



Demographic and social constraints on male chimpanzee behaviour

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Male chimpanzees, *Pan troglodytes*, are well known for affiliating and cooperating in a variety of behavioural contexts. Prior field research indicates that maternal kinship does not affect patterns of affiliation and cooperation by males in the same social group. Two questions remain unclear from this finding. First, why do male chimpanzees not bias their behaviour towards maternal kin? Second, what factors account for who affiliates and cooperates with whom? We conducted behavioural observations of an unusually large community of chimpanzees at Ngogo, Kibale National Park, Uganda, to test the hypothesis that demographic constraints limit the number of maternal kin with whom male chimpanzees can cooperate, and thereby lead them to form selective bonds with nonkin of similar age and status. Results indicated that male age and rank are significantly associated with four measures of social behaviour. Members of the same age class and individuals close in rank were more likely to affiliate and cooperate than males that belonged to different age and rank classes. Additional analyses replicate earlier findings and show that males who affiliated and cooperated were not closely related through the maternal line, as assayed by mtDNA haplotype sharing. These results add to our growing understanding of the important role demographic and social constraints play in animal behaviour.

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Kinship exerts a pervasive influence on the lives of social animals (Alcock 2001). The effects of kinship have been especially well documented among our closest living relatives, the nonhuman primates. Here strong social bonds develop among matrilineally related Old World monkey females, and close genetic relatives are frequently observed to affiliate and cooperate (review in Silk 2001). These empirical observations are easily accommodated and explained by Hamilton's (1963, 1964) concept of inclusive fitness.

Chimpanzees, *Pan troglodytes*, are often used to illustrate how kinship affects primate social behaviour. Chimpanzees live in communities or unit-groups, whose members form temporary parties that vary in size and composition (Nishida 1968; Goodall 1986; Boesch & Boesch-Achermann 2000). Membership in these communities is open due to dispersal (Nishida & Kawanaka 1972;

Pusey 1979). Female chimpanzees usually leave their natal groups after reaching sexual maturity. Males, in contrast, do not disperse. As a result of these dispersal patterns, males within groups are typically more closely related to each other than they are to males from other groups (Morin et al. 1994; Vigilant et al. 2001). Male chimpanzees cooperate to compete with conspecifics both within and between communities (Goodall et al. 1979; Nishida 1983; Nishida et al. 1985; Morin et al. 1994; Nishida & Hosaka 1996; Watts & Mitani 2001). It is generally agreed that kin selection favours males who cooperate together in between-group competition (Morin et al. 1994; Goldberg & Wrangham 1997). Whether a similar selective mechanism shapes cooperative relationships that form for purposes of within-group competition, however, is currently unclear.

Male chimpanzees develop strong social bonds with others in their community. These bonds are manifest in several contexts, including association, grooming, proximity, coalitions, meat sharing and territorial behaviour (Nishida 1968, 1983; Simpson 1973; Riss & Goodall 1977; Goodall et al. 1979; Wrangham & Smuts 1980; Nishida et al. 1992; Nishida & Hosaka 1996; Watts 1998, 2000; Newton-Fisher 1999; Wrangham 1999; Boesch &

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Boesch-Achermann 2000; Mitani & Watts 2001; Watts & Mitani 2001). Recent field studies have called into question the long-standing assumption that genetic relatedness affects the formation and maintenance of social bonds among male chimpanzees that live in the same community. For example, two independent studies now suggest that patterns of social affiliation and cooperation among males are not predicted by maternal relatedness as assayed by mtDNA haplotype sharing and genetic distances (Goldberg & Wrangham 1997; Mitani et al. 2000). These studies raise two important and inter-related questions. First, why do male chimpanzees not bias their behaviour towards maternal kin? Second, what factors account for the observed patterns of affiliation and cooperation among wild male chimpanzees?

Chimpanzee demography and life history have received scant attention with regard to these two questions, yet potentially provide answers to both. Chimpanzees are an extremely long-lived and slowly reproducing species, with females in the wild giving birth to a single offspring only once every 5–6 years (Nishida et al. 1990; Wallis 1997; Boesch & Boesch-Achermann 2000). With an equal sex ratio at birth and high infant and juvenile mortality (see references above), the probability is relatively low that a female will give birth successively to sons that reach adulthood together. Males attain their physical and social prime as adults. At this time, they are most likely to engage in a variety of social behaviours, such as coalitions, meat sharing and territorial defence, whose outcomes have major fitness consequences (Riss & Goodall 1977; Goodall et al. 1979; Nishida 1983; Nishida & Hosaka 1996; Watts 1998; Mitani & Watts 2001). Adolescent males, which are still growing and attempting to integrate themselves into the social worlds of adults, are seldom in a good position to aid their older adult brothers that are striving to improve their reproduction and status. These observations suggest that male chimpanzees only rarely live with maternal kin that can aid them. If kin are not generally available, then males are likely to solicit and use others opportunistically (e.g. deWaal 1982; Nishida 1983; Nishida et al. 1992; Nishida & Hosaka 1996). Individuals in the same age cohort may represent particularly attractive social partners because they grow up together, are generally familiar with each other, and share similar social interests and power throughout their lives (cf. van Hooff & van Schaik 1994; Goldberg & Wrangham 1997). For similar reasons, males close in dominance rank may also be inclined to form strong affiliative and cooperative relationships (cf. deWaal & Luttrell 1986; deWaal 1991; Watts 2000). Males who belong to the same rank class are apt to establish effective bonds insofar as they share similar needs, access to resources and ability to exchange social benefits.

