

RESEARCH ARTICLE

Kinship and Social Bonds in Female Chimpanzees (*Pan troglodytes*)KEVIN LANGERGRABER^{1,2*}, JOHN MITANI², AND LINDA VIGILANT¹¹Primate Department, Max Planck Institute for Evolutionary Anthropology, Leipzig, Germany²Department of Anthropology, University of Michigan, Ann Arbor, Michigan

A large body of theoretical and empirical research suggests that kinship influences the development and maintenance of social bonds among group-living female mammals, and that human females may be unusual in the extent to which individuals form differentiated social relationships with nonrelatives. Here we combine behavioral observations of party association, spatial proximity, grooming, and space use with extensive molecular genetic analyses to determine whether female chimpanzees form strong social bonds with unrelated individuals of the same sex. We compare our results with those obtained from male chimpanzees who live in the same community and have been shown to form strong social bonds with each other. We demonstrate that party association is as good a predictor of spatial proximity and grooming in females as it is in males, that the highest party association indices are consistently found between female dyads, that the sexes do not differ in the long-term stability of their party association patterns, and that these results cannot be explained as a by-product of the tendency of females to selectively range in particular areas of the territory. We also show that close kin (i.e. mother–daughter and sibling dyads) are very rare, indicating that the vast majority of female dyads that form strong social bonds are not closely related. Additional analyses reveal that “subgroups” of females, consisting of individuals who frequently associate with one another in similar areas of the territory, do not consist of relatives. This suggests that a passive form of kin-biased dispersal, involving the differential migration of females from neighboring communities into subgroups, was also unlikely to be occurring. These results show that, as in males, kinship plays a limited role in structuring the intrasexual social relationships of female chimpanzees. *Am. J. Primatol.* 71:840–851, 2009. © 2009 Wiley-Liss, Inc.

INTRODUCTION

In many social mammals, individuals do not distribute their social behaviors equitably among all group members, but instead preferentially affiliate with a small subset of available partners. A growing body of research in several mammalian taxa shows that social bonds can persist for many years [Connor et al., 2000; Lusseau et al., 2003; Mitani, 2009; Silk et al., 2006a,b], and may resemble human friendships in their emotional, psychological, and adaptive functions [Silk, 2003; Taylor et al., 2000]. In baboons, for example, females who concentrate their grooming on a small number of predictable partners have lower levels of glucocorticoids than females with more diverse grooming relationships, and females show higher levels of glucocorticoids following the death of a frequent grooming partner [Crockford et al., 2008; Wittig et al., 2008], indicating that as in humans, social bonds appear to serve an important role in mediating stress [Silk, 2003; Taylor et al., 2000].

If social bonds have positive effects on fitness, as a variety of sources of evidence indicate [Silk, 2007a,b; Silk et al., 2003], kin selection theory predicts that they should preferentially form between relatives [Hamilton, 1963; Hamilton, 1964a,b].

Empirical evidence from many mammalian species confirms that kinship has a strong effect on the development and maintenance of social bonds, particularly between females [Archie et al., 2006; Gero et al., 2008; Holekamp et al., 2007; Silk, 2006; Widdig et al., 2001, 2002]. Among baboons, for example, the vast majority of dyads that form long-term social bonds are close maternal, and to a lesser extent paternal kin, and the number of close kin that

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an individual possesses in a given year is a good predictor of the number of close social bonds that she will form [Silk et al., 2006a,b]. Current socioecological models argue that the additional indirect fitness benefits that females accrue by forming social bonds with relatives is a major selective force in promoting female philopatry in some species [Sterck et al., 1997; van Schaik, 1989; Wrangham, 1980].

Human females also show a tendency to form social bonds with close kin when patterns of postmarital residence allow access to same-sex kin, as occurs in traditional societies that practice female philopatry or in modern industrial societies where high mobility and long-distance communication allow social bonds to persist in the absence of close residential proximity [Bastani, 2009; Dunbar & Spoons, 1995; Marsden, 1987; Moore, 1990]. Ethnographic and genetic data suggest that male philopatry and female dispersal has been the modal pattern of human sex-biased dispersal since at least the rise of agriculture [Murdoch, 1981; Wilkins & Marlowe, 2005]. However, in even the most extremely patrilocal societies where females have no access to relatives, social bonds among females are common, leading to the proposition that humans are unique among mammals in the extent to which social bonds among females occur in the absence of kinship [Rodseth & Novak, 2006].

