

Genetic correlates of social behaviour in wild chimpanzees: evidence from mitochondrial DNA

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(Received 7 August 1996; initial acceptance 14 October 1996;
final acceptance 5 December 1996; MS. number: A7676)

Abstract. This study explored some aspects of chimpanzee social behaviour using mitochondrial DNA sequence data as an index of matrilineal relatedness. The hypothesis tested was that matrilineal relatedness predicts social affiliative preference in wild chimpanzees. Several behavioural measures of individual social preference were examined for chimpanzees from Kanyawara community in Uganda's Kibale Forest. None of the four pairs of strongly affiliative males in this community could have been maternal brothers, since no pair shared the same mitochondrial DNA sequence. Fourteen chimpanzee communities outside Kibale, for which no direct behavioural data were available, were also studied by using communal nesting as a rough index of affiliative preference. Again, chimpanzees that nested together did not tend to be matrilineally related. The results suggest that kin selection is weaker than previously thought as a force promoting intra-community affiliation in chimpanzees.

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Affiliative relationships between adult males are rare in animals. Males form stable social groups in felids (Packer & Pusey 1982; Caro 1994), primates (Van Hooff & Van Schaik 1994) and cetaceans (Connor & Peterson 1994). 'Second-order' affiliative relationships, in which particular males preferentially associate within larger 'first-order' social groupings, occur even more rarely. Such relationships have been documented in bottlenose dolphins, *Tursiops* sp. (Connor et al. 1992), chimpanzees, *Pan troglodytes* (Goodall 1986), and humans, *Homo sapiens* (Wrangham & Peterson 1996).

First-order male relationships are thought to function strategically for between-group competition. Second-order male relationships are thought to function politically, for within-group competition. Initially, kin selection (Hamilton 1964) was thought to be the dominant centripetal force driving the formation of both types of bonds. It is now clear, however, that first-order male

groupings in felids are not primarily determined by kinship (Packer & Pusey 1982; Caro 1994). Male African lions, *Panthera leo*, for example, cooperate mutualistically in the defence of territory, rather than reciprocally or on the basis of kinship (Grinnell et al. 1995). The hypothesis that second-order male affiliations are kinship-driven has not previously been tested.

Social relationships in chimpanzees are largely dominated by cooperative associations between adult males. Wherever long-term research has taken place, social relationships between males are closer and better defined than relationships between females (Goodall 1986; Nishida 1990; Wrangham et al. 1992). Males are generally dominant to females; within-male relationships follow a linear dominance hierarchy, notably different from the more tenuous network of social interactions between females (Nishida 1979; Goodall 1986; Wrangham et al. 1992; but see Sugiyama & Koman 1979; Sugiyama 1988).

Close affiliative relationships between males function on two levels in chimpanzees, for inter-community aggression and for intra-community politics (Wrangham 1986). Inter-community interactions in chimpanzees are almost universally hostile, and often involve premeditated, systematic attacks by groups of coalitional males on

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smaller groups of males from neighbouring communities (Nishida 1979; Goodall 1986; Wrangham & Peterson 1996). By virtue of its ubiquity among chimpanzee communities thus far studied, and because of its existence in humans, cooperative defence of territory by coalitional males has probably been an important component of chimpanzee behaviour at least since the divergence of *Pan* and *Homo* approximately 6 million years ago (Wrangham 1987; Ghiglieri 1989; Wrangham et al. 1994).

All chimpanzee communities in which long-term behavioural observations have taken place also contain particularly interactive male-male dyads that engage in relatively high frequencies of cooperative behaviours (Goodall 1986; Nishida 1990; Wrangham et al. 1992). These male dyadic associations can be viewed proximately as political strategies and ultimately as reproductive strategies (de Waal 1982; Goodall 1986; Nishida & Hiraïwa-Hasegawa 1986; Morin 1993). Cooperative male relationships confer within-community fitness benefits because of the enhanced ability of coalition partners to secure and maintain high dominance rank (de Waal 1982; Goodall 1986; Nishida & Hiraïwa-Hasegawa 1986) as well as to guard mates from rivals (R. W. Wrangham, personal observation). High male rank in turn confers fitness benefits in the form of enhanced mating success during possessive mating attempts (Sugiyama & Koman 1979; Tutin 1979; Hasegawa & Hiraïwa-Hasegawa 1983).

Although the proximate benefits of male coalitional behaviour in chimpanzees are becoming well understood, the decision rules by which males choose alliance partners are not. Research on captive chimpanzees suggests that alliances are formed and broken on the basis of complex political decisions in which personality characteristics of the individual community members play central roles (de Waal 1982). Captivity may necessarily limit the social choices available to chimpanzees, however. In the wild, chimpanzees may have access to a much wider range of potential alliance partners.

