Grouping Patterns and Competition Among Female *Pan troglodytes schweinfurthii* at Ngogo, Kibale National Park, Uganda

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Abstract In mammals, access to mates is probably the most important influence on male reproductive success, whereas foraging efficiency is probably the most important influence on female reproductive success Emlen and Oring (*Science* 197:215–223, 1977). Male chimpanzees (*Pan troglodytes*) are highly gregarious and form cooperative relationships with other males. In contrast, female social relationships vary within and between populations. Females in most East African populations, e.g., Gombe, Mahale, Kibale-Kanyawara, are less gregarious than males and spend most of their time alone or with only their dependent offspring. Researchers have attributed low female gregariousness to the high potential for feeding competition. I provide the first data on association patterns and agonistic interactions of female chimpanzees (*Pan troglodytes schweinfurthii*) from the unusually large Ngogo community, Kibale National Park, Uganda. Ngogo females were less gregarious than males, but spent a mean of 64% of their time in association with ≥1 other females and as much time in all-female parties as they did alone. Further, female dyads associated nonrandomly and they formed associative cliques. Association levels within cliques were similar to those among the relatively gregarious West African chimpanzee females at Taï (*Pan troglodytes verus*) and among bonobo (*P. paniscus*) females. Agonistic interfemale interactions were extremely rare, and monthly mean party size and the numbers of anestrous females per party do not correlate significantly with fruit availability. Thus, Ngogo females maintained relatively high levels of gregariousness, but avoided detrimental feeding competition by preferentially associating with a small subset of other community females.

Keywords association patterns · female socioecology · Ngogo · Kibale National Park · Uganda · *Pan troglodytes schweinfurthii* · party size

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Introduction

The socioecological model for primate female social relationships predicts that food distribution influences the grouping patterns and competitive regimes of female primates, which in turn mold the nature of their social relationships (Koenig 2002; Sterck et al. 1997; van Schaik 1989). Most diurnal primates live in cohesive social groups, presumably because grouping provides protection against predation (van Schaik 1983, 1989). Feeding competition is potentially the most important cost of grouping (MacDonald 1983), especially for females, whose reproductive success is limited mostly by foraging efficiency (Sadleir 1969; Trivers 1972; Wrangham 1979a). When competition is low or scramble competition predominates, females are expected to have egalitarian dominance relationships. Conversely, if contest competition prevails, females should have despotic dominance relationships.

Chimpanzees (Pan troglodytes) fit well with the socioecological model in some respects (Arnold and Whiten 2003; Goodall 1986; Pusey 1979), but inter- and perhaps intrapopulation variation in female association patterns and social relationships still present us with open questions (Pusey et al. 1997; Wittig and Boesch 2003). Chimpanzees live in socially delineated communities, but unlike most diurnal primates, do not form permanent, cohesive groups. Instead, they have a fission-fusion social system in which individuals form flexible parties that fluctuate in size, composition, and duration (Goodall 1968; Nishida 1968; Sugiyama 1968). As in other species with similar fission-fusion social systems (bonobos: Badrian and Badrian 1984; spider monkeys: Klein and Klein 1977; McFarland 1986; and to some extent orangutans: Delgado and van Schaik 2000; van Schaik 1999), subgrouping patterns depend on tradeoffs between the costs and benefits of gregariousness (Chapman et al. 1994, 1995; Hohmann and Fruth 2002; Symington 1988; van Schaik 1999; Wallis 2002; White 1998; Williams et al. 2002b). Large body size should reduce predation risk for chimpanzees and thus reduce the benefits of permanent group formation (Terborgh and Janson 1986; cf. Boesch 1991). Concomitantly, flexible party formation can mitigate the costs of feeding competition; small parties are favored when food abundance is low and the potential for scramble competition is high (Wrangham 1979a). Increased travel costs imposed by scramble competition (Chapman and Chapman 2000; Janson and Goldsmith 1995) should be particularly hard for lactating females to bear because of the energetic costs of both lactation and infant transport (cf. Altmann and Samuels 1992; Wrangham 2000). Chimpanzees concentrate on eating ripe fruit (Nishida and Hiraiwa-Hasegawa 1987); consequently scramble competition should intensify when ripe fruit is scarce (Chapman et al. 1994). Indeed, several studies have shown that chimpanzee parties are larger when fruit is more abundant and decrease during fruit shortages (Anderson et al. 2002; Basabose 2004; Boesch 1996; Chapman et al. 1995; Doran 1997; Fawcett 2000; Hohmann et al. 2006; Matsumoto-Oda et al. 1998; Mitani et al. 2002a; Sakura 1994; Wrangham 1977, 2000; Wrangham et al. 1992). However, most of the studies focus on overall party size or on the numbers of males and estrous females per party. Among bonobos in the Lomako Forest, the number of males in a party correlates positively with fruit abundance, but the number of anestrous females per party is unrelated to fruit abundance (White 1998). Similar analyses of the

influence of food availability on grouping patterns of anestrous female chimpanzees are still rare.

Conversely, gregariousness confers potential benefits; thus individuals are expected to join parties when costs are low. Sociability may facilitate offspring survival (Silk *et al.* 2003), give females and their offspring protection against male aggression (Hohmann *et al.* 1999; Newton-Fisher 2006; Watts and Mitani 2000; Wrangham *et al.* 1992), facilitate formation of alliances between females (Newton-Fisher 2006), give dependent offspring opportunities to gain valuable social experience (Watts and Pusey 1993; Williams *et al.* 2002a) and to engage in social learning (van Schaik, 2003), and provide opportunities to exchange grooming (Hemelrijk and Ek 1991; Henzi and Barrett 1999).

Wrangham (1979a, 2000; *cf.* Wrangham and Smuts 1980) invoked the potentially high costs of scramble feeding competition to explain why female chimpanzees in several East African populations (*Pan troglodytes schweinfurthii*) are generally less gregarious than males are and spend more time alone —including time with only their dependent offspring— than males do (Hasegawa 1990; Nishida 1968, 1979; Pusey 2001; Wrangham 1980; Wrangham *et al.* 1992). In contrast, females at Taï in Côte d'Ivoire (*Pan troglodytes verus*) are more gregarious (Lehmann and Boesch 2008), and female dyads form stable, long-lasting friendships (Boesch and Boesch-Achermann 2000; Lehmann and Boesch 2005). Similar female association patterns occurred in the Sonso community in the Budongo Forest, Uganda (*Pan troglodytes schweinfurthii*: Emery Thompson and Wrangham 2006; Fawcett 2000). At Ngogo, in Kibale National Park, Uganda, estrous females were less gregarious than males or estrous females and associated with other females less than expected if all individuals were equally gregarious (Pepper *et al.* 1999). However, when Pepper *et al.* (1999) took their low overall gregariousness into account, anestrous females actually associated with each other more than expected by chance and actively preferred each other as party members.

