



## Male–Female Association Patterns Among Free-ranging Chimpanzees (*Pan troglodytes schweinfurthii*)

Zarin P. Machanda · Ian C. Gilby ·  
Richard W. Wrangham

Received: 3 May 2013 / Accepted: 8 July 2013 / Published online: 5 September 2013  
© Springer Science+Business Media New York 2013

**Abstract** Although male–female relationships can offer a number of advantages such as protection or social support, they are poorly studied among primates compared to same-sex relationships. We used 12 yr of data from the Kanyawara chimpanzee community to compare three independent measures of association (party association, 5m association, and grooming) among all adult dyads. Party association exhibited by male–female dyads was of intermediate strength between strong male–male and weak female–female association. Male–female dyads were less likely to be within 5m of one another and to groom as male–male dyads, but equally likely to be within 5m and more likely to groom as female–female dyads. Variation in male–female association strength was not related to male rank but was affected by female ranging patterns and female reproductive states. Females with core areas in the center of the home range were more likely to be in parties with males but did not show higher spatial proximity or grooming indices compared to females ranging in the periphery. Party association and 5m indices were higher for dyads of males and estrous females compared to those with anestrus females. These results indicate that male–female dyads are likely to associate with one another more often than female–female dyads because of overlapping ranging patterns and short-term changes in female reproductive state. We conclude that male and female chimpanzees do not exhibit proximity and grooming patterns indicative of strong affiliative bonds. This study also highlights the importance of using multiple independent measures of bond strength in studies of primate social dynamics.

**Keywords** Chimpanzee · *Pan troglodytes schweinfurthii* · Male–female relationships · Social bonds · Association patterns

---

Z. P. Machanda (✉) · R. W. Wrangham  
Department of Human Evolutionary Biology, Harvard University, Cambridge, Massachusetts 02140,  
USA  
e-mail: machanda@fas.harvard.edu

I. C. Gilby  
Department of Evolutionary Anthropology, Duke University, Durham, North Carolina 27708, USA

## Introduction

For the past 30 years researchers have paid considerable attention to the nature and significance of adult social relationships, focusing primarily on same-sex bonds. Bonds between males and females have been studied only in a few primate taxa including gorillas (*Gorilla beringei*: Watts 1992), baboons (*Papio hamadryas*: Palombit 2009; Smuts 1985), macaques (*Macaca fuscata*: Takahata 1982; *Macaca mulatta*: Chapais 1983), and capuchins (*Cebus capucinus*: Perry 1997). In general, it has been assumed that these types of relationships are less important than same-sex bonds because sex-biased dispersal limits both the proportion of their lifetimes that individuals spend together and the potential for kin-selected benefits (Pusey 1987; van Noordwijk and van Schaik 2004). In addition, the optimal reproductive strategy for males is often to limit investment in fertilized females in order to search for more additional mating opportunities (Maynard Smith 1977; Trivers 1972; van Schaik and Kappeler 1997). These considerations suggest that male–female interactions should be limited to short-term contexts. However, for primates that live in permanent heterosexual groups, bonds between males and females could theoretically lead to long-term benefits. Females, for example, can use bonds with males to increase their access to resources (Perry 1997) or receive support in agonistic encounters with other females (Smuts 1985; Watts 1992). In addition, because males are larger and display increased fighting ability, they can offer females and their infants protection against predators (Janson 1985), infanticidal threats (Palombit 2000), and aggression by other males (Smuts 1985). Males may benefit from intersexual bonds by being able to monitor changes in female reproductive condition especially closely and thereby promote access to females when they enter into estrous (Smuts 1985). However, males may also receive social support from females, including against nonresident males attempting to take over groups (Perry 1997; Smuts 1985), or in competition for rank and access to mates (Furuichi 2011; Surbeck *et al.* 2011).

The nature of intersexual relationships is expected to be influenced by the patterns of relationships in the group as a whole and can be better understood in comparison to intrasexual bonds. For example, among primates that exhibit predominantly male dispersal and high levels of intragroup contest competition in feeding, we can expect females to limit their association with other female competitors in favor of association with males to obtain protection against infanticide from non-group males (Sterck *et al.* 1997). This pattern is observed among red-fronted lemurs (*Eulemur fulvus rufus*: Pereira and Kappeler 1997; Pereira and McGlynn 1997) and white-faced capuchins (*Cebus capucinus*: Perry 1997) although in the latter species, it is likely that greater male–female association is driven by males seeking social support against other males more than by the ability to reduce infanticidal threats (Perry 1997). By contrast, in species with high levels of intragroup contest competition in feeding for both males and females, we would expect females to maintain weak association with both sexes, as is the case with brown capuchins (*Cebus apella*: Izar 2004; Janson 1985, 1990a,b). This pattern has also been observed among *Ateles* species where feeding competition among females is high, but females may avoid subgroups with males because of high levels of female-directed male aggression (Slater *et al.* 2009; Symington 1987).

Relative to primates living in stable groups, chimpanzee relationships are complicated by a social system of high fission–fusion dynamics such that no adult dyads are always together (Aureli *et al.* 2008; Sugiyama 1968). Nevertheless, intrasexual bonds

are prevalent and important (Gilby and Wrangham 2008; Langergraber *et al.* 2009; Lehmann and Boesch 2009; Mitani 2009), suggesting in theory that intersexual relationships could likewise occur. After dispersing, female chimpanzees may spend upwards of 40 yr in the same community (Goodall 1986), providing ample opportunity to forge social bonds with philopatric males. In addition, relationships between adult sons and their mothers are sometimes apparently supportive (although rare, given the low probability of a mother and adult son both being alive together; Goodall 1986).

Among chimpanzees, male–male dyads tend to exhibit stronger bonds than female–female dyads (Gilby and Wrangham 2008; Lehmann and Boesch 2005; Mitani 2009; Newton-Fisher 2002). This pattern is thought to result partly from high levels of feeding competition limiting the time that females spend together (Kahlenberg *et al.* 2008b; Wakefield 2008; Wrangham 2000a) as well as the fitness benefits males gain from cooperative behaviors, including boundary patrols and support in dominance competition (Gilby and Wrangham 2008; Gilby *et al.* 2013; Langergraber *et al.* 2007). With regard to interactions between males and females, evidence suggests that males, which are socially dominant to all females (Goodall 1986), can negatively influence female feeding behavior when in parties together for > 2 h/day (Pandolfi 2004; Wrangham and Smuts 1980), and females are often the victims of male aggression (Muller 2002; Muller *et al.* 2009). However, females may also benefit from associating with males because females that spend < 2 h during the day with males show increased time spent feeding compared to those who feed alone (Wrangham and Smuts 1980), and the presence of males in parties reduces aggression between females (Kahlenberg *et al.* 2008a).

Demographic factors are also important in shaping the nature of the relationships between individuals, and relationship strength can fluctuate over time as these characteristics change. For adult males, dominance rank is a particularly important factor in shaping the relationships that males have with each other (Duffy 2006; Mitani 2009; Muller *et al.* 2007; Watts 2000). Male rank also correlates with reproductive success (Gilby *et al.* 2013; Newton-Fisher *et al.* 2010; Wroblewski *et al.* 2009), suggesting that it is an important mediator of interactions between males and females. Female characteristics, especially reproductive variables, can also be important in shaping the patterns of relationships. For example, previous data from the Kanyawara community demonstrated that parity affects the strength of male–female association, as mothers of young offspring are less likely to be in parties with adult males compared to nulliparous females or those with older offspring (Otali and Gilchrist 2006). Estrous state can also affect grouping patterns and relationships within a community as party sizes are larger when estrous females are present (Matsumoto-Oda *et al.* 1998) and females receive more aggression from males when they are fully swollen (Muller *et al.* 2007). In addition, ranging patterns of females affect the probability that individuals interact with each other. Kanyawara females are known to range in overlapping core areas resulting in central, northern, and southern neighborhoods and females are rarely found outside of their preferred neighborhood (Emery Thompson *et al.* 2007).

Here, we report a quantitative analysis of male–female association patterns among free-ranging East African chimpanzees (*Pan troglodytes schweinfurthii*). We use 12 yr of data from the Kanyawara chimpanzee community (Kibale National Park, Uganda) to examine rates of temporal and spatial association and grooming among male–female dyads and compare these indices to those between male–male and

female–female dyads. Given that association with males can both negatively and positively affect female feeding behavior (Wrangham and Smuts 1980) and that females receive both aggression and protection from males (Kahlenberg *et al.* 2008a; Muller 2002; Muller *et al.* 2009), we predict that male–female association should be intermediate in strength between strong male–male and weak female–female bonds. By studying differences in the strength of three separate and independent measures of dyadic association, we are able to understand the complexity of male–female association. For example, females may spend more time in parties with males than with other females to increase their feeding efficiency (Wrangham and Smuts 1980) but they may choose not to be in spatial proximity to males when in these parties to reduce the probability of male-directed aggression (Muller 2002; Muller *et al.* 2009).

