Social dynamics among females and their influence on social structure in an East African chimpanzee community

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Social structure in group-living animals is defined by the nature and patterning of social interactions among members of the society. Social structure is shaped in large part by kinship and competition among group members, but can also be influenced by affiliative interactions among both kin and nonkin and can vary based on sex differences in dispersal patterns and social dynamics. Chimpanzees, *Pan troglodytes*, live in fission–fusion societies in which males form strong dyadic bonds and have social networks that can influence the social structure of the community. Females are generally less gregarious than males and bonding among females is considered rare or absent in East African populations. Although females in some populations are known to form 'neighbourhoods', these are assumed to reflect passive spatial arrangements. In this study I used data on female chimpanzee association and social interactions to examine how social dynamics among the dispersing sex influence social structure at Ngogo, Kibale National Park. Females at Ngogo were relatively gregarious and exhibited association preferences that extended beyond the dyadic level. Females formed distinct association clusters termed 'cliques' within which affiliative interactions occurred more than expected by chance. In addition, association patterns were found to be active social units and not a by-product of space use overlap. These findings demonstrate that intrasexual bonding is not limited to males in this population and that female social relationships, not just those of males, can influence chimpanzee grouping patterns and the corresponding social structure of the community. This study contributes to our growing understanding chimpanzee behavioural diversity.

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A fundamental challenge in behavioural ecology is understanding how individual behaviour influences animal societies (Croft et al. 2008; Whitehead 2008). This includes the typical nature of social interactions and social relationships, which make up the social structure of the society (Hinde 1976; Lee 1994). Social structure is often shaped in large part by kinship and dominance relationships among group members (reviewed in Koenig 2002). More recently though, researchers have emphasized the contribution of social attraction and affiliative interactions (in addition to or in conjunction with competition), even among unrelated pairs, in shaping the dynamics of group social structure (e.g. bottlenose dolphins, *Tursiops truncatus*: Lusseau et al. 2006; meerkats, *Suricata suricatta*: Madden et al. 2009; spider monkeys, *Ateles geoffroyi*: Ramos-Fernandez et al. 2009). In societies with sex-biased dispersal patterns, the dispersing sex will have fewer opportunities to interact with kin. Yet, affiliating with nonkin can still have

important direct fitness benefits to individuals, such as improved health (Seeman 1996; Thorsteinsson & James 1999) and stress reduction (Sapolsky 1998; Carter et al. 2009), particularly among females (Taylor et al. 2000; Cheney & Seyfarth 2009). Thus, while frequently less understood, examining the dynamics of relationships in the dispersing sex holds great interest.

Populations with sex differences in patterning of gregariousness, social interactions and space use can lead to functionally distinct sex-specific influences on social structure. This is seen at its extreme in societies with patterns of sexual segregation, for example many social ungulates (Main et al. 1996), but sexual segregation can also occur to varying degrees in societies with fission–fusion social organization (Ruckstuhl & Neuhaus 2000). Sex differences in social dynamics that shape social structure have been documented in a diverse array of fission–fusion societies, such as African elephants, *Loxodonta africana* (Moss & Poole 1983), sperm whales, *Physeter macrocephalus* (Whitehead & Weilgart 2000), Galápagos sea lions, *Zalophus wollebaeki* (Wolf et al. 2007), and spider monkeys, *Ateles geoffroyi* (Fedigan 1984). Thus, it is important to understand the patterning of social interactions of both sex classes when analysing social structure (Whitehead 2008).

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Here I focus on how intrasexual social relationships and affiliative interactions among females influence the social structure of the Ngogo chimpanzee community in Kibale National Park, Uganda. Chimpanzees, *Pan troglodytes*, live fission–fusion groups in which individuals form subgroups called 'parties' (Sugiyama 1968) that are highly fluid and flexible (Reynolds & Reynolds 1965; Goodall 1968; Nishida 1968). Like other species exhibiting fission–fusion social systems, chimpanzees provide a natural framework for analysing variation in social relationships (Aureli et al. 2008). Females are the dispersing sex in chimpanzees (Pusey 1980); thus, there is low variation in the degree of relatedness between females in the same community, and the majority of female–female dyads will not be closely related (Vigilant et al. 2001). In addition, chimpanzees show considerable sex differences in gregariousness and space use patters (Wrangham 1979). Chimpanzee social structure is traditionally characterized by highly gregarious males that form strong intrasexual bonds and by females that spend the majority of their time alone, but this can vary across populations and with temporal fluctuations in food availability (reviewed in Watts 2012). Male dyadic bonds are reflected in affiliative behaviours such as preferential and nonrandom association, proximity and grooming (reviewed in Mitani 2009). These relationships in turn influence male grouping patterns (Halperin 1979; Newton-Fisher 1999, 2002; Mitani & Amsler 2003; Gilby & Wrangham 2008) and can result in social substructuring or social clique formation (Newton-Fisher 1999; Mitani & Amsler 2003). While a few recent studies have reported that females at some sites are relatively gregarious and spend the majority of their time in social parties and 20% or less of their time alone, including both East African, *P. t. schweinfurthii* (Bugongo: Fawcett 2000; Emery Thompson & Wrangham 2006; Ngogo: Wakefield 2008) and West African, *P. t. verus* (Taï: Lehmann & Boesch 2008) subspecies, the traditional view of chimpanzee social structure still holds strong in the literature (e.g. see Mitani 2009). Competition among and dominance relationships between females have received much attention from researchers (e.g. Pusey 1983; Williams et al. 2002b; Wittig & Boesch 2003; Murray et al. 2006; Newton-Fisher 2006; Emery Thompson et al. 2007), but quantitative data on affiliative social interactions between females remain rare in the literature (but see Lehmann & Boesch 2009); social relationship dynamics among female East African chimpanzees in particular and how they contribute to chimpanzee social structure remain poorly understood.