One plausible hypothesis is that chimpanzees in natural settings preferentially form alliances with kin. Morin et al. (1994) showed that male chimpanzees within a single community in Tanzania are more closely related genetically than are females. Kin selection is thus a viable explanation

for first-order (community-level) territorial groupings in chimpanzees. Within communities, chimpanzees clearly recognize maternally related kin. Close, lasting bonds are characteristic of mothers and their offspring and can persist throughout lifetimes (Goodall 1986). Orphaned infants may be adopted, often by known or suspected maternal siblings (Goodall 1986). These observations suggest that kin selection may also facilitate second-order (intra-community) social relationships, such as male-male alliances.

Lack of male investment in infants, coupled with the generally promiscuous mating system of chimpanzees, would make recognition of paternal kin unlikely. Since primates have been experimentally indicated to discern paternal kin through phenotypic matching, however (Wu et al. 1980; Fredrickson & Sackett 1984), patrilineal relatedness should not be discounted as a possible mediator of social affiliation. The ultimate influence of patrilineal relatedness on the evolution of chimpanzee social behavior may be significant, since the mating system of chimpanzees may facilitate the formation of paternally related age cohorts within communities (Altmann 1979). Nevertheless, an explanation of male social affiliation based on matrilineal relatedness would be most consistent with behavioural observations to date.

In this study, we used mitochondrial DNA sequence data to test the hypothesis that wild chimpanzees of the easternmost subspecies, *P. t. schweinfurthii*, socialize preferentially with maternal kin within communities. Mitochondrial DNA is maternally inherited and can therefore facilitate 'maternity exclusion', since individuals with different mitochondrial DNA sequences cannot be mother-offspring pairs except in the advent of a mutational event. Since even the most quickly evolving regions of the primate mitochondrial genome mutate at rates less than approximately 10^{-3} nucleotide changes per site per generation, however (Vigilant et al. 1991; Ward et al. 1991), mutation can effectively be ignored in the present case.

We examined social relationships at two levels. First, we examined a single chimpanzee community (Kanyawara community in Uganda's Kibale Forest), where social relationships between individuals have been documented through direct behavioural observation (Wrangham et al. 1992). Second, we examined 14 additional communities in which chimpanzees have generally not

been studied. In these communities, we used group nesting behaviour as an assay of affiliative preference.

KIBALE FOREST'S KANYAWARA COMMUNITY

Methods

We compiled behavioural data for 14 chimpanzees from Kibale Forest's Kanyawara community (Wrangham et al. 1992). These chimpanzees represent all of the eight adult males in the community (BB, BF, LB, LM, SL, ST, SY, TU), all of the five subadult males (AJ, MS, NJ, RZ, YB) and one adult female (MG). MG was incorporated because of her unusually close bond with one of the adult males (TU), suggesting a possible maternal relationship.

We compiled data from two types of observations: party compositions and 10 min focal studies (TMS; see also Wrangham et al. 1992). Party composition data consisted of 21 396 observations of the identities of individuals comprising a party, made by observers singly or in pairs between July 1988 and May 1993 (Wrangham et al. 1992). Observations were made every 15 min and were therefore not independent. Furthermore, individuals were not represented equally. For example, RZ was killed in an episode of apparent intercommunity aggression in 1992 and was therefore not represented in subsequent observations. We compiled 10-min focal study data from observations made between March 1993 and March 1995. Raw data consisted of rotating focal observations of individuals in which grooming interactions and nearest-neighbour distances were recorded as a point sample every 2 min (Wrangham et al. 1992). We edited these data for the present analysis to exclude all but the fifth (final) observation in each 10-min focal study, making each of the resulting 1470 observations relatively independent.

We calculated three indices of social interaction using party composition and 10-min focal study data. We calculated dyadic association indices (DAI) from party composition data for all pairs of individuals according to the formula $DAI = C/(A+B+C)$, where A = the number of observations containing individual a without b , B = the number of observations containing individual b without a , and C = the number of observations containing both a and b . We chose this

'twice-weight index' because of its frequent use in studies of chimpanzee behaviour (Nishida 1968; Ghiglieri 1984; Wrangham et al. 1992). We used 10-min focal study data to calculate a 'simple ratio' index of grooming preference, $GP = G/C$, where G = the number of grooming interactions recorded between two individuals and C = the total number of observations in which both individuals were present (Cairns & Schwager 1987). We calculated an analogous index for nearest-neighbour distances.