At the same time, the importance of contest competition for female chimpanzee social relationships is unclear. Contests over food generally occur at low rates (Budongo: Fawcett 2000; Kanyawara, Mahale, Gombe: Muller 2002; Gombe: Murray *et al.* 2006), which could mean that it has little biological importance and makes determining whether females have dominance relationships difficult. Yet long-term analyses at Gombe revealed that reproductive success is related to categorical dominance ranks (Pusey *et al.* 1997) and that high-rank confers some foraging benefits (Murray *et al.* 2006; Pusey *et al.* 1997). At Taï, rates of contests over food are appreciably higher than in East African populations and females exhibit a linear dominance hierarchy (Wittig and Boesch 2003). The behavioral differences highlight the need to examine behavioral diversity and flexibility in social interactions among chimpanzees and to explore the underlying ecological variables associated with behavioral variation (Boesch 2002).

I report new observations of female chimpanzees from the Ngogo community in Kibale National Park, Uganda. I describe the general nature of female association patterns and test hypotheses regarding the effects of habitat-wide fruit availability on party formation of female chimpanzees. The range of the unusually large Ngogo chimpanzee community (Watts 1998) is located in a relatively undisturbed and productive part of Kibale National Park and appears to be particularly good habitat

for chimpanzees (Chapman *et al.* 1997, 1999; Potts *et al.* 2007; Struhsaker 1997). The apparent high and relatively stable abundance of chimpanzee food resources at Ngogo should accordingly reduce feeding competition among females (Chapman *et al.* 1994) and allow them to associate more with other individuals, especially other females. Further, the large number of females gives ample opportunity for females to choose associates; therefore I predict that females will display differential association patterns. However, the large population size and high density (~2.8 females/km^2) of females at Ngogo could increase the importance of contest competition over food (Muller 2002); if so, rates of agonistic interactions between females should be higher than expected by chance during feeding relative to other contexts. Alternatively, females may avoid direct competition with each other by adjusting participation in parties in accordance with food availability. If the latter is the case, then party sizes should be smaller when habitat-wide fruit availability is low relative to times when fruit is abundant. I test the hypotheses via data on female grouping patterns and dyadic associations, and on the frequency of female-female agonistic interactions, especially contests over food. I also utilize monthly indices of habitat-wide fruit availability to test whether females avoid direct feeding competition by joining smaller parties when fruit is scarce. I discuss my findings in relation to the unusual demography and ecology of the Ngogo community.

Methods

Study Site and Subjects

I observed chimpanzees at the Ngogo research site in Kibale National Park, Uganda (0°13′–0°41′N and 30°19′–30°32′E). Ngogo is in central Kibale, *ca.* 10 km southeast of the Kanyawara research site, at *ca.* 1350 m elevation. Mean monthly temperatures are *ca.* 16°C minimum and 23–24°C maximum (Lwanga 2003). Annual mean rainfall is 1395±199 mm (n=8 yr) and is distributed throughout the year, with March–May and September–November usually wetter than average and June–July and December–February usually drier than average (Struhsaker 1997). The vegetation is transitional between lowland and montane rain forest and consists primarily of moist mature evergreen and regenerating forest (Butynski 1990; Ghiglieri 1984; Struhsaker 1997). The Ngogo range encompasses high densities of important chimpanzee food species, e.g., *Pterygota mildbraedii* and *Ficus mucuso*, that are rare or absent at the nearby Kibale site of Kanyawara (Chapman *et al.* 1997; Potts *et al.* 2007); it experiences less extreme temporal fluctuations in fruit availability than Kanyawara (Chapman *et al.* 1999; Potts *et al.* 2007); and fruit abundance does not correlate with seasonal variations in rainfall (Mitani *et al.* 2002a). Published estimates of the size of the Ngogo community's home range vary depending on the method used. Mitani and Amsler (2003) gave a value of 17.5 km^2 based on the locations of first encounters with males on a daily basis, whereas Watts and Mitani (2001) gave a value of 35 km^2 for the total area in which at least some community members foraged. Researchers have continuously observed Ngogo chimpanzees since 1995, focusing primarily on males (Mitani and Amsler 2003; Mitani *et al.* 2000, 2002b; Watts 1998, 2002; Watts and Mitani 2001, 2002). I

collected data on females during 3 field seasons totaling 19 mo over 2 yr, encompassing periods of both wet and dry seasons: April–July 2003; October 2003–May 2004; and October 2004–May 2005.

During this time, there were *ca.* 145 individuals in the Ngogo community, including 42–43 known adult females, 6–14 adolescent females, 25–26 adult males, 12–18 adolescent males, 18–22 juveniles, and 26–28 infants. Three females matured from adolescent to adult, and 12 natal females matured from juvenile to adolescent. Four parous females disappeared and were presumed dead. There were 3 possible adolescent immigrations into the community, but no known emigrations. I did not know exact ages of adult and adolescent females at Ngogo; thus I placed them into broad categories: early adolescent, late adolescent, young adult, prime adult, and old adult (Nishida 1979). I selected 26 well-habituated females, including individuals of varying ages and some with and without infants, as targets for focal data collection. All but 3 target females were parous adults at the beginning of my study; 2 were late adolescent to early adult when I commenced data collection, both conceived and gave birth during my study. The remaining female was a prime adult that is infertile and does not cycle. Two of my female subjects died during the study and are not in the association data set.

