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Male affiliation, cooperation and kinship in wild chimpanzees

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Long-term field research has revealed that male chimpanzees, *Pan troglodytes*, affiliate and cooperate in several contexts. Assuming close genetic relationship among males, affiliative and cooperative behaviour have been hypothesized to evolve through the indirect effects of kin selection. We tested the hypothesis that matrilineal genetic relatedness affects patterns of male social affiliation and cooperation in an unusually large community of chimpanzees at the Ngogo study site, Kibale National Park, Uganda. Field observations indicated that six behavioural measures of affiliation and cooperation among 23 adult males were significantly correlated with each other. Sequences of the first hypervariable portion of the mtDNA genome revealed that three pairs of males and one quintet shared mtDNA haplotypes. Matrix permutation tests using behavioural and genetic data showed that males that affiliated and cooperated with each other were not closely related through the maternal line. These findings add to a growing body of empirical evidence that suggest kinship plays an ancillary role in structuring patterns of wild chimpanzee behaviour within social groups.

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Field studies reveal the important role kinship plays in the evolution of animal behaviour (e.g. Sherman 1977; Emlen & Wrege 1988; Creel et al. 1991; Packer et al. 1991). Kinship is often used to explain patterns of affiliation and cooperation among a wide variety of animals, including insects, anurans, birds and mammals (Trivers & Hare 1976; Blaustein & Waldman 1992; Pusey & Packer 1994; Parker et al. 1995). Hamilton's (1963) inclusive fitness and kin selection theory (Maynard Smith 1964) provide a strong and compelling evolutionary framework to explain why relatives affiliate and cooperate.

Chimpanzees, *Pan troglodytes*, are often cited as a prime example of the pervasive influence kinship has on primate social behaviour (e.g. Goodall 1986). Chimpanzees live in communities (Nishida 1968) whose members associate in temporary parties that vary in size and composition (Halperin 1979; Wrangham et al. 1992; Boesch 1996). Given female-biased natal dispersal (Nishida & Kawanaka 1972; Pusey 1979), male chimpanzees are likely to be more closely related to other males in their community than females are to each other (Morin et al. 1994; but see Gagneux et al. 1999). One hypothesized consequence of the close genetic relationship between male chimpanzees is the formation of strong social bonds. These bonds are reflected through high levels of affiliation and cooperation. Like other primates (Walters & Seyfarth 1987), chimpanzees affiliate by associating,

grooming and maintaining proximity to each other (e.g. Nishida 1968; Simpson 1973; Wrangham & Smuts 1980). Cooperation, both in chimpanzees and other primates, manifests itself through alliances during which two or more individuals direct aggression jointly towards others (Riss & Goodall 1977; Nishida 1983; Walters & Seyfarth 1987; van Hooff & van Schaik 1994). Chimpanzees engage in two additional and unusual forms of cooperative behaviour. Chimpanzees hunt mammalian prey (review in Stanford 1998) and meat is frequently shared between individuals (Boesch & Boesch 1989; Nishida et al. 1992; Stanford 1998; Mitani & Watts 1999). In addition, males occasionally participate in cooperative, territorial boundary patrols, whose outcomes can result in lethal conflict (Goodall et al. 1979). Patterns of male affiliation and cooperation in chimpanzees are generally thought to evolve through the indirect effects of kin selection (e.g. Morin et al. 1994).

Recent behavioural and genetic studies of chimpanzees and their congeners, bonobos, *P. paniscus*, have begun to cast doubt on whether genetic relatedness is a necessary prerequisite for the formation of close social bonds. For example, maternal relatedness does not predict the development of affiliative bonds among female bonobos (Hashimoto et al. 1996). Similarly, male chimpanzees that maintain proximity and groom each other frequently are not necessarily related maternally (Goldberg & Wrangham 1997). Finally, recent genetic analyses indicate that males are no more closely related to other males than females are to each other in one community of West

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African chimpanzees (Gagneux et al. 1999). Although these studies show that a high degree of genetic relatedness is not required for the formation of affiliative ties between wild chimpanzees living within social groups, the extent to which cooperative acts, such as alliances, meat sharing and boundary patrols, depend on kinship has not been investigated specifically. The paucity of empirical data linking kinship to cooperation is a major gap in understanding because the latter has major fitness consequences for male chimpanzees (Riss & Goodall 1977; Goodall et al. 1979; Nishida 1983; Nishida et al. 1992; Watts 1998).