We obtained DNA non-invasively from shed hair. We collected hair opportunistically by searching the ground where individuals had self-groomed, or by sampling sleeping nests which individuals had unambiguously constructed. We stored hairs dry in the field and at room temperature after transport to the United States. Details of laboratory methods, including DNA extraction, polymerase chain reaction (PCR) amplification and DNA sequencing, are given in Goldberg (1996).

The DNA region that we chose to study was a hypervariable segment of the mitochondrial control region, also known as d-loop (Kocher & Wilson 1991). The first hypervariable region of d-loop is the most quickly evolving region in the primate mitochondrial genome (Kocher & Wilson 1991). We sequenced a 368 bp segment (corresponding to Anderson reference sequence coordinates 16042–16410), which includes the first hypervariable region (Anderson et al. 1981). To ensure the accuracy of our DNA sequences, we sequenced each sample at least twice on both the positive and negative strands. We checked all computer reads of our sequences manually, and resolved any ambiguities by resequencing. DNA sequences associated with this project are described elsewhere (Goldberg 1996; Goldberg & Ruvolo 1997), and are obtainable through GenBank (accession numbers U77181–U77293).

Results

Matrices of associative preference between all individuals are presented in Fig. 1 as UPGMA dendrograms (Sokal & Michener 1958), which are standardized to unit length for purposes of comparison. The closest relationship was assigned a distance of zero and the most distant relationship was assigned a distance of 1; intermediate relationships are proportional to their actual

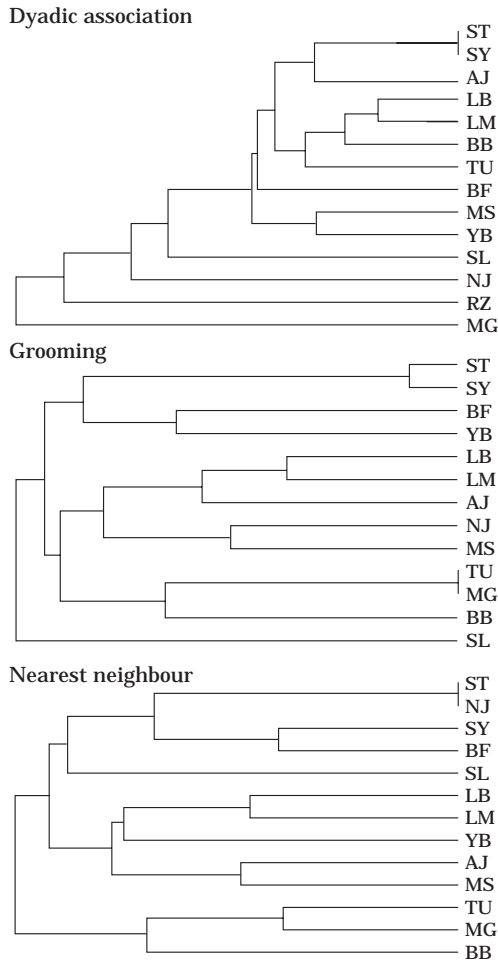


Figure 1. UPGMA dendrograms of social affiliation between Kanyawara individuals calculated for three behavioural measures. Dendrograms are standardized to unit length for comparison.

(unadjusted) distances. RZ, the chimpanzee that died in 1992, does not appear in the dendrograms for grooming and nearest neighbour distance. To test the consistency of the three measures, we performed correlation tests on the unadjusted matrices according to the method of Hemelrijk (1990a, b). Hemelrijk's Kr test is a modified form of the Mantel test of matrix correlation (Mantel 1967). It is superior to the Mantel test for studies of social interaction within groups because it considers intra-individual variation; it is also a more powerful test for matrices containing many 'ties'. We calculated Kr values and one-tailed

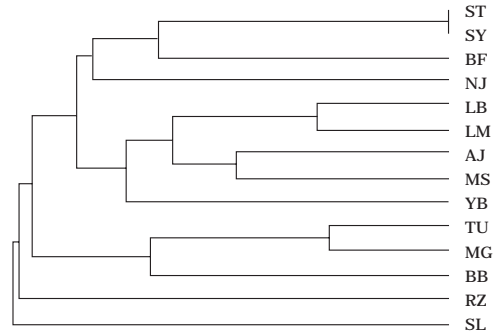


Figure 2. Average UPGMA dendrogram of social affiliation among Kanyawara individuals calculated from the means of dyadic association, grooming and nearest neighbour indices. The dendrogram has been standardized to unit length.

statistical probabilities based on 2000 matrix permutations according to the suggestions of Hemelrijk (1990a) using the computer program MATSQUAR (C. K. Hemelrijk, unpublished software).