Along with humans, chimpanzees are one of the few mammals in which males consistently remain in and females typically disperse from their natal groups (termed "communities") upon reaching sexual maturity [Mitani et al., 2002]. Chimpanzees live in fission-fusion societies, with community members associating in temporary parties that vary in size, duration, and composition [Mitani et al., 2002; Nishida, 1968; Nishida & Kawanaka, 1972]. Male chimpanzees are well known for forming highly differentiated social bonds; dyads that preferentially associate in parties also affiliate and cooperate in other behavioral contexts [Goldberg & Wrangham, 1997; Mitani et al., 2000; Muller & Mitani, 2005]. Although average rates of affiliation and cooperation are lower among females than males [Halperin, 1979; Hasegawa, 1990; Kawanaka, 1984; Williams et al., 2002a; Wrangham & Smuts, 1980], at some study sites certain females associate in parties with one another as frequently as the most strongly bonded male pairs [Gilby & Wrangham, 2008; Lehmann & Boesch, 2008; Pepper et al., 1999], and the sexes do not differ in the stability of their intrasexual party association preferences across time spans of several years [Gilby & Wrangham, 2008]. This has led some to propose that chimpanzee females, like human females, form close social bonds in the absence of kinship [Lehmann & Boesch, 2008; Lehmann & Boesch, 2009; Wakefield, 2008].

This proposal remains controversial for two reasons. First, it is not clear whether long-lasting,

high rates of party association between pairs of females indicate that they share a social bond. In contrast to what is observed in male chimpanzees and other primates that are considered to form strong social bonds [Goldberg & Wrangham, 1997; Mitani et al., 2000], previous research has shown that patterns of female party association are only very weakly mirrored by two other commonly used measures of social bonding: the maintenance of close spatial proximity and social grooming [Gilby & Wrangham, 2008; Lehmann & Boesch, 2009]. The relatively low rates of these affiliative behaviors among female chimpanzees, combined with the small number of female dyads in the communities where female social behavior has been studied thus far, makes it difficult to determine whether this lack of congruence between affiliative behaviors indicates a lack of strong social bonds or a lack of statistical power. In addition, although the strength of this sex difference varies across study sites, females show a stronger tendency than males to range selectively in a subset of the entire community territory, and these ranging patterns can be stable over long periods [Emery Thompson et al., 2007; Lehmann & Boesch, 2005; Williams et al., 2002b]. A high rate of party association between a pair of females over a long time may thus reflect their tendency to selectively range in the same area of the territory rather than any social affinity between them [Gilby & Wrangham, 2008].

A second reason for uncertainty about whether unrelated female chimpanzees form strong social bonds is that genetic relationships are generally unknown. Kin-biased dispersal, a process whereby dispersing individuals join the same groups as their relatives, has been documented or suspected in many bird and mammal species [Bradley et al., 2007; Cheney & Seyfarth, 1983; Koenig et al., 2000; Packer et al., 1991; Sharp et al., 2008b], including chimpanzees [Kawanaka & Nishida, 1974], and may be an important way for individuals to form kin-based social bonds despite dispersing from their natal groups [Heinsohn et al., 2000; Meikle & Vessey, 1981]. Kin-biased dispersal can be based on the recognition of close relatives, as might occur in cases where females selectively disperse into the same community as their maternal or paternal siblings, either at the same time or after the relative has already emigrated. However, kin-biased dispersal need not always involve kin recognition; if dispersal is significantly biased in distance or direction, then dispersing individuals from the same natal group, who are all related to some extent by virtue of their shared descent from the same set of philopatric, related adults [Lukas et al., 2005], will often end up immigrating into the same group [Sharp et al., 2008a].

In this paper we combine behavioral observations of party association, spatial proximity and

grooming with extensive molecular genetic analyses to investigate kinship and social bonding in female chimpanzees living in an unusually large community in the wild. The large sample of individuals allows us to evaluate whether females form strong social bonds with a high degree of statistical power, while our genetic analyses permits us to assess whether bonds form between kin and nonkin alike.

METHODS

Study Site, Subjects, and Data Collection Procedures

We studied the Ngogo community of chimpanzees living in Kibale National Park, Uganda. Ngogo lies at an interface between lowland and montane rainforest and consists primarily of old growth tropical forest, interspersed with *Pennisetum purpureum* grassland [Struhsaker, 1997]. The Ngogo chimpanzee community has been observed continuously since 1995, and most members are well habituated to human presence [Mitani, 2006]. K. L. conducted focal follows of adolescent and adult chimpanzees, which ranged in duration from 1 to 13 hr. For both sexes, at half hour intervals we recorded the identity of individuals who were associating in the same party as the focal, as well as their location on a map of the Ngogo territory overlaid with 500 × 500 m grid cells. For females only, at half hours intervals we also recorded the identities of other females who were within close spatial proximity (≤ 5 m) of the focal individual. We recorded ad libitum all female–female grooming behavior, and in order to facilitate comparisons with previously published results on male chimpanzee affiliative behavior, which used an instantaneous point sampling method [Mitani et al., 2000], we then extracted the identities of females who were observed grooming each other at 10 min intervals. We conducted observations during two separate sampling periods (Period 1: October 2003–September 2004, $N = 4,174$ scan samples; Period 2: October 2007–March 2008, $N = 1,028$ scan samples). Except for the analysis of the temporal stability of party association patterns (see below), all analyses reported here are based on the more extensive data from Period 1. Throughout the study, overall community size remained stable at around 150 members. The subjects of this study are 38 adolescent and adult males who ranged independently from their mother and 39 anestrus adult females who were alive during Period 1. We do not include data from times when females had maximally tumescent sexual swellings, as this has previously been shown to have large effects on female party association and ranging patterns [Matsumoto-Oda, 1999]. One adult female cycled continuously throughout Period 1 and we were unable to obtain a sufficient quantity of data from her during periods when she did not have a