Behavioral Observations

I used several methods to locate target females and to minimize biases toward locating larger parties (Chapman *et al.* 1993), including listening for calls, checking known fruiting trees, and systematically searching the study area. Whenever I located a female I determined the composition of her party, defined as all independent individuals present and in visual range of each other as judged by observers (Mitani *et al.* 2002a; Pepper *et al.* 1999). I considered individuals in the same party to be in association. If the party included 1 of my study subjects, I selected a target female and started a focal sample of her behavior. I tried to follow focal individuals all day, but switched to new targets when I lost focal females irrevocably (average length of focal follows per female per day was 5.1±1.2 h). I conducted 30-min scan samples (Altmann 1974) with help from trained field assistants to record size and composition of parties. The 30-min time interval is statistically independent at Ngogo (Mitani *et al.* 2000), but allows a reasonable estimate of time in association with other conspecifics. The method (*cf.* Wittig and Boesch 2003) provides a more biologically meaningful view of a female's association preferences than considering only morning feeding aggregations or party changes would and it reduces biases to larger parties that first encounter data can introduce (Anderson *et al.* 2002).

I scored sexual swelling for cycling females based on turgidity (Dahl *et al.* 1991), and refer to those with maximal swelling tumescence as estrous females (Tutin 1979). I classified party types into 4 broad categories modified from Goodall (1986): lone female, mixed, all-female, and other (Table I).

I recorded detailed behavioral data for a target female via continuous focal individual sampling for the 25-min intervals between scans. I recorded agonistic interactions between females *ad libitum* for both the focal and other females present. Types of agonistic interactions include pant-grunts, passive deferrals and supplants,

Table I Definitions of party type classification

Party type	Definition
Lone female	Adult or adolescent female alone or if a mother, only with her dependent offspring
Mixed	≥1 adult or adolescent female and ≥1 adult or adolescent male
	Includes:
	Mixed: males, females, and immature offspring
	Mixed adult: no immature individual present
	Mixed sexual: ≥1 estrous female present
All-female	≥2 adult or adolescent females with no independent males present
	Includes:
	Nursery: ≥2 females and dependent offspring
	Female adult: ≥2 adult or adolescent females without immature offspring present
Other	Groupings that do not fit into any of the above categories.
	Includes:
	Family: a mother with her offspring including an independent adolescent offspring
	Babysitter: female alone but with an immature individual that is not her own offspring, most often an orphaned juvenile or possible younger sibling

physical threats without contact (lunge, hit-toward, branch-shake), charges and chases without physical contact, and attacks with physical contact. I recorded as much information as possible surrounding the interaction, including IDs and age/sex class of all individuals involved, behavioral context, response of the receiver(s), and outcome of the interaction. To accommodate subtle agonistic interactions like passive displacements or deferrals that sampling *ad libitum* may miss (Murray *et al.* 2006), I considered all cases in focal data in which one female approached another that then broke proximity in ≤1 min to be passive deferrals.

Data Analysis

All statistical tests were 2-tailed unless otherwise noted. I conducted parametric tests via SPSS 11 for Mac OS X and nonparametric Mann-Whitney U and chi-square χ^2 tests with GraphPad Prism version 4.00 for Mac OSX.

Association patterns To investigate association patterns among females, I used the dyadic association index (DAI) (Martin and Bateson 1993; Nishida 1968) to calculate the frequency of association among female dyads:

$$\mathrm{DAI}_{AB} = \sum AB \Big/ \left(\sum A + \sum B - \sum AB \right)$$

wherein A is the time based on scans I observed individual A, either alone or in association with other independent individuals; B is the time I observed individual B; and AB is the time individuals A and B were in the same party. Because I located only 1 party at a time, this index is equivalent to both the twice-weight and simple ratio association indices (Cairns and Schwager 1987). The DAI is commonly used in chimpanzee studies; it allows for comparisons across studies and communities with caveats owing to variation in data collection methods.

Individuals may vary in gregariousness and their tendency to join parties in general (Pepper *et al.* 1999). Therefore, to test if female dyadic associations deviated

from chance expectations based on individual variation in grouping patterns, I compared the observed DAI to expected values under the null hypothesis that associations are random, not dyad specific. I used the GROUPS computer program with the group randomization method (Pepper *et al.* 1999) to generate the expected values. The program reshuffles the female membership of the observed parties, while maintaining the observed number of females in parties and the number of times each individual appears in the sample. The association index is recalculated after each randomization, and then these values are averaged to generate the expected values. I used 10,000 iterations. A 2-tailed statistical test of the null hypothesis is generated by comparing the ratio of the observed to expected values to the 2.5% tails of the randomized distribution. I provide only the results for the 24 target females, but because the expected association index factors in individual's tendencies to associate with other females in general, I included both target and nontarget females in the null model.

To represent female association relationships graphically, I conducted a hierarchical cluster analysis via the UPGMA (unweighted pair-groups method using arithmetic averages) or average linkage between groups method (Sneath and Sokal 1973). I used the DAI to construct distance matrices between individuals and used squared Euclidean distances to perform the UPGMA analysis. The procedure produces a dendrogram showing the structure of association patterns between individuals for all females in the sample. I identified associative clusters of females by determining the cutoff points that produced well-defined clusters with the deepest branches, i.e., the greatest distance between subsequent splitting events or clusters (Romesburg 2004). To validate statistically that the observed clusters were socially meaningful, I compared the mean DAI for females within and between each cluster and then conducted a resampling procedure with 5000 iterations for each cluster (Manly 1997). The re-sampling procedure retained the observed number of dyads within and between the clusters, and then randomly reshuffled the observed DAIs. I recalculated the difference between mean DAI for within and between the clusters after each randomization event to generate the expected values and test statistic. I use the term association clique to refer to clusters of females that collectively had higher association frequencies than expected by chance or random association patterns.

Influence of fruit availability on party size Ngogo researchers use phenology data on the top 20 chimpanzee food species, combined with data on the densities and mean DBH of each tree species, to calculate a monthly index of habitat-wide ripe fruit availability (FAI; Mitani *et al.* 2002a). For each month in the phenology sample, I calculated mean party size and the mean number of individuals of different sex classes per party. Phenology months center on the days when phenology samples are collected and do not correspond to calendar months (Mitani *et al.* 2002a). For example, May 2003 includes parties recorded from 24 April to 23 May 2003. I included data for 16 months (May–June and November–December 2003; January–May and October–December 2004; January–April 2005), and excluded 3 mo that were truncated by the beginning or end of my field seasons.

