ORIGINAL PAPER

Association patterns among wild chimpanzees (*Pan troglodytes schweinfurthii*) reflect sex differences in cooperation

Ian C. Gilby · Richard W. Wrangham

Abstract Theory predicts that frequent dyadic association should promote cooperation through kin selection or social tolerance. Here we test the hypothesis that sex differences in the strength and stability of association preferences among free-ranging chimpanzees conform to sex differences in cooperative behavior. Using long-term data from the Kanyawara chimpanzee (*Pan troglodytes schweinfurthii*) community (Kibale National Park, Uganda), we calculated indices of intra-sexual dyadic association over a 10-year period. We found that (1) male–male dyads had significantly stronger association indices than female–female dyads, (2) the pattern of association preferences in both sexes changed little over the entire study period, and (3) when comparing periods with different alpha males, changes in association strength were more frequent among males. These results demonstrate that both the strength and stability of association patterns are important components of social relationships. Male chimpanzees, which are characterized by frequent cooperation, had association preferences that were both strong and stable, suggesting that forming long-term bonds is an important dominance strategy. However, the fact that male association patterns were sensitive to upheaval in the male dominance hierarchy suggests that males also take advantage of a changing social climate when choosing association partners. By contrast, the overall strength of female associations was relatively weak. Female association preferences were equally stable as males'; however, this reflected a dyad's tendency to be found in the same party rather than to associate closely within that party. Therefore, in this community, female association patterns appear to be more a consequence of individual ranging behavior rather than a correlate of cooperation.

Introduction

In this paper, we test the hypothesis that sex differences in the strength and stability of association among chimpanzees conform to sex differences in cooperative behavior. Throughout, we use 'association' to describe the frequency with which two individuals are seen together, either in the same temporary subgroup or in close spatial proximity. Theory predicts that for at least two reasons, frequent association between two individuals should promote cooperation (joint action for mutual benefit (Mesterton-Gibbons and Dugatkin 1992; Clements and Stephens 1995)). First, genetically related individuals should cooperate to defend resources and offspring, and to compete with non-kin for dominance rank, thereby increasing the probability of propagating shared alleles (Hamilton 1964). Such behavior is facilitated by preferential association among close kin and has repeatedly been documented, particularly in species with a matrilineal dominance hierarchy (e.g., female savannah baboons, *Papio cynocephalus* (Silk et al. 2006a), see Kapsalis (2003) for review). Second, there is growing evidence that cooperation requires a 'tolerant' relationship (chimpanzees, Melis et al. 2006; bonobos, *Pan paniscus*, Hare et al. 2007). As predicted, non-relatives in several species characterized by frequent cooperation exhibit strong and differentiated dyadic association preferences (e.g.,

I. C. Gilby (✉) · R. W. Wrangham
Department of Anthropology, Harvard University,
Cambridge, MA, USA
e-mail: gilby@fas.harvard.edu

bottlenose dolphins, *Tursiops* spp. (Connor et al. 2001) and wild dogs, *Lycaon pictus* (de Villiers et al. 2003)).

Studies of association patterns are typically cross-sectional and therefore concentrate upon the strength rather than the duration of a dyad's tendency to associate. Here we investigate whether the temporal stability (consistency) of association is also an informative measure for understanding the extent to which association preferences predict cooperative behavior. We explore the relationship between association and cooperation by taking advantage of sex differences in cooperation within a single species, chimpanzees. Chimpanzees are an appropriate species to study for several reasons. First, males and females differ considerably in the degree to which they cooperate, with males cooperating more frequently and in a wider range of contexts. Second, chimpanzees have a fission–fusion social system in which community members travel in fluid subgroups of changing size and composition (Nishida 1968; Wrangham and Smuts 1980; Goodall 1986). Individuals therefore have considerable freedom to choose with whom to associate. Third, since male chimpanzees are philopatric (and therefore are more likely to be genetically related (but see Vigilant et al. 2001)), kin-selected cooperation is expected to be more prevalent among males than females, which typically disperse. Langergraber et al. (2007) showed that cooperation is more likely among close maternal kin than either paternal kin or unrelated dyads. However, cooperation is also common among unrelated males (for review, see Muller and Mitani 2005).

Sex differences in chimpanzee cooperation

Male chimpanzees frequently cooperate (for review, see Muller and Mitani 2005). At the group level, they patrol the edges of their home range, attacking and killing conspecifics from neighboring communities (Watts and Mitani 2001; Wilson and Wrangham 2003; Wilson et al. 2004; Watts et al. 2006). In the Ngogo community (Kibale National Park, Uganda), rates of joint patrol participation were correlated with association and grooming rates (Watts and Mitani 2001), suggesting that close associates were more likely to cooperate in this context. On the other hand, Wilson et al. (2001) found no individual differences among males in their tendency to respond aggressively to playbacks of stranger males, a result that does not support the notion that a male's participation may be contingent upon the presence of a frequent associate.

Males also communally hunt red colobus monkeys (*Procolobus* spp.), although there is debate over the degree to which this is cooperative (Boesch 1994; Mitani and Watts 2001; Boesch 2002; Gilby et al. 2006, 2008). At the individual level, males cooperate by grooming and sharing meat, actions which may serve to cement social bonds

(Stanford 1998; Mitani and Watts 2001; Watts 2002; Mitani 2005; but see Gilby 2006). Finally, male chimpanzees frequently form coalitions, in which two individuals jointly direct aggression toward a third (de Waal and Harcourt 1992). These coalitions may occur in the context of mate guarding (Watts 1998), but are most often associated with acquisition and maintenance of dominance rank (Riss and Goodall 1977; Bygott 1979; Nishida 1983; Goodall 1986; de Waal 1992; Mitani et al. 2000; Newton-Fisher 2002). In theory, frequent, close association between two individuals should facilitate the formation of reciprocal cooperative coalitions, thus providing a mutual benefit. In support of this idea, Goodall (1986) describes several "enduring alliances" between males at Gombe National Park, Tanzania. These males preferentially associate with one another, exhibit high grooming rates, and support each other in dominance disputes with other males. While many studies acknowledge that such relationships exist (for review, see Muller and Mitani 2005), few offer empirical evidence or a formal measure to identify allied dyads.

Less is known about cooperation among female chimpanzees. While two captive studies in particular have highlighted the frequency and importance of female coalitions (de Waal 1984; Baker and Smuts 1994), female chimpanzees in the wild rarely cooperate. Females of the East African subspecies, *P. t. schweinfurthii*, are considerably less gregarious than males, tending to travel alone with their dependent offspring (Wrangham and Smuts 1980; Wrangham 2000; Williams et al. 2002a). For a discussion of sex differences in sociality among West African chimpanzees, *P. t. verus*, see Lehmann and Boesch (2007). When they do join groups, females rarely groom one another (Wrangham et al. 1992) and are seldom in a position to voluntarily share meat, since they tend to lose meat to males. At Gombe, where some females remain in their natal community, mothers and daughters tend to have high association rates (Williams et al. 2002b), and occasionally form kin-based coalitions against other females (Goodall 1986). Reports of coalitions between non-kin (directed primarily by mothers towards recent immigrant females) are rare (Townsend et al. 2007; Kahlenberg et al. 2008).