In this paper we examine the relationships among genetic relatedness, social affiliation and cooperation between male chimpanzees living in an extremely large community at the Ngogo study site in the Kibale National Park, Uganda. We took advantage of unique demographic and social features displayed by the Ngogo chimpanzees and we extended prior research by explicitly asking whether maternal relatives display a preference for cooperating with each other. Our results add to a growing body of evidence that suggests kinship plays an auxillary role in structuring social interactions and relationships between wild chimpanzees.

METHODS

Study Site and Subjects

We observed adult male chimpanzees at the Ngogo study area in the Kibale National Park, Uganda, which lies between lowland and montane rain forest and has been a site of primate field research since 1974 (Struhsaker 1997). The Ngogo chimpanzee community moves over a home range of approximately 25 km^2. Ghiglieri (1984), Butynski (1990) and Struhsaker (1997) provide more detailed descriptions of the study site.

The Ngogo chimpanzees have been observed previously by Ghiglieri (1984), who conducted field work during 18 months between 1976 and 1978 and an additional 5 months in 1981. Subsequent observations of chimpanzees were made by Wrangham et al. (1992) between 1988 and 1995, B. Grieser-Johns and field assistants between 1992 and 1993, and D. Watts from June to August 1993. Along with D. Watts, we have maintained continuous observations of the Ngogo chimpanzees since 1995 (Watts 1998; Mitani et al. 1999; Mitani & Watts 1999; Pepper et al. 1999).

Chimpanzees at Ngogo have never been provisioned, and the group is exceptionally large compared with other communities. As of August 1999, we have identified 148 individuals, including 26 adult males, 47 adult females, a single noncycling adult female, 15 adolescent males, 9 adolescent females and 50 dependent young. The results presented here derive from 870 h of observations by J.C.M. during two observation periods: June–August 1997 and January–June 1998. Our analyses include observations of 23 of the 26 individually identifiable adult males that were present during both 1997 and 1998. Each male was observed a minimum of 30 h ($\bar{X} \pm SD = 38 \pm 6$, range 30–51 h).

Behavioural Observations

By virtue of prior field work, the Ngogo chimpanzees were habituated to human presence at the start of our observations in 1997. During both observation periods, all 23 male subjects tolerated our presence to within a few metres. We observed social behaviour during hour long sessions of target males. During each session, we used scan samples at 10 min intervals to record the target's behaviour, including grooming and proximity to other chimpanzees.

We assessed male affiliation through associations, proximity and grooming. We scored associations between male subjects during observations of target individuals. Two males were defined to be in association whenever they came within visual range of each other. We scored proximity between two males during scan samples to be whenever the male came within 5 m of the target. Grooming was recorded whenever two males were observed performing this behaviour during scan samples. We examined behavioural records from 51 h of observation of one adult male (bt, Fig. 1) to determine the minimum sample interval that could be treated as statistically independent (Altmann 1974). Samples of behaviour separated by 10 and 20 min were interdependent (χ^2 test: $P<0.05$ for both tests), but those recorded every 30 min were independent (χ^2 test: NS). We accordingly employed behavioural observations of associations, grooming and proximity made at 30 min intervals in the following analyses.

Male cooperation was evaluated through ad libitum observations of participation in alliances, meat sharing and boundary patrols. Alliances ($N=55$) between two males were defined to occur whenever they directed aggression together towards a third individual (e.g. Nishida 1983; de Waal 1984; Mitani & Nishida 1993). Meat sharing ($N=113$) was recorded during hunting episodes of mammalian prey (Mitani & Watts 1999). We scored sharing whenever meat was exchanged between two males. Sharing included apparent cooperative exchange and did not involve the theft of meat by one individual from another. We also recorded adult male participation in a small number of boundary patrols ($N=16$). Patrols were characterized by an unique suite of behaviours similar to those displayed by chimpanzees at other sites (Goodall et al. 1979). During patrols the Ngogo chimpanzees became unusually silent as they approached the periphery of their range. Upon reaching territorial boundaries, they began to move together in single file, while often stopping, scanning and changing directions several times without calling. Chimpanzees were extremely attentive to any arboreal or terrestrial movements and would stop and actively search the area whenever motion was detected. Single-file movements and the silent nature of boundary patrols are two of the most salient features of boundary patrols and these behaviours differ markedly from the behaviour displayed by chimpanzees most other times. Chimpanzees are highly vocal and use loud calls to coordinate movements between individuals, which are typically widely separated (Mitani & Nishida 1993).