An intermediate level of association among male–female dyads compared to intrasexual dyads may be the result of a consistent pattern of intermediate level interactions between males and females or from averaging periods of high and low association. Therefore, we also examine how variation in male rank, female estrous state, and female ranging patterns affects the strength of the male–female bond. This allows us to interpret the resulting comparison of male–female association patterns with those of same-sex dyads and the demographic factors that shape male–female association patterns. We predict that low-ranking males should exhibit higher association rates with females than high-ranking males do. Although male rank is positively correlated with reproductive success, some individuals are able to father infants despite being low-ranking (Gilby *et al.* 2013; Newton-Fisher *et al.* 2010; Wroblewski *et al.* 2009). Although there are a number of strategies that these males can use to increase the probability of fathering offspring (Tutin 1979; Wroblewski *et al.* 2009), male–female dyads that maintain higher association in both estrous and anestrus periods are more likely to copulate with one another (Matsumoto-Oda 2002). Therefore, low-ranking males may increase their mating opportunities by associating more with females. Males and estrous females should also associate more than males and anestrus females because parties with estrous females often contain many adult males and because female chimpanzees attempt to mate with all available adult males when in estrus in an attempt to confuse paternity (Emery Thompson and Wrangham 2008; Matsumoto-Oda and Oda 1998; Watts 2007). Finally, males at Kanyawara range preferentially in the central neighborhood of females, which contains resources of higher quality. We predict, therefore, that central females should be in parties with males more often than peripheral females. However, because peripheral and immigrant females receive more aggression from other females (Kahlenberg *et al.* 2008a), it is possible that they might maintain higher spatial or grooming association with males compared to central females.

## Methods

### Study Site and Community

The Kanyawara chimpanzees live in Kibale National Park in southwestern Uganda and have been studied continuously by the Kibale Chimpanzee Project since 1987. All males and most females in the community were successfully habituated by 1990.

At the beginning of this study (January 1995), the community consisted of 43 individuals (11 adult males, 6 nonadult males, 16 adult females, and 10 nonadult females). By the end of the study (December 2006), it numbered 45 individuals (9 adult males, 12 nonadult males, 13 adult females, and 11 nonadult females). In total, over the entire 12-yr study, there were 78 male–male dyads, 273 male–female dyads, and 120 female–female dyads, although not every dyad was represented in each 2-yr period.

### Data Collection

Field assistants of the Kibale Chimpanzee Project entered the forest daily and located parties by either going to areas where the chimpanzees nested the previous evening, waiting at fruit trees, or listening for vocalizations. We analyzed two sets of long-term data collected daily by pairs of field assistants. One assistant collected party composition data by recording the identity of all individuals in a party at 15-min intervals. Field assistants considered individuals to be in the same party if they were within 50 m of one another, using a chain rule. They also scored the sexual state of each observed female daily as 1 (no swelling of the anogenital tissue), 2 (anogenital tissues swollen but submaximal), and 3 (anogenital tissues maximally swollen). We classified only females with a swelling of 3 as estrous and all others as anestrus. A second field assistant collected 10-min focal observations that provided data on the activity of a focal chimpanzee and the identity of all individuals within 5 m of the focal individual. When observation of a party began, the field assistant selected the least-frequently observed adult as the first focal target, subsequently rotating among available adults within the party. If a fission event occurred, the field assistants stayed with the party of the focal individual at the time. Focal observations lasted for 10 min each, with data collected at 2-min intervals. To minimize potential influences of the initial behavior on decisions to select a focal individual and begin a focal observation, we used only the last scan of each 10-min focal observation in this analysis. We refer to these as “focal scans” through the rest of this article.

We analyzed association data from 1995–2006 and divided the data set into six 2-yr periods, which is a long enough interval to obtain a large sample of observations, yet short enough to capture changes in association patterns (Gilby and Wrangham 2008). For each period, we included only individuals that were alive and adult during the entire period. Adult males were  $\geq 15$  yr old while adult females had been observed with a full sexual swelling and had mated with adult males. Table I lists the adult males and adult females that we included in this study in different periods along with the frequency with which they were observed in parties and were the subject of a 10-min focal observation.

### Calculation of Association and Grooming Indices

We calculated dyadic association and grooming indices for all male–female, male–male, and female–female dyads in each of the six 2-yr periods. To calculate the association indices, we followed Gilby and Wrangham (2008), a study of intrasexual association in chimpanzees at Kanyawara. The first index was a temporal measure of party association based on the Simple Ratio Index (Cairns and Schwager 1987),

**Table 1** The number of observations of a) adult male chimpanzees and b) adult female chimpanzees at Kanyawara during the six 2-yr periods (1995–2006). *P* refers to the number of 15-min party composition scans in which an individual was observed and *T* refers to the number of times an individual was the subject of a 10-min focal observation. Empty cells indicate that those individuals were either not alive or not adults for that period. For females, the number in parentheses refers to number of scans a female was observed with a swelling grade of 3

Males	ID	Birth	Death	Period										
				1995–1996		1997–1998		1999–2000		2001–2002		2003–2004		2005–2006
				T	P	T	P	T	P	T	P	T	P	T
	AJ	1974		199	8604	280	7393	133	10129	184	9524	187	8922	243
	BB	1966		191	6474	234	5938	113	6774	119	8013	193	8924	233
	BF	1966	1998	111										
	KK	1985							9669	189	11245	256	13541	622
	LB	1968	2001	192	7581	268	6790	171						
	LK	1982					9132	259	11726	221	12618	235	13834	567
	MS	1979		205	9181	331	9193	224	10676	226	12811	268	12200	437
	PG	1988											12398	380
	SL	1971	2005	70	3208	103	3593	57	5838	73	8023	88		
	ST	1955		203	8158	270	6751	158	9219	160	12609	196	8854	257
	SY	1964	2000	206	7275	314								
	TU	1960		99	4896	119	4911	116	7372	133	10806	192	8208	180
	YB	1973		185	8257	323	7440	203	9646	184	11420	222	12037	450

**Table I** (continued)

Females	ID	Birth	Death	Period		1995-1996		1997-1998		1999-2000		2001-2002		2003-2004		2005-2006	
				P	T	P	T	P	T	P	T	P	T	P	T	P	T
AL	1982	4516 (2545)	230 (138)	5122 (1835)	200 (96)	5445 (491)	82 (12)	7013 (136)	75 (1)	6861 (1606)	86 (11)	13334 (2046)	348 (29)				
AR	1943	1589 (0)	159 (0)	3824 (494)	179 (22)	2627 (0)	91 (0)	2587 (0)	36 (0)	3375 (0)	112 (0)	5198 (154)	163 (1)				
BL	1960	53 (0)	0 (0)	1122 (0)	20 (0)	2229 (0)	17 (0)	4550 (354)	53 (6)	6089 (429)	37 (3)	7129 (0)	143 (0)				
EK	1974	135 (0)	6 (0)	430 (99)	9 (0)	2170 (438)	27 (11)	1521 (229)	17 (6)	4429 (736)	83 (13)	10277 (0)	268 (0)				
FG	1955	2790 (222)	156 (4)														
GO	1957	494 (0)	38 (0)	1722 (809)	50 (23)	1165 (0)	6 (0)										
HH	1993																
JO	1960	2001	160 (0)	343 (0)	0 (0)	1954 (415)	38 (11)										
KL	1970	2000	2569 (0)	235 (0)	4168 (1000)	307 (137)											
LP	1955	2004	4014 (0)	245 (0)	9911 (0)	534 (0)	206 (1)	8542 (446)	175 (7)	3147 (0)	20 (0)						
LR	1989							8600 (3781)	153 (49)	7306 (2125)	112 (25)	14146 (0)	753 (0)				
MG	1945	1998	986 (0)	40 (0)													
MU	1970																
NG	1955	1997	204 (149)	10 (6)	17 (0)	1 (0)	4 (0)	157 (0)	2 (0)	1628 (0)	38 (0)	2689 (13)	84 (0)				
NL	1982																
OU	1979																
PE	1970	2003	252 (0)	9 (0)	6203 (858)	279 (54)	159 (49)	7354 (896)	89 (8)	5596 (1433)	56 (8)	13570 (432)	501 (3)				
PU	1955	2003	237 (27)	17 (0)	337 (0)	9 (0)	10 (0)	219 (33)	0 (0)	8264 (1106)	112 (31)	16320 (519)	504 (13)				
TG	1980																
UM	1981																
WA	1991																

which measures how often a dyad is present together in the same 15 minute party scan. The party association index for chimpanzees A and B would be:

$$\text{Party Association} = \frac{P_{AB}}{P_A + P_B - P_{AB}} \quad (1)$$

where  $P_{AB}$  is the number of party scans containing A and B together,  $P_A$  is the number of party scans containing A, and  $P_B$  is the number of party scans containing B. In the denominator,  $P_{AB}$  is subtracted to avoid counting individuals twice because the  $P_A$  and  $P_B$  both include party scans where individuals A and B are seen together. The second index was a metric of spatial association, the 5m index, which measures the frequency with which two individuals were within 5m of one another when one was the subject of a 10-min focal observation and the other was in the same party. The spatial proximity between individuals A and B is calculated using the following formula:

$$5m_{AB} = \frac{A_f B_5 + B_f A_5}{A_f B_p + B_f A_p} \quad (2)$$

where  $A_f B_5$  and  $B_f A_5$  are equal to the number of focal scans where A or B is the focal and the other individual is within 5m of the focal, and  $A_f B_p$  and  $B_f A_p$  are the number of focal scans where A or B is the focal and the other is in the same party. Finally, we calculated a measure of grooming association by counting the number of focal scans in which individuals were observed grooming each other divided by the number of scans that one individual was the focal and the other was within 5m of the focal. It is calculated for chimpanzees A and B as follows:

$$\text{Groom}_{AB} = \frac{A_f B_{\text{groom}} + B_f A_{\text{groom}}}{A_f B_5 + B_f A_5} \quad (3)$$

where  $A_f B_{\text{groom}}$  and  $B_f A_{\text{groom}}$  are the number focal scans in which A or B is the focal and the other is the grooming partner and  $A_f B_5$  and  $B_f A_5$  are as stated for equation (2). We calculated the 5m index only for dyads that were in the same party together for at least ten 15-min scans, i.e. where the denominator was  $\geq 10$ , in a given period. Similarly, we calculated the grooming index only for dyads that were within 5m of each other in  $\geq 10$  scans. Therefore, there are some dyads for which the data were not available to calculate one or both of these indices.

Our three indices represent independent measures of association. For example, the 5m index is not influenced by the number of times that two individuals were seen in the same party. Therefore, a dyad that was rarely in the same party (and therefore had a low party association value) could nevertheless in theory have a high 5m index value. This approach allows us to characterize the specific nature of adult association patterns.

To compare association patterns of male–female dyads with male–male and female–female dyads, we standardized each dyadic index by dividing by the mean index of all intra- and intersexual dyads in the community for each period. Therefore the value of the association index is a measure of how much each dyad deviated from the average dyad in the community at that time. A dyad with an index value  $> 1$  associated more often than the average dyad.

## Variation Among Male–Female Association Patterns

To understand the source of variation in the relationship strength of male–female dyads, we examined correlations between male–female association indices and male rank, female neighborhood affiliation and female reproductive state. We determined male dominance ranks for each period using data on the frequency and direction of pant-grunts (a vocalization given by subordinate individuals to dominant individuals; Goodall 1986), as well as the outcomes of decided, dyadic agonistic interactions. We calculated Landau's index of linearity ( $H'$ ) using the Matman (version 1.1, Noldus Information Technology; de Vries *et al.* 1993), which orders males into a hierarchy while minimizing the number of inconsistencies and missing data between dyads. We used a two-step randomization procedure with 10,000 iterations (de Vries 1995) to determine that the male dominance hierarchy in each period was significantly linear. We assigned a rank to each male in each period, with 1 being the alpha (highest ranking). We also classified males into rank categories with individuals ranked 1–3 as high-ranking, 4–7 as mid-ranking, and 8 and above as low-ranking.

To examine female ranging patterns, we assigned females to different neighborhoods (central, northern, and southern) within the community range based on the locations of overlapping core areas for each 2-yr period (Emery Thompson *et al.* 2007). We considered any female who was not assigned to the central neighborhood (including those that had just immigrated or were observed infrequently), as peripheral. We used these neighborhood categories in models that compared variation in male–female and female–female association patterns.

Examining the effect of female estrous state on association patterns is more complicated because it is not possible to calculate the party association index separately for male–estrous female and male–anestrous female dyads. This is because a female has to be observed in order to be assigned a swelling score. In general, there is only one party under observation during any given 15-min scan. Therefore, when we observe males on days without a particular female, it is not possible to know her estrous state. Hence, in equation (1), if individual A is a male and individual B is an estrous (or anestrous) female,  $P_A$  will be equal to  $P_{AB}$ . Therefore, instead of a party association index, we calculated the proportion of 15-min scans that females were in parties with individual males on days when they were in estrous and anestrous. In other words, for each male (A) and female (B) dyad in a period, we divided the number of 15-min scans that a male and female in a particular estrous state were seen together, e.g.  $P_{AB(\text{estrous})}$ , by the number of 15-min scans that the female was observed in that same estrous state, e.g.  $P_{B(\text{estrous})}$ . We calculated the 5m and grooming indices for male–estrous female dyads and male–anestrous female dyads in each period as shown in equations (2) and (3) respectively because these indices are dependent on the male and female being in the same party together. Therefore during each 2-yr period we calculated two separate 5m and grooming indices for each male–female dyad — one for each female estrous state (see Table 1b for the number of observations of each female with a maximal swelling).

During the 12-yr study there were six adult male–female dyads composed of close kin (mother–son or matrilineal siblings). The sample size for these related male–female dyads was too small during any particular period to allow us to test quantitatively predictions about the relationship between relatedness and male–female association.

## Comparing Association Strength

We ran generalized linear models (GLMs) to compare the mean party association, 5m, and grooming indices of male–male, male–female, and female–female dyads. In the models, we used the different indices as the response variables and the sex composition of the dyad as the predictor variable. We controlled for repeated sampling of individuals by using males and females as subjects and the 2-yr period as an intrasubject effect. This allowed us to control for the possibility that some chimpanzees might be more gregarious than others and the fact that we had repeated sampling of dyads across periods. To examine variation within male–female association values in party association, 5m and grooming indices, we used the indices as response variables, and male rank (either continuous or categorical) and female neighborhood affiliation as predictor variables in the GLMs. Again, we included males and females as subject variables and period as an intrasubject variable. For the proportion of time that females spent in parties with males when in estrous or anestrus, and for the 5m and grooming indices, we also included estrous state (estrous/anestrus) as an intrasubject variable in the GLM. This accounts for the fact that we have repeated measures on males and females in different periods and that in some 2-yr periods there are females with scores during times when they are in estrous and anestrus. We also ran the GLM with the different indices just for dyads of male–estrous female dyads to test whether male rank would predict association with females only during periods when females were fully swollen. We kept female neighborhood affiliation as a predictor in this model to control for the fact that ranging patterns might affect association with males even when a female is in estrous. Finally, to understand fully the effect of female neighborhood affiliation on male–female association, we examined variation in party association between female–female dyads to see whether females living in the same neighborhood exhibited stronger association values than individuals ranging in different neighborhoods. In this analysis, the party association, 5m, and grooming indices were included as response variables in the GLM with female neighborhood as the predictor variable. Individual female IDs were included as subject variables and the 2-yr period as an intrasubject variable to control for repeated measures on individuals. The mean values of the relationship indices and the standard errors that are presented in this article are the predicted values provided by the model. These and all other statistical analyses were performed using SPSS v.20 (SPSS Inc., Chicago, IL).

## Variation in the Direction of Grooming

The grooming index described in equation (3) does not distinguish between the groomer and the recipient. To do this, we identified every focal scan between 1995 and 2006 in which an adult male and adult female were grooming. We used a binomial test to determine whether grooming direction in these bouts differed significantly from the expected distribution of 50% (if each sex was equally likely to groom the other). We then used a generalized linear mixed model to examine the effects of male rank, female estrous state, and female neighborhood on the probability that the male was grooming the female in the grooming scan. In this model, we controlled for

repeated measures of the male–female dyad in the dataset by using the dyad ID as a random effect.

## Results

From 1995 to 2006, there were 129,483 15-min scans of chimpanzee parties from which we calculated the party association index. During this study period, adult males were the subjects of 12,032 10-min focal follows (4448 in parties alone or with other adult males and 7584 in parties with adult females; see Table II for a breakdown by period). Adult females were the subjects of 9649 10-minute focal follows in total, with 951 on days with a full sexual swelling. Of these focal scans, 4401 were of adult females alone or in parties with other adult females and 5248 in parties with adult males (Table II). When females were observed with full sexual swellings, they were in parties with other adult males for 846 of the 951 focal scans.