Association patterns and cooperation

These sex differences in cooperation generate contrasting predictions regarding the strength and stability of long-term dyadic intra-sexual association patterns among wild chimpanzees. Since males cooperate more frequently, in more contexts and in more dangerous situations, they are expected to exhibit stronger measures of association than females. They are also expected to exhibit more stable association patterns, in part because kinship will be important

for some dyads, and in part because cooperation depends on the establishment of trust and tolerance, which take time to achieve. However, if frequent association is important primarily because it facilitates coalition formation, we expect male association preferences to vary over time in accordance with changing dominance relationships. In particular, after an alpha male takeover, each male's relative value as a coalition partner is likely to change, thus prompting individuals to adjust their association preferences.

Comparable considerations apply to females. Since females rarely form coalitions, we might expect female association patterns to be relatively weak and undifferentiated. However, in at least two sites in East Africa, female chimpanzees concentrate their space use in small core areas that overlap to form distinct 'neighborhoods' to which they remain faithful from year to year (Gombe, Williams et al. 2002a; Murray et al. 2007; Kanyawara, Emery Thompson et al. 2007). This micro-geographic structuring suggests that female association patterns are likely to be quite stable, even if weak. In other words, due to similar ranging patterns, certain female dyads (that occupy the same neighborhood) are expected to be likely to associate. Thus, female association patterns should exhibit long-term stability, since changes in the male dominance hierarchy are not known to affect female ranging patterns.

In sum, male association preferences are expected to be strong and consistent until a major change occurs in the hierarchy, while female association preferences are expected to be weak and consistent, regardless of a change in the male hierarchy.

Methods

Study site and long-term data collection

The Kanyawara chimpanzee community occupies approximately 38 km^2 (Wilson 2001) within Kibale National Park, Uganda. The community was partially habituated to the presence of humans by M. Ghiglieri in 1979–1980, and then by G. Isabirye-Basuta in 1983–1985. R. Wrangham founded the Kibale Chimpanzee Project in 1987, and systematic data collection has been continuous since 1988. The chimpanzees were habituated without provisioning, and adult males could be observed systematically by January 1990. Since the project's inception, the size and composition of the Kanyawara community has remained relatively stable, averaging about 50 individuals, with 9–12 adult males and 12–15 adult females.

Each day, two or more Ugandan field assistants locate a party of chimpanzees using nesting information from the previous day, listening for vocalizations, or checking recent feeding sites. After locating chimpanzees, the team follows the party for as long as possible, usually until the animals build their night nests. If the party splits, observers follow the larger subgroup. Such party-level follows maximize the number of social interactions that are recorded, allowing for detailed analyses of association patterns. While this method may increase the number of observations of more social individuals, daily follows over several years ensure that all individuals are adequately sampled.

At 15-min intervals, one observer uses scan sampling (Altmann 1974) to record which chimpanzees are present in the party. A second observer collects ten-minute focal (TMF) data. He chooses a chimpanzee at random and conducts scan samples at 2-min intervals. During each scan, he records which chimpanzees are within 5 m of the focal individual and the identity of its nearest neighbor. After the fifth scan, the observer chooses another focal individual and starts another TMF. He rotates through all chimpanzees in the party. In order to reduce biased sampling of "interesting" behavior (which might prompt an observer to initiate a TMF), we used only the last scan of each TMF in our analyses.

The observers were carefully trained by R. Wrangham, and are usually accompanied in the field by graduate students, colleagues, and/or the project field manager, who check the accuracy of the data. Observers averaged over 95% accuracy in inter-observer reliability tests of 5-m and nearest-neighbor data collection (Kibale Chimpanzee Project, unpublished data). All data, along with detailed demographic information on each chimpanzee, are digitized and stored in a relational database in the Department of Anthropology at Harvard University.

Time periods

We analyzed four 2-year time periods covering the tenure of two alpha males. BB was alpha male from March 1994 through early 1998, when MS replaced him. We classified each analysis period according to the identity of the alpha male and sequence number: BB: 1995–1996; MS$_I$: 1999–2000; MS$_{II}$: 2001–2002; MS$_{III}$: 2003–2004. We chose to start with the second year of each alpha male's tenure to allow for the hierarchy to stabilize after the takeover.

We identified all individuals that were adults at the beginning and alive at the end of each period. We considered only these individuals in our analyses. Adult males were those that were at least 15 years old, according to known and estimated birthdates. There were 11 adult males in period BB and nine in MS$_I$, MS$_{II}$, and MS$_{III}$ (Table 1A). The adult male cohort was identical in periods MS$_{II}$ and MS$_{III}$. Adult females were those that had been observed with a full sexual swelling and were seen to mate with adult males. There were 16 adult females in period BB, 15 in MS$_I$, 13 in MS$_{II}$, and 11 in MS$_{III}$ (Table 1B). One female (PE) was rarely seen between 2001 and 2004, and

Table 1 Number of observations of (A) adult males and (B) adult females

| ID | Birth | Death | Period | | | | | | |
| | | | BB | MS$_I$ | | MS$_{II}$ | | MS$_{III}$ | |
			P	P	T	P	T	P	T
(A)									
AJ	1974		389	499	131	805	177	514	185
BB	1966		334	400	110	478	119	427	190
BF	1966	1998	234						
LB	1968	2001	374	465	168				
KK	1985					808	183	653	256
LK	1982			626	249	977	219	732	234
LM	1950	1996	321						
MS	1979		414	650	222	938	223	749	267
SL	1971		215	234	57	446	71	425	88
ST	1955		366	451	151	719	156	675	195
SY	1964	2000	305						
TU	1960		238	331	114	597	128	574	189
YB	1973		334	495	300	788	181	629	221
Mean			320	461	166	728	161	597	202
S.D.			66.6	131	76	187	49	121	52
(B)									
AL	1982		516	517	82	656	75	555	86
AR	1943		183	257	91	259	36	297	112
BL	1960		11	186	17	408	53	494	37
EK	1974		25	176	27	157	17	371	83
FG	1955	1998	319						
GO	1957	2001	77	98	6				
JO	1960	2001	27	194	38				
KL	1970	2000	319	344	103				
LP	1955	2004	444	508	206	710	175	269	20
LR	1989					774	153	578	112
MG	1945	1998	137						
MU	1970		28	32	4	14	2	133	38
NG	1955	1997	23						
NL	1982			473	159	671	89	429	56
OU	1979		441	574	128	877	88	696	112
PE	1970		27	60	10				
PU	1955	2003	39	177	17	193	19	3	
TG	1980		448	466	111	682	72	628	130
UM	1981			38	8	31	2	57	12
Mean			191	272	65	402	59	377	69
S.D.			189	190	62	314	52	231	44

P the number of parties in which an individual was seen; *T* the number of times an individual was the subject of a ten-minute focal

was therefore excluded from all analyses of periods MS$_{II}$ and MS$_{III}$. Table 1 lists the number of observations of each individual per period.