Genetic Analyses

Shed hair samples were gathered in the field (by J.C.M.) between February and June 1998 under CITES import (U.S.A. No. US830142) and export (Uganda No. 103) permits. All samples were collected noninvasively from subjects on the ground following self-grooming episodes. Care was taken to ensure that we collected samples from isolated individuals that had scratched and shed hair several metres from other chimpanzees. Following collection, all samples were stored dry at ambient temperature in the field and frozen at $-20°C$ after transport to the laboratory.

We assessed matrilineal genetic relatedness between male chimpanzees by sequencing the first hypervariable segment of the mitochondrial control region or D-loop (Kocher & Wilson 1991). The haploid nature and maternal inheritance of mtDNA combine with its lack of recombination and high mutation rate to make it an ideal choice for studies of within-species genetic variation (Harrison 1989). Our use of mtDNA is especially appropriate given that there is a high probability chimpanzees are able to discriminate individuals on the basis of matrilineal relatedness. Chimpanzee mothers and their offspring display enduring social bonds (Goodall 1968, 1986), thus making it likely that maternal siblings are able to recognize each other (cf. Parr & de Waal 1999). In contrast, internal fertilization coupled with a promiscuous mating system (Tutin 1979; Gagneux et al. 1999) render it doubtful that male chimpanzees possess an ability to distinguish paternal relatives.

We extracted mtDNA from single hair follicles using a Chelex extraction protocol. Following extraction, polymerase chain reaction (PCR) amplification (Saiki et al. 1988) was carried out using Amplitaq Gold at the manufacturer's recommended conditions. We amplified samples in 50 µl PCR reactions using primers covering a 349 bp segment corresponding to Anderson reference sequence coordinates 16026–16375 (Anderson et al. 1981). 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′), respectively. Primers were removed using Microcon 100 000 MW cut-off filters, and 100 ng of product were used as template for a dye-labelled dideoxy terminator cycle sequencing reaction using ABI's FS Dye Terminator Kit. After vacuum-concentrating the samples dry, they were rehydrated in formamide/EDTA/Dextran Blue loading buffer and electrophoresed through a Long Ranger Singel on an ABI 377XL automated sequencer. Sequences were aligned and corrected using ABI's Sequence Navigator program. We sequenced all samples in both the forward and reverse direction using the external or internal nested primers.

Statistical Analyses

To quantify affiliation among males, we used the occurrences of association, grooming and proximity during scan samples to compute simple ratio indices (Cairns & Schwager 1987). We assessed cooperation by employing ad libitum observations of the number of times two males participated together in alliances, meat sharing and boundary patrols. These procedures generated a 23×23 matrix of pairwise affiliation and cooperation values for each of the six behaviours. Two analogous matrices of matrilineal genetic relatedness between males were assembled with the mtDNA sequence data. One genetic matrix reflected haplotype identity or nonidentity and contained cells with values of ones or zeros, respectively. We constructed a second matrix by applying Kimura's (1980) two-parameter model to estimate mtDNA genetic distances between the 23 subjects. For these calculations, we employed a transversion to transition ratio of 10:1.

We computed neighbour-joining trees (Saitou & Nei 1987) to display graphically levels of affiliation and cooperation between adult males. The neighbour-joining algorithm employs distance measures between individuals to produce trees or dendrograms that provide a visual representation of the relationships between them. Neighbour joining is conceptually similar to cluster analytical techniques that have been widely adopted in ethological studies (e.g. Morgan et al. 1976; Goldberg & Wrangham 1997). Cluster analysis dendrograms primarily display the topological relationships between individuals and are thus generally less informative than neighbour-joining trees insofar as the latter provide data regarding both the topology and distances separating individuals. For our purposes, individuals that affiliate and cooperate closely will be linked together at shared nodes and isolated by relatively short distances on neighbour-joining trees. In contrast, individuals that affiliate and cooperate infrequently will be separated widely in absolute distance and will not share common nodes. Unlike cluster analysis, neighbour joining permits unequal branch lengths between subjects. In our behavioural dendrograms, unequal branch lengths that link two individuals reflect different amounts of change that have occurred between them relative to all other nodes on the tree. Because the neighbour-joining algorithm operates on distance metrics, we converted measures of affiliation and cooperation by dividing each pairwise value by the largest score in the matrix and subtracting these from 1. All behavioural trees were thus standardized to unit length with the highest and lowest levels of affiliation and cooperation assigned distances of zero and one, respectively. We constructed one additional neighbour-joining tree to illustrate levels of mtDNA genetic relatedness between our male subjects. Here we calculated trees based on the Kimura two-parameter model estimates of mtDNA distances between individuals. In this genetic tree, males that share mtDNA haplotypes are connected at zero branch lengths. Other closely related males share common nodes and distantly related individuals are linked together at further distances.