The three indices of social affiliation were highly correlated (dyadic association indices and nearest-neighbour distance: $Kr=235$, $P=0.0005$; dyadic association indices and grooming: $Kr=181$, $P=0.0015$; nearest neighbour distance and grooming: $Kr=250$, $P=0.0010$). We also tested these associations using standard Mantel tests; probabilities were virtually identical in each case. The concordance between the three measures is encouraging, and reflects the fact that affiliative preferences in chimpanzees manifest themselves at different behavioural levels. Autocorrelational effects could account in part for the correlation between nearest-neighbour distance and grooming, but not between either of these measures and dyadic association indices, which is an independent measure. The dendrograms are not identical, however, presumably because of a combination of sampling error and real variation in the expression of affiliative preferences across the three behavioural dimensions examined.

Correlation between the three matrices justifies the calculation of a combined matrix of social affiliation, in which each cell represents an average associative index, calculated as the mean standardized distance across all three behavioural measures (Fig. 2). Values for RZ, who appeared only in the dyadic association indices matrix, are mean values for grooming and nearest-neighbour

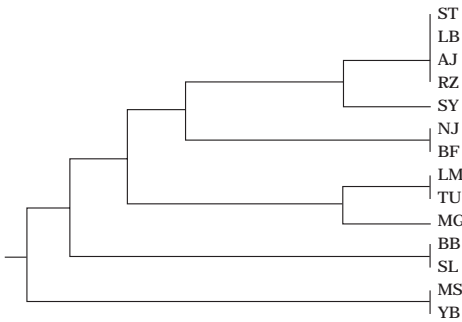


Figure 3. UPGMA tree of mitochondrial haplotypes for Kanyawara individuals. Zero branch lengths indicate haplotype identity.

distances calculated across all other individuals for which data were available. The dendrogram in Fig. 2 is quantitatively meaningless in that it combines behavioural data calculated in different units, but it is qualitatively useful for identifying consistently affiliative dyads.

Four dyads stand out as particularly close. The closest, SY–ST, were the alpha and beta males, respectively, from 1987 to 1994 (Wrangham et al. 1992). The next closest relationship, that between TU and MG, is unusual in that MG is an adult female and TU an adult male. The relationship is asymmetrical, with MG showing intense but generally unreciprocated interest in TU, and is reminiscent of mother–son relationships in Gombe (Goodall 1986). The third closest relationship, LB–LM, represents another affiliative relationship between adult males. The fourth closest relationship, that between the two subadult males AJ and MS, may represent a nascent cooperative dyadic association between males on the cusp of adulthood. Finally, although BB and TU do not stand out as particularly close in any of the dendrograms presented, BB and TU are currently the alpha and beta males, having displaced ST and SY in 1994. Their close affiliative relationship has been documented by Wrangham et al. (1992), and they are currently each other's closest allies (R. W. Wrangham, personal observation).

Figure 3 shows a UPGMA tree of genetic relationships for the same chimpanzees based on mitochondrial control region DNA sequences. The dendrogram is unstandardized, with zero branch lengths representing actual haplotype identity. Kanyawara haplotypes differed from one another by a minimum of zero nucleotides and a

maximum of six nucleotides. For the purposes of discerning potential maternal kin, only two levels of genetic similarity are relevant: identity and non-identity. Mutational events are possible, but their low frequency renders them statistically non-significant for the present analysis (Kocher & Wilson 1991; Vigilant et al. 1991; Ward et al. 1991). Sequencing errors are also possible, although the two-stranded, multiple sequencing strategy used in this study minimized such errors. Individuals sharing the same haplotype (joined by zero branch lengths) may therefore be members of the same matriline. Individuals with different haplotypes (joined by branches of greater-than-zero length) cannot be members of the same matriline.

None of the five aforementioned affiliative dyads shared the same mitochondrial haplotype. ST and SY were not maternal brothers (different by one nucleotide), nor were LB and LM (different by three nucleotides), AJ and MS (different by five nucleotides) or BB and TU (different by five nucleotides). This observation represents a strong rejection of the hypothesis that Kanyawara males form cooperative alliances on the basis of matrilineal kinship. Furthermore, MG and TU also did not share the same haplotype (different by one nucleotide) and were not therefore mother and son. Extra-genealogical factors must account for this unusual female–male bond.