Association measures

Party-level association

The first dyadic association measure we used was the Simple Ratio Index (SRI) (Cairns and Schwager 1987),

which measured a dyad's tendency to be present in the same party. To reduce pseudoreplication, we sampled each party of unique composition (of a given sex) once per day. For example, if one party contained the same six males between 6:00 and 13:00, and then two males joined the party at 13:15 and remained for the rest of the day, we recorded two unique adult male parties in our analyses of male association patterns, regardless of any changes in the number of adult females. We then calculated the SRI for each same-sex pair in each period. For individuals A and B,

the SRI is the proportion of total sightings of both individuals in which they were together in the same party, or:

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

where P_{AB}=the number of parties containing both A and B, P_A=the number of parties containing A, and P_B=the number of parties containing B.

To ensure that our subsampling procedure did not bias our results, we repeated the procedure using all 15-min samples. Both sampling methods yielded very similar results. SRI indices calculated using party composition scans taken every 15 min were significantly correlated with SRI indices calculated using daily unique parties (e.g., males (2003–2004); K_r=218, r=0.96, $p<0.0001$; females (2003–2004); K_r=212, r=0.82, $p<0.0001$).

To enable meaningful comparison across indices (see below) and between sexes, we standardized each value by dividing by the mean of all dyads for a given period ($SRI = SRI_{AB}/SRI_{mean}$, where $SRI_{mean} = mean(SRI_{female-female}+SRI_{male-male})$). Note that the denominator equals the average SRI value for both male–male and female–female dyads. Thus, numbers greater than one indicated that a dyad was present in the same party more often than the average dyad.

Spatial proximity—5 m

The second dyadic association measure was the "five-meter association index" (5M), which measured the frequency with which two individuals were observed within 5 m of one another, given that both were present in the same party and one was the subject of a TMF scan:

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

where $A_f(B_5)$=the number of instances A was the TMF focal and B was within 5 m of A, $B_f(A_5)$=the number of instances B was the TMF focal and A was within 5 m of B, $A_f(B_p)$=the number of instances A was the TMF focal and B was in same party, and $B_f(A_p)$=the number of instances B was the TMF focal and A was in same party. Note that this controls for the number of times two individuals were present in the same party (by including the variables B_p and A_p), resulting in an index that is independent of party-level association. A dyad that is rarely observed in the same party could therefore have a high 5M index value and vice versa. Again, we divided each value by the mean of all same-sex dyads to identify pairs that associated more often than expected ($5M = 5M_{AB}/5M_{mean}$, where $5M_{mean} = mean(5M_{male-male}+5M_{female-female})$).

Spatial proximity—nearest neighbors

The third dyadic association measure was the "nearest neighbor association index" (NN), which measured the frequency with which two individuals were seen as nearest neighbors, given that one was the focal of a TMF and the other was within 5 m, or:

$$NN_{AB} = \frac{A_f(B_{nn}) + B_f(A_{nn})}{A_f(B_5) + B_f(A_5)} \quad (3)$$

where $A_f(B_{nn})$=the number of instances A was the TMF focal and B was its nearest neighbor and $B_f(A_{nn})$=the number of instances B was the TMF focal and A was its nearest neighbor. Again, this index controls for the frequency with which individuals were observed within 5 m of one another, and is therefore independent of the 5M (and party-level) index. As above, we standardized the index by dividing each value by the mean: ($NN = NN_{AB}/NN_{mean}$, where $NN_{mean} = mean(NN_{male-male} + NN_{female-female})$).

Combined association index

Each of the indices described above provides an independent measure of dyadic association. When considered together, they allow us to assess a dyad's overall temporal and spatial association patterns. We assume that individuals that are frequently seen both in the same party and as nearest neighbors have a stronger tendency to associate than those with high party-level association rates only. Therefore, in addition to analyzing each index separately, we also developed an index that captures a dyad's overall tendency to associate. For males, our "Combined Association Index" (CAI), measured a dyad's average deviation from the mean across the three indices during a given time period:

$$CAI_{AB} = \frac{(SRI_{AB}/SRI_{mean}) + (5M_{AB}/5M_{mean}) + (NN_{AB}/NN_{mean})}{3} \quad (4)$$

This method of combining association indices is similar to the way in which Alberts (1999) and Silk et al. (2006b) classified social bonds in wild baboons. A dyad with above average values for all three component indices will have a higher CAI value than one that is frequently seen in the same party, but rarely within 5 m. Sample sizes were too small to calculate NN for adult females in any period (Table 1B). Therefore, the CAI for adult females measured the mean of the observed/expected values of the SRI and 5M indices only. We also calculated a similar combined measure based on the Pairwise Affinity Index (Pepper et al. 1999), which controls for gregariousness (but does not use independent component indices). For the sake of brevity, we do not include these

analyses, as they generated very similar results to those reported here.

Stability of association patterns

We used the K_r matrix correlation procedure (Hemelrijk 1990) to test for similarity in association patterns between time periods. The K_r test is an iterative row-wise variation of the Mantel test (Mantel 1967) that takes individual differences into account. For a given index, a significant positive correlation between time periods indicates that, on average, dyads with a high index value in one period had a high value in the other. Following Mitani et al. (2002), we log-transformed the observed/expected values so that above- and below-expected values would be weighted equally in the matrix analyses ($\log(x)$ and $\log(1/x)$ have the same absolute value, but different sign). To avoid undefined values, we changed observed/expected ratios of 0 to 0.01 before log-transformation. We performed all K_r tests using MatMan 1.1.4 (Noldus Information Technologies, Wagenigen, The Netherlands) and report one-tailed p-values based on 10,000 iterations.

Visualizing association patterns

We generated unrooted phylograms to graphically display the strength of association among individuals. An unrooted phylogram is a non-hierarchical tree without an outgroup. Branch lengths are proportional to the degree to which two individuals associate, with shorter distances representing closer association. To create these diagrams, we converted index values into distances by dividing each by the greatest value (for a given time period), and then subtracting from one. This created a distance matrix with values ranging from zero (closest association) to one. We used PAUP 4.0.0b10 (Swofford 2003) to create the phylograms.

Preferred social partners

While the methods described above are powerful, they cannot distinguish between "mutual" and "one-sided" relationships. In other words, the same value would be generated if A and B mutually associated with one another or if B had a strong affinity for A but not vice versa. Therefore, for a given index (SRI, 5M, NN), we classified individuals A and B as "mutual associates' if the value was 1/2 standard deviation greater than the means of both A and B. Thus, mutual associates were those that had a higher index than was typical for both of them, therefore controlling for overall sociality. We designated members of a dyad as "preferred social partners" (PSPs) if they were mutual associates for at least two of the three independent indices.