maximally tumescent swelling. This female was excluded from all analyses reported here, although her inclusion did not qualitatively alter any of our results. All eight adolescent females who were present during Period 1 were also excluded entirely because unlike individuals in the other three age–sex classes, adolescent females are not necessarily permanent, full-time members of a single chimpanzee community. During Period 2, 34 of the 38 male and 33 of the 39 female subjects from Period 1 were still present in the community. These individuals were used to evaluate the long-term stability of social bonds. Although we have attempted to achieve an unbiased and representative sample of chimpanzee party association patterns, our focal follows were biased toward females, and we thus may have undersampled male associations in parties that did not contain at least one adult female. However, this bias is not likely to be large enough to qualitatively alter any of our conclusions regarding sex differences in social bonds. This research complied with protocols approved by the University of Michigan Committee on the Use and Care of Animals and the legal requirements of Uganda.

Measurement and Comparison of Intrasexual Bonds in Males and Females

For each female dyad we calculated the pairwise affinity index (PAI; [Pepper et al., 1999]) for each of the three affiliative behaviors (i.e. party association, proximity, and grooming). For each male dyad we calculated the PAI for party association. Numerically this index is:

$$\frac{I_{ab}^* \sum S_i (S_i - 1)}{\sum a_i (S_i - 1)^* \sum b_i (S_i - 1)}$$

where I_{ab} = the number of instantaneous point records where individuals a and b are in the same group, a_i = the total number of instantaneous point records of a , b_i = the total number of instantaneous point records of b , S_i = the size of group i , where a “group” is defined as the individuals occurring in the same party, in spatial proximity, or engaging in grooming with each other. Before using these observed indices, we normalized them by dividing by their expected values under the null hypothesis that social behaviors were generic rather than dyad specific. We produced these expected values using a randomization technique. This procedure repeatedly re-shuffled the membership of observed parties, while retaining both the observed number of appearances of each individual and the observed distribution of party sizes. After each of 10,000 randomizations, the PAI was calculated for each dyad, and these randomized values were averaged to generate an expected value for each pair. We log transformed the observed/expected ratios to ensure that dyadic interactions above and below expected

levels would have equal weight. To avoid undefined values resulting from observed or expected values of zero, we truncated the range of the log-transformed values to $-2 \leq x \leq 2$, corresponding to a floor of 0.01 and a ceiling of 100 for observed/expected ratios. A particularly useful feature of the PAI that makes it useful for assessing social bonds is that it factors out each individual's gregariousness, or tendency to interact with conspecifics irrespective of their individual identity. As a result, it reflects only the interaction intensity that is specific to the dyad, rather than being generic to either individual's behavior.

We used Kr matrix permutation tests [Hemelrijk, 1990] to determine the strength and statistical significance of the concordance between our three measures of female affiliation, and compared the results with those obtained using the same methods in a previous study of male chimpanzee affiliation at Ngogo [Mitani et al., 2000]. As results showed that party association was approximately as predictive of spatial proximity and grooming in female dyads as in male dyads (see results below), all further analyses of social bonding were based on PAIs of party association, as this allowed us to assess sex differences across the same time periods.

We compared average male and female intrasexual PAIs of party association with matrix permutation tests. For this test we created a categorical matrix whose entries consisted of the sex of the dyad (i.e. male or female) and a corresponding matrix of PAIs of party association. We held the categorical matrix constant while randomly permuting the order of individuals in the rows and columns of the PAI matrix, with the order of individuals in columns kept the same as that in rows in order to preserve the diagonal. After each of 10,000 permutations we calculated the difference between the sexes in the mean PAI, and obtained a *P*-value by computing the proportion of permutations in this expected distribution where the mean difference was as large as or larger than that in the observed data.

We conducted two additional tests to assess whether the social relationships of females were more differentiated than those of males. First, we used a matrix permutation procedure similar to that described in the previous paragraph to determine whether the standard deviation of male and female PAIs of party association were significantly different. Second, following previous research [Silk et al., 2006b], we classified dyads that were above the 90th percentile of intrasexual PAIs of party association as having a strong social bond, and used a permutation test to determine whether males and females differed in the percentage of dyads that were strongly socially bonded. In this test a categorical sex matrix was held constant and a corresponding PAI of party association matrix was randomly permuted.

After each of 10,000 permutations, the difference between the sexes in the percentage of dyads that have a PAI value above the 90th percentile was determined. A *P*-value was calculated by computing the proportion of permutations in the expected distribution that was as large as or larger than that of the observed data.