We assessed the degree of congruence between our behavioural measures of affiliation and cooperation by using Hemelrijk's (1990) K_r test. The K_r test is a matrix permutation procedure and variant of the Mantel (1967) test for matrix correlation. We employed the K_r test rather than the Mantel procedure because the former takes

interindividual variation in behaviour into account. We used the K_r test additionally to compare observed levels of affiliation and genetic relatedness. Here our tests involved six comparisons, utilizing three matrices of male affiliation and two matrices of genetic relatedness, and we therefore adjusted the statistical criterion of significance to 0.008 using a Bonferroni correction (Sokal & Rohlf 1995). We also compared matrices of male participation in alliances, meat sharing and patrols against the two matrices of male relatedness with the K_r test. Given a family of six tests, we set alpha levels here to 0.008. Two-tailed P values of all K_r tests were based on 10 000 iterations of the data. Although not used for analytical purposes, Pearson correlation coefficients are provided to illustrate the associations between behavioural measures as well as those between behavioural measures and mtDNA genetic distances.

RESULTS

Figure 1 shows neighbour-joining trees of association, grooming and proximity and illustrates the level of affiliation between the 23 male subjects. Additional neighbour-joining trees were constructed to display levels of male cooperation as assayed by participation in alliances, meat sharing and patrols (Fig. 2). Six pairs of males, mw–ru, el–hr, lo–ty, ay–mi, mo–pi and di–or, showed high degrees of affiliation and cooperation; each of these pairs showed strong relationships in two or more measures of social behaviour.

Matrix permutation tests indicated that measures of affiliation and measures of cooperation were consistent. All three measures of affiliation showed strong correlations with each other (Table 1; K_r tests: $P \leq 0.004$ for all three comparisons). Similarly, the three measures of cooperation displayed strong and significant associations (Table 1; K_r tests: $P \leq 0.01$ for all three comparisons). Each measure of affiliation was also correlated with each measure of cooperation (Table 1; K_r tests: $P \leq 0.03$ for all nine tests). These results suggest that our six measures of social behaviour effectively assay a single, general aspect that reflects affiliation and cooperation among male chimpanzees.

Figures 1 and 2 also show the genetic relatedness between males based on mtDNA haplotype identity. Three pairs of males (ay–mz, co–hr, ru–ty) and one quintet (el, ho, mo, or, st), shared mtDNA haplotypes. Examination of our behavioural measures in light of these genetic data indicated that pairs that affiliated and cooperated often were not related matrilineally. Identical mtDNA haplotypes were not shared by individuals in any of the six dyads that showed high levels of behavioural interaction (see above). Moreover, there were no significant associations between any measure of male affiliation and cooperation and mtDNA haplotype identity (K_r tests: two-tailed $P \geq 0.45$ for all six comparisons; Figs 1, 2, Table 1). Similarly, male affiliation and cooperation were not correlated with levels of male relatedness as assayed by genetic distances based on mtDNA sequences (Fig. 3, Table 1; K_r tests: two-tailed $P \geq 0.20$ for all six comparisons).

DISCUSSION

The preceding analyses indicate that matrilineally related adult male chimpanzees living within the same social group do not affiliate with each other closely. At Ngogo, high levels of affiliation, as measured through associations, grooming and proximity, were not predicted by mtDNA haplotype sharing. Our results are consistent with Goldberg & Wrangham's (1997) research on the neighbouring Kanyawara chimpanzee community at Kibale. In their study, mtDNA haploytpe sharing was not related to levels of affiliation reflected by grooming and nearest-neighbour distances. High levels of associations were positively correlated with mtDNA genetic relatedness, although a composite measure of social affiliation based on associations, grooming and nearest-neighbour distances showed no correlation with the degree of male genetic relatedness. From these results, Goldberg & Wrangham (1997) concluded that kinship exerted little influence on patterns of male chimpanzee social behaviour. Taken together with our observations, an emerging consensus based on currently available empirical evidence suggests that male chimpanzee affiliation within social groups is largely unaffected by matrilineal kinship.