The possibility still exists that matrilineality predicts affiliative preference in general (i.e. that close, but non-dyadic, social affiliations are mediated by matrilineal kinship). To test this possibility, we ran matrix correlations between each of the behavioural matrices and a matrix of genetic distance based on mitochondrial control region sequences. The behavioural matrices were the unstandardized dyadic association indices, grooming and nearest neighbour matrices, calculated as described above. The genetic matrix contained cells with values of either zero or one, representing haplotype non-identity and haplotype identity, respectively. We ran Mantel tests (Mantel 1967; Smouse et al. 1986) using the computer package 'The R Package' (Legendre & Vaudour 1991). We calculated one-tailed probabilities using a Monte Carlo procedure involving 2000 matrix permutations (Hope 1968).

The association between nearest neighbour distance and genetic identity was not significant (Mantel $Z=154$, $P=0.3378$), nor was the

association between grooming preference and genetic identity (Mantel $Z=6$, $P=0.9270$). A significant relationship emerged for the comparison between dyadic association indices and genetic identity (Mantel $Z=550$, $P=0.006$). We repeated these same analyses using Hemelrijk's Kr test, with the same results (nearest neighbour: $Kr=1$, $P=0.4908$; grooming: $Kr=-33$, $P=0.8821$; dyadic association indices: $Kr=82$, $P=0.0005$). We also ran Mantel tests and Kr tests to compare the standardized combined matrix of social affiliation (Fig. 2) with the matrix of genetic identity. The correlation was not significant by either test (Mantel $Z=4.96$, $P=0.2650$; $Kr=23$, $P=0.2559$). To account for the possibility that small genetic differences between individuals were not real, but resulted from sequencing errors, we repeated the above analysis using a matrix of absolute genetic distances in place of the binary genetic matrix. Levels of statistical significance did not change appreciably for any analysis.

These observations confirm that, in general, chimpanzees in Kanyawara community do not tend to associate on the basis of matrilineal relatedness. The hypothesis cannot, however, be rejected for association in the same party (dyadic association indices).

SOCIAL BEHAVIOUR OUTSIDE KANYAWARA

Methods

We searched 14 forest locations outside Kibale Forest's Kanyawara community for chimpanzee sleeping nests, which the animals construct of woven branches both during the day and at night (Nissen 1931; Goodall 1962). These nests provide a 'fossil record' from which chimpanzee behaviour can be inferred (Sept 1992; Fruth & Hohmann 1994b). Nests have also been used to estimate population densities (Kano 1972; Ghiglieri 1984; Tutin & Fernandez 1984) and to study cultural variability between populations (McGrew 1985; Fruth & Hohmann 1994a).

The locations from which we sampled nests spanned a representative range of habitat types within the geographical range of *P. t. schweinfurthii* (Goldberg 1996). We recorded both the height of each nest encountered and its relative age. We assigned relative ages to nests using a

five-point scale. Nests of age 1 (youngest) contained only green leaves. Nests of age 2 contained a mixture of green and brown leaves, and nests of age 3 contained brown leaves only. Nests of ages 4 and 5 contained only brown leaves and had missing sections. Nests of age 4 were missing less than 50% of the nest material, and nests of age 5 (oldest) were missing more than 50% of the nest material.

We also recorded the number and identities of all nests found in the same spatial cluster. We defined spatial clusters as aggregates of nests that were within visual range of each other when observed from the forest floor. This definition is conservative with respect to identifying communal nesting events. It does not, for example, account for the fact that visibility may be greater across the forest canopy than from the ground. Similarly, it ignores the possibility that chimpanzees maintain contact with nesting partners using non-visual (e.g. auditory) cues. Aggregates of nests representing actual communal nesting events were therefore almost certainly more dispersed than were our spatial clusters, which generally spanned 5–20 meters.

When we encountered a nest, we searched it for shed hairs, which we stored dry in the field and frozen after transport to the United States. We extracted, amplified and sequenced DNA as described above. A single nest thereby ultimately yielded a single DNA sequence. Nests yielding different DNA sequences could be unambiguously assigned to different chimpanzee individuals (within the bounds of error associated with sequencing). Nests yielding identical DNA sequences, however, may have been constructed by the same individual.

Results

Variation in mean nest heights and mean numbers of nests per cluster was considerable both within and between forests (Table I). Analysis of variance revealed a significant association between location and nest height ($r^2=0.340$, $P=0.0001$), as well as between nest cluster size and location ($r^2=0.201$, $P=0.01$).