Results

Association strength

Males were consistently more likely to associate than females. In all periods, mean party-level association index (Simple Ratio Index, SRI) values were significantly higher for male dyads than female dyads (Table 2A). To examine whether this result could be a byproduct of the fact that males are simply more gregarious than females, we also examined sex differences in spatial proximity within a party. Mean five-meter index (5M) values were significantly higher for male dyads than female dyads (Table 2B). Thus, males were more likely than females to form specific dyadic associations,

Table 2 Sex differences in association strength

Period	Male dyads	Female dyads	T	df	p-value
(A) Mean Simple Ratio Index (SRI) values of party-level association					
BB: 1995–1996	1.84	0.62	−7.5	173	<0.0001
MS$_I$: 1999–2000	2.15	0.60	−15.2	139	<0.0001
MS$_{II}$: 2001–2002	1.76	0.59	−11.4	97.1	<0.0001
MS$_{III}$: 2003–2004	1.57	0.54	−14.4	78.3	<0.0001
(B) Mean Five-meter Index (5M) values of spatial association					
MS$_I$: 1999–2000	1.46	0.57	−6.6	72	<0.0001
MS$_{II}$: 2001–2002	1.44	0.60	−6.3	71	<0.0001
MS$_{III}$: 2003–2004	1.54	0.44	−8.3	62.9	<0.0001
(C) Mean Combined Association Index (CAI) values					
MS$_I$: 1999–2000	1.54	0.52	−13.2	139	<0.0001
MS$_{II}$: 2001–2002	1.40	0.49	−10.4	92.7	<0.0001
MS$_{III}$: 2003–2004	1.37	0.46	−12.5	79	<0.0001

Across all periods, males had significantly higher mean Simple Ratio Index (A), Five-meter (B) and Combined Association Index (C) values than females. All indices were standardized by dividing by the mean of all same-sex dyads, as described in the text. Values greater than one characterize dyads that associated more than expected

rather than merely being more gregarious. Finally, Combined Association Index (CAI) values were significantly higher for male–male dyads than female–female dyads (Table 2C). Note that, before calculating means and conducting statistical tests, we standardized all indices by dividing by the mean of all same-sex dyads, as described above.

Histograms showing the distribution of CAI values across all dyads demonstrate considerable variability within

sexes (Fig. 1). Several female dyads had stronger association indices than some male dyads. In fact, in MS_{II}, one female dyad (the only mother–daughter pair in the community) had an association index that was comparable to the strongest male dyad. However, most female dyads had CAI values considerably less than one, while most male dyads had CAI values greater than one. In general, female CAI values were skewed to the left, demonstrating that most female dyads were characterized by relatively weak association.
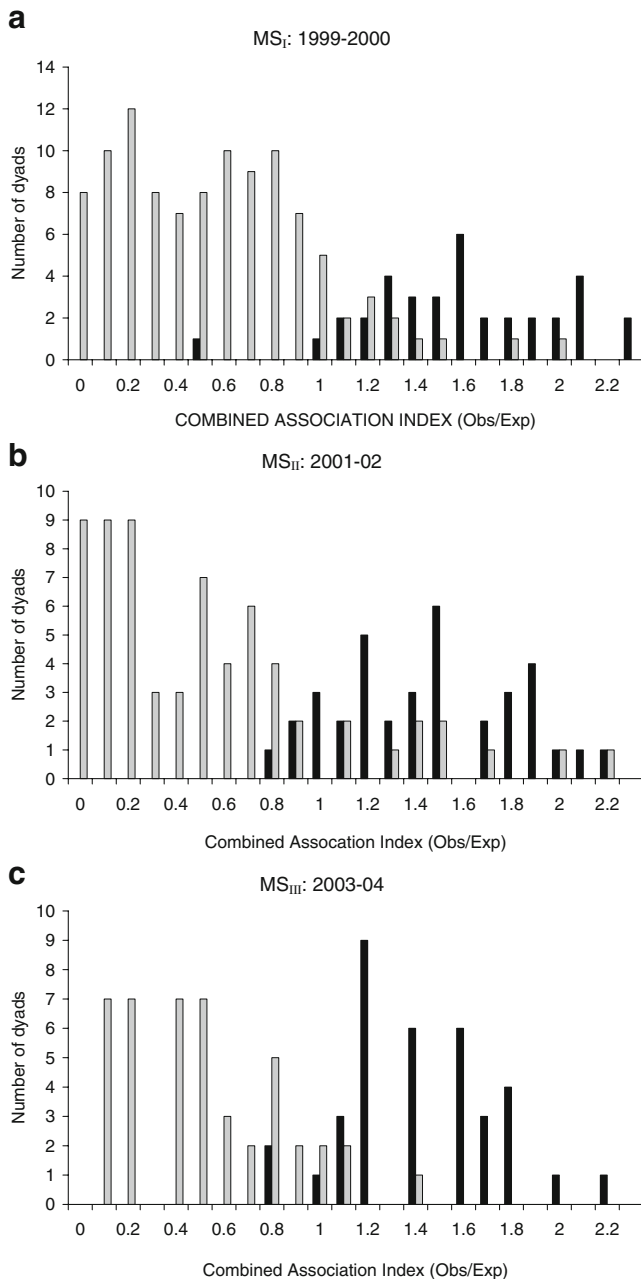
Association stability

1999–2004 (alpha male = MS)

Party-level association (SRI) values for both male and female dyads were significantly positively correlated across the three periods when MS was alpha male (Table 3). For males, the spatial association (5M and NN) indices were positively correlated in all but one comparison (NN index, MS_I:MS_{III}, Table 3A). In females, by contrast, spatial association indices were positively correlated in only one comparison (MS_I:MS_{II}, Table 3B—note the relatively low Pearson's r of 0.089).

Our combined association index (CAI) provides a more meaningful measure of a dyad's likelihood of associating, for it incorporates independent temporal and spatial variables. Again, matrix permutation tests demonstrated that, for both sexes, the overall pattern of association changed little during MS's tenure as alpha male. For males, the CAI values from periods MS_I and MS_{II} were positively correlated ($K_r=128$, $p=0.0001$, Pearson's $r=0.47$, Table 3A), as were those from MS_{II} and MS_{III} ($K_r=200$, $p=0.0001$, Pearson's $r=0.80$), and MS_I and MS_{III} ($K_r=100$, $p=0.004$, Pearson's $r=0.33$). The same was true for adult females: CAI values for periods MS_I and MS_{II} were positively correlated ($K_r=415$, $p=0.0002$, Pearson's $r=0.61$), as were those from MS_{II} and MS_{III} ($K_r=402$, $p=0.0001$, Pearson's $r=0.76$), and MS_I and MS_{III} ($K_r=261$, $p=0.002$, Pearson's $r=0.44$). These results show that, for both males and females, a positive dyadic relationship in one period was likely to be positive in the next. However, for both sexes, the relatively low correlation coefficients (Pearson's r-values) from these analyses indicate that some important changes occurred.