The data presented here go further by indicating that kinship does not underlie patterns of male cooperation. There were no significant relationships between mtDNA genetic relatedness and levels of cooperation, as assayed by participation in alliances, meat sharing and patrols. Cooperation is of greater evolutionary significance than affiliation alone because only the former is likely to have important fitness consequences among chimpanzees (Goodall et al. 1979; Nishida 1983; Nishida et al. 1992; Nishida & Hosaka 1996). In addition to alliances, meat sharing and patrols, male chimpanzees at Ngogo engage in another form of cooperation with direct fitness consequences. When large groups of adult males aggregate and make it difficult for a single male to mate-guard an oestrous female successfully, duos or trios of males cooperate in communal mate-guarding episodes (Watts 1998). Participants in these coalitions are generally of high rank, however, and the genetic data presented here indicate that previously observed coalition partners do not share mtDNA haplotypes.

The results of our analyses are unexpected given the putative importance ascribed to kinship in chimpanzee society. Based on her long-term observations at the Gombe National Park, Goodall (1968, 1986) has consistently emphasized the enduring maternal bonds that form between chimpanzee mothers and their offspring. Equally important are the long-lasting relationships that are thought to exist between maternal siblings. Morin et al. (1994) recently suggested that indirect fitness benefits have been largely responsible for the evolution of several aspects of male chimpanzee social behaviour. Few empirical data exist, however, to support this proposition. For example, maternally related brothers have been hypothesized to cooperate in order to acquire and maintain high male rank (Riss & Goodall 1977). Most previous behavioural studies have nevertheless failed to ascertain with certainty the genetic relationships between cooperating
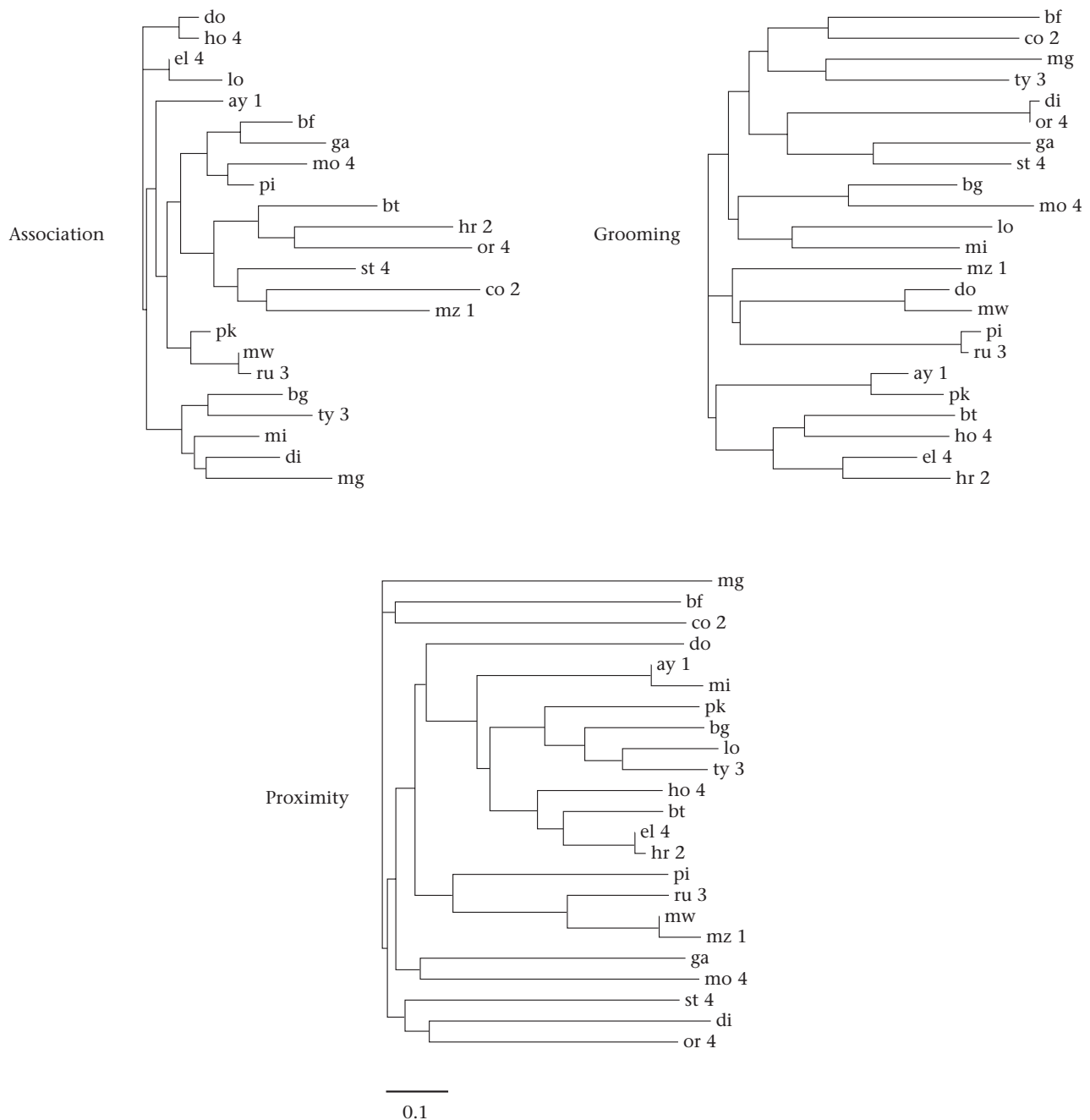
Figure 1. Neighbour-joining trees of affiliation between adult male chimpanzees. Three measures of affiliation are shown, with trees standarized to unit length for comparison. Males that share mtDNA haplotypes are indicated by shared numbers, while unmarked males possess unique haplotypes. Trees were generated using 863, 334 and 573 observations of associations, grooming and proximity, respectively. The ranges for the number of times individuals were paired in each tree were: 0–201 (associations), 0–26 (grooming) and 0–36 (proximity).