The mean \pm SE nest height (7.83 ± 0.23 m), the median height (7.0 m) and the range of heights observed (0–27 m) are comparable to values reported for other chimpanzee populations across a range of geographical locations and habitat types

Table I. Mean \pm SE nest heights and mean \pm SE nest cluster sizes for 14 chimpanzee populations

Forest	Location name ^a	Nests (N)	Height (m)	Clusters (N)	Cluster size
1 Bugoma	Mwela Sawmill	29	7.50 \pm 0.67	20	1.45 \pm 0.40
2 Budongo	Pabidi	25	10.12 \pm 0.72	12	2.08 \pm 0.52
3 Budongo	Sonso Sawmill	28	5.68 \pm 0.69	12	2.33 \pm 0.52
4 Itwara	Rwebikuya	33	5.17 \pm 0.53	9	3.67 \pm 0.60
5 Ituri	Afarama	36	8.92 \pm 0.60	16	2.25 \pm 0.45
6 Ituri	Avakubi NE	22	9.18 \pm 0.77	7	3.14 \pm 0.68
7 Ituri	Avakubi SW	16	8.16 \pm 0.91	5	3.20 \pm 0.80
8 Ituri	Lenda	27	6.06 \pm 0.70	10	2.70 \pm 0.57
9 Kibale	Kanyanchu	17	11.59 \pm 0.88	7	2.43 \pm 0.68
10 Kibale	Ngogo	15	11.10 \pm 0.94	8	2.00 \pm 0.64
11 Kalinzu	Kalinzu Sawmill	31	5.84 \pm 0.65	12	2.58 \pm 0.52
12 Rwenzori	Katebwa	18	14.44 \pm 0.86	5	3.60 \pm 0.81
13 Semliki	Mbume-Busaru	13	4.85 \pm 1.01	6	2.17 \pm 0.74
14 Tshopo	Bafwabalinga	13	9.23 \pm 1.01	8	1.63 \pm 0.64

^aDetails of sampling locations in Goldberg (1996).

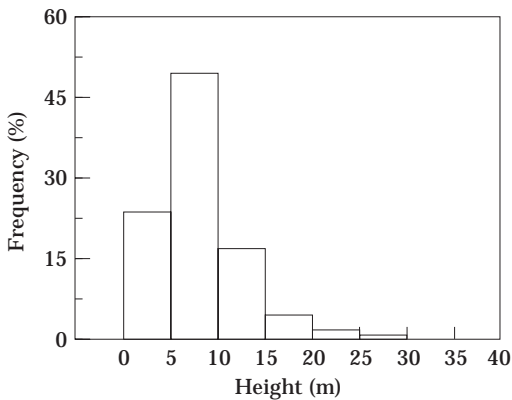


Figure 4. Frequency distribution of nest heights for 14 sampling locations ($N=323$ observations).

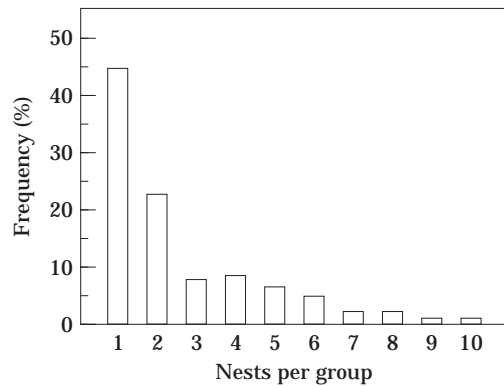


Figure 5. Frequency distribution of nest group sizes for 14 sampling locations ($N=138$ observations).

(Fruth & Hohmann 1994a; Fig. 4). Furthermore, the shape of the distribution is comparable to that reported for chimpanzees in Lopé, Gabon (Wroegmann 1992). These observations suggest that the nests collected in the present study do not represent a severely biased sample of the population of nests at large. Very high nests may be under-represented in the sample, although the remarkable skills of locally hired tree climbers minimized this bias.

Figure 5 shows a frequency distribution of nest group sizes for the 323 nests (138 groups) for which data were available. Within each location, we defined nests as in the same 'group' if they were

in the same spatial cluster and if they were of identical relative age (measured as described above). For example, a spatial cluster of 10 nests in which half were scored as age 2 and the other half as age 3 would be scored as two separate groups of five. This age-dependent measure differentiates nest clusters representing simultaneous nesting events by social groups of chimpanzees from those representing the habitual use of a nesting site by a few individuals over time. Choice of a restrictive definition of group identity may account for the absence of very large groups (>10) in Fig. 5, even though large clusters of nests have been reported in low frequency in

Table II. Association between communal nesting and identity of haplotype for chimpanzees in 14 locations