Long-Term Stability of Intrasexual Party Association Patterns in Males and Females

We used Kr tests to assess congruence across time periods in the intrasexual PAIs of party association. This test involved 34 males and 34 females who were present during both Periods 1 and 2. We also used a matrix permutation test to determine whether male and females differed in the percentage of dyads whose PAIs were in the same general direction (i.e. both negative, indicating the dyad associated with parties less often than expected, or both positive, indicating the dyad associated in parties more often than expected) across time periods.

The Influence of Space Use on Intrasexual Party Association Patterns in Males and Females

We summed how often each individual used each 500 × 500 m grid cell, and calculated Spearman rank correlation coefficients of grid cell usage frequency for all dyadic combinations to assess similarity in ranging patterns [Doncaster, 1990]. This "Doncaster Index" (DI) varies from 1 (the ranks of grid cell usage frequency for two individuals are identical) to -1 (the two individual never use the same grid cell). If females tend to range selectively in different areas of the territory, while males tend to range over the territory more evenly, then variability in intrasexual DIs should be higher in females than males. We tested this hypothesis using a matrix permutation test similar to that described above. Here we employed sex differences in the standard deviation of DIs rather than PAIs of party association. To assess the extent to which ranging behavior influenced party association patterns, we performed Kr tests using matrices of intrasexual DIs and PAIs for both male and female dyads. To determine how the use of space influenced party association patterns between females and between males, we defined an individual's "core area" as the minimum set of grid cells where 50% of her or his party association scans occurred. We then removed individuals from all parties that occurred inside her or his core area, and recalculated PAIs to obtain a measure of dyadic party association outside of the portions of the territory where both of the individuals typically ranged. We compared male and female means, standard deviations, and percentages of

values above the 90th percentile using matrix permutation tests.

The Role of Kinship in the Intrasexual Party Association Patterns of Females

We genotyped 203 chimpanzees at up to 44 autosomal and 13 X-linked microsatellite loci, and sequenced them at 473 bases of the first hypervariable segment of the mitochondrial DNA (mtDNA) control region, following standard procedures to produce genotypes from noninvasively collected fecal samples [Langergraber et al., 2007a]. Autosomal and X-linked genotypes were 95% complete, and mtDNA sequences were 100% complete. The sample included 163 Ngogo chimpanzees, including all 38 of the mature males and 39 mature females who were the subjects of this study, and 40 chimpanzees from the nearby Kanyawara community. Individuals in the latter community were 10 km away from Ngogo and occupied a nonneighboring territory. Chimpanzees at Kanyawara were genotyped to increase the number of unrelated dyads in the sample, and thereby minimize the negative bias in relatedness values that results from allele frequencies being calculated from the same set of individuals whose relatedness is being assessed.

We used likelihood-based parentage analyses to identify mother–daughter dyads between the 39 mature Ngogo females in our sample. To identify maternal and paternal siblings, we used a combination of dyadic relatedness (R) values [Lynch & Ritland, 1999] calculated from the autosomal loci, likelihood-based KINSHIP analysis [Goodnight & Queller, 1999] using the X-linked loci, and mtDNA haplotype sharing information. To determine the most accurate criteria to identify maternal and paternal siblings among our adult female study subjects, we first tested a variety of classification schemes on a large sample of (mostly immature) female dyads whose maternal and paternal sibship status was known from parentage analyses and behavioral observations ($N = 15$ dyads known to be maternal siblings, $N = 15$ dyads known to be paternal siblings, $N = 2,661$ dyads known to be neither maternal nor paternal siblings). Many individuals in this “test” data set were not genotyped at all 44 autosomal and 13 X-linked loci. To make up for these gaps in the data, we randomly assigned individuals one allele from their mother and one allele from their father at each incomplete locus, when both parents were available. In this way, our sample of test dyads with known sibship status was approximately as complete as the sample of adult females whose sibship status we wished to determine.

After systematic testing of various cut-off values, we determined that the following classification scheme produced the highest percentage of correct classifications: (1) Maternal siblings: dyads

that shared the same mtDNA haplotype, and had either an autosomal R -value above 0.2313, or an autosomal R -value above 0.1207 and a KINSHIP likelihood ratio-value above 0.5994 for the hypothesis that the dyad was related at the X-linked loci at the level of 0.5 versus 0; (2) Paternal siblings: dyads that had either an autosomal R -value above 0.1768 and a KINSHIP likelihood ratio value above 3.003 for the hypothesis that the dyad was related at the X-linked loci at the level of 1.0 vs. 0, or an autosomal R -value above 0.0082 and a KINSHIP likelihood ratio value above 4.8216 for the hypothesis that the dyad was related at the X-linked loci at the level of 1.0 vs. 0; (3) Unrelated: all other dyads.