To examine whether grouping patterns were more sensitive to the availability of different classes of fruit, I divided the FAI into 3 categories: total FAI for all of the top 20 chimpanzee food species, FAI for only nonfig species (FAI_{nf}), and FAI for

only *Ficus mucuso* (FAI$_{fm}$). Considering *Ficus mucuso* separately is valuable because individuals of the species are large (average DBH of phenology samples is 115 cm ±38 cm) with abundant fruit crops that can support large parties of chimpanzees. Its fruit is available throughout the year (some ripe fruit of *Ficus mucuso* was available in all months of the study) and it is both a staple food (Potts *et al.* 2007) and the top food in the diet of Ngogo chimpanzees (Watts *et al.*, *unpub. long-term data*). However, *Ficus mucuso* occurs at low densities relative to other phenology trees and consequently does not contribute significantly to the overall FAI. Further, its ripe fruit score is independent of the index for nonfig fruit (Watts *et al.*, *unpub. long-term data*). Therefore, I expect females will occur in larger parties during times when ripe fruit of *Ficus mucuso* is more abundant.

The presence and number of estrous females might vary with fruit availability if variation in energetic status influences the probability that females cycle (Anderson *et al.* 2006; Wallis 2002); estrous females may in turn influence party size and composition (Anderson *et al.* 2002; Boesch 1996; Hashimoto *et al.* 2001; Matsumoto-Oda 1999; Matsumoto-Oda *et al.* 1998; Mitani *et al.* 2002a; Newton-Fisher 1999; Wallis 2002; Wrangham 2000). Therefore, I also examined the effects of food availability on the number of adult estrous females in parties, and how the number of estrous females in turn affects party size and membership.

I used linear regression analysis to examine the effects of fruit availability on overall party size and the number of both anestrous and estrous females in parties, and to examine the effects of estrous females on party size and composition. I used the tests to identify potential interacting variables and then conducted partial correlation analyses to control for the confounding variables. I used the Shapiro-Wilk's W statistic to test for normal distribution in my samples of monthly FAIs and mean monthly party size/composition values (Shapiro and Wilk 1965). The W statistic has more power than alternative tests for normality and remains sensitive with small samples (Shapiro *et al.* 1968). I used a square root transformation on any data set that was not normally distributed to satisfy the assumptions of analysis of variance and Pearson's correlation coefficient. I employed a Bonferroni correction (Sokal and Rohlf 1995) to guard against type I errors occurring from conducting multiple tests; I tested each hypothesis 3 times in relation to 3 different FAI measure; thus I set the significance level at $\alpha' = \alpha/k = 0.017$. I predicted a positive relationship between all tests of fruit availability and party/sex class size; therefore, all tests are 1-tailed.

Results

Party Types and Sizes

I observed female chimpanzees for 1700 h and recorded 3393 complete 30-min scans on parties containing ≥1 female. Females participated most frequently in mixed parties (55.9%), and spent similar amounts of time in all-female parties and alone (19.7% and 20.0% respectively).

Mean party size is 7 independent individuals, but considerable variation occurred (range = 1–44; SD=7.0, Table II), with a skew toward smaller parties. Party size for

Table II Party size and number of males or females per party across different party types

	All Parties (n=3393)		Mixed (n=1895)		All-female (n=667)	
	Mean ± SD	Median (range)	Mean ± SD	Median (range)	Mean ± SD	Median (range)
Ngogo, this study						
Total party size	6.68±7.02	4 (1–44)	10.25±7.60	8 (2–44)	3.35±1.49	3 (2–8)
Females	3.08±2.56	2 (1–15)	3.93±2.91	3 (1–15)	3.16±1.41	3 (2–8)
Adult females	2.67±2.14	2 (0–14)	3.40±2.45	3 (0–14)	2.67±1.18	2 (1–7)
Adolescent females	0.41±0.75	0 (0–4)	0.54±0.85	0 (0–4)	0.49±0.73	0 (0–4)
Males	3.23±5.10	1 (0–33)	5.74±5.67	4 (0–33)	–	–
Ngogo 1998–1999[a]						
Total party size (*n*=827)	10.27±10.24	4 (1–47)	–	–	–	–

[a] From Mitani *et al.* (2002a).

my subjects is smaller than the average of 10 Mitani *et al.* (2002a) reported for Ngogo. However, I include only parties with ≥1 female, whereas Mitani *et al.* (2002a) collected data during research focusing on males. Because males are more gregarious than females are, the different results are likely explained by the differences in grouping patterns of males and females. Accordingly, parties in my sample that include males, i.e., mixed parties, should be larger than all-female parties. Party size varied across party type; mixed parties were the largest ($\bar{x} = 10.3 \pm 7.6$, *n*=1895), and all-female parties ($\bar{x} = 3.4 \pm 1.5$, *n*=667) were significantly smaller (Mann-Whitney test: U=180,700, p<0.0001). The number of females in mixed parties ($\bar{x} = 3.9 \pm 2.9$) and in all-female parties ($\bar{x} = 3.2 \pm 1.4$) varied less than overall party size. Thus, the number of males in the party primarily accounted for the larger size of mixed parties. Mitani *et al.* (2002a) gave party size figures similar to those for mixed parties of my subjects (Table II).