Table III shows the number of male–male, male–female, and female–female dyads for which we had enough observations to calculate each association index. Across periods, it was possible to calculate 5m indices for all male–male dyads and grooming indices for 71–100% of those same dyads. Females were seen often enough to calculate party association indices for every dyad, but other indices were less available. Thus for male–female pairings, we calculated 5m indices for only 61–100% of all dyads and grooming indices for 12–44% of dyads. For female–female dyads, we calculated 5m indices for 33–100% of dyads and grooming indices for 2–26% of dyads. The range of values for the party association index across all periods was 1.02–4.87 for male–male dyads, 0–5.16 for female–female dyads, and 0–3.83 for male–female dyads. For the 5m index, the range of values was 0–4.22 for male–male dyads, 0–3.27 for female–female dyads, and 0–5.06 for male and female dyads. For the grooming index, the range of values was 0–4.18 for male–male dyads, 0–2.18 for female–female dyads and 0–4.84 for male–female dyads.

**Table II** The number of 10-min focal follows for males and females in each 2-yr period. Males were the subject of focal follows either alone or in parties with other adult males or in parties with at least one female. Females were the subject of focal follows either alone or in parties with other adult females or in parties with at least one adult male

Period	Males		Females	
	Alone or with other adult males	With at least one adult female	Alone or with other adult females	With at least one adult male
1995–1996	459	1202	791	830
1997–1998	979	1263	843	1103
1999–2000	606	828	449	558
2001–2002	481	1008	289	506
2003–2004	571	1266	213	585
2005–2006	1352	2017	1816	1666

**Table III** The total number of male–female, male–male, and female–female chimpanzee dyads at Kanyawara in each period (1995–2006) and the number of dyads for which we calculated individual association indices in each period

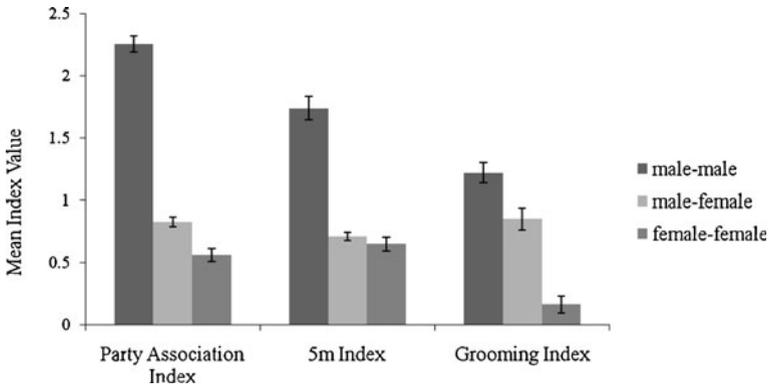
Period	Total			Party association			5m			Grooming		
	MF	MM	FF	MF	MM	FF	MF	MM	FF	MF	MM	FF
1995–1996	160	45	120	160	45	120	98	45	39	19	32	6
1997–1998	126	36	91	126	36	91	88	36	32	28	29	5
1999–2000	126	36	91	126	36	91	95	36	30	19	36	6
2001–2002	117	36	78	117	36	78	90	36	38	15	36	5
2003–2004	99	36	55	99	36	55	98	36	42	16	35	1
2005–2006	108	36	66	108	36	66	108	36	66	48	36	17

### Comparing Intersexual and Intrasexual Association Strength

The party association index, which measured the proportion of time that members of a dyad were seen in a party together, was significantly different among male–male (highest), male–female (intermediate), and female–female dyads (lowest) ( $\chi^2=472.3$ ,  $df = 2$ ,  $P<0.0001$ ; Fig. 1). Male–female party association values (mean =  $0.83 \pm 0.04$ ) were significantly different from both male–male dyads (mean =  $2.26 \pm 0.07$ ,  $\chi^2=362.5$ ,  $df = 1$ ,  $P<0.0001$ ) and female–female dyads (mean =  $0.56 \pm 0.05$ ,  $\chi^2=18.5$ ,  $df = 1$ ,  $P<0.0001$ ). However, mean party association values for male–female dyads were more similar to values for female–female dyads than to male–male dyads. Both male–female and female–female values were below the mean community value of 1.

The 5m index (the frequency that two individuals were within 5m of one another given that one was the focal and the other was in the party) was also significantly different between male–male, male–female, and female–female dyads ( $\chi^2=114.9$ ,  $df=2$ ,  $P<0.0001$ ; Fig. 1). However, although male–male 5m index values (mean =  $1.74 \pm 0.09$ ) were significantly greater than both the male–female (mean =  $0.71 \pm 0.03$ ,  $\chi^2=107.6$ ,  $df = 1$ ,  $P<0.0001$ ) and female–female values (mean =  $0.65 \pm 0.05$ ,  $\chi^2=101.4$ ,  $df = 1$ ,  $P<0.0001$ ), the male–female values and female–female values did not differ significantly from each other ( $\chi^2=0.8$ ,  $df = 1$ ,  $P = 0.366$ ). Both were lower than the community mean value of 1.

The strength of the grooming index (the frequency with which two individuals were grooming partners given that they were within 5m of one another) was significantly different between male–male, male–female, and female–female dyads ( $\chi^2=103.5$ ,  $df=2$ ,  $P<0.0001$ ; Fig. 1). Similar to the party association index, male–male dyads showed the highest levels of grooming (mean =  $1.22 \pm 0.08$ ), which were significantly greater than both male–female (mean =  $0.85 \pm 0.09$ ,  $\chi^2=9.1$ ,  $df = 1$ ,  $P = 0.003$ ) and female–female values (mean =  $0.16 \pm 0.07$ ,  $\chi^2=97.0$ ,  $df = 1$ ,  $P<0.0001$ ). Male–female values were also significantly different from female–female values ( $\chi^2=38.3$ ,  $df = 1$ ,  $P<0.0001$ ). However, unlike the other indices, although the mean male–female grooming index was below the community mean of 1, it was closer in value to the male–male value than the female–female value.



**Fig. 1** Comparison of the mean ( $\pm$  SE) party association, 5m, and grooming indices for male–male, male–female, and female–female of chimpanzees of the Kanyawara community from 1995 to 2006. The index values shown here as well as the standard error bars are estimated means from the general linear models evaluating variation in the association indices by dyad composition.

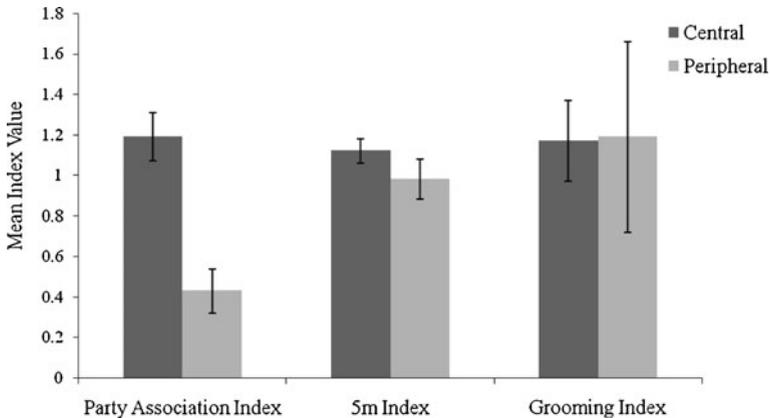
### Variation in Male–Female Association

Male dominance rank had no effect on variation in the male–female party association index (continuous rank:  $\chi^2=0.02$ ,  $df=1$ ,  $P=0.881$ ; categorical rank:  $\chi^2=0.26$ ,  $df=1$ ,  $P=0.877$ ), the 5m association index (continuous:  $\chi^2=2.6$ ,  $df=1$ ,  $P=0.103$ , categorical:  $\chi^2=1.2$ ,  $df=1$ ,  $P=0.549$ ), or the grooming index (continuous:  $\chi^2=1.6$ ,  $df=1$ ,  $P=0.2$ , categorical:  $\chi^2=1.9$ ,  $df=1$ ,  $P=0.387$ ). Therefore, we removed rank from subsequent models although the results remained the same regardless of its inclusion.

Female neighborhood affiliation (see Fig. 2) was a significant predictor of variation in party level association ( $\chi^2=313.8$ ,  $df=1$ ,  $P<0.0001$ ). Central females were more likely than peripheral females to be in parties with adult males (mean male–female party association for central females:  $1.19 \pm 0.12$ , vs. that of peripheral females:  $0.43 \pm 0.11$ ). Among female–female dyads, neighborhood affiliation was significantly related to party association indices ( $\chi^2=53.5$ ,  $df=2$ ,  $P<0.0001$ ). Dyads of central females exhibited high mean values (mean party association for central–central female dyads =  $1.15 \pm 0.12$ ); dyads of peripheral females had intermediate values (mean party association for peripheral–peripheral female dyads =  $0.51 \pm 0.07$ ) and dyads of central–peripheral females had the lowest values (mean party association for central–peripheral female dyads =  $0.29 \pm 0.02$ ).