We found that using these criteria, of the 15 dyads known to be maternal siblings, 13 (86.7%) were correctly classified as maternal siblings, and 2 (13.3%) were incorrectly classified as being unrelated. Of the 15 dyads known to be paternal siblings, 13 (86.7%) were correctly classified as paternal siblings, and two (13.3%) were incorrectly classified as unrelated. Of the 2,661 dyads known to be unrelated, 2,658 (99.1%) were correctly classified as being unrelated, and three ($< 0.1\%$) were incorrectly classified as maternal siblings. Overall, the vast majority of dyads ($2,684/2,691 = 99.7\%$) were correctly classified. These results indicate that these criteria allowed us to assign both maternal and paternal sibship status to the adult female dyads with a high degree of accuracy even in the absence of parentage information.

We conducted a series of additional analyses to test whether a geographically based form of kin-biased dispersal by more distantly related individuals was occurring at Ngogo. Results reported below showed that the females could be divided into subgroups whose members associated in parties frequently with each other but rarely with others, whereas graphical displays of the grid cell usage frequency of subgroup members showed that the core areas of subgroup members tended to differentially cluster in relatively discrete areas of the Ngogo territory (data not shown). Thus, subgroups of females who preferentially associated in parties differed in their proximity to the 4–6 neighboring chimpanzee communities surrounding Ngogo. By virtue of their descent from the same set of paternally related males [Langergraber et al., 2007b], females from the same natal community should be on average more closely related to one another than are females who originate in different communities. We tested this assumption by examining R -values of natal infant, juvenile and adolescent females from Ngogo and Kanyawara, and found that average dyadic R -values were significantly higher within ($\bar{X} = 0.01, N = 236$ dyads) than between ($\bar{X} = -0.03, N = 550$) communities (matrix permutation test, $P < 0.05$). Thus, if females who immigrate into Ngogo establish core areas in the area of the

territory closest to their natal source community, this could increase relatedness within subgroups in the absence of biased dispersal by close, recognizable relatives. We test this possibility by comparing the average autosomal genetic relatedness of females belonging to the same and different subgroups.

We assigned females to subgroups based on simple ratio indices of party associations using Newman's [Newman, 2006] eigenvector-based method of community division by modularity. The validity of the community subdivision was assessed with Newman's [Newman, 2004] modularity coefficient, Q , which is the sum of party associations for all dyads belonging to the same subgroup minus its expected value if dyads associated in parties at random. The best division of a network is the division that maximizes Q . In practice, Q is rarely larger than 0.7 [Clauset et al., 2004], and values greater than 0.3 are considered to indicate a useful division of the population [Newman, 2004]. This coefficient also has the advantage of permitting the possibility that all individuals belong to only one cluster. A high Q -value is a necessary but not sufficient criterion of meaningful subdivision in a network, as random networks can sometimes have fairly high Q -values by chance [Croft et al., 2008; Guimera et al., 2004]. Following [Lusseau et al., 2008], we employed a bootstrapping procedure to address uncertainty surrounding the observed Q -value and the assignment of individuals to subgroups. In this procedure, we resampled with replacement our scans of party association 4,174 times (i.e. the number of party association scans in the data set) and calculated simple ratio indices of party association using these resampled data. We repeated this procedure to produce 100 matrices of simple ratio indices of party association. We then applied the community division of modularity algorithm to each of these 100 matrices. This allowed us to determine a 90% confidence interval for our observed Q -value and to determine whether it was significantly greater than 0.3.

We performed two tests to determine whether average genetic relatedness was significantly higher among dyads that belonged to the same vs. different subgroups. First, we assigned individuals to subgroups using the divisions calculated from the original (unresampled) party association data, and

used a matrix permutation test to determine whether average relatedness was significantly higher within than between subgroups. This test is similar to the permutation test for sex differences in mean intrasexual PAI of party association described above, except that dyadic categories represent individuals who belong to the same or different subgroup rather than male and female, and permuted rows and columns contain dyadic relatedness rather than dyadic PAI values. Second, to account for the fact that any method that divides a network into subgroups has a certain degree of uncertainty, for each of the 100 divisions from the bootstrapped data, we calculated the difference between the average relatedness of dyads within vs. between subgroups. We examined the range of values in the resulting distribution to assess how different divisions into subgroups affected our conclusions regarding whether individuals who belonged to the same subgroup were more closely related to each other than were members of different subgroups.

RESULTS

Comparison of Intrasexual Bonds in Males and Females

All three measures of female affiliation were significantly positively correlated with one another, at levels very similar to those previously reported for males at Ngogo [Mitani et al., 2000] (Table I). Average intrasexual pairwise affinity indices of party association were significantly higher for male (0.0016) than female dyads (-0.5691) (matrix permutation test, $P = 0.0001$), indicating that even after controlling for their higher gregariousness, males on average prefer to associate in parties with members of the same sex more strongly than do females. However, an examination of the actual values for male and female dyads (Fig. 1) shows that the network of social relationships is actually more differentiated in females than males. The standard deviation of female PAIs (1.0264) was significantly higher than that of male PAIs (0.2655) (matrix permutation test, $P = 0.0001$). The lowest PAIs occurred among females, with many dyads never observed to associate in parties for the whole

TABLE I. Correlations between measures of affiliation in female and male chimpanzees

	Males		Females	
	Pearson correlation coefficient	<i>P</i> -value	Pearson correlation coefficient	<i>P</i> -value
Association–Proximity	0.37	0.0002	0.21	0.0006
Association–Grooming	0.21	0.0004	0.39	0.0003
Proximity–Grooming	0.55	0.0002	0.31	0.0005

Values shown are from 741 female dyads (data from this study) and 256 male dyads [data from Mitani et al., 2000]. Two-tailed *P*-values are based on Kr matrix permutation tests with 10,000 permutations.