The preceding considerations suggest that age and rank, rather than maternal kinship, will be good predictors of patterns of wild male chimpanzee social behaviour. In this paper, we test these hypotheses by examining the relationships between age and rank and affiliative and cooperative behaviour among males living in an extremely large chimpanzee community at Ngogo, Kibale National Park, Uganda. We extend results of prior analy-

ses by also investigating the association between maternal genetic relatedness and social behaviour in a larger sample of males that includes both adults and adolescents. Our results are consistent with those that we have reported previously (Mitani et al. 2000), and add to our understanding by clarifying some of the demographic and social constraints on male chimpanzee social behaviour.

METHODS

Study Site and Animals

We observed chimpanzees at the Ngogo study site in Kibale National Park, Uganda. J.C.M. and D.P.W. collected behavioural observations during 22 months between January 1998 and August 2000. Ngogo lies at an interface between lowland and montane rainforest and is covered primarily with moist, evergreen forest. Ghiglieri (1984) Butynski (1990) and Struhsaker (1997) provide detailed descriptions of the Ngogo study area.

The Ngogo chimpanzee community is the largest thus far described in the wild. Approximately 150 individuals live within the Ngogo community, including 23–24 adult males, 15 adolescent males, and more than 45 adult females during the period considered here. We have maintained continuous observations of the chimpanzees at Ngogo since 1995, and as a result, subjects were well habituated to our presence.

Behavioural Observations

We made observations of social behaviour during hour-long samples of target males. During each observation period, scan samples were made at 10-min intervals to record the target's behaviour, including grooming and proximity to other chimpanzees. We scored associations between male subjects during observations of target individuals, with two males defined to be in association whenever they came within visual range of each other as assessed by human observers. We scored proximity during scan samples, defining other individuals to be in proximity to targets whenever they came within 5 m. Grooming was recorded whenever two males were observed performing this behaviour during scan samples. Because prior analyses indicated that observations recorded every 30 min were statistically independent (Mitani et al. 2000), we employed this interval for behavioural observations of associations, grooming and proximity. Analyses of social behaviour were based on 1415 h of observations, with each of the 38 males present throughout the study followed a minimum of 30 h ($\bar{X} \pm SD = 37 \pm 3$, range 30–51).

We scored male participation in coalitions, meat sharing and boundary patrols ad libitum. Coalitions ($N=709$) between two males were defined to occur whenever they directed aggression together towards others (e.g. Nishida 1983; deWaal 1984; Mitani et al. 2000) Meat sharing ($N=397$) was recorded during hunting episodes of mammalian prey (Mitani & Watts 1999, 2001; Watts & Mitani

2002a, b). Males frequently exchange meat with the same individual several times at the same hunt. To preserve statistical independence, we recorded sharing between two males only once during the same hunt irrespective of the number of times meat was transferred. We also recorded adult male participation in boundary patrols ($N=56$). Patrols were characterized by a unique suite of behaviours similar to those displayed by chimpanzees at other sites (e.g. Goodall et al. 1979; Boesch & Boesch-Achermann 2000). During patrols the Ngogo chimpanzees move silently to the periphery of their range seeking signs of individuals from other communities (Watts & Mitani 2001). Such searches resulted in encounters with members of other groups 39% of the time, with males from the Ngogo community killing infants from neighbouring communities four times (Watts & Mitani 2000; D. Watts, J. C. Mitani & H. Sherrow, unpublished observations).

Ascertainment of Ages

We used a classification scheme originally developed and subsequently refined by Goodall (1968, 1983, 1986) and divided males into five age categories (Table 1; cf. Goodall 1986; Nishida et al. 1990; Boesch & Boesch-Achermann 2000). We assigned males to one of these five age classes using standard morphological and behavioural criteria. We followed previous convention and assigned adolescent males to one of two categories, early and late. We classified adult males into three categories, young, prime and old. We departed from convention in our categorization of adults by collapsing a typically used 'middle-age' class into the group of 'prime' males. Given the well-known anatomical and behavioural variability that exists among chimpanzees (e.g. Goodall 1986), we found it especially difficult to differentiate males during middle adulthood. For this reason, we took a conservative approach, adopted by others (e.g. Boesch & Boesch-Achermann 2000), and pooled males at this life-history stage.

Given the relatively short duration of our field observations at Ngogo, we cannot assign specific ages to any of our 38 study subjects with absolute certainty. Age estimates were made independently, and without consultation, by J.C.M. and D.P.W. Both were responsible for all field observations, and each possesses over 22 years of experience working with a variety of primates in the wild. Both showed remarkable congruence in their assignments, concurring on 37 of 38. For purposes of the following analyses, we classified the one adult male, EL, on which we did not concur, as a 'prime' adult male instead of an 'old' adult male. Altering EL's classification did not affect the results of any of the analyses presented below in an appreciable way.