We used unrooted phylograms to visualize these changes (Fig. 2). We found that there were no dramatic changes in the direction of association preferences (e.g., from positive to negative), but the strength (indicated by phylogram branch length) of certain dyads changed. Males MS, ST, TU, and BB were relatively close together in all periods, as were YB and LK (Fig. 2a). AJ and SL were less social. Periods MS_{II} and MS_{III} were remarkably similar. The only major difference was that the closest dyad in period MS_{II}

Fig. 1 Comparison of the strength of male (black) and female (grey) Combined Association Index (CAI) values in each time period. a MS_I: 1999–2000; b MS_{II}: 2001–02; c MS_{III}: 2003–04. Males consistently showed significantly stronger association indices than females

Table 3 Summary of matrix correlation tests between periods for males (A) and females (B)

	Party-level (SRI)		Spatial (5M)		Spatial (NN)		Combined (CAI)	
	r	p	r	p	r	p	r	p
(A) Males								
BB:MS$_I$ 1995–1996:1999–2000	**0.19**	**0.012**	–	–	–	–	–	–
MS$_I$:MS$_{II}$ 1999–2000:2001–2002	**0.70**	**0.0001**	**0.44**	**0.0002**	**0.08**	**0.003**	**0.47**	**0.0001**
MS$_{II}$:MS$_{III}$ 2001–2002:2003–2004	**0.81**	**0.0001**	**0.65**	**0.0001**	**0.63**	**0.0001**	**0.80**	**0.0001**
MS$_I$:MS$_{III}$ 1999–2000:2003–2004	**0.57**	**0.0014**	**0.21**	**0.0001**	0.08	0.24	**0.33**	**0.004**
(B) Females								
BB:MS$_I$ 1995–1996:1999–2000	**0.39**	**0.0001**	–	–			–	–
MS$_I$:MS$_{II}$ 1999–2000:2001–2002	**0.66**	**0.0001**	0.12	0.28			**0.61**	**0.0002**
MS$_{II}$:MS$_{III}$ 2001–2002:2003–2004	**0.74**	**0.0001**	**0.089**	**0.019**			**0.76**	**0.0001**
MS$_I$:MS$_{III}$ 1999–2000:2003–2004	**0.43**	**0.0034**	0.003	0.279			**0.44**	**0.0001**

Values in bold are statistically significant after Bonferroni adjustment

was MS–TU, and the closest dyad in period MS$_{III}$ was MS–ST. Note however, that this simple change affected the strength of several relationships. For example, while AJ and TU associated closely in both periods, the strength of their

Fig. 2 Unrooted phylograms of **a** adult male and **b** adult female association patterns based on the Combined Association Index, during MS's tenure as alpha male. The summed distance between individuals is inversely proportional to the strength of their association. Shorter distances represent closer association

association was much stronger in MS$_{III}$ than MS$_{II}$. For females, the phylograms illustrate that one cluster (OU–TG–NL–AL) in particular was consistent across all three periods (Fig. 2b). Similarly, BL and AR consistently fall relatively close together. UM and MU did not associate closely with any females in any period. Note that female branches are typically much longer (and more variable) than the males'. This is consistent with our earlier result that, on average, females had lower association indices than males.

With the exception of one period (MS$_{III}$), males and females showed similar likelihoods of having a preferred social partner (PSP). In period MS$_I$, we classified 13.8% (5/36) of male dyads and 11% of female dyads (six of 55 with adequate data) as PSPs (Fig. 3). In period MS$_{II}$, 16.7% (6/36) of male dyads and 10% (4/40) of female dyads were classified as PSPs. This includes the mother–daughter pair (LP–LR) mentioned earlier. In MS$_{III}$, 16.7% (6/36) of male dyads were PSPs, compared to only 5% (2/36) for females.

The duration of PSPs was also similar for males and females. Two male PSPs (BB–MS, MS–ST) lasted for the entire 6-year period, and three (LK–YB, AJ–LK, BB–TU) lasted for at least 4 years. By our age criterion, KK was not an adult in MS$_I$, and therefore was not eligible for a PSP during that period. Female rates of PSP stability were similar—AL–NL lasted for at least 6 years, while AL–TG and OU–TG lasted for at least 4 years. Deaths (KL, LP) and lack of data (PE) prevented us from determining the stability of the other female PSPs.
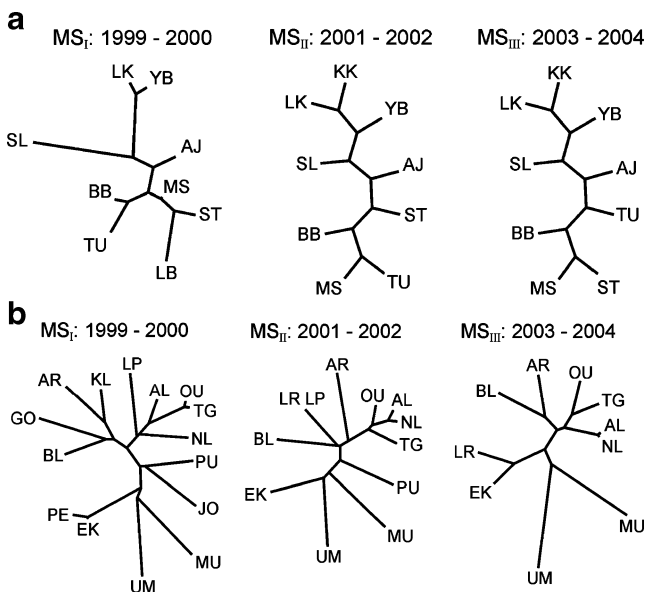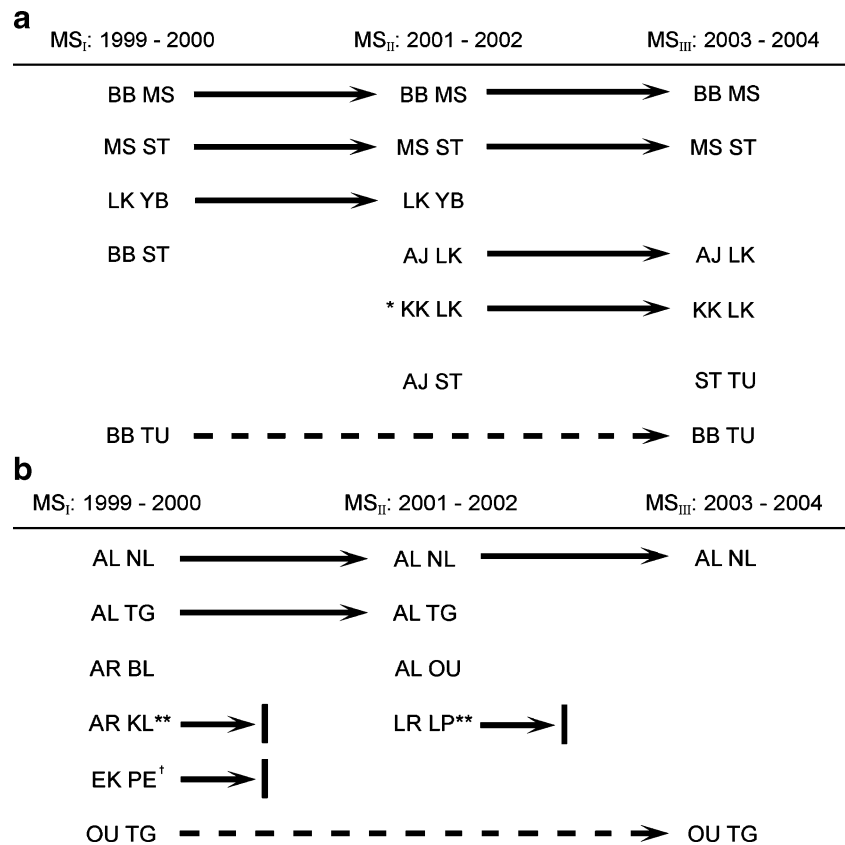
a