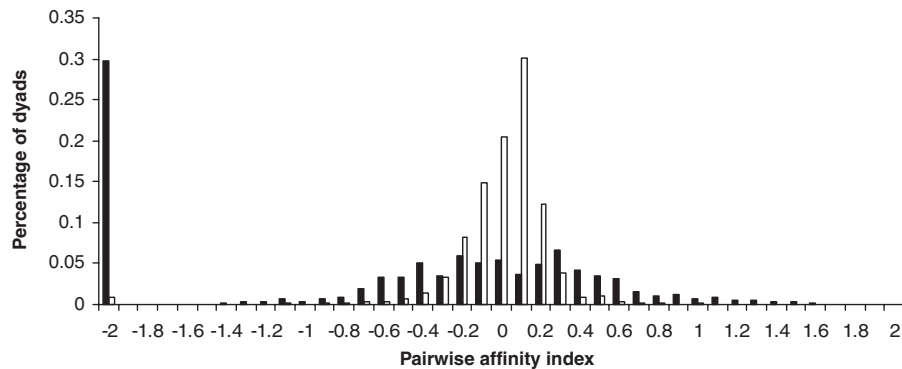


Fig. 1. Pairwise affinity indices of male (open bars) and female (black bars) associations. Values shown are rounded to one decimal place.

duration of the study (i.e. dyads with PAIs of -2.0 in Fig. 1). The very strongest social bonds occurred much more frequently in females than males, with significantly more female ($126/741 = 17.0\%$) than male ($18/703 = 2.6\%$) dyads having PAIs above the 90th percentile (>0.36) (matrix permutation test, $P = 0.0001$).

Long-Term Stability of Intrasexual Party Association Patterns in Males and Females

Both sexes exhibited long-term stability in party association patterns across the 4-year time period. Intrasexual PAIs were significantly positively correlated between the two time periods in both males (Kr test, Pearson's $r = 0.50$, $P = 0.0001$) and females (Kr test, Pearson's $r = 0.52$, $P = 0.0001$). The percentage of dyads that were consistent between time periods in the sign of their PAIs did not significantly differ between males ($387/561 = 69.0\%$) and females ($383/528 = 72.5\%$) (matrix permutation test, $P = 0.48$).

Comparing the Influence of Space Use on Intrasexual Bonds in Males and Females

The standard deviation of Doncaster indices of space use similarity was significantly higher among females (0.27) than males (0.19) (matrix permutation test, $P = 0.04$), and a significantly higher percentage of female ($136/741 = 18.4\%$) than male ($8/703 = 1.1\%$) dyads had DIs above the 90th percentile (>0.59) (matrix permutation test, $P = 0.0035$). PAIs and DIs were less strongly correlated in males (Kr test, Pearson's $r = 0.52$, $P = 0.001$) than females (Kr test, Pearson's $r = 0.73$, $P = 0.001$). Together, these results indicate that females showed greater interindividual variation in their use of space, and that ranging patterns had a stronger influence on the intrasexual party association patterns of females than males.

Nevertheless, additional analyses indicated that party associations between females could not be explained solely by differential patterns of space use. As with PAIs calculated from the entire data set, the

average PAIs of dyads calculated on sightings of individuals only when outside of their core areas were significantly higher in males (0.01) than females (-0.65) (matrix permutation test, $P = 0.0001$). Also consistent with analyses of the entire data set, the standard deviation of these PAIs was significantly higher in females (1.07) than males (0.37) (matrix permutation test, $P = 0.0001$), and significantly more female ($124/741 = 16.7\%$) than male ($20/703 = 2.8\%$) dyads had values above the 90th percentile (>0.37) (matrix permutation test, $P = 0.0001$) (Fig. 2).

The Role of Kinship in the Intrasexual Party Association Patterns of Females

There was only one adult, mother–daughter pair. There were no maternal siblings and only one pair of paternal siblings among the 39 adult females in our behavioral sample. However, the adult female we excluded from the behavioral analyses because she was cycling throughout Period 1 had a maternal sister among the 39 adult females, whereas three of the adult females had daughters who were adolescents during the study period but have since given birth and will presumably remain in the Ngogo community. The paucity of close female kin in our sample indicates that, as at most other chimpanzee study sites [Mitani et al., 2002], the vast majority of females at Ngogo are nonnatal. The small number of maternal and paternal siblings further suggests that female chimpanzees do not often migrate into communities containing close, potentially recognizable relatives.