Rank Determinations

We employed 1208 observations of pant grunts between individuals and an additional 580 dyadic aggressive interactions to determine dominance ranks of the 38

Table 1. Male chimpanzee study subjects

Individual	Age class	Rank	Rank class
AY	Old adult male	21	Low
BA	Young adult male	16	Middle
BD	Early adolescent	31	Very low
BF	Prime adult male	8	High
BG	Prime adult male	11	Middle
BR	Late adolescent	25	Low
BT	Prime adult male	2	High
CO	Prime adult male	5	High
CR	Late adolescent	36	Very low
DI	Prime adult male	30	Low
DO	Prime adult male	13	Middle
DX	Late adolescent	29	Low
EL	Prime adult male	3	High
EV	Late adolescent	19	Middle
GA	Young adult male	24	Low
GR	Late adolescent	23	Low
GZ	Early adolescent	32	Very low
HO	Prime adult male	7	High
HR	Prime adult male	6	High
LO	Prime adult male	1	High
MG	Prime adult male	12	Middle
MI	Prime adult male	15	Middle
MO	Prime adult male	22	Low
MT	Late adolescent	28	Low
MW	Old adult male	4	High
OR	Young adult male	10	Middle
PI	Prime adult male	20	Middle
PK	Prime adult male	17	Middle
RH	Early adolescent	33	Very low
RI	Early adolescent	37	Very low
RO	Early adolescent	38	Very low
RU	Old adult male	14	Middle
ST	Prime adult male	27	Low
TA	Late adolescent	38	Very low
TY	Prime adult male	9	Middle
WA	Late adolescent	34	Very low
WB	Late adolescent	18	Middle
WY	Early adolescent	35	Very low

Males and their ages, ranks and rank classes are shown.

male study subjects. Pant grunts are distinctive calls given by low-ranking individuals to higher-ranking animals (Bygott 1979; deWaal 1982). We used the distribution of these calls along with the outcomes of aggressive interactions to construct a 38×38 dominance matrix. We employed a scaling method developed by Batchelder et al. (1992; Jameson et al. 1999) to assign dominance ranks to our 38 study subjects (Table 1). For subsequent analyses (see below), we computed the absolute values of the difference in rank between each male pair and classified every individual into one of four rank categories, either high, middle, low or very low (Table 1). We used the distribution of the number of individuals each male dominated as the basis for classification (Fig. 1). We grouped the top eight males, which dominated at least 60% of all others, into the high-ranking class. We categorized the next 12 males in the hierarchy into a middle-ranking class. These males dominated at least 20% of all other individuals. The low-ranking class consisted of the next nine males, which dominated between 14 and 24% of all others. We classified the lowest nine males in our

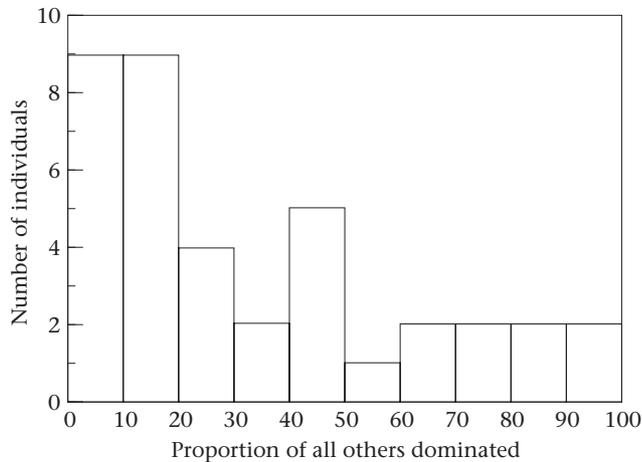


Figure 1. Distribution of the percentage of individuals dominated. Bars show the number of males that dominated a given proportion of other males.

hierarchy into the 'very low-ranking' class. Members of this group never or only rarely dominated others as revealed through aggressive interactions and by pant grunts.

Genetic Analyses

We obtained data regarding mtDNA genetic relatedness using shed hair and faecal samples. Shed hair samples were gathered in the field under CITES import (U.S.A. number US830142) and export (Uganda number 103) permits. All samples were collected noninvasively from the ground following self-grooming episodes of subjects. Care was taken to ensure that samples were collected from isolated individuals who had scratched and shed hair several metres from other chimpanzees. Following collection, all samples were stored dry in sealed envelopes at ambient temperature in the field and frozen at -2°C after transport to the laboratory. Faecal samples consisted of approximately 5 g of faeces collected from each male following defecation on the ground. Samples were placed in 50-ml tubes containing 20 g of desiccant silica gel (Wasser et al. 1997) and stored at ambient temperature in the field and at 4°C with fresh silica following transport to the laboratory.

We assessed matrilineal genetic relatedness between male chimpanzees by sequencing the first hypervariable segment of the mitochondrial control region (Kocher & Wilson 1991). Our use of mtDNA is biologically appropriate given the high probability chimpanzees are able to discriminate individuals on the basis of maternal relatedness. Chimpanzee mothers and their offspring display enduring social bonds (Goodall 1968, 1986), making it likely that maternal siblings are able to recognize each other. In contrast, internal fertilization coupled with a promiscuous mating system (Tutin 1979; Watts 1998) may render it difficult for chimpanzees to discriminate paternal relatives.