MS$_I$: 1999 - 2000	MS$_{II}$: 2001 - 2002	MS$_{III}$: 2003 - 2004
BB MS →	BB MS →	BB MS
MS ST →	MS ST →	MS ST
LK YB →	LK YB	
BB ST	AJ LK →	AJ LK
	* KK LK →	KK LK
	AJ ST	ST TU
BB TU - - - - - - - - - - →		BB TU

b

MS$_I$: 1999 - 2000	MS$_{II}$: 2001 - 2002	MS$_{III}$: 2003 - 2004
AL NL →	AL NL →	AL NL
AL TG →	AL TG	
AR BL	AL OU	
AR KL** →		LR LP** →	
EK PE† →			
OU TG - - - - - - - - - - →		OU TG

1995–2000 (alpha males = BB, MS)

To examine whether long-term associations were resistant to major changes in the male dominance hierarchy, we tested whether association patterns were significantly different when comparing periods before and after a change in alpha male. As few focal data were available for BB's alpha tenure, we used the simple ratio index (SRI, Eq. 1) to compare association patterns between BB and MS$_I$.

For both male and female dyads, SRI values from periods BB and MS$_I$ were positively correlated (males, K_r= 132, p=0.012, Pearson's r=0.19; females, K_r=596, $p<$ 0.0001, Pearson's r=0.39). This demonstrates that, at the group level, both sexes were relatively consistent in their patterns of association, even after an alpha male takeover. Associations that were positive during BB's alpha tenure generally persisted after MS became alpha. However, the correlation coefficient (Pearson's r) for females was double that for males. This indicates that, between alpha male periods, the strength of male association preferences changed more than those of females.

We compared these results to those from an equivalent time span when the dominance hierarchy was stable—between MS$_I$ and MS$_{III}$. We have already reported that, for males, matrices of SRI values from periods MS$_I$ and MS$_{III}$ were positively correlated (Table 3A). Note, however, that the

correlation coefficient was almost three times higher than it was between BB and MS$_{III}$ (0.57 vs. 0.19). This indicates that the strength of male association preferences changed more over the time when the alpha male changed than when the hierarchy was stable. This was not the case for females (Table 3B), which showed similar correlation coefficients between BB:MS$_I$ (r=0.39) and MS$_I$:MS$_{III}$ (r=0.43), illustrating that, in contrast to males, the strength of female association preferences changed relatively little after the alpha male takeover.

Discussion

Our study offers three important results. First, male chimpanzees at Kanyawara exhibited closer dyadic intrasexual associations than females did, even when sex differences in gregariousness were taken into account. Second, the overall pattern of association preferences in both sexes changed little over 6–10 years. Dyads that frequently associated in one period were highly likely to do so in another. However, relatively low matrix correlation coefficients and phylograms illustrate that, while there were no major directional changes (e.g., from positive to negative), the strength of some association preferences did change. Third, when comparing periods with different alpha

males, we found that changes in association strength were more prevalent among males while female association patterns were less sensitive to changes in the male hierarchy. Below, we discuss these findings and their implications for sex differences in cooperation.

Males

Theory predicts that frequent association facilitates cooperation through the development of tolerance (Melis et al. 2006) and/or the opportunity for reciprocation (Trivers 1971; Axelrod and Hamilton 1981). Therefore, since male chimpanzees are considerably more cooperative than females, males should exhibit stronger and more stable associations than females. Our study supports both of these predictions. The average male dyad spent more time in close association than the average female dyad. Critically, this result was not simply due to the fact that males are typically found in larger parties than females, as our association indices incorporated spatial components that measured a dyad's likelihood of being observed in close proximity within a party.

These are the first formal comparisons of sex differences in association strength and stability among East African chimpanzees, and they clarify several issues. First, until now, the degree to which association patterns persist over time has been poorly understood. On the one hand, it has often been reported that certain male dyads form long-term cooperative alliances characterized by repeated, reciprocal coalitions (reviewed in Muller and Mitani 2005). On the other hand, several studies have shown that males frequently team up with recent adversaries against recent coalition partners (Nishida 1983; de Waal 1984; Nishida and Hosaka 1996; Newton-Fisher 1999, 2002; Watts 2002). Such 'allegiance fickleness' (Nishida 1983) suggests that male association patterns should be flexible, changing with the availability of profitable coalition partners. Our results are consistent with both views of male chimpanzee dominance strategies. First, the high consistency of male association patterns at Kanyawara supports the idea that long-term relationships are important for males: some dyads exhibited frequent association year after year. Interestingly, the two dyads of preferred social partners (PSPs) that lasted for at least 6 years included the alpha male (MS), suggesting that forming a long-term cooperative relationship may be particularly important for maintaining high rank (cf. Duffy et al. 2007). This is consistent with recent findings from Kanyawara suggesting that high-ranking males form closer social bonds than low-ranking males (Duffy 2006). Future work will reveal whether this sort of strategy is adopted by all alpha males or only by individuals that are unable to achieve and maintain dominance by their individual effort.

Second, while the overall pattern of male associations was consistent over time, the strength of many relationships changed. In other words, while remaining 'friends', males often became more or less affiliative over time. This is consistent with reports of allegiance fickleness, suggesting that males alter their association preferences based on a changing social climate. Such flux was particularly apparent after major disruption of the male dominance hierarchy—association patterns in periods straddling an alpha male takeover were less tightly correlated compared to periods of relative hierarchy stability.

Finally, our results add to the growing body of data suggesting that kinship is not the only factor promoting cooperation among male chimpanzees (Muller and Mitani 2005; Langergraber et al. 2007). While genetic data on the entire Kanyawara community are not yet available, of the nine PSPs from MS's tenure, only one (AJ–LK) consisted of suspected maternal brothers.