Although the small sample of closely related dyads precludes formal statistical analysis, we note that the mother–daughter had a PAI of party association of 1.04 , which is within the top 1.5% of intrasexual PAIs, whereas the paternal sister pair had a PAI of 0.54 , which is in the top 5.9%.

The modularity coefficient Q of the community division was 0.45 (90% confidence interval = 0.42 – 0.46), which is significantly higher than the minimum value of 0.3 that is considered to indicate a meaningful division of a network

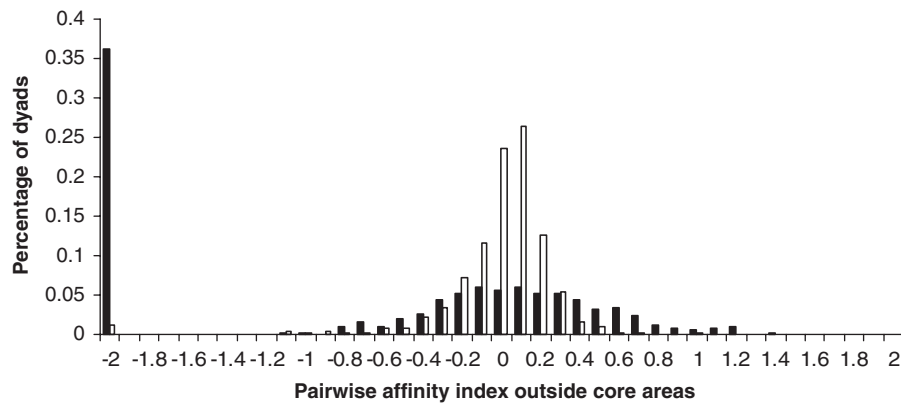


Fig. 2. Pairwise affinity indices of male (open bars) and female (black bars) associations, calculated from observations of individuals only when outside of their core area to control for sex differences in selective ranging behavior. Values shown are rounded to one decimal place.

[Newman, 2004]. The initial subdivision revealed four female subgroups, each consisting of 7–14 individuals. The average within subgroup relatedness was low in each of the four subgroups (range: -0.0106 to 0.0046), and the overall level of average relatedness did not differ within (-0.0004) and between (-0.0008) subgroups (matrix permutation test, $P = 0.16$). Examination of the bootstrap replicates revealed that some individuals were not always allocated to the same subgroup; although a division into four subgroups was the most common ($N = 89$), divisions into five ($N = 7$) and six subgroups ($N = 4$) also occurred. Additional analyses, however, indicated that uncertainty in subgroup assignments was unlikely to affect our conclusions regarding the average levels of relatedness of females belonging to the same and different subgroups. Most of the differences in average relatedness within and between subgroups from the bootstrap replicates of alternative community divisions were positive (74/100). The average difference, however, was very small (0.0008), and the largest difference in all of the replicates was only 0.0030. In sum, these results fail to provide conclusive evidence that females from neighboring communities show a pattern of differential migration into subgroups at Ngogo. The extremely small differences in average relatedness of females who occupy different subgroups indicate that if such a process is occurring, it is taking place at very low levels.

DISCUSSION

Our study provides two main results. First, we furnish some of the first evidence, especially for the East African subspecies, that long-term party associations between female chimpanzees result from a genuine social affinity rather than a passive by-product of selective ranging behavior. We found that female party association patterns were strongly correlated with proximity and grooming and were

stable across time. In these ways, the behavior of females is similar to what has been described for male chimpanzees [Mitani, 2009; Mitani et al., 2000]. Furthermore, although average levels of dyadic party association were higher among males, the majority of dyads with extremely high intrasexual party association indices were female. These same general patterns held after incorporating additional results showing that females showed less overlap in their ranging patterns than did males. Second, we found that because there were so few closely related female dyads, the overall impact of kinship on female party association patterns was very limited. As at other chimpanzee study sites [Gilby & Wrangham, 2008; Williams et al., 2002a], the few female kin dyads present in the community appeared to form strong social bonds. However, there were many more female dyads that developed strong social bonds than there were dyads that were closely related, mirroring a result shown earlier for male chimpanzees at Ngogo [Langergraber et al., 2007a]. Low levels of relatedness among females living in the same subgroups additionally suggest that individuals from neighboring communities were unlikely to migrate and settle in the same areas of the Ngogo territory.