Our model did not reveal a significant difference between central and peripheral females for the 5m index ( $\chi^2=1.6$ ,  $df=1$ ,  $P=0.201$ , mean 5m index for central females:  $1.12 \pm 0.22$ , mean 5m index for peripheral females:  $0.98 \pm 0.24$ ; Fig. 2). Similarly, female neighborhood affiliation was not a significant predictor of grooming frequency (female neighborhood:  $\chi^2=0$ ,  $df=1$ ,  $P=0.989$ ; Fig. 2). Therefore, once males were in parties with females, female neighborhood affiliation did not affect either the pattern of 5m association or the frequency of grooming.

Males were more likely to be observed in parties with a female when she was in estrous than when she was anestrus ( $\chi^2=273.8$ ,  $df=1$ ,  $P<0.0001$ , mean proportion of scans of males and estrous females:  $0.73 \pm 0.01$  and mean proportion of scans of males and anestrus females:  $0.46 \pm 0.02$ ; Fig. 3). Our model also revealed different patterns for the 5m index ( $\chi^2=13.0$ ,  $df=1$ ,  $P<0.0001$ ), with estrous females exhibiting



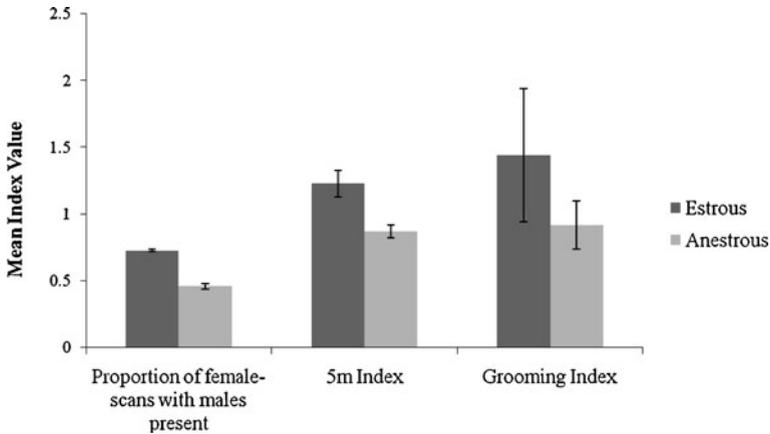
**Fig. 2** Comparison of the mean ( $\pm$  SE) party association, 5m, and grooming indices for male–central female and male–peripheral female dyads of chimpanzees of the Kanyawara community from 1995 to 2006. The index values shown here as well as the standard error bars are estimated means from the general linear models evaluating variation in the association indices by female neighborhood.

higher spatial association with males than anestrus females did (mean 5m index for estrous females:  $1.24 \pm 0.11$  and mean 5m index for anestrus females:  $0.87 \pm 0.05$ ). However, female estrous state was not a significant predictor of grooming (female estrous:  $\chi^2=1.0$ ,  $df=1$ ,  $P=0.316$ , male–estrous female mean:  $1.35 \pm 0.51$ , male–anestrus female mean:  $0.91 \pm 0.16$ ). When we ran the GLM on just the association indices for male–estrous female dyads, we found that male rank (as either a continuous variable or categorical variable) was not related to the proportion of 15-min scans that estrous females spent in parties with males (continuous rank:  $\chi^2=0.1$ ,  $df=1$ ,  $P=0.704$ , categorical rank:  $\chi^2=0.2$ ,  $df=1$ ,  $P=0.909$ ) nor did it predict the grooming index of a male–estrous female dyad (continuous rank:  $\chi^2=0.6$ ,  $df=1$ ,  $P=0.428$ , categorical rank:  $\chi^2=0.7$ ,  $df=1$ ,  $P=0.721$ ). However, in the model, male rank was significantly and negatively related to the strength of the 5m index for male–estrous female dyads, although only when rank was used as a continuous variable ( $\chi^2=6.5$ ,  $df=1$ ,  $P=0.011$ ) and not as a categorical variable ( $\chi^2=5.0$ ,  $df=1$ ,  $P=0.083$ ).

#### Variation in the Direction of Grooming

Between 1995 and 2006, there were 1506 dyadic male–male grooming scans (1403 unidirectional) and 87 female–female scans (84 unidirectional). There were 497 male–female scans (450 unidirectional) in which an adult male and female were grooming. In these bouts, males were significantly more likely to be the groomer than the female was (60.4% [272/450], binomial test,  $P<0.0001$ ). Of the 93 grooming scans between males and estrous females, the male was the groomer in 75 (80.6%) scans. Of the 357 scans between males and anestrus females, the null hypothesis of a 50% distribution between males and females being the groomer cannot be rejected (binomial test,  $P=0.057$ , males groomed females in 197 of 357 scans).

Male rank, measured either as a continuous or a categorical variable, was not a significant predictor of the probability that males were grooming females (continuous male rank:  $F=0.59$ ,  $df_1=1$ ,  $df_2=429$ ,  $P=0.442$ , categorical male rank:  $F=0.23$ ,  $df_1=2$ ,



**Fig. 3** Comparison of the mean ( $\pm$  SE) party association, 5m, and grooming indices for male–estrous female and male–anestrous female dyads of chimpanzees of the Kanyawara community from 1995 to 2006. The index values shown here as well as the standard error bars are estimated means from the general linear models evaluating variation in the association indices by female reproductive state.

$df_2=428$ ,  $P=0.816$ ). When rank was removed from the model, female neighborhood affiliation was still not a significant predictor ( $F=2.8$ ,  $df_1=1$ ,  $df_2=430$ ,  $P=0.095$ ). As expected from the binomial test, female estrous state was a significant predictor in the model ( $F=14.50$ ,  $df_1=1$ ,  $df_2=430$ ,  $P<0.0001$ ) with the probability of male grooming being higher when the female of the dyad was swollen.

## Discussion

In this study, male–female dyads showed intermediate levels of party association, falling between male–male and female–female values. Strong association patterns among male chimpanzees have been suggested to reflect increased cooperative behavior compared to females and the importance of these social bonds in chimpanzee communities (Gilby and Wrangham 2008; Muller and Mitani 2005). Given the intermediate value that we found, our results raise the possibility that male–female relationships are also valuable in this community. However, we demonstrate that males and females were as likely to be within 5m of one another in parties as female–female dyads and significantly less so than male–male dyads. This contrasts with male–male dyads, which tended to be in parties together and also maintained close spatial proximity within those parties. Comparison of the grooming index also showed that male–female dyads had values that fall between those of male–male and female–female dyads. Female–female dyads exhibited very little grooming over the 12-yr study, and although male–female grooming indices were more similar to those exhibited between males, they were still lower than the mean grooming index of the community.

The intermediate pattern of association for male–female dyads is consistent with results from other primate species including the red-fronted lemur (Pereira and Kappeler 1997; Pereira and McGlynn 1997) and white-faced capuchins (Perry 1997). For these species, the benefits of male–female association are generally thought to be related to a social system of male dispersal (Pereira and McGlynn 1997; Perry 1997; Sterck *et al.* 1997) that is not characteristic of chimpanzees. Instead, chimpanzees live in a social

system with high fission–fusion dynamics and female dispersal. This social system is similar to that of many *Ateles* spp. that also exhibit weak male–female association patterns compared to male dyads as a result of females avoiding aggression from males (Slater *et al.* 2009; Symington 1987). The high rates of aggression male chimpanzees direct toward females (Muller 2002; Muller *et al.* 2009) may also explain why male–female association patterns were weaker than those between male–male dyads in our study. Because female chimpanzees do not reside in groups with their kin owing to male philopatry, they do not receive social support from other females against male kind of aggression (Smuts 1992). In fact, females often act aggressively toward each other, and the presence of males in parties may serve to police this aggression (Kahlenberg *et al.* 2008a). Female chimpanzees, therefore, may exhibit reduced association with one another in favor of males to reduce the threat of female–female aggression. Among bonobos (*Pan paniscus*), which also live in a system with high fission–fusion dynamics, Hohmann *et al.* (1999) reported that associations between males and females were not as strong as female–female associations. The differences in our results compared to bonobo association patterns are most likely the result of a lower levels of feeding competition allowing female bonobos to be more gregarious with one another and a reduction in male bonobo aggression against females (Kano 1992).

The weak association between female–female dyads in chimpanzees is likely also the result of high levels of intragroup competition for food (Gilby and Wrangham 2008; Wrangham 2000b). This pattern has also been found among female brown capuchins but in this species, females also avoid associating with males to avoid food competition (Janson 1985, 1990a,b). Although our data do not specifically test the role that feeding competition plays in shaping male–female association patterns, our results are consistent with data from Gombe showing that females that spend a fraction of the day with males spend more time feeding compared to when they spent all or none of their day with males (Wrangham and Smuts 1980). If increased feeding time is beneficial to females, then spending too much or too little time with adult males will negatively impact female feeding behavior. Therefore, females may obtain benefits from associating with males but not to the same degree that males do from male–male association. However, because increased feeding time may not accurately reflect increased caloric intake, future studies of the impact of males on female feeding efficiency in chimpanzees are necessary to better understand how males have a positive or negative impact on female feeding behavior.