We extracted mtDNA from single hair follicles using the Chelex (BioRad, Hercules, California, U.S.A.) extrac-

tion protocol. Following extraction, PCR amplification (Saiki et al. 1988) was carried out using Amplitaq Gold (Perkin-Elmer, Foster City, California, U.S.A.) at the manufacturer's recommended conditions. We amplified hair samples in PCR reactions using primers covering a 349 base pair segment corresponding to Anderson et al.'s (1981) reference sequence coordinates 16026–16375. Primer pairs included 16026Ch-For (5' CTT TCA TGG GGA AGC AAA TTT AAG 3') and 16375Ch-Rev (5' GGC ATC CGT GGG GAC GAG G 3'), yielding 306 bases of usable sequence. Primers were removed using Microcon 100 000 MW cutoff filters.

We used the QIAamp DNA Stool Kit (Qiagen, Chatsworth, California, U.S.A.) to extract mtDNA from faecal samples and the Degenerate Oligonucleotide Priming (DOP) method (Cheung & Nelson 1996) to amplify DNA. We used the DOP-PCR product as template for subsequent PCRs with Platinum *Taq* (Invitrogen). We amplified a 592 base pair segment from the faecal DNA samples using primers spanning Anderson et al.'s reference coordinates 15912–16504. Primers included 15912Ch-For (5' CAC CGG TCT TGT AAA CCG GAA AC 3') and 16504Ch-Rev (5' CCA GAT GTC GGA TAC AGT TCA CTT T 3'), resulting in 544 bases of usable sequence. PCR reactions were digested with Exo I enzyme to remove primers and filtered through Millipore Multiscreen plates.

PCR products were used as templates in dye-labelled dideoxy terminator cycle sequencing reactions employing the ABI Prism FS or BigDye Terminator kits (Perkin-Elmer). Sequencing reactions were purified with alcohol precipitation, then rehydrated in formamide/EDTA/Dextran Blue loading buffer and electrophoresed in denaturing polyacrylamide gels (Long Ranger Singel pack, BioWhittaker Molecular Applications, Rockland, Maine, U.S.A.) on an ABI 377XL automated sequencer. We sequenced all samples in both the forward and reverse direction. Sequences were aligned using ABI's Sequence Navigator program. All sequences were scored and confirmed a minimum of two times (range 2–4) from independent samples collected from each male.

We constructed a neighbour-joining tree (Saitou & Nei 1987) to illustrate mtDNA genetic relatedness between our male subjects. We used the Kimura (1981) two-parameter model, with a 15:1 transition:transversion ratio, to estimate mtDNA genetic distances between all pairs of individuals. We implemented Felsenstein's (1993) DNADist program contained in PHYLIP Version 3.5 to estimate distances and then used the Neighbor program in PHYLIP to generate the neighbour-joining tree.

Statistical Analyses

We used three different statistical approaches to evaluate the effects of maternal kinship, age and rank on male social behaviour: matrix correlation tests, resampling tests and paired *t* tests.

Matrix correlation tests

For matrix correlation tests we constructed a 38×38 matrix of pairwise values for each predictor variable:

maternal kinship, age difference and rank difference. We also constructed matrices for each measure of social affinity: association, grooming, proximity, coalitions, meat sharing and territorial behaviour. We then tested whether each predictor matrix was correlated with each social affinity matrix.

The maternal kinship matrix reflected mtDNA haplotype identity or nonidentity and contained values of one or zero, respectively. The age matrix also included ones and zeros, representing pairs of males of the same or different age classes, respectively. Entries in the rank matrix consisted of the absolute values of the difference in rank between each male pair.

To construct behavioural matrices we used the pairwise affinity index (Pepper et al. 1999):

$$\frac{I_{AB}}{I_A + I_B}$$

where I_{AB} is the total number of interactions observed between individuals A and B, I_A is the total number of interactions observed between individual A and all other individuals, and I_B is the total number of interactions observed between individual B and all others. Here an 'interaction' is defined as two individuals appearing together in the same group (i.e. party, patrol and proximity sample, or conventional dyadic social interaction, such as grooming, coalition or meat sharing). The advantage of this index over other association indices is that it factors out each individual's general gregariousness or tendency to interact. Consequently, it reflects only the interaction intensity that is specific to a particular dyad, rather than being generic to either individual's behaviour (Pepper et al. 1999).

Before using the observed pairwise affinity values, we normalized them by dividing by their expected values under the null hypothesis that social behaviours were generic rather than dyad specific. To generate these expected values we used the GROUPS computer program, which implements the group randomization method (Pepper et al. 1999). Here 'groups' were defined in terms of one of the six social behaviours we recorded. This procedure repeatedly reshuffles the membership of observed groups, while retaining both the observed number of appearances of each individual and the observed distribution of group sizes. After each randomization we calculated the affinity index for each dyad, and averaged these randomized values to generate an expected value for each dyad. We performed 10 000 randomizations to generate null expectations.