male pairs, thus making it impossible to test the predicted effect of kinship on patterns of male social behaviour.

Although our results do not implicate indirect fitness effects as an important force in the evolutionary maintenance of male chimpanzee social behaviour within groups, several caveats are necessary. First, the failure to uncover strong relationships between male kinship and levels of affiliation and cooperation are consistent with our recent observations that, after controlling for the relatively high levels of gregariousness among adult

males, they do not on average show a preference for associating with adult males over members of other age and sex classes (Pepper et al. 1999). In contrast, adult males and adolescent males associate with each other above levels predicted by chance (Pepper et al. 1999). Given its extremely large size, the Ngogo community is likely to contain pairs of closely related males, and whether kinship forms the basis of the observed patterns of affiliation between adult and adolescent males awaits further study. Second, the nature of the mtDNA data
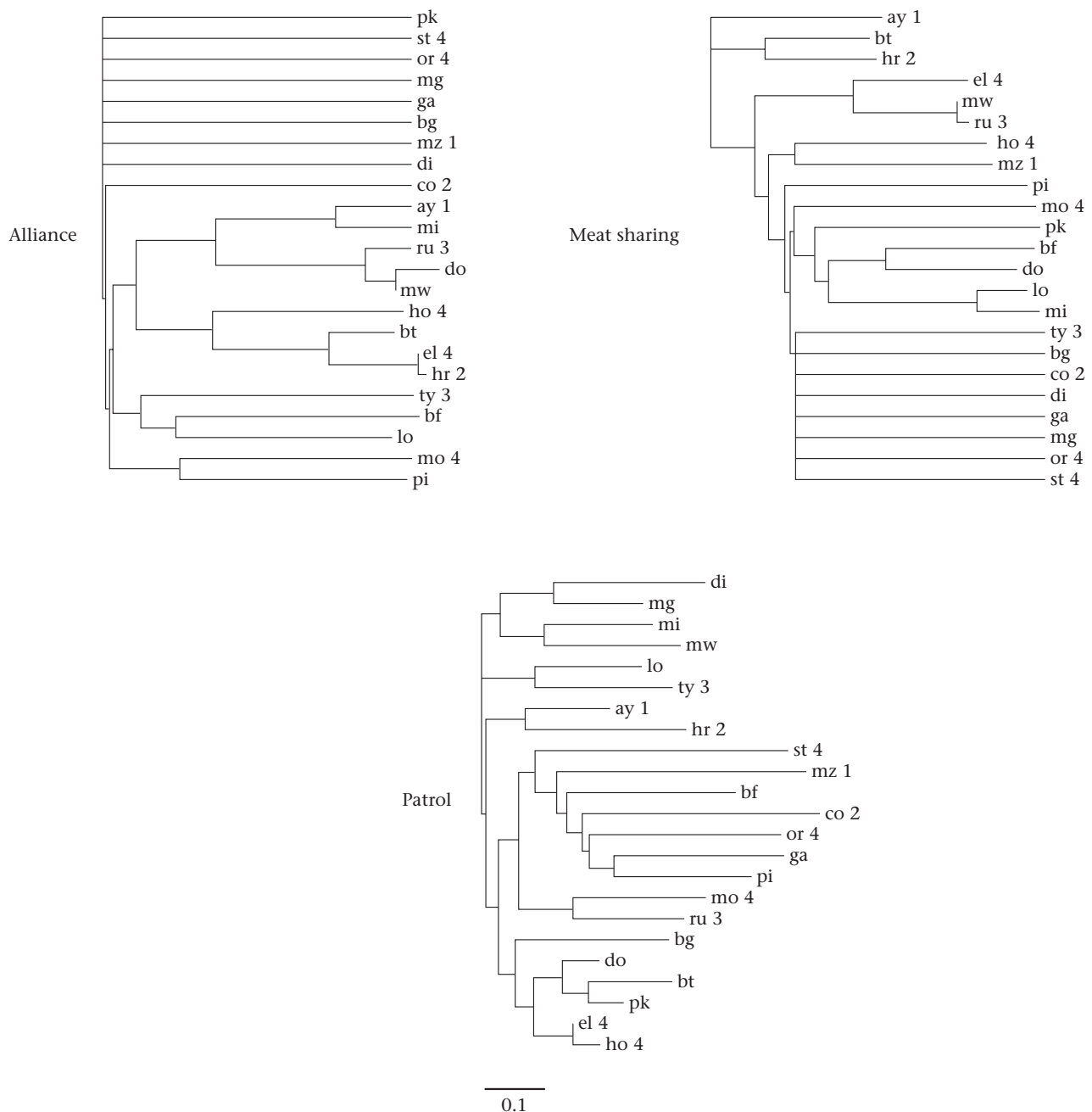
Figure 2. Neighbour-joining trees of cooperation between adult male chimpanzees. Three measures of cooperation are shown, with trees standarized to unit length for comparison. Males that share mtDNA haplotypes are indicated by shared numbers, while unmarked males possess unique haplotypes. Trees were generated using 55, 113 and 16 observations of alliances, meat sharing and patrols, respectively. The ranges for the number of times individuals were paired in each tree were: 0–4 (alliances), 0–9 (meat sharing) and 0–9 (patrols).

allows us to ascertain only matrilineal genetic relationships among males. It is still possible that individuals that share haplotypes at Ngogo are more distantly related matrilineally, for example at the level of cousins, and that none of the adult males in our sample are maternal brothers. While recent research suggests that chimpanzees may use visual cues alone to recognize kin relationships between mothers and sons (Parr & de Waal 1999), it is doubtful that this ability extends to more distantly related individuals. These limitations under-

score the need for further genetic characterization of the Ngogo chimpanzee community. Additional assays that utilize nuclear STR loci will be required to provide more precise estimates of male genetic relatedness (e.g. Ely et al. 1998; Gagneux et al. 1999). Whether such estimates will reveal that genetically related males affiliate and cooperate closely remains an important area for future research.