Location ^c	N ^d	With age criterion ^a		Without age criterion ^b	
		<i>r</i> ^e	<i>P</i> ^f	<i>r</i> ^e	<i>P</i> ^f
1	13	0.216	0.049	0.135	0.174
2	12	-0.075	0.543	-0.075	0.543
3	15	0.291	0.023	0.090	0.316
4	12	-0.109	0.513	-0.075	0.570
5	13	0.177	0.254	0.130	0.337
6	12	-0.029	0.803	-0.024	0.572
7	13	-0.052	0.565	0.267	0.038
8	17	0.032	0.864	0.032	0.864
9	14	-0.074	0.472	-0.052	0.519
10	13	0.074	0.390	0.235	0.053
11	13	-0.047	0.849	-0.059	0.778
12	13	-0.086	0.591	-0.089	0.576
13	9	-0.112	0.580	-0.134	0.650
14	10	0.059	0.894	0.401	0.040

^aNests were assigned to the same 'group' only if they were spatially associated and of the same relative age.

^bNests were assigned to the same 'cluster' regardless of age, on the basis of spatial proximity alone.

^cLocation numbers refer to Table I.

^dNumbers of DNA sequences obtained.

^eStandardized form of the Mantel *Z* statistic (Smouse *et al.* 1986).

^fProbabilities computed from 2000 matrix permutations following Hope (1968).

other populations (Fruth & Hohmann 1994a). The mean \pm SE group size (2.44 ± 0.15) and the median group size (2) were consistent with observations from other study sites (Fruth & Hohmann 1994a).

For each population, we created a matrix of haplotype identity. We assigned a value of 1 to pairs of nests yielding the same haplotype and a value of 0 to pairs of nests yielding different haplotypes. For these same nests, we also created a matrix of group identity. Pairs of nests from the same spatial cluster which were also of the same age were placed in the same group and assigned a value of 1; pairs of nests from different spatial clusters, or of different ages, were assigned a value of 0. For each population, we correlated the genetic identity matrix with the group identity matrix using a Mantel test (Mantel 1967). Because of unequal sample sizes between locations, we used a standardized form of the Mantel *Z* statistic, *r* (Smouse *et al.* 1986). We calculated probabilities (one-tailed) from 2000 matrix permutations using a Monte Carlo permutation technique (Hope 1968).

Twelve of the 14 locations showed no association between nesting in the same group and identity of haplotype (Table II). Two locations (1 and 3) showed probabilities below 0.05 (0.049 and 0.023, respectively). These probabilities are marginal, however, and most likely represent type I error resulting from the large number of independent correlations run (14). A level of significance of 0.0036 ($\alpha' = 0.05/14$) would be required to reject the null hypothesis of no general association, given the number of simultaneous tests run. The observed values of *r* for each location also suggest no general trend (six positive and eight negative). Data from 14 independent locations therefore support the overall conclusion that chimpanzees did not associate in sleeping groups on the basis of matrilineal kinship.

We repeated the analysis described above without the criterion that nests need be of the same age to be classified in the same group (i.e. we assigned pairs of nests a matrix value of 1 solely on the basis of being in the same spatial cluster). This analysis is useful since nests decompose at varying rates (Ghiglieri 1984; Tutin & Fernandez 1984;

Plumptre & Reynolds 1996). A cluster of nests assigned different ages may therefore have been simultaneously constructed. A cluster of nests assigned the same age may analogously have been constructed at different times. Relaxing the age criterion also tests for the possibility that spatial clusters of nests were constructed by one or a few individuals during a short period of localized habitat use. This would be the case if individual chimpanzees preferred to re-use nesting sites (Goodall 1986; Sept 1992). Relaxing the age criterion is therefore also a test of the hypothesis that double-sampling of individuals was a significant sampling problem.

With the age criterion relaxed, 12 of the 14 populations again showed no association between genetic identity and nest cluster identity (Table II). Two probabilities were only marginally significant, and may represent type I error. As in the original test, no trend is suggested by values of r , seven of which are positive and seven negative. This observation provides evidence that that double-sampling of individuals has not significantly influenced the data. Again, replacement of the binary genetic matrix with a matrix of actual genetic distances among haplotypes did not change the results described above, indicating that genetically similar but non-identical haplotypes (which could have resulted from sequencing error) did not bias these results.

The overall result from both tests suggests that no association exists between nesting partner preference and haplotype identity. This analysis therefore confirms, in 14 independent populations, that matrilineal relatedness is not a strong force mediating social affiliation.