Association Patterns

Two or more females were in association for 64% of scans. There were 1728 possible female-female dyads; I documented 1019 dyads in association at least once. Including data from only the 24 target females, there were 276 possible dyads; I observed 233 of them in association ≥1 time. The association frequencies varied considerably between dyads (mean DAI=0.06±0.08, range = 0–0.58) and all dyads had DAIs that significantly deviated, either positively or negatively, from the expected DAIs based on the null hypothesis of random association (group randomization method: p<0.05 for all dyads, mean p-value = 0.0004±0.0013, range = 0.0184–0.0002, *n*=276 dyads). The results from the UPGMA analysis show that the 24 target females formed 4 clusters representing association cliques (Fig. 1). The re-sampling tests confirmed that the cliques were statistically distinct and nonrandom: the mean DAIs were significantly higher within than between cliques than expected by chance (p<0.001 for all 4 cliques, Fig. 2). I did not include all of the community's females in the dendrogram, but adding data on another 14 females that were not targeted leaves it largely unchanged, with simply more females per clique. Thus, females did not associate equally or randomly with other females, but instead preferentially associated with a subset of potential partners.
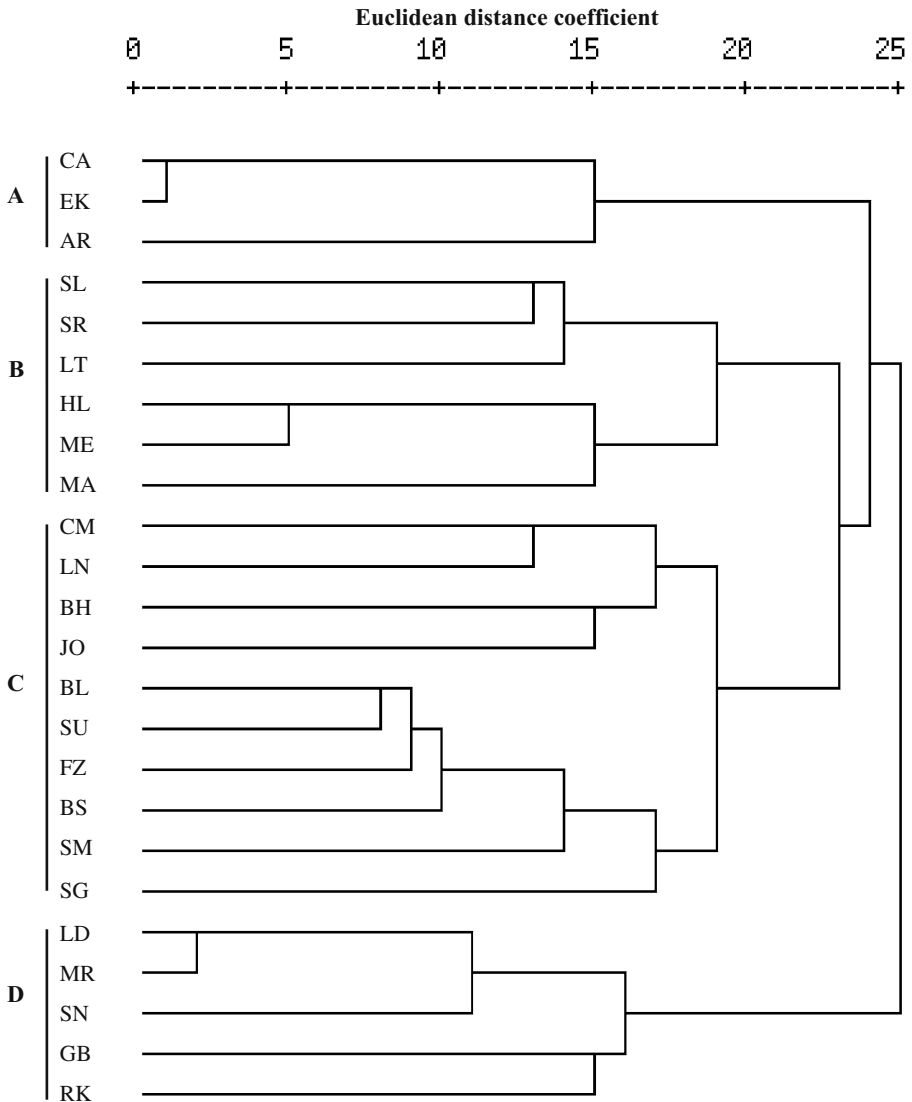
Fig. 1 Dendrogram of the results of the UPGMA cluster analysis calculated from the dyadic association indices for target females. Females clustered into 4 association cliques demarcated with capital letters.

The average DAI among females across all 276 target dyads is within the range in other East African chimpanzee communities (Table III). However, given that female associations are nonrandom, highly variable, and are organized into statistically distinct cliques, it is meaningful to examine DAIs within cliques. The mean DAI within cliques (0.20±0.09, range 0.13–0.32) is higher than values reported for other East African communities and within the range of Taï chimpanzee and bonobo females (Table III).

Fig. 2 Mean observed/expected dyadic association indices (DAI) for dyads within (gray bars) and between (white bars) each of 4 association cliques. Positive values indicate individuals associated more than expected by chance and negative values indicate individuals associated less than expected by chance. Error bars represent 1 SD of the mean. *$p < 0.001$ assessed via resampling tests.
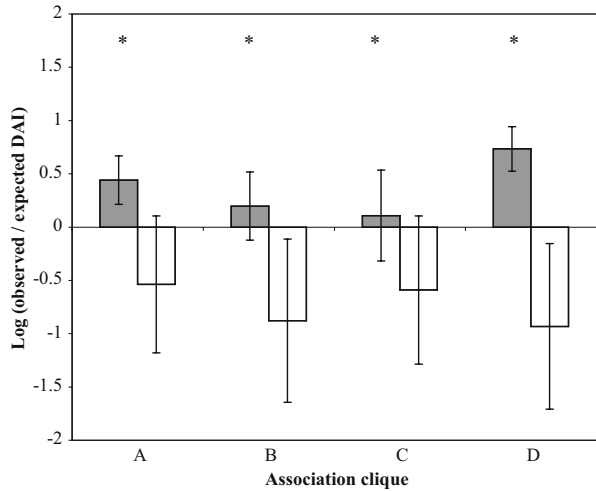
Agonistic Interactions

Decided agonistic interactions, including pant-grunts, rarely occurred between females (Table IV). In 1700 h of observation, including 1080 h of females in association, I observed 20 pant-grunts that a female unambiguously emitted to another, instead of possibly to a nearby male, and another 27 decided agonistic interactions: 18 aggressive and 7 nonaggressive, e.g., supplants or passive deferrals. Even if one considers only target females, the samples are too small for statistical tests of linearity in the outcome of agonistic interactions (Table IV).

In 31 (66% of) decided agonistic interactions, submission was clearly directed from younger to older females, which is a conservative estimate because I included only dyads with a clear difference in age class. The remaining 16 (34% of) interactions occurred between dyads in the same age class. I never observed a

Table III Comparisons of average female-female dyadic association indices across different chimpanzee (*Pan troglodytes*) and bonobo (*Pan paniscus*) communities

Population	Average F-F DAI	Source
Pan troglodytes:		
Budongo (Sonso)	0.09	Fawcett 2000
Gombe (Kasakela)	0.05	Goodall 1986
Kibale (Kanyawara)	0.08	Wrangham *et al.* 1992
Taï (North group: 1987–1989)	0.11	Boesch and Boesch-Achermann 2000
Taï (North group: 1996–1999)	0.27	Wittig and Boesch 2003
Kibale (Ngogo)	0.06	This study
Ngogo clique A	0.32	
Ngogo clique B	0.13	
Ngogo clique C	0.13	
Ngogo clique D	0.20	
Pan paniscus:		
Lomako	0.25	Hohmann and Fruth 2002