The randomization procedure simulates a scenario in which individuals may vary in their tendency to interact, but do not discriminate among potential partners. It controls for potentially confounding factors, such as the number and sizes of observed groups and the differing number of appearances of individuals, by explicitly incorporating them into the null model. The resulting ratio of observed to expected values indicates the direction and magnitude of each dyad's deviation from generic or indiscriminant behaviour. The user-friendly program and manual is available on request.

So that dyadic interactions above and below expected levels would have equal weight, we log transformed the observed/expected ratios (e.g. after log transformation, x and $1/x$ have the same magnitude but opposite sign). To avoid undefined values resulting from observed or expected values of zero, we truncated the range of the log-transformed values to $-2 \leq x \leq 2$, corresponding to a floor of 0.01 and a ceiling of 100 for observed/expected ratios.

To test the null hypotheses that maternal relatedness, age and rank were unrelated to a given social behaviour, we used the K_r test for correlation between two matrices (Hemelrijk 1990a). The K_r test is a matrix permutation procedure and variant of the Mantel (1967) test for matrix correlation. We performed three sets of six comparisons, testing maternal relatedness, age and rank against each social behaviour. To correct for the increased probability of committing type I errors when making these six comparisons, we adjusted our criteria of significance downward using the sequential Bonferroni technique (Holm 1979). For k multiple tests, we set our adjusted alpha levels, α' , at $\alpha' = \alpha / (1 + k - i)$, where $\alpha = 0.05$ is the overall experimentwise error rate and i is the i th sequential test from first to last.

Matrix correlation tests indicated that two potential predictor variables, age and rank, were strongly correlated with each other ($P = 0.0002$). We therefore examined whether significant relationships between predictor variables and measures of social behaviour were affected by a hidden third variable using a matrix partial correlation test (Hemelrijk 1990b). In this test, the association between two variables (e.g. rank and meat sharing) is examined while controlling for the effects of a third variable (e.g. age). The matrix partial correlation procedure provides a multivariate version of Kendall's S statistic (tau K_r) corrected for sample sizes and ties (Hemelrijk 1990b).

Resampling tests

We used a resampling procedure as an alternate means to assess the effects of maternal kinship, age and rank on male social behaviour. This analysis included three steps. First, we used the group randomization method to identify 'close dyads'. These included pairs of males with significantly elevated affiliation (i.e. within the top 2.5% of the distribution generated by group randomization; see above) in each of the six measures of social behaviour. Second, for each social behaviour we counted the number of close dyads that shared mtDNA haplotypes or included males belonging to the same age and rank class. We used the ratios of these numbers to the total number of close dyads as test statistics. Finally, for each combination of predictor variable and affinity index we used a resampling procedure to determine whether test statistics exceeded chance expectation.

To generate expected values, we constructed for each predictor variable a half-matrix with $38 \times 38 = 703$ entries, one for each male dyad in the Ngogo community. Values were either 1 or 0, with 1 indicating similarity (i.e. same mtDNA haplotype, age class or rank class) and 0 indicating dissimilarity. We randomly selected pairs of numbers

from these matrices N times, where N equalled the total number of close dyads. After making these N selections, we counted the number of times individuals with the same haplotype, rank or age class were selected (i.e. the number of times two ones were drawn). We used this count as a single data point and iterated this process 10 000 times to generate a frequency distribution of expected values. We compared observed test statistics to the tails of the expected distribution to assess the null hypothesis that social affinity was independent of the predictor variable. We used the sequential Bonferroni correction to adjust the lengths of these tails in each test.

Paired t tests

Both the matrix correlation tests and the resampling tests indicated that differences in age and rank had significant effects on cooperative behaviour. If maternally related dyads differed more in age and rank than other dyads, this might mask the direct effects of maternal relatedness. To control for this potential confound, we performed a third and final set of tests in which we removed the effects of age and rank before examining the relationship between maternal genetic relatedness and behaviour. Here we used paired Student t tests to compare the social behaviour of related and unrelated dyads that were matched in age and rank. To ensure statistical independence, we allowed each individual to appear only once in these analyses, either in a related or unrelated dyad. Related dyads consisted of four related pairs, and one randomly drawn pair each from two quartets and one trio of related individuals (Fig. 2). Dyads matched in age and rank to these related pairs were randomly selected from the remaining pool of unrelated individuals. Two groups of six and 10 males shared mtDNA haplotypes (Fig. 2). We did not consider males from either of these two groups as potential candidates for related dyads due to our inability to match them in age and rank to others in the remaining sample of nonrelatives. Some males that appear in these analyses did not form coalitions or share meat. We therefore conducted only four tests using the other measures of social behaviour.

