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Demographic and social constraints on male chimpanzee behaviour

JOHN C. MITANI,*DAVID P. WATTS,† JOHN W. PEPPER‡, & D. ANDREW

MERRIWETHER*

*Department of Anthropology, University of Michigan, Ann Arbor

†Department of Anthropology, Yale University

‡Santa Fe Institute

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Correspondence: John Mitani, Department of Anthropology, University of Michigan, Ann Arbor, MI 48109 - 1382 (email: mitani@umich.edu). D. Watts is at the Department of Anthropology, Yale University, New Haven, CT 06520-8277. J. Pepper is at the Santa Fe Institute, 1399 Hyde Park Road, Santa Fe, NM 87501. D. A. Merriwether is at the Department of Anthropology, University of Michigan, Ann Arbor, MI 48109 – 1382.

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

16

16 Kinship exerts a pervasive influence on the lives of social animals (Alcock 2001). The effects of
17 kinship have been especially well-documented among our closest living relatives, the nonhuman
18 primates. Here strong social bonds develop among matrilineally related Old World monkey
19 females, and close genetic relatives are frequently observed to affiliate and cooperate (review in
20 Silk 2001). These empirical observations are easily accommodated and explained by Hamilton's
21 (1963, 1964) concept of inclusive fitness.

22

23 Chimpanzees, *Pan troglodytes*, are often used to illustrate how kinship affects primate social
24 behaviour. Chimpanzees live in communities or unit-groups, whose members form temporary
25 parties that vary in size and composition (Nishida 1968; Goodall 1986; Boesch & Boesch-
26 Achermann 2000). Membership in these communities is open due to dispersal (Nishida &
27 Kawanaka 1972; Pusey 1979). Female chimpanzees usually leave their natal groups after
28 reaching sexual maturity. Males, in contrast, do not disperse. As a result of these dispersal
29 patterns, males within groups are typically more closely related to each other than they are to
30 males from other groups (Morin et al. 1994; Vigilant et al. 2001). Male chimpanzees cooperate to
31 compete with conspecifics both within and between communities (Goodall et al. 1979; Nishida
32 1983; Nishida et al. 1985; Morin et al. 1994; Nishida & Hosaka 1996; Watts & Mitani 2001). It
33 is generally agreed that kin selection favours males who cooperate together in between group
34 competition (Morin et al. 1994; Goldberg & Wrangham 1997). Whether a similar selective
35 mechanism shapes cooperative relationships that form for purposes of within group competition,
36 however, is currently unclear.

37

38 Male chimpanzees develop strong social bonds with others in their community. These bonds
39 are manifest in several contexts, including association, grooming, proximity, coalitions, meat-
40 sharing, and territorial behaviour (Nishida 1968, 1983; Simpson 1973; Riss & Goodall 1977;
41 Goodall et al. 1979; Wrangham & Smuts 1980; Nishida et al. 1992; Nishida & Hosaka 1996;
42 Watts 1998, 2000; Newton-Fisher 1999; Wrangham 1999; Boesch & Boesch-Achermann 2000;
43 Mitani & Watts 2001; Watts & Mitani 2001). Recent field studies have called into question the
44 long-standing assumption that genetic relatedness affects the formation and maintenance of
45 social bonds among male chimpanzees that live in the same community. For example, two
46 independent studies now suggest that patterns of social affiliation and cooperation among males
47 are not predicted by maternal relatedness as assayed by mtDNA haplotype sharing and genetic
48 distances (Goldberg & Wrangham 1997; Mitani et al. 2000). These studies raise two important
49 and inter-related questions. First, why don't male chimpanzees bias their behaviour toward
50 maternal kin? Second, what factors account for the observed patterns of affiliation and
51 cooperation among wild male chimpanzees?