Table IV Observed number and rates of decided agonistic interactions between females and the number and proportion of different dyads engaging in interactions

| Variables | Type of decided agonistic interaction | | | | Target dyad observations only |
| | All observations | | | | |
	Pant-grunts	Food conflicts	Other	All combined	All combined
No. of observed interactions	20	12	15	47	20
Hourly rate[a]	0.012 (0.019)/h	0.001 (0.011)/h	0.016 (0.025)/h	0.028 (0.044)/h	0.012 (0.019)/h
No. of dyads	19	10	14	41	18
Proportion of possible dyads[b]	1.1 (1.8)%	0.5 (0.9)%	1.3 (2.1)%	2.4 (3.8)%	6.5 (7.7) %

[a] Rate calculated from 1700 total observation hours and 1080 observation hours of females in association (in parentheses).
[b] Percentage of 1728 total possible female dyads and of 1019 observed female dyads (in parentheses) for all observations; percentage of 276 total possible female dyads and of 233 observed female dyads (in parentheses) for target dyad observations.

decided agonistic interaction wherein the aggressor was clearly younger than the receiver. In addition, 19 (40% of) decided agonistic interactions involved an adolescent female (18 adolescent-adult dyads, 1 adolescent-adolescent dyad). The proportion of adolescent to adult females varied from 12.5% to 24.5%. At Gombe (Pusey 1980, 1990) and Mahale (Nishida 1989), newly immigrated females received frequent aggression from resident females. I observed 3 acts of aggression from resident females toward 2 possible new immigrant adolescents.

If contest competition over food is important to female chimpanzees, aggression and agonistic interactions should occur most frequently in feeding contexts, as occurs at Gombe (Goodall 1986), Kanyawara (Muller 2002), and Taï (Wittig and Boesch 2003). Pant-grunts generally occur during greetings or approaches, so excluding pant-grunts, 12 (41%) of the remaining 27 decided agonistic interactions and 2 undecided acts of aggression between females occurred during feeding. Target females in parties with ≥2 females fed or foraged during 39% of scans. Thus, agonistic interactions among females did not occur more than expected by chance during feeding contexts in proportion to time spent feeding (chi-square test: $\chi^2=0.072$, ns).

Influence of Fruit Availability on Party Size

Mean monthly values for party size range from 2.8 to 12.6 independent individuals across all party types (Fig. 3). The number of independent females per party varies from 1.4 to 4.8, and anestrous adult females range from 1.2 to 3.3 individuals (Fig. 3). The monthly FAI (Fig. 3) had little effect on the grouping patterns of females (Fig. 4). Monthly party size is not significantly related to either overall fruit availability, via linear regression with a Bonferroni correction (FAI: $F_{1,14}=2.61$, $r^2=0.16$, $p=0.13$), or the availability of nonfig fruit (FAI$_{nf}$: $F_{1,14}=2.67$, $r^2=0.16$, $p=0.12$), or the availability of *Ficus mucuso* (FAI$_{fm}$: $F_{1,14}=0.80$, $r^2=0.05$, $p=0.39$). Likewise, the number of adult anestrous females per party did not relate to any

Fig. 3 Temporal variation in total ripe fruit availability (FAI) by each month included in analysis plotted with monthly variation in party size and number of anestrous adult females per party. I conducted observations on parties containing ≥1 female. Months included are based on the phenology month and include 16 mo between 2003 and 2005.
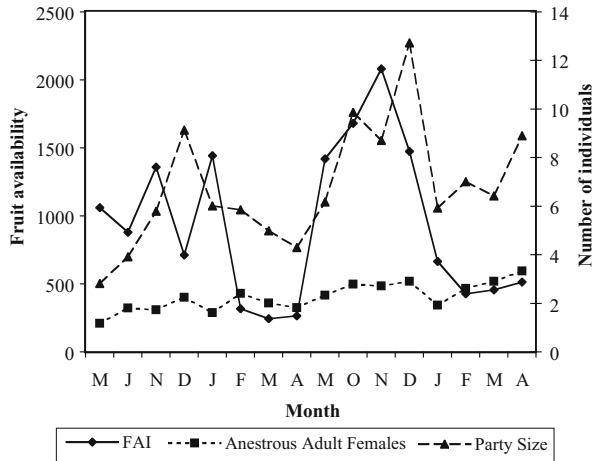
category of FAI (FAI: $F_{1,14}=0.01$, $r^2=0.00$, $p=0.91$; FAI$_{nf}$: $F_{1,14}=0.01$, $r^2=0.00$, $p=0.92$; FAI$_{fm}$: $F_{1,14}=2.27$, $r^2=0.14$, $p=0.15$), nor did the number of males (FAI: $F_{1,14}=3.58$, $r^2=0.20$, $p=0.08$; FAI$_{nf}$: $F_{1,14}=3.73$, $r^2=0.21$, $p=0.07$; FAI$_{fm}$: $F_{1,14}=0.35$, $r^2=0.03$, $p=0.56$). However, the data set includes only parties with ≥1 female present; neither all-male nor lone-male parties are represented here and many parties contained no male. Consequently, the analysis does not necessarily reflect the response of males to fruit availability, but reflects variation in the number of males with which females associate in parties, either actively or passively, under different ecological conditions.

The number of adult estrous females per party did not significantly relate to any fruit availability measures (FAI: $F_{1,14}=2.17$, $r^2=0.13$, $p=0.16$; FAI$_{nf}$: $F_{1,14}=2.26$, $r^2=0.14$, $p=0.16$; FAI$_{fm}$: $F_{1,14}=0.28$, $r^2=0.02$, $p=0.61$), but overall party size ($F_{1,14}=34.98$, $r^2=0.71$, $p<0.001$) and the number of males per party ($F_{1,14}=45.90$, $r^2=0.77$, $p<0.001$) increased significantly with the number of estrous females. However, if the number of males is controlled for, overall party size did not correlate with the number of estrous females (partial correlation: $r=0.16$, $p=0.29$). In addition, the number of adult anestrous females did not significantly relate to the number of estrous females ($F_{1,14}=4.51$, $r^2=0.24$, $p=0.05$).