Females

Even though female chimpanzees rarely cooperate, their association patterns were consistent over time. Similar correlation coefficients indicate that female association patterns were neither more nor less stable than males'. Why do females have consistent association patterns? We suggest that female association is largely a result of individual ranging patterns. There is growing evidence that female East African chimpanzees increase their fitness by establishing core areas in high-quality areas of the community range (Pusey et al. 1997; Williams et al. 2002a; Emery Thompson et al. 2007; Murray et al. 2007). At Gombe and Kanyawara, such competition results in the formation of 'neighborhoods' of overlapping core areas where adult females forage alone or with their dependent offspring for several years (Williams et al. 2002a; Emery Thompson et al. 2007). Hence, females in the same neighborhood should be more likely to be seen together in the same party, simply by chance. If this is true, and there is little social incentive for females to associate, then we would expect that association indices based on presence in the same party would be highly correlated over time, but that those based on spatial proximity within the social group would not. This is exactly what we found. Party-level association (SRI) values were highly correlated across all periods, while values of the 5M index were only correlated between MS_{II} and MS_{III}, and even then, the correlation coefficient was very low ($r=0.089$). As expected, the pattern of female association corresponded closely with neighborhood membership (Emery Thompson et al. 2007).

Within a given period, the strength and number of close associates varied considerably among female dyads. Some females (e.g., UM and MU) rarely associated with other

females, while others (OU, AL, NL, and TG) were frequently seen together. Again, this is consistent with the idea that female association patterns are largely a byproduct of the location of their core area, which affects whom they frequently encounter. Peripheral females rarely encounter other females. This result may contribute to explaining why captive female chimpanzees at Arnhem zoo were shown to have strong, stable bonds (de Waal 1984). In captivity, females are not food-limited and have little ability to forage solitarily. The ecological factors that affect female ranging and association patterns in the wild have effectively been removed. Limited ranging options intensify female social interactions, increasing the importance of forming cooperative relationships.

Due to almost universal female dispersal at Kanyawara, females did not typically have the opportunity to associate with adult female kin. However, the single female to remain in the community (LR) associated very closely with her mother (LP). More research is needed to determine whether kin selection plays a more prominent role at sites such as Gombe, where females exhibit a lower rate of transfer (Williams 2000).

Conclusions

Our results support the hypothesis that frequent association is important for facilitating cooperation. While we have not examined the direction of causality, we have shown that both the strength and stability of association are important for evaluating sex differences in cooperation. Male chimpanzees, which are characterized by frequent cooperation, exhibited dyadic associations that were both strong and stable. By contrast, the overall strength of female associations was relatively weak. While female association preferences were as equally stable as males', this reflects a dyad's likelihood of being found in the same party rather than associating closely within that party. Therefore, it seems that female association patterns are more a consequence of individual ranging patterns rather than a correlate of cooperation.

References

Alberts SC (1999) Paternal kin discrimination in wild baboons. Proc Roy Soc London, Ser B 266:1501–1506

Altmann J (1974) Observational study of behavior: sampling methods. Behaviour 49:227–267

Axelrod R, Hamilton WD (1981) The evolution of cooperation. Science 211:1390–1396

Baker KC, Smuts BB (1994) Social relationships of female chimpanzees: diversity between captive social groups. In: Wrangham RW, McGrew WC, de Waal FBM, Heltne PG (eds) Chimpanzee cultures. Harvard University Press, Cambridge, pp 227–242

Boesch C (1994) Cooperative hunting in wild chimpanzees. Anim Behav 48:653–667

Boesch C (2002) Cooperative hunting roles among Taï chimpanzees. Hum Nature-Int Bios 13:27–46

Bygott JD (1979) Agonistic behaviour, dominance and social structure in wild chimpanzees of the Gombe National Park. In: Hamburg DA, McCown ER (eds) The great apes. Benjamin/Cummings, Menlo Park, pp 405–427

Cairns SJ, Schwager SJ (1987) A comparison of association indices. Anim Behav 35:1454–1469

Clements KC, Stephens DW (1995) Testing non-kin cooperation: mutualism and the Prisoner's Dilemma. Anim Behav 50:527–535

Connor RC, Heithaus MR, Barre LM (2001) Complex social structure, alliance stability and mating access in a bottlenose dolphin 'super-alliance'. Proc Roy Soc London, Ser B 268:263–267

de Villiers MS, Richardson PRK, van Jaarsveld AS (2003) Patterns of coalition formation and spatial association in a social carnivore, the African wild dog (Lycaon pictus). J Zool (London) 260:377–389

de Waal FBM (1984) Sex differences in the formation of coalitions among chimpanzees. Ethol Sociobiol 5:239–255

de Waal FBM (1992) Coalitions as part of reciprocal relations in the Arnhem chimpanzee colony. In: Harcourt AH, de Waal FBM (eds) Coalitions and alliances in humans and other animals. Oxford University Press, Oxford, pp 233–257

de Waal FBM, Harcourt AH (1992) Coalitions and alliances: a history of ethological research. In: Harcourt AH, de Waal FBM (eds) Coalitions and alliances in humans and other animals. Oxford University Press, Oxford, pp 1–19

Duffy KG (2006) Social dynamics of male chimpanzees: adaptive significance of male bonds. PhD thesis, University of California, Los Angeles, Los Angeles, CA

Duffy KG, Silk JB, Wrangham RW (2007) Male chimpanzees exchange political support for mating opportunities. Curr Biol 17:R586–R587

Emery Thompson M, Kahlenberg SM, Gilby IC, Wrangham RW (2007) Core area quality is associated with variance in reproductive success among female chimpanzees at Kibale National Park. Anim Behav 73:501–512

Gilby IC (2006) Meat sharing among the Gombe chimpanzees: harassment and reciprocal exchange. Anim Behav 71:953–963

Gilby IC, Eberly LE, Pintea L, Pusey AE (2006) Ecological and social influences on the hunting behaviour of wild chimpanzees (Pan troglodytes schweinfurthii). Anim Behav 72:169–180

Gilby IC, Eberly LE, Wrangham RW (2008) Economic profitability of social predation among wild chimpanzees: individual variation promotes cooperation. Anim Behav 75:351–360

Goodall J (1986) The chimpanzees of Gombe: patterns of behavior. Harvard University Press, Cambridge

Hamilton WD (1964) The genetical evolution of social behavior. J Theor Biol 7:1–52

Hare B, Melis AP, Woods V, Hastings S, Wrangham RW (2007) Tolerance allows bonobos to outperform chimpanzees on a cooperative task. Curr Biol 17:619–623

Hemelrijk CK (1990) Models of, and tests for, reciprocity, unidirectionality and other social interaction patterns at a group level. Anim Behav 39:1013–1029

Kahlenberg SM, Emery Thompson M, Wrangham RW (2008) Female competition over core areas among Kanyawara chimpanzees, Kibale National Park, Uganda. Int J Primatol. In press