In societies with flexible grouping patterns, dyadic associations are thought to reflect social relationships and preferences among individuals (e.g. African buffalo, *Syncerus caffer*: Cross et al. 2005; Asian elephants, *Elephas maximus*: de Silva et al. 2011; bottlenose dolphins, *Tursiops* spp.: Gero et al. 2005; spotted hyaenas, *Crocuta crocuta*: Holekamp et al. 1997). However, association patterns could form randomly or passively, even among dyads with higher-than-expected association frequencies (e.g. Ramos-Fernandez et al. 2009), and thus do not always reflect active social preferences (Newton-Fisher 1999). For example, party membership could reflect aggregations at mutually attractive resources, rather than attraction to conspecifics (dusky dolphins, *Lagenorhynchus obscurus*: Pearson 2009; orang-utans, *Pongo pygmaeus*: Sugardjito et al. 1987; chimpanzees: Wrangham 1977), or association patterns could be a by-product of limited ranging flexibility and/or site fidelity (e.g. false killer whales, *Pseudorca crassidens*: Baird et al. 2008; Galapagos sea lions, *Zalophus wollebaeki*: Wolf & Trillmich 2007). Thus it is important when analysing animal social structure to distinguish between active versus passive or random association (e.g. Mitani et al. 1991; Whitehead 1997; Bejder et al. 1998; Newton-Fisher 1999; Whitehead & Dufault 1999). Both of these factors have the potential to influence female chimpanzee grouping patterns. Females in some East African communities form spatial clusters known as 'neighbourhoods' in which a subset of females have overlapping core ranging areas in the same general part of their community's territory (Kanyawara: Emery Thompson et al. 2007; Mahale: Hasegawa 1990; Gombe: Williams et al. 2002b). Females show strong site fidelity to core areas (Murray et al. 2007) and, if range overlap compounded by shared resources within their ranges increases the likelihood that two individuals are found together, then association frequencies could be a by-product of range overlap rather than an expression of social affinity (Gilby & Wrangham 2008).

The aims of this paper are two-fold. First, I used data on party formation to test the null hypotheses that female association patterns reflect passive or random aggregations resulting from (1) mutual attraction to resources and/or (2) a by-product of space use overlap compared to the alternative hypothesis that female association patterns reflect active social preferences (sensu Newton-Fisher 1999). Second, I analyse association patterns to investigate female social structure and to explore whether females form social bonds that exist at a higher level than the dyadic pair, as found in male chimpanzees in the unusually large Ngogo community (Mitani & Amsler 2003). I expand on previous reports of female substructures at Ngogo (Wakefield 2008; Langergraber et al. 2009) to examine the social component of these units. I use data on affiliative (proximity and grooming) and agonistic social interactions to investigate the social dynamics of female social structure to test the hypotheses that (1) female substructures represent active social units based on mutual affinity and (2) rates of agonism are lower among frequent associates due to stable dominance relationships (Emery Thompson et al. 2007). Proximity and grooming patterns are widely considered effective measures of the value of social relationships in primates (Cords 1997) and are accordingly commonly used to meaningfully evaluate social bonds (e.g. female chimpanzees, *P. t. verus*: Lehmann & Boesch 2009; male chimpanzees, *P. t. schweinfurthii*: Newton-Fisher 2002; white-faced capuchins, *Cebus capucinus*: Perry 1996; female baboons, *Papio cynocephalus*: Silk et al. 2006).

METHODS

Study Site and Animals

I observed chimpanzees at the Ngogo research site, Kibale National Park, Uganda for 19 months between April 2003 and May 2004 (Period 1) and between October 2004 and June 2005 (Period 2). Ngogo is in the centre of Kibale in an area transitional between lowland and montane rain forest that consists primarily of moist mature evergreen and regenerating forest (Ghiglieri 1984; Butynski 1990; Struhsaker 1997).

The Ngogo community is the largest known chimpanzee community and, at the start of my study, the community included 44 adult females, 6 adolescent females, 26 adult males, 13 adolescent males, 22 juveniles and 29 infants. I selected 24 well-habituated females, including individuals of varying ages and some with and others without infants, as targets for focal data collection (total focal observation time = 1418 h; see Appendix). Twenty-one targets were parous adults at the start of data collection, two were nulliparous, but became pregnant during the first period of data collection, and one adult female was infertile and never cycled. Of the 276 dyads included in my sample, two were mother–adult daughter dyads (EK and CA; ME and HL) and the remaining 274 dyads were not close kin (Langergraber et al. 2009).

Data Collection

I used several methods to locate target females and to minimize biases towards larger parties, including listening for calls, checking fruiting trees and systematically searching the study area (Chapman et al. 1993). I collected data using a combination focal

and scan sampling techniques (Altmann 1974). I conducted instantaneous scan samples at preset 30 min intervals (on the hour and half hour) to document association patterns, proximity data and location of the focal within the community range. I conducted continuous focal animal samples for 25 min between scan samples to record detailed data on behaviour and social interactions. I chose a 30 min interval for scans because it is statistically independent at Ngogo (Mitani et al. 2000) but allows for a measure of social preferences that approximates time spent in association with other conspecifics (Wakefield 2008). I conducted all-day focal follows on target females, but switched to a new target when I lost a focal irrevocably (mean ± SD length of focal follows = 5.1 ± 1.2 h; minimum time between switching subjects was one scan period of 30 min to allow time to relocate my original focal).

Association patterns

To be consistent with previous work at Ngogo, I defined a party as all independent individuals (adults, adolescents and orphaned juveniles) present and judged to be in visual range of each other (Pepper et al. 1999; Mitani et al. 2002a) and I considered individuals in the same party to be in association. When I initially located a female, I identified all individuals present, allowing sufficient time to identify individuals initially obscured by vegetation. I subsequently recorded party composition data during scan samples, but with the help from trained field assistants, I continuously monitored party composition between scans and noted the arrivals and departures of individuals. In this way I avoided missing counts of individuals that were temporarily out of view, but still present in the party.

Space use

During scan samples, I either recorded the location of the focal to the nearest trail on the grid system, or monitored the location with a handheld GPS unit. I used a minimum convex polygon (MCP) method with 100% of points to determine the congruence of space use among female dyads and calculated the percentage of dyadic space use overlap. I included all scans in spatial analyses because eliminating scans reduces the sample size and results in representation of only a portion of the animal's movements, which in turn reduces the biological relevance and accuracy of the data (de Solla et al. 1999; Amsler 2009). In addition, because my objective was to test whether observed association patterns are a by-product of space use patterns, it was important to utilize the same data set (i.e. scan data) in both analyses and not create biases by limiting a portion of the data in one, but not the other. Thus, I included 100% of points in the MCP analysis.

Social interactions

I documented social interactions (proximity, grooming, agonistic) between target females and other adult or independently ranging adolescent females (excluding the target's own adolescent daughter) as follows. I recorded proximity during scan samples and scored all females within 5 m of the focal female as 'in proximity'. I extracted female–female grooming data from continuous focal animal samples on who groomed with whom independent of direction or duration of grooming and tallied the number of grooming bouts for each dyad. I defined grooming bouts as a continuous grooming interaction between two individuals (Barrett et al. 1999); interactions separated by more than 1 min or by a break in proximity of partners were scored as separate bouts. When visibility permitted I supplemented focal data with ad libitum sampling of female–female grooming. I considered each bout as a single dyadic interaction to facilitate calculating an index of dyadic grooming partner preferences (the pairwise affinity index, see below under Social network analysis: Matrix correlation tests). I recorded agonistic interactions between females ad libitum for both the focal and any other females present. Types of agonistic interactions included pant-

grunts, supplants, passive deferrals, physical threats without contact (lunge, hit-towards, branch-shake), charges and chases without physical contact, and attacks with physical contact. To accommodate subtle agonistic interactions like passive deferrals that ad libitum sampling may miss (Murray et al. 2006), I considered passive deferrals to include all cases where one female approached another individual who then broke proximity within 1 min.