RESULTS

Figure 2 displays the maternal relationships among the 38 male subjects as assayed by mtDNA. Matrix correlation tests revealed that maternal kinship at Ngogo, as measured by mtDNA haplotype sharing, is not a good predictor of patterns of male chimpanzee social behaviour (K , tests: NS for five of six tests; Table 2). One possible exception existed. Males tended to associate with others that shared mtDNA haplotypes, but this tendency was nonsignificant ($P=0.01$, $\alpha'=0.0083$). Results of the resampling tests reinforced conclusions derived from matrix correlations. Twenty-six male dyads out of 703 total groomed more often than expected by chance. Of these, only four (15%) shared mtDNA haplotypes, a proportion that did not exceed chance expectation of 11% (resampling test: $P>0.30$; Fig. 3a). Similar compari-

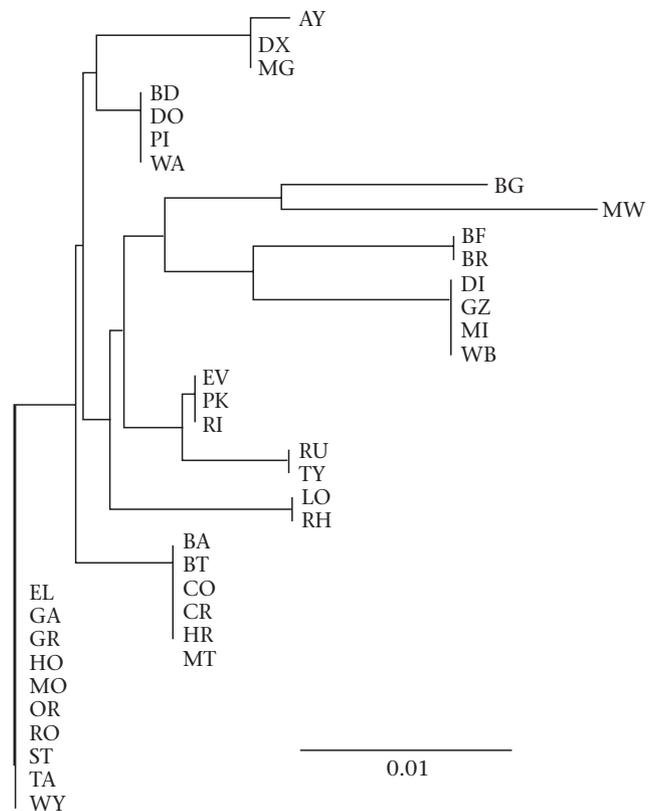


Figure 2. Neighbour-joining tree of mtDNA genetic distances between male chimpanzees. Males linked at zero branch lengths share mtDNA haplotypes.

sons involving the five other measures of social behaviour also showed that males related through the maternal line neither affiliated nor cooperated closely with each other (resampling tests: NS for all five tests; Fig. 3a).

Some of the mtDNA genetic relationships shown in Fig. 2 differ from those that we have previously reported for this community of chimpanzees (Figure 3 in Mitani et al. 2000). Differences are due to prior scoring errors in the sequences of four adult male chimpanzees, BT, DI, GA and PI. Fewer mtDNA haplotypes exist as a result of these scoring errors, now verified through multiple and longer sequences for each individual. We used the corrected mtDNA genetic data to reanalyse the relationships that we have reported before between mtDNA haplotype sharing and adult male social behaviour (Mitani et al. 2000). Results of these reanalyses do not alter any of our previous findings. As is the case for the larger sample of adults and adolescents analysed here, adult males when considered alone do not preferentially affiliate or cooperate with others who are closely related through the maternal line.

While maternal kinship had little power in predicting who affiliated and cooperated, male chimpanzees at Ngogo appeared to bias their social behaviour towards members of the same age class. Males that formed coalitions, shared meat and patrolled together more often than expected by chance were frequently members of the same age class (resampling test: coalitions: $P=0.0001$,

Table 2. Relationships between mtDNA haplotype sharing, age and rank with social behaviour

	mtDNA haplotype sharing		Age		Rank	
	K_r	P	K_r	P	K_r	P
Association	924	0.01	838	0.12	-1707	0.03
Grooming	388	0.15	553	0.13	-905	0.08
Proximity	391	0.22	847	0.07	-1691	0.001
Coalitions	54	0.71	740	0.02	-980	0.001
Meat sharing	90	0.56	636	0.02	-885	0.01
Patrols	127	0.66	738	0.11	-1549	0.03

K_r matrix correlation statistics and associated P values are shown. Entries highlighted in bold indicate those that were less than the sequential Bonferroni criterion.

$\alpha'=0.0083$; meat sharing: $P=0.0001$, $\alpha'=0.0100$; patrols: $P=0.0102$, $\alpha'=0.0125$; Fig. 3b). Associations, grooming and proximity were not strongly affected by age, however (Fig. 3b). Matrix correlation tests revealed positive but nonsignificant associations between similarity in age and the tendencies to form coalitions and share meat (K_r tests: $P \leq 0.02$ for both tests, starting sequential Bonferroni $\alpha'=0.0083$; Table 2).

A third set of analyses showed that rank had an equally strong effect on patterns of male behaviour. Significant negative associations existed between distance in rank and three of the six measures of social behaviour, proximity, coalitions and meat sharing (K_r tests: proximity: $P=0.0058$, $\alpha'=0.0083$; coalitions: $P=0.0098$, $\alpha'=0.0100$; meat sharing: $P=0.0112$, $\alpha'=0.0125$; Table 2). Matrix partial correlation tests indicated that all three of these relationships still persisted after controlling for the effects of age (coalitions: $P=0.0158$, $\alpha'=0.0167$; meat sharing: $P=0.0236$, $\alpha'=0.0250$; proximity: $P=0.0298$, $\alpha'=0.0500$). Rank showed strong, but nonsignificant relationships with associations and patrols (K_r tests: $P=0.03$, $\alpha'=0.0167$; Table 2). Results of resampling tests tended to support those derived from matrix correlations. Males that formed coalitions and shared meat more often than expected by chance were frequently members of the same rank class (coalitions: $P=0.0001$, $\alpha'=0.0083$; meat sharing: $P=0.001$; $\alpha'=0.01$; Fig. 3c).