Kapsalis E (2003) Matrilineal kinship and primate behavior. In: Chapais B, Berman C (eds) Kinship and behavior in primates. Oxford University Press, Oxford, pp 153–176

Langergraber KE, Mitani JC, Vigilant L (2007) The limited impact of kinship on cooperation in wild chimpanzees. Proc Natl Acad Sci USA 104:7786–7790

Lehmann J, Boesch C (2007) Sexual differences in chimpanzee sociality. Int J Primatol 29:65–81

Mantel N (1967) The detection of disease clustering and a generalized regression approach. Cancer Res 27:209–200

Melis AP, Hare B, Tomasello M (2006) Engineering cooperation in chimpanzees: tolerance constraints on cooperation. Anim Behav 72:275–286

Mesterton-Gibbons M, Dugatkin LA (1992) Cooperation among unrelated individuals: evolutionary factors. Q Rev Biol 67:267–281

Mitani JC (2005) Reciprocal exchange in chimpanzees and other primates. In: Kappeler PM, van Schaik CP (eds) Cooperation in primates: mechanisms and evolution. Springer, Heidelberg, pp 101–113

Mitani JC, Merriwether DA, Zhang C (2000) Male affiliation, cooperation and kinship in wild chimpanzees. Anim Behav 59:885–893

Mitani JC, Watts DP (2001) Why do chimpanzees hunt and share meat. Anim Behav 61:915–924

Mitani JC, Watts DP, Pepper JW, Merriwether DA (2002) Demographic and social constraints on male chimpanzee behaviour. Anim Behav 64:727–737

Muller MN, Mitani JC (2005) Conflict and cooperation in wild chimpanzees. Adv Stud Behav 35:275–331

Murray CM, Mane SV, Pusey AE (2007) Dominance rank influences female space use in wild chimpanzees, Pan troglodytes: towards an ideal despotic distribution. Anim Behav 74:1795–1804

Newton-Fisher NE (1999) Association by male chimpanzees: a social tactic. Behaviour 136:705–730

Newton-Fisher NE (2002) Relationships of male chimpanzees in the Budongo Forest, Uganda. In: Boesch C, Hohmann G, Marchant L (eds) Behavioural diversity in chimpanzees and bonobos. Cambridge University Press, Cambridge, pp 112–124

Nishida T (1968) The social group of wild chimpanzees in the Mahali mountains. Primates 9:167–224

Nishida T (1983) Alpha status and agonistic alliance in wild chimpanzees (Pan troglodytes schweinfurthii). Primates 24:318–336

Nishida T, Hosaka K (1996) Coalition strategies among adult male chimpanzees of the Mahale Mountains, Tanzania. In: McGrew WC, Marchant L, Nishida T (eds) Great ape societies. Cambridge University Press, Cambridge, pp 114–134

Pepper JW, Mitani JC, Watts DP (1999) General gregariousness and specific social preferences among wild chimpanzees. Int J Primatol 20:613–632

Pusey AE, Williams JM, Goodall J (1997) The influence of dominance rank on the reproductive success of female chimpanzees. Science 277:828–831

Riss D, Goodall J (1977) The recent rise to the alpha-rank in a population of free-living chimpanzees. Folia Primatol 27: 134–151

Silk JB, Alberts SC, Altmann J (2006a) Social relationships among adult female baboons (Papio cynocephalus) II. Variation in the quality and stability of social bonds. Behav Ecol Sociobiol 61:197–204

Silk JB, Altmann J, Alberts SC (2006b) Social relationships among adult female baboons (Papio cynocephalus) I. Variation in the strength of social bonds. Behav Ecol Sociobiol 61:183–195

Stanford CB (1998) Chimpanzee and red colobus. Harvard University Press, Cambridge

Swofford DL (2003) PAUP*: phylogenetic analysis using parsimony (*and other methods), 4th edn. Sinauer Associates, Sunderland

Townsend SW, Slocombe KE, Emery Thompson M, Zuberbühler K (2007) Female-led infanticide in wild chimpanzees. Curr Biol 17: R355–R356

Trivers RL (1971) The evolution of reciprocal altruism. Q Rev Biol 46:35–57

Vigilant L, Hofreiter M, Siedel H, Boesch C (2001) Paternity and relatedness in wild chimpanzee communities. Proc Natl Acad Sci USA 98:12890–12895

Watts DP (1998) Coalitionary mate guarding by male chimpanzees at Ngogo, Kibale National Park, Uganda. Behav Ecol Sociobiol 44:43–55

Watts DP (2002) Reciprocity and interchange in the social relationships of wild male chimpanzees. Behaviour 139:343–370

Watts DP, Mitani JC (2001) Boundary patrols and intergroup encounters in wild chimpanzees. Behaviour 138:299–327

Watts DP, Muller MN, Amsler SJ, Mbabazi G, Mitani JC (2006) Lethal intergroup aggression by chimpanzees in Kibale National Park, Uganda. Am J Primatol 68:161–180

Williams JM (2000) Female strategies and the reasons for territoriality in chimpanzees: lessons from three decades of research at Gombe. PhD thesis, University of Minnesota, Minneapolis, MN

Williams JM, Pusey AE, Carlis JV, Farm BP, Goodall J (2002a) Female competition and male territorial behaviour influence female chimpanzees' ranging patterns. Anim Behav 63:347–360

Williams JM, Liu H-Y, Pusey AE (2002b) Costs and benefits of grouping for female chimpanzees at Gombe. In: Boesch C, Hohmann G, Marchant L (eds) Behavioural diversity in chimpanzees and bonobos. Cambridge University Press, Cambridge, pp 192–203

Wilson ML (2001) Imbalances of power: how chimpanzees respond to the threat of intergroup aggression. PhD thesis, Harvard University, Cambridge, MA

Wilson ML, Wrangham RW (2003) Intergroup relations in chimpanzees. Ann Rev Anthropol 32:363–392

Wilson ML, Hauser MD, Wrangham RW (2001) Does participation in intergroup conflict depend on numerical assessment, range location or rank for wild chimpanzees. Anim Behav 61:1203–1216

Wilson ML, Wallauer WR, Pusey AE (2004) New cases of intergroup violence among chimpanzees in Gombe National Park, Tanzania. Int J Primatol 25:523–549

Wrangham RW (2000) Why are male chimpanzees more gregarious than mothers? A scramble competition hypothesis. In: Kappeler PM (ed) Primate males: causes and consequences of variation in group composition. Cambridge University Press, Cambridge, pp 248–258

Wrangham RW, Smuts B (1980) Sex differences in the behavioral ecology of chimpanzees in the Gombe National Park, Tanzania. J Reprod Fertil, Supplement 28:13–31

Wrangham RW, Clark AP, Isabirye-Basuta G (1992) Female social relationships and social organization of Kibale forest chimpanzees. In: Nishida T, McGrew WC, Marler P, Pickford M, de Waal FBM (eds) Topics in primatology. Vol. 1. Human origins. Tokyo University Press, Tokyo, pp 81–98