Data Analysis

Due to the nonindependence of dyadic data, all correlation tests described below were run using matrix and partial matrix correlation procedures with the tau K_r test statistic in MatrixTester v.2.2.3 (Hemelrijk 1990a, b). I ran 10 000 permutations for each test, which was the number of iterations needed to produce a stable P value (Whitehead et al. 2005). All P values are two tailed with an alpha of 0.05 unless otherwise noted.

Dyadic association index

To investigate association patterns among females, I used the dyadic association index (DAI) to calculate the frequency of association among dyads (Nishida 1968; Martin & Bateson 1993): $DAI_{AB} = \sum AB / (\sum A + \sum B - \sum AB)$. Where A is the time based on scans individual A was seen, either alone or in association with other independent individuals; B is the time individual B was seen; and AB is the time individuals A and B were in the same party. Because I only located one party at a time, this index is equivalent to both the twice-weight and simple ratio association indices (Cairns & Schwager 1987). The twice-weight association index is the least biased index when there is a sampling bias towards finding individuals together (Cairns & Schwager 1987).

Individuals may vary in their general tendencies to join parties (Pepper et al. 1999). Therefore, to test whether female dyadic associations deviated from chance expectations based on individual variation in gregariousness, I compared the observed DAIs to values expected under the null hypothesis that associations are random, not dyad specific. I used the GROUPS computer program with the group randomization method to generate the expected values using 10 000 iterations (Pepper et al. 1999). I only present the results for the 24 target females, but since the expected association index factors in individuals' tendencies to associate with other females in general, both target and nontarget females were included in the null model.

Association dynamics: tests of active versus passive association

Newton-Fisher (1999) proposed the theory that the nature of dyadic relationships (random, passive, or active) in fission–fusion societies can be gauged by analysing the relationship between the tendency for two individuals to associate and the average size of parties in which they are together, thus producing testable predictions (Table 1). Under this model, if individuals associate at random with no discrimination among potential partners, then dyadic association strength will vary little and will be independent of variation in party size. Alternatively, individuals could be independently attracted to the same resources regardless of the presence or absence of other individuals. If party size increases with the value/size of the resource and the probability that individuals associate passively increases with party size, dyadic association strength should increase with the size of the party in which dyad members are jointly present. Conversely, if specific social affinities influence grouping decisions, then the correlation between dyadic association strength and the size of joint parties should be negative. If individuals actively associate with specific other individuals, then at the community level, preferential associates will on average be in smaller parties together, whereas infrequent associates will tend to be found together by chance in larger parties. In the case of female

Table 1
Hypotheses and predictions for association dynamics in fission–fusion groups (modified from Newton-Fisher 1999)

Hypothesis	Explanation	Predicted relationship between dyadic association strength and mean dyadic party size
H_0: *Random association*	Individuals encounter each other randomly and there is little variation in dyadic association frequencies (all dyads have similar dyadic association indices)	No relationship
H_1: *Passive association*	Individuals are independently attracted to a common resource such as a food patch regardless of other individuals that may or may not be present	Positive
H_2: *Active association*	Dyadic association patterns reflect specific social affinities among individuals with preferred associates seeking each other out as party members	Negative

chimpanzees, smaller parties provide opportunities for preferred associates to interact and for their offspring to play in a more benign environment with reduced risk of aggression and/or harassment from male chimpanzees.

To test these hypotheses for female chimpanzees at Ngogo, I followed Newton-Fisher (1999) and converted the DAI to a relative measure of dyadic association across all females, called the dyadic association strength. This was derived for each dyad using a *Z* score expressed as: $Z_{AB} = (I_{AB} - I)/s$. Where I_{AB} is the DAI for dyad AB, I is the mean DAI across all dyads, and s is the sample standard deviation. In addition, I calculated the mean dyadic party size for each dyad included in the sample (i.e. the average party size for all scans in which individuals A and B were in association). I log-normalized both variables' increasing dyadic association strength by an increment of 1 to make all values positive before transformation.

I used the partial matrix correlation procedure to examine the relationship between the log-normalized variables, dyadic association strength and mean dyadic party size. The partial matrix correlation technique utilizes three matrices and measures the association between two test matrices while holding the effects of a third (control) matrix constant (Hemelrijk 1990a). In this test I utilized a dummy matrix as the control matrix to partial out missing variables representing dyads that had zero association levels and, therefore, that had undefined values for mean dyadic party size.

Association patterns: cluster analysis

To investigate female social networks based on associations, I conducted a hierarchical cluster analysis of observed DAIs using the UPGMA or average linkage between groups method (Sneath & Sokal 1973) and statistically validated the observed clusters with a resampling procedure as described by Wakefield (2008). I use the term clique to refer to clusters of females that had higher association frequencies as a group than expected by chance.

Association patterns: matrix correlation tests

I used partial matrix correlation tests to examine the relationship of clique membership with grooming and proximity behaviour to test the predictions that pairs of females who belonged to the same clique should have been overrepresented among those dyads that engaged in affiliative behaviours more often than expected by chance (where chance levels are those expected if frequencies depend only on time in association), while dyads belonging to different cliques should have been underrepresented. I tested two alternative hypotheses for agonistic interactions within and between cliques. First, if females establish dominance relationships in

the process of forming cliques and if relationships within the clusters are thereafter stable, then it follows that females in separate cliques are less likely to establish clear dominance relationships and that rates of agonistic interactions should be higher per unit time in association between individuals belonging to separate cliques than between those in the same clique. Alternatively, it could be more important for females to reinforce dominance with frequent associates because they are more likely to forage together and face feeding competition. This leads to the prediction that agonistic interactions will occur more frequently within than between cliques.

To test these predictions, each test consisting of three matrices: a clique membership matrix (a 1, 0 matrix reflecting whether each dyad belonged to the same or a different clique), a social behaviour matrix (index of grooming, proximity or agonistic interactions), and a control matrix with the DAI to control for association frequency. I conducted separate tests for grooming, proximity and agonistic interactions, and used a Bonferroni correction to guard against type I errors (Sokal & Rohlf 1995), where $\alpha = 0.05/k$ number of tests $= 0.05/3 = 0.017$.