The preceding results indicate that both age and rank have significant effects on male chimpanzee social behaviour. To remove their effects and thus discern any possible influence of maternal relatedness on male behaviour, we compared the social behaviour of related and unrelated dyads matched in age and rank. Results showed that maternal relatives neither associated, groomed, maintained proximity nor patrolled with each other more frequently than did unrelated individuals (Student's t tests: associations: $t_7=0.87$; grooming: $t_7=0.78$; proximity: $t_7=1.03$; patrols: $t_7=0.16$, NS for all four comparisons, $\alpha'=0.0125$; Fig. 4).

DISCUSSION

Results of the preceding analyses replicate earlier research showing that maternally related male chimpanzees do

not affiliate or cooperate more often than expected by chance (Goldberg & Wrangham 1997; Mitani et al. 2000). The observations reported here complement those presented before through the analysis of a larger sample of males. Our prior results were derived from a study of 23 adult males living in the Ngogo community (Mitani et al. 2000). Anecdotal observations of persistent associations between selected pairs of adolescent and adult males (e.g. OR-GR, MG-DX, ST-TA, BF-RI; Table 1, Fig. 1), led us to hypothesize that some of these represented cases of maternal brothers. From this it seemed logical to conclude that we would find a strong effect of maternal kinship on male social behaviour if we included adolescent males with the adults in a single analysis. Our results are not consistent with this expectation. Although it is likely that older brothers will sometimes be in position to help their younger half-siblings (Riss & Goodall 1977), it is now clear that such effects take on a secondary role, at least when examining the general patterns of social relationships among male chimpanzees on a community-wide basis at Ngogo.

If male chimpanzees do not consistently bias their affiliative and cooperative behaviour towards maternal kin, what factors do play a role? Here our findings extend prior research by revealing that age and rank exert important influences on structuring patterns of male chimpanzee social behaviour. Both of these variables have an especially important impact on behaviours that are likely to have major fitness consequences. Males preferentially formed coalitions, shared meat and patrolled territorial boundaries with members of the same age and rank classes.

Prior assumptions that male chimpanzees selectively affiliate and cooperate with close relatives have been based on kin selection theory (Hamilton 1963, 1964). Theory predicts that individuals will behave altruistically towards kin whenever $rB > C$, where r is the coefficient of relatedness between actor and recipient, B is the benefit of altruism to the recipient and C is the cost to the actor. Here relatedness, in the form of r , is a primary factor that affects who will do what with whom. In cases where r is high, the expectation is that individuals will behave altruistically towards others to increase their inclusive fitness.