Although the data presented here cannot be used to define the genetic relationships between males completely, limitations apply to our observations of social

Table 1. Correlations between genetic relatedness and behavioural measures of affiliation and cooperation

	Association	Grooming	Proximity	Alliance	Meat sharing	Patrol	Genetic distance	mtDNA haplotype
Association	—	0.0004	0.0002	0.0054	0.002	0.0002	0.5432	0.4804
Grooming	0.21	—	0.0002	0.023	0.0332	0.0006	0.2730	0.9378
Proximity	0.37	0.55	—	0.0004	0.002	0.0002	0.2270	0.9266
Alliance	0.23	0.29	0.46	—	0.0004	0.0198	0.9228	0.6104
Meat sharing	0.28	0.20	0.44	0.53	—	0.198	0.9916	0.7138
Patrols	0.62	0.23	0.42	0.17	0.21	—	0.8822	0.7004
Genetic distance	0.02	−0.11	−0.16	−0.09	−0.03	−0.01	—	—

Pearson correlation coefficients between measures are shown in the bottom half of the matrix, while associated two-tailed P values based on the K_r test are displayed in the top half of the matrix. The 'genetic distance' row and column refer to estimates of mtDNA genetic distances between males. The last column indicates whether males shared identical mtDNA haplotypes. Correlation coefficients are not presented for these mtDNA haplotype sharing data given the dichotomous nature of the dependent variable. Analyses are based on $N=253$ pairs of individuals. P values from K_r tests are derived from 10 000 iterations.

behaviour as well. For instance, all of our behavioural observations were made over a relatively short time. Chimpanzee social relationships are well known to vary temporally (Nishida 1983; Goodall 1986), and given a dynamically changing situation, it is unclear whether observations of affiliation and cooperation gathered over longer periods will appreciably affect our results. Finally, it is important to note that our results pertain to aspects
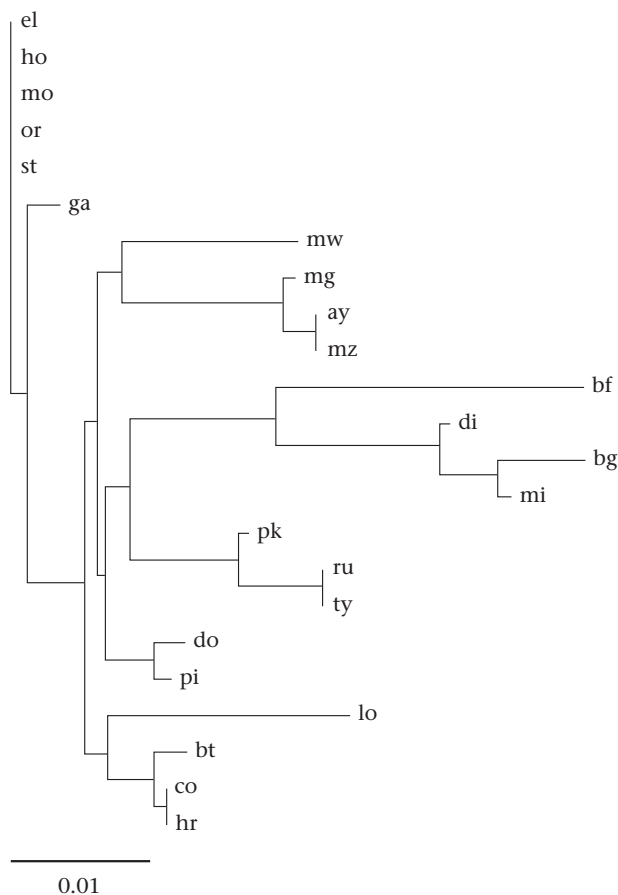

Figure 3. Neighbour-joining tree of mtDNA genetic distances between adult male chimpanzees. The tree is based on mtDNA sequence data. Zero branch lengths indicate sequence identity.

of male chimpanzee behaviour that occur within social groups. Thus far, current evidence suggests that genetic relatedness does not structure these within-community, 'second-order' relationships, but this should not obscure the fact that kinship is likely to affect 'first-order' relationships that exist between males living in different communities (cf. Goldberg & Wrangham 1997). If chimpanzee males from the same social group are more closely related to each other than they are to those from other communities, then kin selection is still apt to explain why males from the same social group cooperate to compete against members from different groups (Nishida et al. 1985; Goodall 1986).

In summary, our results suggest that male chimpanzees do not always choose important social partners on the basis of genetic ties. Two critical questions remain unanswered. First, why do male chimpanzees not bias their behaviour toward matrilineally related kin? Second, what factors account for male affiliation and cooperation in lieu of the indirect effects of kin selection? Future research on these questions will require thorough consideration of the relative costs and benefits of recognition errors as well as alternative mechanisms for the evolution of cooperation (Dugatkin 1997; Keller 1997).

Acknowledgments

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