At present, it is not clear how or whether strong social bonds among female chimpanzees enhance the reproductive success of individuals who form them. However, our finding that females tend to form strong bonds with individuals with similar ranging patterns offers some insight into this issue. Research from other chimpanzee study sites in East Africa suggest that food is not evenly distributed across chimpanzee territories, that females compete to occupy high quality core areas, and that females who successfully obtain such areas achieve high reproductive success [Emery Thompson et al., 2007; Murray et al., 2006; Murray et al., 2007; Pusey & Williams, 1997]. Although female aggression is rare [Muller, 2002], most is directed to new immigrants who are attempting to establish core areas in their

new communities [Kahlenberg et al., 2008]. Although quantitative data are lacking given the low frequency of female aggression, anecdotal observations suggest that coalitionary aggression by long-term party associates may have important consequences for female fitness; recent reports of infanticide by coalitions of females, some of whom appeared to be long-term party associates, have been interpreted as a result of competition over space [Murray et al., 2008; Townsend et al., 2007]. These data highlight the need for further long-term research to assess whether long-term social bonds facilitate coalitionary defense by females who range in similar areas of the community territory.

If it can be assumed that social bonds do enhance female fitness, this raises the question of why females do not often form them with kin, either through kin-biased dispersal or female philopatry. Demographic constraints probably limit the potential for kin-biased dispersal in chimpanzees. High levels of male reproductive skew could facilitate kin-biased dispersal of paternal siblings, both when individuals disperse together in age cohorts of paternal siblings [Boinski et al., 2005; Jack & Fedigan, 2004], and when individuals dispersing alone use age proximity as a cue to recognize their older paternal siblings who left previously [Altmann, 1979]. But age proximity may be less well correlated with paternal sibship in chimpanzees than other primate species, as male reproductive skew at any time is less extreme, and males produce appreciable numbers of offspring throughout their lifespan rather than during a narrow time window [Boesch et al., 2006; Constable et al., 2001; Inoue et al., 2008; Vigilant et al., 2001; Wroblewski et al., 2009]. Similarly, female reproductive parameters may explain why kin-biased dispersal of maternal siblings does not frequently occur: with a 50–50 sex ratio at birth, high infant mortality, an average interbirth interval of 5–6 years, and an average dispersal age of 11 years [Boesch & Boesch-Achermann, 2000; Nishida et al., 2003; Sugiyama, 2004], dispersing females will not always have maternal sisters who will recognize them or that they will recognize as such by virtue of a bond they shared as immatures with their mother in their natal group.

Although demographic and kin recognition constraints may explain why female chimpanzees do not routinely disperse into communities with close relatives, they do not explain why females do not simply gain access to kin by remaining philopatric. Theory predicts that whichever sex benefits more from social bonds should remain philopatric to obtain additional indirect fitness benefits by forming them with relatives [Le Galliard et al., 2006; Perrin & Goudet, 2001; Perrin & Lehmann, 2001]. Although currently available data do not allow us to determine whether social bonds are more important to the fitness of male or female chimpanzees, our results

showing that the social relationships of females are more strongly differentiated than those of males suggest that social bonds increase fitness in different ways in the two sexes. The strength and distribution of intrasexual bonds result from a balance of the forces of competition with individuals within groups and between groups [Cheney, 1992; Di Bitetti, 2000; Sterck et al., 1997; van Hoof, 2000]. Strong social bonds are thought to evolve when they aid individuals in competition with other group members for fitness limiting resources. However, when competition also occurs at the between-group level, affiliative social behaviors are predicted to be more equally distributed among group members. In the latter case, the development of strong social bonds and highly differentiated social structure is attenuated, as individuals need to maintain a certain minimum level of relationship with all of the members of their group to effectively compete with other groups. Chimpanzees are unusual among mammals in that they also regularly engage in between-group coalitionary aggression, and several lines of evidence indicate that success in lethal between-group competition can have important fitness consequences [Williams et al., 2004; Wrangham et al., 2004]. The fact that between-group competition is an overwhelmingly male activity [Wilson & Wrangham, 2003] may thus contribute to the more even distribution of their social relationships.

It has also been hypothesized that the larger role that men have played in between-group competition (i.e. warfare) may explain similar sex differences in the nature of intrasexual relationships in humans [Baumeister & Sommer, 1997; Byrd-Craven & Geary, 2007; Geary, 2006]. A growing body of research suggests that although men tend to form weak social relationships with many other individuals, females tend to form close dyadic relationships with a few individuals [Aukett et al., 1988; Barth & Kinder, 1988; Vigil, 2007]. These sex differences are associated with cognitive differences in the ability to process different forms of social information [Gabriel & Gardner, 1999; Markovits et al., 2006; Seeley et al., 2003], are reflected in actual behavior as well as stated preferences [Markovits et al., 2001], and emerge early in development and in many cultures across the world [Baumeister & Sommer, 1997; Byrd-Craven & Geary, 2007; Taylor et al., 2000]. Thus, in addition to sharing a unique propensity for female bonding in the absence of kinship, humans and chimpanzees may also share a history of selective pressures that have resulted in a similar male social structure. Ultimately, testing the role of within- and between-group competition in the evolution of intrasexual social relationships in humans and other social animals will require more data on the taxonomic distribution of social bonds and a better understanding of how they contribute to variation in individual fitness.

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