To construct the behaviour matrices I used the pairwise affinity index (PAI: Pepper et al. 1999; Mitani et al. 2002b): $AB \times \sum s_i(s_i - 1)/\sum A_i(s_i - 1) \times \sum B_i(s_i - 1)$. Where AB is the number of interactions observed between individuals A and B, A_i is the number of interactions of A, B_i is the number of interactions of B, s_i is the size of group i (in theses analyses 'group' is defined in terms of a dyadic interaction, thus group size remains constant at two). The PAI factors in the tendency for each individual to engage in the given behaviour and reflects the strength of the specific dyadic relationship rather than the general tendency of either individual to engage in it. I normalized the PAI by dividing the observed value by the expected value under the null hypothesis that the social behaviours are generic, not dyad specific. The expected index assumes that individuals vary in their tendency to engage in the behaviour but do not discriminate among potential partners. I used GROUPS to generate the indices and the null expectations for the PAI in the same way as described above for the DAI (under *Dyadic association index*).

Female space use overlap

I used matrix correlation to compare the percentage space use overlap for females within and between cliques. To test whether clique membership is a by-product of space use overlap, I ran a partial matrix correlation comparing association frequencies within and between cliques while controlling for space use overlap. If clique membership is purely based on overlapping space use among members of the same clique, then controlling for overlap should nullify the relationship between clique membership and association frequency.

RESULTS

Association Dynamics: Tests of Active versus Passive Association

Mean $\pm$ SD party size for parties containing females was 6.72 ± 7.03 individuals ($N = 3186$, median $= 4.0$, range 1–44). The mean $\pm$ SD number of females per party was 3.11 ± 2.56 ($N = 3186$, median $= 2.0$, range 1–15). On average, females spent 81% of their time in association with at least one other independent individual and 65% of their time with at least one other independent female; the remaining 19% of their time was spent alone (with only their dependent offspring and/or an adolescent offspring). Females varied in their tendencies to associate: DAIs ranged from 0 to 0.59, and normalized dyadic association strength ranged from -0.74 to $+6.69$ ($N = 24$ individuals, 276 dyads). There was a significantly negative relationship between dyadic association strength and mean dyadic party size (partial matrix correlation: tau $K_{r\ xy,z} = -0.359$, $N = 233$

dyads, $P = 0.0002$; Fig. 1a). The negative relationship was more pronounced among dyads with positive or greater-than-average dyadic association strength scores (tau $K_{r\ xy,z} = -0.469$, $N = 86$ dyads, $P = 0.0002$; Fig. 1b). These results support the hypothesis for active association and are inconsistent with predictions of the alternative hypotheses (random association, passive association).

Association Patterns: Cluster Analysis and Association Cliques

All dyads had observed DAIs that significantly deviated, either positively (72 or 26% of dyads) or negatively (204 or 74% of dyads), from the expected DAIs based on the null hypothesis of random association (group randomization method: $P < 0.05$ for all dyads, mean $\pm$ SD P value $= 0.0004 \pm 0.0013$, range $0.0184-0.0002$, $N = 276$ dyads). Cluster analysis revealed that females formed four association cliques (Fig. 2). Mean DAIs were significantly higher within cliques than between cliques (resampling procedure: $P < 0.001$ for all four cliques). Thus, cliques represented statistically distinct units, with females associating significantly more with members of their own clique than expected by chance (Fig. 3). While I only included target females in this analysis to avoid sampling biases, when I ran a cluster analysis on a larger sample including 38 females, the results were largely unchanged, with
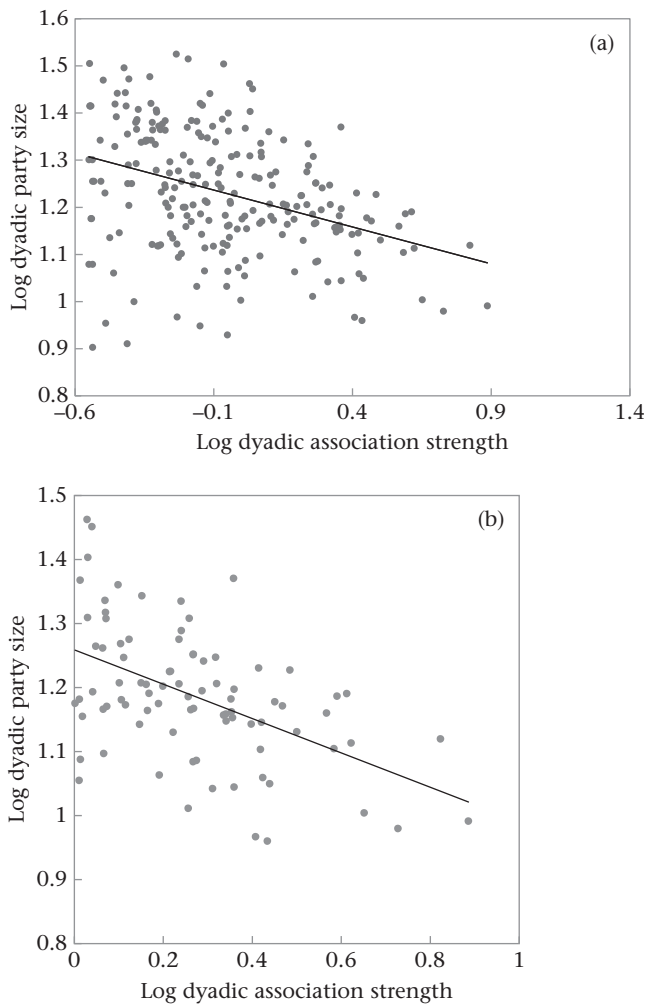
simply more females per clique, which is consistent with other work from Ngogo (Wakefield 2008; Langergraber et al. 2009).

Because the twice-weight DAI is commonly used, it allows for comparisons across chimpanzee studies, with some caution, because data collection methods vary. The overall mean for Ngogo (mean $\pm$ SD $= 0.06 \pm 0.08$) falls within the range of values reported for other East African chimpanzee communities, but the within-clique mean was considerably higher (mean $\pm$ SD $= 0.20 \pm 0.09$, range $0.13-0.32$) and within the range of female chimpanzees at Taï and bonobo females (Table 2).