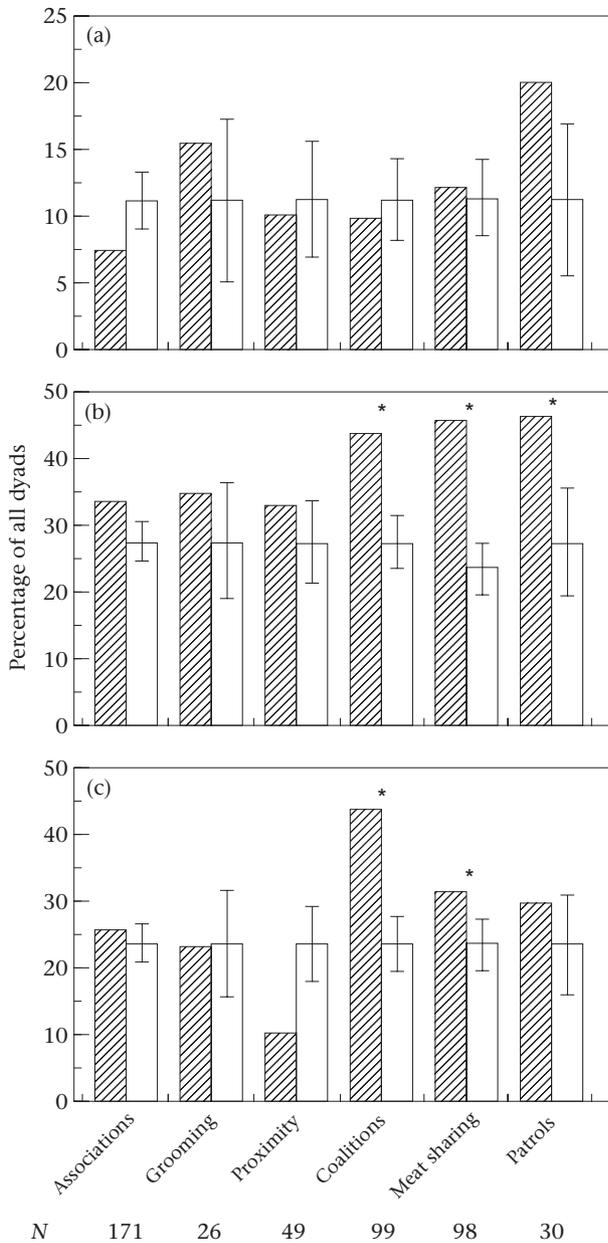


Figure 3. Effects of maternal kinship, age class membership and difference in rank on male social affinity. The number of male dyads (N) that engaged in each of six social behaviours more often than expected by chance were first computed in a social preference analysis. Displayed are the observed (▨) and expected (□) percentage of these dyads that: (a) shared mtDNA haplotypes; (b) were members of the same age class; and (c) belonged to the same rank class. Expected ± 1 SD values were calculated using a resampling technique. * $P < \text{sequential Bonferroni } \alpha'$.

Descriptions of alliances between presumed maternal brothers have led to the belief that male chimpanzees cooperate in part to gain indirect fitness benefits (Goodall 1986). Despite this long-standing assumption, our findings now indicate that demographic constraints may limit what is functionally possible (cf. Sherman 1981). While it may be in the reproductive interests of male chimpanzees to behave altruistically towards and cooper-

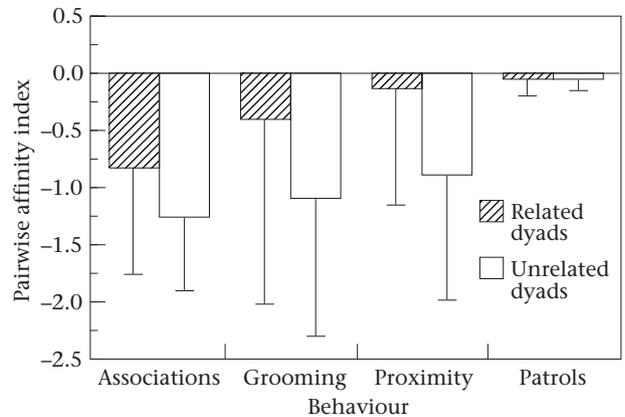


Figure 4. Comparison of the behaviour of related and unrelated male chimpanzee dyads matched in age and rank. The means and standard deviations of pairwise affinity indices between related and unrelated pairs are shown. $N=7$ matched dyads.

ate with close male kin, slow female reproduction may provide few opportunities for such interactions. An emerging body of theory and empirical research may also be germane to our results. Here theory suggests (Frank 1998; Taylor 1992; Wilson et al. 1992) and observations indicate (Dunn et al. 1995; Clutton-Brock et al. 1999, 2000; West et al. 2001) that limited dispersal may combine with high levels of local competition to offset potential inclusive fitness benefits. These findings may be especially relevant to chimpanzees, a species that displays male philopatry along with extremely high levels of within-group male-male competition (Bygott 1979; Pusey 1979; Nishida 1983; Goodall 1986; Nishida & Kawanaka 1972; Muller 2002).

We realize that some of the suggestions made here are not entirely new. For example, primatologists have long recognized the importance of demographic constraints on behaviour. Altmann & Altmann (1979) were the first to describe how demographic variables can affect, and in turn, be affected by behaviour, and studies of Old World monkeys have provided some possible empirical examples of how alliance formation might be influenced by group structure and demographic processes (Dunbar 1984; Datta 1989). Research on New World monkeys furnish other illustrations of demographic effects on primate social relationships (Pope 2000; Strier 2000). The data presented here can now be added to the growing body of evidence regarding demographic constraints on primate behaviour.

Our results also highlight the tactical decisions male chimpanzees make to develop and maintain alliances. Considerable evidence from the wild shows that male chimpanzees use grooming, meat sharing and decisions about associations with conspecifics as tactics to form and maintain alliances (e.g. Nishida et al. 1992; Nishida & Hosaka 1996; Newton-Fisher 1999; Mitani & Watts 2001). Given that the value of potential partners varies, that kin may be unavailable or unsuitable as allies and that unrelated individuals make tactical decisions to cooperate in other primates (e.g. bonobos, *Pan paniscus*: Hohmann et al. 1999; baboons: Noë 1992; red howler monkeys,

Alouatta seniculus: Pope 2000) and nonprimates (e.g. dolphins: Connor et al. 2000; lions: Packer et al. 1991), the absence of consistent maternal kinship effects on male chimpanzee social behaviour is not entirely unexpected.

We conclude by noting that kinship might still have important effects on male social relationships if there is high reproductive skew and male chimpanzees selectively cooperate with agemates, who are paternal siblings (Altmann 1979). Although current evidence indicates that Old World monkeys are unable to discriminate paternal relatives (Fredrikson & Sackett 1984; Erhart et al. 1997), a recent study suggests that chimpanzees may be able to identify kin relationships between others on the basis of facial features alone (Parr & deWaal 1999). This raises the intriguing possibility that male chimpanzees might be able to recognize their paternal relatives. We are unable to assess this possibility given our current lack of information regarding nuclear and Y chromosome markers. Obtaining these data remains a high priority for future study.

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