Although we hypothesized that low-ranking males would maintain higher association with females to increase mating opportunities, male rank had no effect on party association, 5m association, or grooming between male–female dyads. Because male rank is often related to many other aspects of chimpanzee social behavior, including male rates of aggression (Muller *et al.* 2007), male–male grooming patterns (Mitani 2009; Watts 2000), and male social relationships (Duffy 2006), this suggests that association with females is a relatively unimportant aspect of male social relationships. Instead, the tendency of males to be in parties with females and the variation among male–female dyads in their 5m indices appears to be driven by female estrous. Although the grooming index was not predicted by female estrous, males were more likely to be the groomer during bouts with a female in estrous. In addition, male rank was a significant predictor of the variation in the 5m index only between males and estrous females, suggesting that males change their behavior toward females during the time that they are fully swollen. As predicted, lower ranking males were more likely to be in spatial proximity to females in estrous than high-

ranking males, which may be the result of these males trying to increase their access to mating opportunities. Although male rank did not significantly predict the proportion of time that estrous females spent in parties with males nor the grooming index between male–estrous female dyads, it is important to remember that estrous refers to the time that a female is maximally swollen and includes several days before the periovulatory period when high-ranking males show more interest in estrous females (Deschner *et al.* 2004; Emery Thompson 2005). These results are consistent with various aspects of chimpanzee sexual behavior where males may mate-guard or be attracted to unguarded females (Wroblewski *et al.* 2009) or unguarded females may choose to be close to males (Emery Thompson and Wrangham 2008; Matsumoto-Oda 2002). Females could prefer to be near males to reduce the possibility of being harassed by other males in the party (Muller *et al.* 2007, 2009), to avoid aggression from females (Kahlenberg *et al.* 2008a; Pusey *et al.* 2008), or to express mate choice (Pieta 2008; Stumpf and Boesch 2006). In any case, male–female association patterns are affected by short-term changes in the reproductive state of the female.

Instead of being driven by a consistent social preference, variation in male–female association patterns was significantly affected by female ranging patterns: central females had stronger party level association with males than peripheral females. Emery Thompson *et al.* (2007) analyzed ranging data of the Kanyawara chimpanzees from 1996–2004 and found that male ranging patterns overlapped more closely with the core areas of central females than those of peripheral females. In addition, they showed that the central female core areas contained higher quality resources than the noncentral neighborhoods and suggested that this may explain the increased presence of males in these areas. We therefore propose that males and females show increased party association in the central part of the community range primarily as a result of their overlapping range use. This conclusion is supported by our finding of no effect of female neighborhood on the mean spatial association or grooming indices between males and females. Therefore males were more likely to be in parties with central females, but there was no difference in male proximity or grooming with these females when they were in the same party. In addition, we also looked at the effect of female neighborhood on female–female association and found that females with overlapping ranges had higher levels of party level association than females whose neighborhoods did not overlap. This pattern, along with the results of a recent study among the Ngogo chimpanzees (Wakefield 2013), indicate that space use is important in determining the structure of community relationships for females. Future work is necessary at Kanyawara to determine whether females with overlapping ranging patterns also exhibit higher proximity and grooming indices with one another as they do at Ngogo (Wakefield 2013).

Our conclusion that overlapping ranging patterns account for patterns of male–female association may also explain male–female association patterns observed in the Tai chimpanzees in West Africa. These chimpanzees have been described as bisexually bonded, meaning that the sexes are equally gregarious (Lehmann and Boesch 2005). As such, males and females use the entire home range equally and have individual ranges that overlap extensively both among females and between females and males. This pattern of range overlap could therefore account for the association patterns in female–female dyads and male–female dyads, which are reported to be of equal strength in Tai (Lehmann and Boesch 2008). The difference between party association and spatial association between males and females may also explain other behavioral patterns at this site. Interestingly, at Tai, the tendency to reconcile, a measure

of the value of a relationship, was stronger for intrasexual dyads than for male–female dyads (Wittig and Boesch 2005). Like grooming, reconciliation might require spatial proximity within a party and it is possible that male and female chimpanzees at Tai exhibit high party association but not close spatial proximity within the party.

A further difference between male–male dyads and those involving females is indicated by the fact that we were unable to calculate the grooming index for the majority of male–female or female–female dyads in any 2-yr period, because many individuals were rarely within 5m of each other. Although we were able to calculate grooming indices for up to 100% of male–male dyads, the best coverage of grooming indices in any period was 44% of male–female dyads and 26% of female–female dyads. Our criteria for calculating the grooming index was that individuals had to be seen within 5m of one another during  $\geq 10$  scans during a 2-yr period. Considering that many of the females in our dataset were followed for hundreds to thousands of scans, this likely reflects major differences in how females distribute themselves spatially in parties. More detailed observations of proximity and grooming between males and females (including information on who initiates grooming behavior and the duration of bouts) would be valuable to better understand relationships among chimpanzees. Some male–female dyads also exhibited a wide range of association values with some dyads exhibiting as strong or stronger association index values as some male–male dyads. This might be an indication that at least some male–female dyads benefit from associating with one another but this needs to be addressed further.

Of further methodological concern is the possibility that our results may be skewed because females are less gregarious than males and they can be difficult to follow when alone or in parties without adult males (Wrangham 2000b). For example, if our data are biased toward following females when adult males are present, then the reduced female–female association patterns that we found may be the result of limited data on females in all-female parties. Data from Kanyawara have shown that social interactions between females change when males are absent with increased rates of female–female aggression, especially against immigrant females (Kahlenberg *et al.* 2008a). The absence of males in parties may also create a more relaxed environment for females and increase the rate of affiliative behaviors among female–female dyads (Wakefield 2013; Williams *et al.* 2002). In our dataset, adult females were the subject of focal follows 4401 times when they were either alone or in parties with only other adult females (and their dependent offspring) and 5248 in parties with at least one adult male. Although females are slightly more likely to be followed in parties with adult males, it seems unlikely that this small difference would account for the reduced association indices of female–female dyads. However, any future studies of chimpanzee association patterns should consider party composition as an important variable when collecting data. This is also true of any species that exhibits high fission–fusion dynamics.

Given that increased male–male association allows for stronger male–male social bonds and for more cooperative behavior among males (Gilby and Wrangham 2008), the reduced consistency of association between males and females at Kanyawara is an indication that affiliative social bonds between the sexes are relatively unimportant compared to male–male bonds. Furthermore, male–female association patterns are clearly affected by overlapping ranging patterns and do not necessarily reflect a strong bond. In addition, changes in female reproductive state also affect association patterns, suggesting that short-term reproductive relationships are more important than long-term bonds between the sexes. This study demonstrates the importance of using multiple

independent measures of association when trying to understand variation in social relationships within a group. The finding that temporal, spatial, and grooming indices did not exhibit the same patterns shows that measures of association at the party level might be explicable by geographical similarities but are not necessarily a good indicator of social preferences for male–female dyads.

In a broadly similar study of male–female sociospatial patterns, Langergraber *et al.* (2013) analyzed the Ngogo chimpanzee community (also in Kibale) using measures that resembled ours. Our results are similar to theirs in some ways, but different in others. At Kanyawara, we found that party association values were lower for male–female dyads than for male–male dyads. Although this pattern matches the results from Ngogo, we did not find a similar increase in 5 m association among male–female dyads reported from this site. Unfortunately the meaning of this difference from our results is unclear because Langergraber *et al.* (2013) tallied the 5m and grooming indices in a different way from our procedure. Specifically, their indices did not appear to control for time spent in parties together, meaning that their indices were not independent of one another and therefore did not offer independent measures of the strength of dyadic relationships. Therefore, whether males and females are more likely to form bonds at Ngogo compared to Kanyawara cannot be addressed with current data.

Interestingly, Ngogo males and females whose ranging areas were more overlapping were also more likely to reproduce with one another (Langergraber *et al.* 2013). Even though it was not clear whether (according to our definition) reproducing pairs at Ngogo tended to have affiliative bonds, this result suggests that overlapping core areas can be an important factor in determining reproductive success in chimpanzees. The Kanyawara community exhibits much less differentiation among males in the spatial use of the territory (Wilson *et al.* 2012), suggesting that the opportunity for differential use of space to influence paternity at Kanyawara is less than at Ngogo. Thus whether the location of male core areas has a relatively strong influence on which females they are likely to impregnate may depend on whether individual males use the whole territory relatively evenly or more heterogeneously.