Social Behavioural Correlates of Association Cliques

Target females had another female in proximity during 371 scans; in 275 of these cases, the target was in proximity to another target adult female. I observed 280 grooming bouts between target females and other females; 189 of these occurred between two target adult females. Since proximity and grooming are predicated upon association, both interactions were correlated with association frequencies (matrix correlation: proximity: tau $K_{r\ xy,z} = 0.433$, $P = 0.0002$; grooming: tau $K_{r\ xy,z} = 0.373$, $P = 0.0002$). However, both proximity (partial matrix correlation controlling for association frequency: tau $K_{r\ xy,z} = 0.171$, $P = 0.0052$) and grooming (tau $K_{r\ xy,z} = 0.209$, $P = 0.0018$) occurred significantly more among dyads within cliques and less among dyads between cliques than expected based on association frequencies. Thus, affiliations within cliques were not a mere by-product of time spent in association, as predicted by the hypothesis that association cliques represent social units.

I observed 48 agonistic interactions among females; 19 occurred between target females. Results of the matrix correlation tests
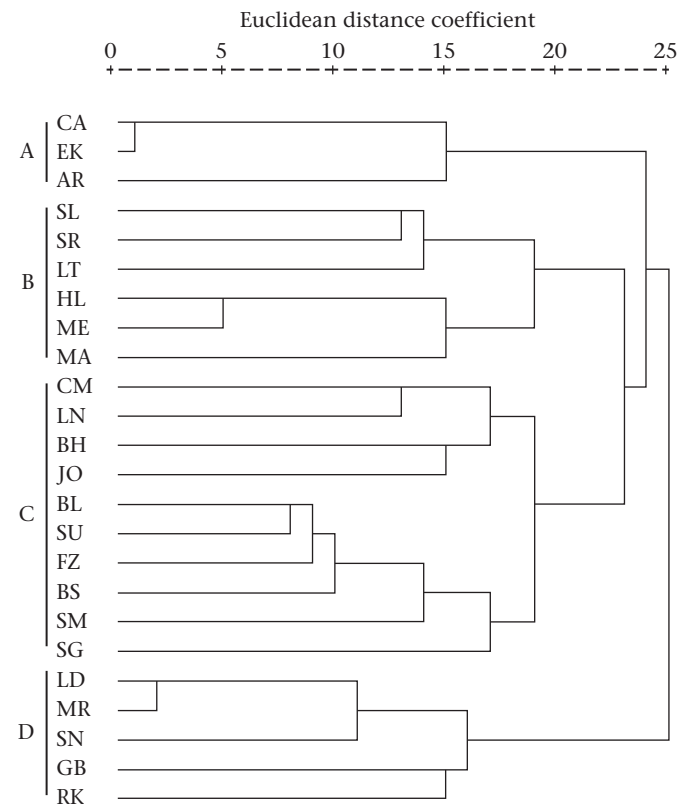

Figure 1. Mean dyadic party size of female chimpanzees at Ngogo as a function of mean dyadic association strength for (a) all dyads in the sample excluding dyads with zero association (tau $K_{r\ xy,z} = -0.359$, two-tailed $P_l = 0.0002$) and (b) only dyads with positive association strength (tau $K_{r\ xy,z} = -0.469$, two-tailed $P_l = 0.0002$). Best-fit lines are shown for visual representation.

Figure 2. UPGMA cluster analysis of the dyadic association indices for target chimpanzee females. 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). Females clustered into four association cliques, A, B, C and D.
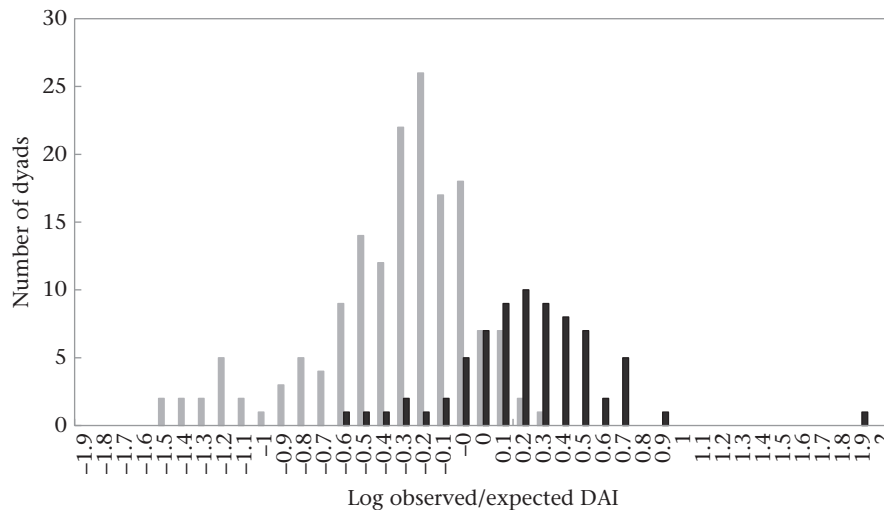
Figure 3. Distribution of observed/expected dyadic association indices (DAIs) for female chimpanzee dyads within the same clique (dark bars) and dyads belonging to different cliques (light bars). Forty-three dyads were never observed in the same party (0 association frequency) and are not shown here. The remaining 233 dyads associated at least once and had DAIs that deviated significantly from chance values. Values are log normalized so that negative numbers (left side) represent dyads that associated significantly less than expected based on a null hypothesis of random association and positive values (right side) represent dyads that associated significantly more than expected.

failed to support either alternative hypothesis clearly: the occurrence of agonistic interactions was positively correlated with association frequency alone (matrix correlation: tau $K_r = 0.256$, $P = 0.0002$), but the rates did not deviate from chance expectations either within or between cliques (partial matrix correlation: tau $K_{r\ xy,z} = 0.003$, $P = 0.9328$). However, due to the rarity of agonistic interactions and thus low statistical power, the results of this test are only preliminary.

Female Space Use

Each clique displayed distinctive, but nonuniform, space use (Fig. 4). Dyadic space use overlap was significantly higher within

cliques than between cliques (mean ± SE percentage overlap: within: $74.2 \pm 0.02\%$; between: $50.0 \pm 0.01\%$; matrix correlation: tau $K_r = 0.388$, $P = 0.0002$) and space use overlap was correlated with association frequency (matrix correlation: tau $K_r = 0.350$, $P = 0.0002$). Given that being in the same location is a requisite for an association, high association is expected to be correlated with ranging overlap. However, space use overlap was also high between cliques and, importantly, association frequency remained significantly higher within cliques than between cliques after controlling for space use overlap (partial matrix correlation: tau $K_{r\ xy,z} = 0.455$, $P = 0.0002$). Thus, clique formation among females at Ngogo cannot be explained by space use alone.