Fig. 4 Relationship between overall party size (black triangles), number of anestrous adult females (gray squares) per party, and total ripe fruit (FAI) availability. Data points represent mean monthly values.
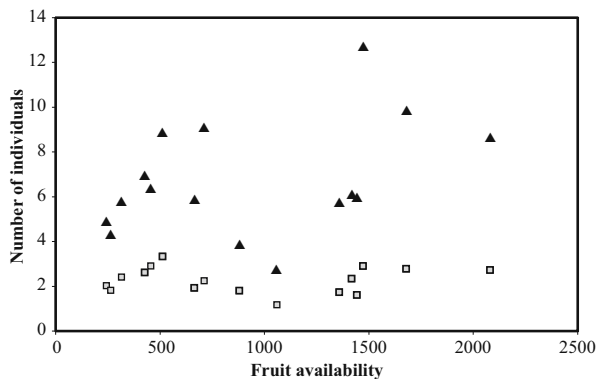
Discussion

My results demonstrate that female chimpanzees at Ngogo associated with ≥1 other female more often than they remained alone. Further, females preferentially associated with small subsets of other females and formed association cliques. However, tolerance among females was high; signals of formal dominance and decided agonistic interactions rarely occurred between females; and most females did not have clear dominance relationships. Yet females did not appear to avoid contest competition by adjusting their associations with other females based on habitat-wide fruit availability, which also suggests that the observed association patterns do not merely reflect passive groupings at fruiting trees. However, considering the large number of females at Ngogo, an average of 3–4 females per party is not high. Therefore, it appears that females at Ngogo circumvented potentially detrimental effects of feeding competition while maintaining relatively high levels of gregariousness by preferentially associating in cliques with a limited subset of community females.

Female association cliques appeared to be the principal social unit among females at Ngogo rather than the community-wide unit. Many females rarely or never encountered each other, while I regularly observed others together. It is possible that some females from different cliques did not know each other, which could have interesting implications regarding chimpanzee social structure (Wrangham 1979b). However, it is also likely that all individuals know and recognize each other as community members, but some dyads associated so rarely that I missed it in my sample. The low average dyadic association index at the community-wide level could be interpreted as generally low gregariousness among Ngogo females. However, examining dyadic association at the clique level showed a very different picture of female sociability and indicates that females formed bonds with at least some other females. The levels of association within female cliques are comparable to the association levels among Taï females in West Africa (Boesch and Boesch-Achermann 2000; Wittig and Boesch 2003), which are highly gregarious, forming stable bonds and friendships (Boesch and Boesch-Achermann 2000), and to Lomako bonobo females (Hohmann and Fruth 2002), which are highly cohesive and affiliative (Idani 1991; White 1996), though like among chimpanzees, there is considerable intra- and intersite behavioral variation (Hohmann and Fruth 2002; White and Burgman 1990). In addition, female clique membership appears to persist over time. Most were apparent when I began working at Ngogo in 2001 and continued through my study.

Female association cliquing behavior adds another dimension to the spatial range use clusters or neighborhoods found at Gombe (Williams *et al.* 2002b; Wrangham and Smuts 1980), Kanyawara (Emery Thompson *et al.* 2007), and to a certain extent Mahale (Hasegawa 1990). Data not presented here show that like at other sites, Ngogo females do not use space uniformly; however, range overlap is high among both individual females and cliques and the integrity of the cliques is maintained even in overlapping areas or when females travel far away from their typical ranging areas (Amsler and Wakefield, *unpub. data*). Moreover, females at Ngogo groomed with and maintained proximity within cliques more than expected by association levels (Wakefield 2007). Thus, association cliques among Ngogo females presumably

have social components and are not just spatial clusters. I will investigate female social relationships and demographic correlates within and between cliques in detail in future analyses.

It remains unclear whether females at other sites display associative clustering behavior like that at Ngogo. Nishida (1989) observed similar behavior at Mahale after the K-group dissolved and several females transferred to the M-group. After transfer, former K-group females primarily associated, groomed, and shared ranges with females from their original community. Conversely, Fawcett (2000) found that Budongo females did not form clear association clusters, but instead displayed a nested association pattern, which may be due in large part to greater sociability of peripheral females (Emery Thompson and Wrangham 2006). Taï females also do not appear to form association clusters; instead, females are affiliative and cohesive at the community level (Wittig and Boesch 2003). Detailed investigations into the association levels within female neighborhoods at Gombe and Kanyawara are not available in the literature, but Murray *et al.* (2006) reported higher association indices within female neighborhoods at Gombe than between them.

Mitani and Amsler (2003) also documented association clusters, termed subgroups, among the males of Ngogo. Even though the underlying social and ecological pressures leading to clique formation presumably differ between males and females, the unusual demography of the Ngogo community almost certainly contributes significantly to the behavior in both sexes. Owing to the costs of travel, finite resources, and time limitations, the large number of females precludes uniform affiliation among all females in the community, and cliquing allows females to be gregarious at levels that do not exceed the costs. Therefore, female association clique formation at Ngogo may represent a behavioral variation among chimpanzee populations. However, my study also highlights the importance of examining female social relationships at the level that is meaningful to the female; investigations at the community-wide level may mask important relationships and understate female sociability.

In recent years, there has been a growing body of research on competitive regimes and dominance relationships among female chimpanzees. Researchers at a few sites have documented decided dominance relationships among females, both categorical (Gombe: Murray *et al.* 2006; Pusey *et al.* 1997; Budongo: Newton-Fisher 2006) and linear (Taï: Wittig and Boesch 2003). Thus far, my data indicate that dominance relationships are not salient among Ngogo females, either at the community level or within cliques. Given the large number of females at Ngogo, one might predict that rates of direct contests would be accordingly high, but that was not the case. Muller (2002) suggested that territory size and the density of females could influence rates of aggression within a community; rates of aggression should be lower among females at sites where there is less competition for space. However, this cannot explain the low rate at Ngogo. Based on Muller's (2002) data, rates of aggression between females are as low at Ngogo as they are at Kanyawara despite a density of females at Ngogo more than triple that at Kanyawara. Using total area used by chimpanzees as a comparative measure of community home range size, the density of adult females at Ngogo is *ca.* 1.2 females/km^2 vs. 0.4 females/km^2 at Kanyawara (15–16 adult females, community home range 37.8 km^2: Wilson *et al.* 2001). In contrast, in 1 study on the Northern community at Taï, the rate of female food