DISCUSSION

From long-term field studies, the closest and most important bond formed in a chimpanzee's life is that with its mother (Goodall 1986; Nishida 1990). Comparably important are thought to be the relationships among maternal siblings during childhood, which persist at least up to the time of weaning, and probably through adolescence. Goodall (1986, page 205) wrote, 'Bonds that develop between the siblings themselves during these years [juvenile and adolescent years] are likely to endure, particularly those between brothers; this may well be crucial in determining social

rank in later life.' By expectation, positive associations between haplotype identity and social affiliation should therefore have emerged in the analyses described above.

Among Kanyawara individuals, pairs of coalitional males proved not to be maternal brothers. Associating in the same party (as measured by the dyadic association index) did correlate with haplotype identity. However, the two 'closest' behavioural measures of social affiliation, grooming and nearest-neighbour distance, did not correlate with genetic relatedness. Chimpanzees in Kanyawara community did not, therefore, preferentially associate with maternal kin in ways which would lead to the formation of rank-enhancing alliances.

Potential alliance partners from the same matriline may simply be scarce in Kanyawara. Kanyawara females are noted for their unusually long inter-birth interval, currently estimated at over 7 years (Wrangham et al., in press). The probability that a male seeking an alliance partner would be able to select a maternal brother of comparable age and social maturity to himself may therefore be low. It is demographically likely, however, that some maternal brother pairs do exist in Kanyawara. A female reproductive lifespan of 15 years (Goodall 1986; Harvey et al. 1987) and an inter-birth interval of 6–7 years (Wrangham et al., in press) implies that a Kanyawara female may expect, on average, three offspring during her lifetime. There are six unique ordered combinations in which these offspring may appear (M=male; F=female): MMM, FFF, MMF, FFM, MFM, FMF. Thus, 5/9 of males will have an 'adjacent' maternal brother, assuming a 50:50 sex ratio. Only adjacent maternal brothers are likely to be close enough in age to serve as potential alliance partners, since the male 'window of opportunity' for dominance is probably, at most, 10 years (Goodall 1986). In a community of 13 adult and subadult males (such as Kanyawara), $5/9 \times 13$, or 7.2 males probably have a maternal brother who is also a potential alliance partner. Therefore, 7.2/2, or 3.6 (between 3 and 4) maternal brother pairs probably exist in Kanyawara. Indeed, 10 pairs of Kanyawara males are potential maternal brothers in that they share the same mitochondrial haplotype (Fig. 3). Given the potential for fraternal cooperative dyads in Kanyawara, it is therefore especially intriguing that they do not occur.

The lack of association between genetic identity and nesting preference in 14 communities other than Kanyawara suggests lack of a general trend. Nesting in the same group may simply be too crude an index of affiliative preference; mother-offspring relationships are invisible to the analysis of nesting, since mothers and dependent offspring share both sleeping nests and mitochondrial haplotypes. Nevertheless, contrary to the claims of Goodall (1986), the data in general do not confirm the presence of enduring matrilineal bonds.

The most parsimonious explanation of these data is that chimpanzees in the wild are making social decisions much as they do in captivity, by choosing to consort with individuals with whom they share complementary social goals and abilities (de Waal 1982). 'Second-order' political relationships among chimpanzees within communities may therefore be qualitatively different from 'first order' community-level territorial groupings, which may indeed be facilitated by consanguinity and thus kin selection (Morin et al. 1994). To discover the extent to which this distinction is truly generalizable we may have to await detailed observational and genetic data from a statistically meaningful number of chimpanzee communities throughout Africa.

ACKNOWLEDGMENTS

Many thanks to Maryellen Ruvolo for providing laboratory facilities. David Pilbeam and Mark Leighton provided invaluable intellectual advice. Colin and Lauren Chapman, John and Terese Hart, Tuhairwe Peter Atwooki, Katembo Mushgezni Vital and the faculty and staff of Makerere University Biological Field Station (Kanyawara, Uganda) and the Centre de Formation et de Recherche en Conservation Forestière (Epulu, Zaïre) were instrumental during the sample collection phase.

The Wenner-Gren Foundation for Anthropological Research, the L. S. B. Leakey Foundation, the Charles A. and Anne Morrow Lindbergh Foundation, the Mellon Foundation, and the Department of Anthropology at Harvard University generously funded laboratory and field research. Harvard University, the U.S. Department of Education, and the Cora Du Bois Charitable Trust provided additional funds that

significantly facilitated the completion of the project. The field work component of this project was funded by NSF grants BNS-8704458 and DEB-9120960. The Uganda National Council for Science and Technology and the government of Zaire kindly permitted fieldwork.

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