Table 2
Comparisons of female association patterns in wild *Pan troglodytes* (five sites) and *Pan paniscus* (one site)*

Population, community	Females (N)/total community size	Average F–F DAI	Source	Spatial and F–F association pattern
Pan troglodytes				
Budongo, Sonso	12/56	0.09	Fawcett 2000	Bisexually bonded ranging (Fawcett 2000; Reynolds 2005); no distinct association cliques (Fawcett 2000)
Gombe, Kasakela	8/54	0.05	Goodall 1986	Spatial neighbourhoods (Williams et al. 2002b); active social component unknown
Kibale, Kanyawara	6/~40	0.08	Wrangham et al. 1992	Spatial neighbourhoods (Emery Thompson et al. 2007); no active social component (Gilby & Wrangham 2008†)
Taï, North-group, 1987–1989	25–27/66–80	0.11	Boesch & Boesch-Achermann 2000	Bisexually bonded ranging (Lehmann & Boesch 2005); evidence for cliques when group size was large (Lehmann & Boesch 2009)
Taï, North-group, 1996–1999	11/31	0.27‡	Wittig & Boesch 2003	Females cohesive with low differentiation in DAI when community size was small (Wittig & Boesch 2003)
Kibale, Ngogo (cliques A–D)§	24/~150	0.06	This study	Active association cliques (this study)
Ngogo clique A	(3)	(0.32)		
Ngogo clique B	(6)	(0.13)		
Ngogo clique C	(10)	(0.13)		
Ngogo clique D	(5)	(0.20)		
Pan paniscus				
Lomako	11–14/33	0.25	Hohmann et al. 1999; Hohmann & Fruth 2002	Females range and actively associate cohesively (Waller 2011)

DAI: dyadic association index; F–F: female–female.

* Comparison of all studies (to the best of my knowledge) that used comparable methods/indices as in the present study. Note, I excluded two chimpanzee studies: (1) at Mahale, where estimates of female–female DAIs ranged from 0.05 to 0.39 (Nishida 1968; Nishida & Hosaka 1996; see also Boesch & Boesch-Achermann 2000), because these data were collected at artificial feeding stations; and (2) at Gombe, where DAIs of neighbours (0.154) were significantly higher than those of non-neighbours (0.096) during 1995–2004 (Murray et al. 2006), because DAIs were calculated using a half-weight association index.

† The Kanyawara community had ~50 individuals (including ~19 adult females) at the time of Gilby & Wrangham's (2008) study.

‡ Between the first and second study periods (1987–1989 and 1996–1999, respectively), there was a sharp decline in the Taï population due to an Ebola outbreak, which may have led to the significant increase in group cohesion (Boesch & Boesch-Achermann 2000).

§ Data are combined for all females, then given separately for each clique.
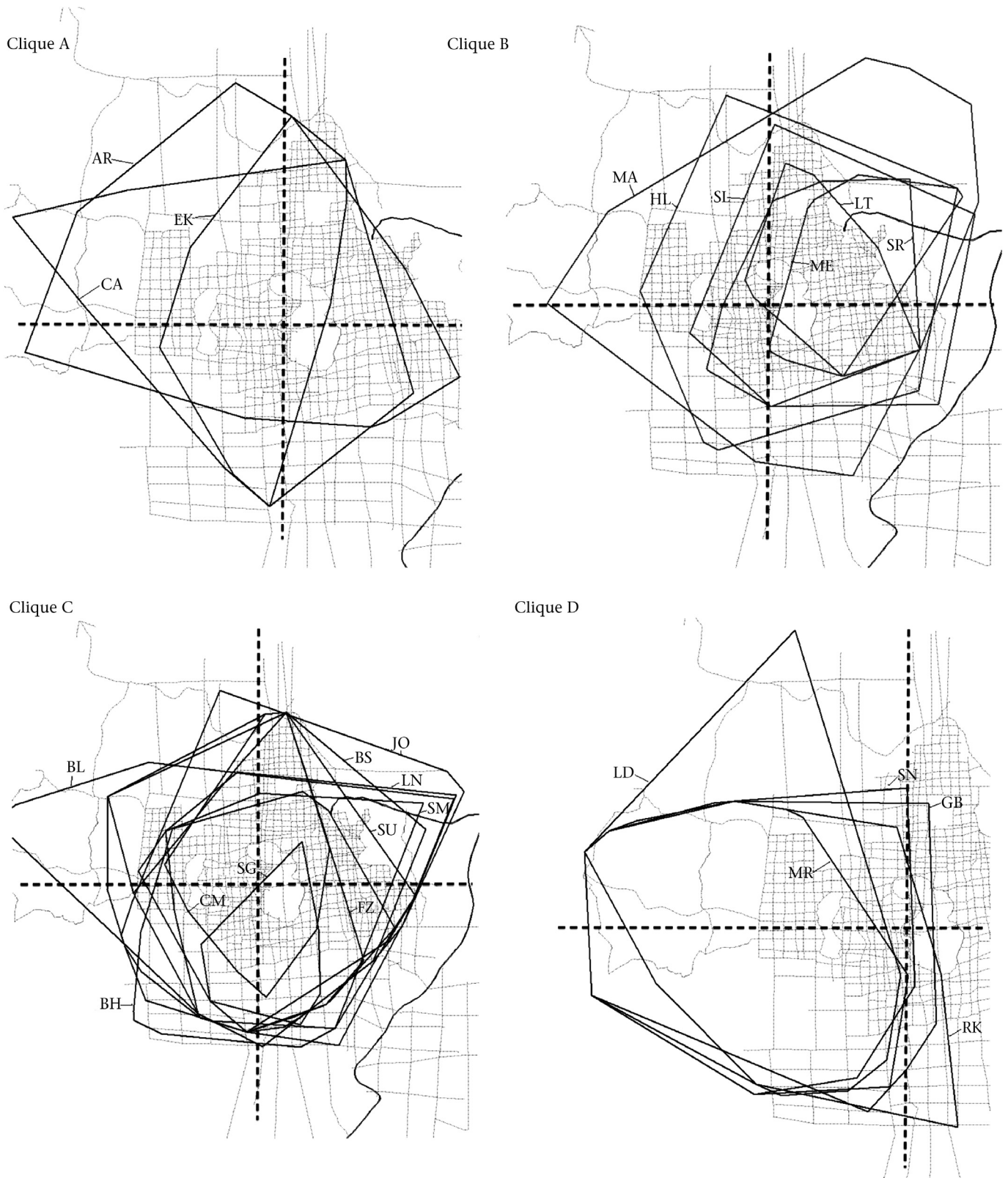
Figure 4. Space use of target females separated by association cliques A–D. Two-letter codes for females are defined in the Appendix, Table A1. The grey hashed cross denotes the approximate centre of the Ngogo trail system and is in the same location on each figure for ease of comparison.