conflicts alone was 0.1/h (Wittig and Boesch 2003), 10-fold the rate of food conflicts at Ngogo, but the density of females at the time was only *ca.* 0.6 females/km^2 (10.5 adult females and community home range size in 1996 ~17.1 km^2: Lehmann and Boesch 2003). Thus it appears that female density alone cannot account for variation in rates of agonistic interactions among females. At Taï, Wittig and Boesch (2003) proposed that leopard predation pressure leads to high levels of cohesiveness among females, which in turn increases contest competition over food, leading to the formation of a linear dominance hierarchy, whereas Ngogo females do not face similar predation pressure to remain cohesive in the face of feeding competition. Another option is that low rates of agonistic interactions indicate stable dominance relationships instead of their absence (Emery Thompson *et al.* 2007; Nishida 1989). The age-biased directionality of agonistic interactions lends some support to this; adolescent females seemed to receive slightly more aggression proportionately than adult females do. However, the interactions were still very rare and only 3 involved possible new immigrants into the community. Heightened aggression from adult to adolescent females could also be a byproduct of smaller body size in adolescent females and therefore lowered competitive ability than that of adults.

The fruit-rich and relatively undisturbed Ngogo habitat (Chapman and Chapman 1997; Chapman *et al.* 1999; Struhsaker 1997) probably reduces feeding competition and can support the higher density of females vs. sites with more disturbed, patchy, and edge habitats that experience marked lean fruit seasons, such as Gombe (Pusey *et al.* 2005; Williams *et al.* 2002b) and Kanyawara (Chapman *et al.* 2000, 1999). Competition for quality space at such sites should be accordingly high. Indeed, at both Gombe (Murray *et al.* 2006) and Kanyawara (Emery Thompson *et al.* 2007), researchers found there is variation in food quality between neighborhoods that correlates with variation in female reproductive success. Accordingly, generally high habitat-wide fruit abundance at Ngogo may reduce the importance of dominance in regard to nutritional intake and reproductive success vs. these and other sites. Given marked variation in demography and ecology across chimpanzee populations and communities, researchers expect to find corresponding behavioral diversity (Boesch 2002). Though more longitudinal data on Ngogo females are needed before drawing any decisive conclusion about female dominance relationships, the evidence thus far suggests that there could be a real difference in dominance relationships among females across populations and Ngogo represents another facet of the variation.

Given that females are expected to be more sensitive to fluctuations in food availability than males are, the finding that party size showed no significant relationship to indices of habitat-wide fruit availability is surprising. The relatively high and stable food productivity at Ngogo may in part account for the findings. Hashimoto *et al.* (2003) proposed that monthly fruit availability should influence party sizes only at sites where fruit availability reaches low enough levels to limit party size for a substantial portion of the year. Comparative phenology data of Chapman *et al.* (1999) showed that Ngogo did not experience predictable lean fruit seasons that occurred at nearby Kanyawara; accordingly fruit availability may not have reached a low enough threshold during my study to have a negative influence on average party size. Also, chimpanzees may sometimes use several feeding patches (Newton-Fisher *et al.* 2000) that are too far apart for them to be in visual

contact, but still maintain vocal contact (Itoh and Nishida 2007). Earlier researchers at Ngogo found a significant positive correlation between monthly party size and food availability (Mitani *et al.* 2002a). The research period for the study by Mitani *et al.* (2002a) included a period of fruit scarcity more extreme than anything experienced during my study, which could in part explain the different results and lend further support to the hypothesis of Hashimoto *et al.* (2003). Further, Mitani *et al.* (2002a) focused on male behavior, whereas I focused on females. It is likely that males and females respond differently to fluctuating fruit availability. Males may gain high social benefits by joining large parties with other males, and thus do so when food permits (Mitani and Watts 1999, 2005; Watts 2000). However, for anestrous females, the costs of being in large parties with many males, such as received aggression from males (Nishida 2003; Otali and Gilchrist 2006; Wrangham 2002), may outweigh the benefit even when fruit supply is high. This may also in part explain why the number of males per party increased with the number of estrous females, but the number of anestrous females did not. Aggression and excitement are often intensified in sexual parties (McGinnis 1973; Watts 1998; Wrangham 2002); consequently, anestrous females, particularly lactating ones, may often avoid them.

Other potentially important ecological factors not considered here could influence female grouping patterns. I incorporated only fruit abundance into the fruit availability index, whereas fruit dispersion can also effect party size (Basabose 2004; Newton-Fisher *et al.* 2000). In addition, the index is based only on ripe fruit, but other nonfruit food resources such as young leaves may play an important role in reducing feeding competition and influence grouping patterns (Fawcett 2000). Terrestrial herbaceous vegetation (THV) is an important food resource for chimpanzees at Kanyawara and may serve as a fallback food (Chapman *et al.* 1994; Wrangham *et al.* 1991), but chimpanzees at Ngogo spend very little time feeding on THV, so it is unlikely to influence grouping patterns. However, when overall habitat-wide fruit availability is low, chimpanzees may sometimes rely on large, scattered fruiting trees, like *Ficus mucuso*, that can still support large parties. This illustrates the need to investigate the relationship of female gregariousness to food availability on a smaller spatial and temporal scale, such as individual patches. Moreover, interindividual differences and differences in reproductive state among females may influence gregariousness. Finally, researchers have suggested multiple additional potential costs and benefits to gregariousness by females, consideration of which are beyond the scope of this paper, including opportunities for offspring socialization (Watts and Pusey 1993; Williams *et al.* 2002a), assessment of future mates (Matsumoto-Oda 1999), risk of and protection from infanticide (Arcadi and Wrangham 1999; Sterck *et al.* 1997; van Schaik and Kappeler 1997; Watts and Mitani 2000), and opportunities to confer benefits on relatives (Williams *et al.* 2002a). Forthcoming genetic data will address the influence of relatedness on female-female association and social relationships (Langergraber, *pers. comm.*). Relatedness may be an important influence on some dyads, but its limited influence on male-male association and relationships, even given male philopatry (Langergraber *et al.* 2007), suggests that it has limited importance for females.

On the basis of my data taken together, I propose that females at Ngogo form association cliques as an adaptation to balance the potential benefits of gregariousness

while minimizing the costs of feeding competition in an unusually large chimpanzee community. Accordingly, the social structure of females at Ngogo is an example of behavioral flexibility in chimpanzees and contributes to the growing body of literature on chimpanzee behavioral diversity.

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