Although we were unable to test whether association strength is stronger for related male–female dyads, mother–son bonds are strong among bonobos and these bonds are important for male reproductive success (Furuichi 2011; Surbeck *et al.* 2012). Future analyses involving larger and longer-term datasets could offer insight into how mothers and sons associate with one another. However, for unrelated dyads, females may be subject to a number of costs by associating with males such as aggression and feeding competition, which restricts the formation of any meaningful relationship between the sexes other than during short-term reproductive contexts.

**Acknowledgments** This research was funded by Harvard University, NSF grants 0416125 and 0849380 (to R. W. Wrangham) and by a Wenner–Gren Hunt Fellowship (to Z. P. Machanda). We thank the Uganda National Council for Science and Technology, the Uganda Wildlife Authority, and the Makerere Biological Field Station for permission to conduct research within Kibale National Park. This research complies with the current laws of Uganda. This project would not have been possible without the hard work and dedication of the field research team, especially Francis Mugurusi, Christopher Muruuli, Peter Tuhairwe, Christopher Katongole, James Kyomuhendo, Solomon Musana, Sunday John, Wilberforce Tweheyo, Edgar Mugenyi, and the late Donor Muhangyi and John Barwogeza as well as field managers Michael Wilson, Martin Muller, Katherin Pieta, Carole Hooven, Kimberly Duffy, Alain Houle, and Emily Otali. Martin Muller and Melissa Emery Thompson provided useful comments on earlier versions of this manuscript. We also thank the editor and two anonymous reviewers for their feedback.

## References

- Aureli, F., Schaffner, C. M., Boesch, C., Bearder, S. K., Call, J., Chapman, C. A., et al. (2008). Fission-fusion dynamics new research frameworks. *Current Anthropology*, *49*, 627–654.
- Cairns, S. J., & Schwager, S. J. (1987). A comparison of association indexes. *Animal Behaviour*, *35*, 1454–1469.
- Chapais, B. (1983). Adaptive aspects of social relationships among adult rhesus monkeys. In R. A. Hinde (Ed.), *Primate social relationships: An integrated approach* (pp. 286–289). Oxford: Blackwell.
- Deschner, T., Heistermann, M., Hodges, K., & Boesch, C. (2004). Female sexual swelling size, timing of ovulation, and male behavior in wild West African chimpanzees. *Hormones and Behavior*, *46*, 204–215.
- de Vries, H. (1995). An improved test of linearity in dominance hierarchies containing unknown or tied relationships. *Animal Behaviour*, *50*, 1375–1389.
- de Vries, H., Netto, W. J., & Hanegraaf, P. L. H. (1993). Matman—A program for the analysis of sociometric matrices and behavioral transition matrices. *Behaviour*, *125*, 157–175.
- Duffy, K. G. (2006). *Social dynamics of male chimpanzees: Adaptive significance of male bonds*. Ph.D. thesis, University of California, Los Angeles.
- Emery Thompson, M. (2005). Reproductive endocrinology of wild female chimpanzees (*Pan troglodytes schweinfurthii*): Methodological considerations and the role of hormones in sex and conception. *American Journal of Primatology*, *67*, 137–158.
- Emery Thompson, M., Kahlenberg, S. M., Gilby, I. C., & Wrangham, R. W. (2007). Core area quality is associated with variance in reproductive success among female chimpanzees at Kanyawara, Kibale National Park. *Animal Behaviour*, *73*, 501–512.
- Emery Thompson, M., & Wrangham, R. W. (2008). Male mating interest varies with female fecundity in *Pan troglodytes* of Kanyawara, Kibale National Park. *International Journal of Primatology*, *29*, 885–905.
- Furuichi, T. (2011). Female contributions to the peaceful nature of bonobo society. *Evolutionary Anthropology*, *20*(4), 131–142.
- Gilby, I. C., Brent, L. J. N., Wroblewski, E. E., Rudicell, R. S., Hahn, B. H., Goodall, J., & Pusey, A. E. (2013). Fitness benefits of coalitionary aggression in male chimpanzees. *Behavioral Ecology and Sociobiology*, *67*(3), 373–381.
- Gilby, I. C., & Wrangham, R. W. (2008). Association patterns among wild chimpanzees (*Pan troglodytes schweinfurthii*) reflect sex differences in cooperation. *Behavioral Ecology and Sociobiology*, *62*(11), 1831–1842.
- Goodall, J. (1986). *The chimpanzees of Gombe: Patterns of behavior*. Cambridge, MA: Belknap Press.
- Hohmann, G., Gerloff, U., Tautz, D., & Fruth, B. (1999). Social bonds and genetic ties: Kinship association and affiliation in a community of bonobos (*Pan paniscus*). *Behaviour*, *136*, 1219–1235.
- Izar, P. (2004). Female social relationships of *Cebus apella nigrinus* in a southeastern Atlantic Forest: An analysis through ecological models of primate social evolution. *Behaviour*, *141*, 71–99.
- Janson, C. H. (1985). Aggressive competition and individual food consumption in wild brown capuchin monkeys (*Cebus apella*). *Behavioral Ecology and Sociobiology*, *18*, 125–138.
- Janson, C. H. (1990a). Ecological consequences of individual spatial choice in foraging groups of brown capuchin monkeys, *Cebus apella*. *Animal Behaviour*, *40*, 922–934.
- Janson, C. H. (1990b). Social correlates of individual spatial choice in foraging groups of brown capuchin monkeys, *Cebus apella*. *Animal Behaviour*, *40*, 910–921.
- Kahlenberg, S. M., Emery Thompson, M., & Muller, M. N. (2008a). Immigration costs for female chimpanzees and male protection as an immigrant counterstrategy to intrasexual aggression. *Animal Behaviour*, *76*, 1497–1509.
- Kahlenberg, S. M., Emery Thompson, M., & Wrangham, R. W. (2008b). Female competition over core areas in *Pan troglodytes schweinfurthii*, Kibale National Park, Uganda. *International Journal of Primatology*, *29*(4), 931–947.
- Kano, T. (1992). *The last ape: Pygmy chimpanzee behavior and ecology*. Stanford, CA: Stanford University Press.
- Langergraber, K., Mitani, J., & Vigilant, L. (2009). Kinship and social bonds in female chimpanzees (*Pan troglodytes*). *American Journal of Primatology*, *71*(10), 840–851.
- Langergraber, K. E., Mitani, J. C., & Vigilant, L. (2007). The limited impact of kinship on cooperation in wild chimpanzees. *Proceedings of the National Academy of Sciences of the USA*, *104*(19), 7786–7790.
- Langergraber, K. E., Mitani, J. C., Watts, D. P., & Vigilant, L. (2013). Male-female socio-spatial relationships and reproduction in wild chimpanzees. *Behavioral Ecology and Sociobiology*, *67*, 861–873.