DISCUSSION

There is a growing body of evidence that social bonds among females can have strong adaptive benefits that extend beyond kin selection (e.g. female feral horses, *Equus caballus*: Cameron et al. 2009; baboons, *Papio hamadryas ursinus*: Silk et al. 2010). Yet bonds among female chimpanzees have rarely been documented (but see Langergraber et al. 2009; Lehmann & Boesch 2009). The

preceding analyses demonstrate that females at Ngogo spent the majority of their time in association with other females, and actively associated and formed intrasexual social bonds based on mutual affinity. These bonds extended beyond the dyadic pair and females formed higher-level association cliques within which affiliative interactions, but not agonistic interactions, were relatively common. This study is the first to demonstrate that female chimpanzee substructuring within a community has a social component beyond a spatial component and that females' affiliative social relationships, not just those of males, can have an influence on the structure of East African chimpanzee societies.

Here I expanded upon theory of association dynamics in male chimpanzees put forth by Newton-Fisher (1999) to test for active association patterns in female chimpanzees. The results of my study were consistent with Newton-Fisher's predictions of active association: association levels within cliques were higher than expected by chance, and frequent associates typically formed smaller parties, whereas rare associates tended to encounter each other in large parties (i.e. preferred partners actively associated, while nonpreferred partners encountered one another randomly or passively). This relationship was even more evident among females with greater-than-average dyadic association strength, which included most within-clique dyads. Newton-Fisher (1999) referred to this form of active association among males as 'tactical association'. Tactical association may be particularly important for males because alliances are important in their competition for status (de Waal 1982). Frequent association gives males ample opportunity to develop and maintain alliances, and association in small parties could reduce the chance that rivals interrupt interactions between allies and also give them more opportunity to exchange benefits like grooming (Newton-Fisher 1999, 2002). Female chimpanzees at Ngogo are not likely to be so politically motivated in their relationships with other females given that rates of agonism among females are low (0.026/h, this study) and coalition formation is rare (three female–female coalitions in 1700 h of observation, this study). However, this does not preclude females from forming social bonds with other females, but female social relationships could be motivated more by friendship than by political strategies (de Waal 1984; Goodall 1986; Nishida & Hosaka 1996; Silk 2002). Smaller parties provide a more relaxed environment in which females can socialize and exchange benefits like grooming free from the frequent harassment and aggression, both direct and indirect, that they receive when in larger parties with males (Arcadi & Wrangham 1999; Muller 2002; Wrangham 2002; Nishida 2003; Newton-Fisher 2006; Otali & Gilchrist 2006). Successfully extending Newton-Fisher's (1999) theory of association dynamics to female chimpanzees demonstrates the effectiveness and utility of this test for examining social structure in fission–fusion societies.

Cliques appeared to be the principal social unit for relationships among females at Ngogo. Association patterns were extremely differentiated across dyads: 16% of dyads were never observed in association, while 28% of dyads had significantly positive association frequencies (Fig. 3). Although this differentiation resulted in a low community-wide mean DAI, association frequencies within female cliques were comparable to those of West African Taï females (Boesch & Boesch-Achermann 2000; Wittig & Boesch 2003), which are highly gregarious and form stable bonds and friendships (Boesch & Boesch-Achermann 2000; Lehmann & Boesch 2008), and to those of bonobo females at Lomako (Hohmann & Fruth 2002), which are characterized by high cohesion and affiliation (Idani 1991; White 1996; Table 2). Additionally, cliques were quite stable over time; most were apparent when I began working at Ngogo in 2001 and continued through my study. While there was a spatial component to association patterns since, by definition, individuals in association are in the same location, space use alone could not

account for high within-clique association frequencies. In contrast, Gilby & Wrangham (2008) found that, at Kanyawara, female association occurred only by chance based on neighbourhood membership. At Gombe, neighbours have higher association indices than non-neighbours, but it was not tested whether this departs from chance based on space use (Murray et al. 2006). Given that Gombe females spend the majority of their time alone, the extent to which spatial associations reflect social structuring is not clear. Thus, the active social component to Ngogo cliques seems to differentiate cliques from spatially defined neighbourhoods.

Clique formation at Ngogo is likely the result of a combination of two factors: reduced feeding competition and large community size. The Ngogo site contains high densities of food species important to chimpanzees and does not experience extreme temporal fluctuations in food availability (Chapman et al. 1999; Potts et al. 2009), which reduces feeding competition among females, enabling heightened gregariousness (Wakefield 2008, 2010b). Additionally, rates of agonistic interaction at Ngogo were even lower than those reported for other eastern chimpanzee communities (Wakefield 2008). Even though agonistic interactions are infrequent at both Gombe and Kanyawara, females seem to compete over space at these sites; thus, low rates of agonism may be the result of stable dominance relationships rather than lack of dominance relationships (Murray et al. 2006; Emery Thompson et al. 2007). If the low rates of female agonism at Ngogo are also the result of stable dominance relationships, then rates of agonistic interactions per unit time spent in association should be lower within established cliques than between cliques, but this was not supported. Furthermore, the finding that rates of agonism were significantly correlated with association frequency alone is counter to what would be expected if low rates indicate stable dominance relationships. I did not quantify variation in habitat quality in this study, but the high space use overlap and the ranging flexibility among females are inconsistent with high competition over space. This pattern is similar to that found in the Budongo Forest in northern Uganda, where individual female ranging patterns are differentiated, but females show extensive overlap in space use, and they show no evidence of competition over core areas (Fawcett 2000; Reynolds 2005).

Reduced feeding competition and heightened gregariousness alone cannot account for the formation of cliques. For example, at Budongo, feeding competition is reduced due to stable resources (Newton-Fisher et al. 2000), and females are relatively gregarious (Emery Thompson & Wrangham 2006), yet female association patterns are more cohesive at the group level and clique formation has not been reported (Fawcett 2000). The Ngogo community is about three times the size of the Budongo community (Table 2). Thus, given the large size of the Ngogo community, food availability and associated travel costs will place an upper limit on party size despite reduced levels of feeding competition (Wakefield 2010b) and may prevent the many females at Ngogo from cohesively associating with each other. Clique formation can enable them to maintain consistent social relationships while minimizing any costs of gregariousness. A similar demographic influence on female grouping patterns was found at Taï: when the community size was at its smallest, females associated and ranged cohesively, leading to higher mean dyadic association indices (Wittig & Boesch 2003; Lehmann & Boesch 2009), whereas when the community size was larger, there was evidence of differential social preferences and clustering among females, resulting in lower mean dyadic association indices (Lehmann & Boesch 2009; Table 2).