- Lehmann, J., & Boesch, C. (2005). Bisexually bonded ranging in chimpanzees (*Pan troglodytes verus*). *Behavioral Ecology and Sociobiology*, 57(6), 525–535.
- Lehmann, J., & Boesch, C. (2008). Sexual differences in chimpanzee sociality. *International Journal of Primatology*, 29(1), 65–81.
- Lehmann, J., & Boesch, C. (2009). Sociality of the dispersing sex: The nature of social bonds in West African female chimpanzees, *Pan troglodytes*. *Animal Behaviour*, 77(2), 377–387.
- Matsumoto-Oda, A. (2002). Social relationships between cycling females and adult males in Mahale chimpanzees. In C. Boesch, G. Hohmann, & L. F. Marchant (Eds.), *Behavioural diversity in chimpanzees and bonobos* (pp. 168–180). Cambridge, U.K: Cambridge University Press.
- Matsumoto-Oda, A., Hosaka, K., Huffman, M. A., & Kawanaka, K. (1998). Factors affecting party size in chimpanzees of the Mahale mountains. *International Journal of Primatology*, 19(6), 999–1011.
- Matsumoto-Oda, A., & Oda, R. (1998). Changes in the activity budget of cycling female chimpanzees. *American Journal of Primatology*, 46, 157–166.
- Maynard Smith, J. (1977). Parental investment—prospective analysis. *Animal Behaviour*, 25, 1–9.
- Mitani, J. C. (2009). Male chimpanzees form enduring and equitable social bonds. *Animal Behaviour*, 77(3), 633–640.
- Muller, M. N. (2002). Agonistic relations among Kanyawara chimpanzees. In C. Boesch, G. Hohmann, & L. F. Marchant (Eds.), *Behavioural diversity in chimpanzees and bonobos* (pp. 112–124). Cambridge: Cambridge University Press.
- Muller, M. N., Kahlenberg, S., & Wrangham, R. (2009). Male aggression against females and sexual coercion in chimpanzees. In M. Muller & R. Wrangham (Eds.), *Sexual coercion in primates: An evolutionary perspective on male aggression against females* (pp. 184–217). Cambridge, MA: Harvard University Press.
- Muller, M. N., Kahlenberg, S. M., Emery Thompson, M., & Wrangham, R. W. (2007). Male coercion and the costs of promiscuous mating for female chimpanzees. *Proceedings of the Royal Society of London B: Biological Sciences*, 274, 1009–1014.
- Muller, M. N., & Mitani, J. (2005). Conflict and cooperation in wild chimpanzees. *Advances in the Study of Behavior*, 35, 275–331.
- Newton-Fisher, N. (2002). Male chimpanzee relationships in the Budongo Forest, Uganda. In C. Boesch, G. Hohmann, & L. F. Marchant (Eds.), *Behavioural diversity in chimpanzees and bonobos* (pp. 125–137). Cambridge, U.K: Cambridge University Press.
- Newton-Fisher, N. E., Thompson, M. E., Reynolds, V., Boesch, C., & Vigilant, L. (2010). Paternity and social rank in wild chimpanzees (*Pan troglodytes*) from the Budongo Forest, Uganda. *American Journal of Physical Anthropology*, 142(3), 417–428.
- Otali, E., & Gilchrist, J. S. (2006). Why chimpanzee (*Pan troglodytes schweinfurthii*) mothers are less gregarious than nonmothers and males: The infant safety hypothesis. *Behavioral Ecology and Sociobiology*, 59(4), 561–570.
- Palombit, R. A. (2000). Infanticide and the evolution of male-female bonds in animals. In C. P. van Schaik & C. H. Janson (Eds.), *Infanticide by males and its implications* (pp. 239–292). Cambridge, U.K: Cambridge University Press.
- Palombit, R. A. (2009). Friendships with males: A female counterstrategy to infanticide in the Okavango chacma baboons. In M. N. Muller & R. W. Wrangham (Eds.), *Sexual coercion in primates and humans: An evolutionary perspective on male aggression against females* (pp. 377–409). Cambridge, MA: Harvard University Press.
- Pandolfi, S. S. (2004). *Ecological sex differences in Gombe chimpanzees* (*Pan troglodytes*). Ph.D. thesis, Duke University.
- Pereira, M. E., & Kappeler, P. M. (1997). Divergent systems of agonistic behaviour in lemurid primates. *Behaviour*, 134, 225–274.
- Pereira, M. E., & McGlynn, C. A. (1997). Special relationships instead of female dominance for redfronted lemurs, *Eulemur fulvus rufus*. *American Journal of Primatology*, 43(3), 239–258.
- Perry, S. (1997). Male-female social relationships in wild white-faced capuchins (*Cebus capucinus*). *Behaviour*, 134, 477–510.
- Pieta, K. (2008). Female mate preferences among *Pan troglodytes schweinfurthii* of Kanyawara, Kibale National Park, Uganda. *International Journal of Primatology*, 29(4), 845–864.
- Pusey, A., Murray, C., Wallauer, W., Wilson, M., Wroblewski, E., & Goodall, J. (2008). Severe aggression among female *Pan troglodytes schweinfurthii* at Gombe National Park, Tanzania. *International Journal of Primatology*, 29(4), 949–973.
- Pusey, A. E. (1987). Sex-biased dispersal and inbreeding avoidance in birds and mammals. *Trends in Ecology & Evolution*, 2(10), 295–299.

- Slater, K. Y., Schaffner, C. M., & Aureli, F. (2009). Sex differences in the social behavior of wild spider monkeys (*Ateles geoffroyi yucatanensis*). *American Journal of Primatology*, 71(1), 21–29.
- Smuts, B. (1992). Male aggression against women: An evolutionary perspective. *Human Nature*, 3(1), 1–44.
- Smuts, B. B. (1985). *Sex and friendship in baboons*. New York: Aldine.
- Sterck, E. H. M., Watts, D. P., & van Schaik, C. P. (1997). The evolution of female social relationships in nonhuman primates. *Behavioral Ecology & Sociobiology*, 41, 291–309.
- Stumpf, R. M., & Boesch, C. (2006). The efficacy of female choice in chimpanzees of the Tai Forest, Cote d'Ivoire. *Behavioral Ecology and Sociobiology*, 60(6), 749–765.
- Sugiyama, Y. (1968). Social organization of chimpanzees in the Budongo Forest, Uganda. *Primates*, 9, 225–258.
- Surbeck, M., Deschner, T., Schubert, G., Weltring, A., & Hohmann, G. (2012). Mate competition, testosterone and intersexual relationships in bonobos, *Pan paniscus*. *Animal Behaviour*, 83(3), 659–669.
- Surbeck, M., Mundry, R., & Hohmann, G. (2011). Mothers matter! Maternal support, dominance status and mating success in male bonobos (*Pan paniscus*). *Proceedings of the Royal Society of London B: Biological Sciences*, 278(1705), 590–598.
- Symington, M. M. (1987). Sex-ratio and maternal rank in wild spider monkeys—When daughters disperse. *Behavioral Ecology and Sociobiology*, 20(6), 421–425.
- Takahata, Y. (1982). Social relationships between adult males and females of Japanese monkeys in the Arashiyama B Troop. *Primates*, 23(1), 1–23.
- Trivers, R. L. (1972). Parental investment and sexual selection. In B. Campbell (Ed.), *Sexual selection and the descent of man: 1871–1971* (pp. 136–179). Chicago: Aldine.
- Tutin, C. E. G. (1979). Mating patterns and reproductive strategies in a community of wild chimpanzees (*Pan troglodytes schweinfurthii*). *Behavioral Ecology and Sociobiology*, 6(1), 29–38.
- van Noordwijk, M. A., & van Schaik, C. P. (2004). Sexual selection and the careers of primate males: Paternity concentration, dominance acquisition tactics and transfer decisions. In P. M. Kappeler & C. P. van Schaik (Eds.), *Sexual selection in primates: A comparative perspective* (pp. 208–229). Cambridge, U.K.: Cambridge University Press.
- van Schaik, C. P., & Kappeler, P. M. (1997). Infanticide risk and the evolution of male-female association in primates. *Proceedings of the Royal Society of London B: Biological Sciences*, 264(1388), 1687–1694.
- Wakefield, M. L. (2013). Social dynamics among females and their influence on social structure in an East African chimpanzee community. *Animal Behaviour*, 85, 1303–1313.
- Wakefield, M. L. (2008). Grouping patterns and competition among female *Pan troglodytes schweinfurthii* at Ngogo, Kibale National Park, Uganda. *International Journal of Primatology*, 29(4), 907–929.
- Watts, D. P. (1992). Social relationships of immigrant and resident female mountain gorillas. I. Male-female relationships. *American Journal of Primatology*, 28(3), 159–181.
- Watts, D. P. (2000). Grooming between male chimpanzees at Ngogo, Kibale National Park. II. Influence of male rank and possible competition for partners. *International Journal of Primatology*, 21(2), 211–238.
- Watts, D. P. (2007). Effects of male group size, parity, and cycle stage on female chimpanzee copulation rates at Ngogo, Kibale National Park, Uganda. *Primates*, 48(3), 222–231.
- Williams, J. M., Liu, H.-Y., & Pusey, A. E. (2002). Costs and benefits of grouping for female chimpanzees at Gombe. In C. Boesch, G. Hohmann, & L. F. Marchant (Eds.), *Behavioural diversity in chimpanzees and bonobos* (pp. 192–203). Cambridge: Cambridge University Press.
- Wilson, M. L., Kahlenberg, S. M., Wells, M., & Wrangham, R. W. (2012). Ecological and social factors affect the occurrence and outcomes of intergroup encounters in chimpanzees. *Animal Behaviour*, 83, 277–291.
- Wittig, R. M., & Boesch, C. (2005). How to repair relationships—Reconciliation in wild chimpanzees (*Pan troglodytes*). *Ethology*, 111(8), 736–763.
- Wrangham, R. W. (2000a). Why are male chimpanzees more gregarious than mothers? A scramble competition hypothesis. In P. Kappeler (Ed.), *Male primates* (pp. 248–258). Cambridge, U.K.: Cambridge University Press.
- Wrangham, R. W. (2000b). Why are male chimpanzees more gregarious than mothers? A scramble competition hypothesis. In P. M. Kappeler (Ed.), *Primate males: Causes and consequences of variation in group composition* (pp. 248–258). Cambridge, U.K.: Cambridge University Press.
- Wrangham, R. W., & Smuts, B. (1980). Sex differences in the behavioral ecology of chimpanzees in the Gombe National Park, Tanzania. *Journal of Reproduction and Fertility (Supplement)*, 28, 13–31.
- Wroblewski, E. E., Murray, C. M., Keele, B. F., Schumacher-Stankey, J. C., Hahn, B. H., & Pusey, A. E. (2009). Male dominance rank and reproductive success in chimpanzees, *Pan troglodytes schweinfurthii*. *Animal Behaviour*, 77(4), 873–885.