Long-term data will be needed to understand the fitness benefits of female social cliques and high levels of gregariousness at Ngogo. The heightened gregariousness among West African females may be a function of the presence of danger and leopard predation risk (Boesch 1991; Sakura 1994; Wittig & Boesch 2003) and may also be a factor for female bonobos at Lomako in the Democratic Republic of Congo

(Hohmann & Fruth 2002). Leopards are regionally extinct in Kibale (Struhsaker 1997); thus, predation is not a major threat to chimpanzees at Ngogo. Another possibility is that females could form cliques for direct protection from male harassment through coalitions against males (White 1992; Newton-Fisher 2006). However, female–female coalitions against males are extremely rare at Ngogo (M. L. Wakefield, personal observation), probably because large numbers of males typically found in mixed-sex parties at Ngogo (Wakefield 2008) make female coalitions too risky. However, both inter- and intracommunity infanticide is relatively common at Ngogo (Watts & Mitani 2000; Watts et al. 2002) and female–female gregariousness may provide some protection in numbers against infanticide. Testing this possibility will require long-term data on offspring survivorship, but one line of supporting evidence from the present study was the cohesiveness of female clique D (Fig. 2). This clique numbered around 14 females, including five from my sample, that showed high association frequencies and were highly cohesive. These females mostly used the far western edge of the community territory (Fig. 4), where they could have been at relatively high risk of intergroup encounters and, thus, may have formed larger, more cohesive groups as protection against infanticidal attacks. While infanticide protection may be an added benefit to associating in cliques, it is not sufficient to explain their existence since infanticide is a general feature of most chimpanzee communities (Arcadi & Wrangham 1999).

Only females with young infants can gain immediate benefits from infanticide protection, but cliques contained females in a mix of ages and reproductive states, and varying composition of offspring (Appendix). Chimpanzees are long-lived species with relatively slow life histories; it is probably more beneficial for females to form stable, long-term bonds with other individuals than to form temporary associations based on current reproductive state. In this way, females can receive long-term reciprocal or mutualistic benefits of association (as seen in female bottlenose dolphins, *Tursiops* spp.: Conner et al. 2000; Pearson 2011). Associating in small, stable cliques, within which individuals have positive affiliative interactions, increases the familiarity and predictability of relationships in fission–fusion societies. Small and stable social networks can lower social risks and reduce stress (Engh et al. 2006; Crockford et al. 2008; Wittig et al. 2008) even in the absence of frequent agonistic interactions. In addition, even though females did not form direct coalitions against male aggression, social bonds could provide a buffer against the stress of received aggression and harassment from males, which could be especially important at Ngogo with the large number of males in the community. Small stable cliques may also provide benign environments for females to exchange benefits such as offspring socialization (Williams et al. 2002a) and reciprocal grooming (Gomes et al. 2009), which are possibilities that merit further testing (Wakefield 2010a).

Previously, I proposed that Ngogo females reduce the costs of feeding competition while still obtaining benefits from gregariousness by associating in small, but stable association cliques (Wakefield 2008). My finding that cliques have strong affiliative components and represent active social networks provides further support for this hypothesis. This study highlights the importance of examining female social relationships at a level that is meaningful to the female; investigations at the community-wide level may mask important relationships and understate female sociability. Additionally, this study demonstrates that female social relationships, not just those of males, can actively influence chimpanzee party formation and thus contribute to our growing understanding of chimpanzee behavioural flexibility and social structure.

Acknowledgments

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Appendix

Table A1
Summary of target female chimpanzees divided into two periods to document demographic changes

Name (ID)	Focal time (min)	No. of scans present	Clique	Age class	Period 1 Reproductive class	Period 1 Infant/juvenile/known adolescent	Period 2 Reproductive class	Period 2 Infant/juvenile/known adolescent
Aretha (AR)	6681	449	A	PA	Lactating	F/M/M	Lactating	F/M/M
Brunhilde (BH)	4290	471	C	LAd to YA	Cycling	–/–/–	Cycling	–/–/–
Bartoli (BL)	5684	473	C	YA	Lactating	F/–/–	Cycling	–/F/–
Bessie (BS)	3811	397	C	PA	Infertile, does not cycle	–/–/–	Infertile, does not cycle	–/–/–
Callas (CA)	5335	391	A	YA	Lactating /cycling	M/–/–	Pregnant	–/M/–
Carmen (CM)	1230	194	C	PA	Lactating	F/–/–	Cycling	–/F/–
Elektra (EK)	3957	343	A	PA	Lactating	F/F/–	Lactating	F/–/F
Fitzgerald (FZ)	3708	327	C	YA	Lactating	M/–/–	Lactating	M/–/–
Garbo (GB)	2577	152	D	OA	Cycling	–/M/–	Cycling	–/M/–
Halle (HL)	3778	283	B	YA	Cycling	–/–/–	Lactating	F/–/–
Jolie (JO)	5627	476	C	YA	Cycling	–/–/–	Lactating	F/–/–
Lady Day (LD)	2296	125	D	PA	Lactating	F/–/–	Cycling	–/F/–
Leonora (LN)	4426	340	C	PA	Cycling	–/F/–	Lactating	F/F/–
Lita (LT)	6735	339	B	PA	Lactating /cycling	M/–/–	Lactating	F/M/–
Marlene (MA)	3075	292	B	OA	Postreproductive	–/F/–	Postreproductive	–/–/F
Merrill (ME)	2507	179	B	PA	Cycling	–/F/–	Cycling	–/–/F
Ma Rainy (MR)	748	90	D	OA	Lactating	M/–/–	Cycling, postreproductive?	–/–/M
Rusalka (RK)	2495	160	D	LAd to YA	Cycling	–/–/–	Lactating	M/–/–
Sigourney (SG)	801	120	C	PA	Lactating	F/F/–	Lactating	F/F/–
Sills (SL)	4049	336	B	PA	Lactating	M/M/–	Lactating	M/M/–
Salome (SM)	1802	340	C	OA	Lactating	M/F/–	Lactating	M/–/F
Senta (SN)	1617	147	D	YA	Cycling/pregnant	–/–/–	Lactating	M/–/–
Sarah (SR)	3308	337	B	PA	Lactating	F/F/–	Lactating	F/F/–
Sutherland (SU)	4533	393	C	OA	Lactating	M/F/M	Cycling/pregnant	M/–/F

Period 1: April 2003–May 2004; Period 2: October 2004–June 2005. LAd: late adolescent; YA: young adult; PA: prime adult; OA: old adult; F: female; M: male.