52

53 Chimpanzee demography and life history have received scant attention with regard to these
54 two questions, yet potentially provide answers to both. Chimpanzees are an extremely long-lived
55 and slowly reproducing species, with females in the wild giving birth to a single offspring only
56 once every 5 - 6 years (Nishida et al. 1990; Wallis 1997; Boesch & Boesch-Achermann 2000).
57 With an equal sex ratio at birth and high infant and juvenile mortality (ibid.), the probability is
58 relatively low that a female will give birth successively to sons that reach adulthood together.
59 Males attain their physical and social prime as adults. At this time, they are most likely to engage
60 in a variety of social behaviours, such as coalitions, meat-sharing, and territorial defense, whose

61 outcomes have major consequences (Riss & Goodall 1977; Goodall et al. 1979; Nishida 1983;
62 Nishida & Hosaka 1996; Watts 1998; Mitani & Watts 2001). Adolescent males, which are still
63 growing and attempting to integrate themselves into the social worlds of adults, are seldom in a
64 good position to aid their older adult brothers that are striving to improve their reproduction and
65 status. These observations suggest that male chimpanzees only rarely live with maternal kin that
66 can aid them. If kin are not generally available, then males are likely to solicit and use others
67 opportunistically (e.g. deWaal 1982; Nishida 1983; Nishida et al. 1992; Nishida and Hosaka
68 1996). Individuals in the same age cohort may represent particularly attractive social partners
69 because they grow up together, are generally familiar with each other, and share similar social
70 interests and power throughout their lives (cf. van Hooff & van Schaik 1994; Goldberg &
71 Wrangham 1997). For similar reasons, males close in dominance rank may also be inclined to
72 form strong affiliative and cooperative relationships (cf. deWaal & Luttrell 1986; deWaal 1991;
73 Watts 2000). Males who belong to the same rank class are apt to establish effective bonds insofar
74 as they share similar needs, access to resources and ability to exchange social benefits.

75

76 The preceding considerations suggest that age and rank, rather than maternal kinship, will be
77 good predictors of patterns of wild male chimpanzee social behaviour. In this paper, we test these
78 hypotheses by examining the relationships between age and rank and affiliative and cooperative
79 behaviour among males living in an extremely large chimpanzee community at Ngogo, Kibale
80 National Park, Uganda. We extend results of prior analyses by also investigating the association
81 between maternal genetic relatedness and social behaviour in a larger sample of males that
82 includes both adults and adolescents. Our results are consistent with those that we have reported

83 previously (Mitani et al. 2000), and add to our understanding by clarifying some of the
84 demographic and social constraints on male chimpanzee social behaviour.

85

86

METHODS

87

88 **Study Site and Animals**

89

90 We observed chimpanzees at the Ngogo study site in Kibale National Park, Uganda. Mitani
91 and Watts collected behavioural observations during 22 months between January 1998 – August
92 2000. Ngogo lies at an interface between lowland and montane rain forest and is covered
93 primarily with moist, evergreen forest. Ghiglieri (1984) Butynski (1990) and Struhsaker (1997)
94 provide detailed descriptions of the Ngogo study area.

95

96 The Ngogo chimpanzee community is the largest thus far described in the wild.
97 Approximately 150 individuals live within the Ngogo community, including 23 – 24 adult males,
98 15 adolescent males, and > 45 adult females during the period considered here. We have
99 maintained continuous observations of the chimpanzees at Ngogo since 1995, and as a result,
100 subjects were well-habituated to our presence.

101

102 **Behavioural Observations**

103

104 We made observations of social behaviour during hour-long samples of target males. During
105 each observation period, scan samples were made at 10 minute intervals to record the target's

106 behaviour, including grooming and proximity to other chimpanzees. We scored associations
107 between male subjects during observations of target individuals, with two males defined to be in
108 association whenever they came within visual range of each other as assessed by human
109 observers. We scored proximity during scan samples, defining other individuals to be in
110 proximity to targets whenever they came within 5 metres. Grooming was recorded whenever two
111 males were observed performing this behaviour during scan samples. Because prior analyses
112 indicated that observations recorded every 30 minutes were statistically independent (Mitani et
113 al. 2000), we employed this interval for behavioural observations of associations, grooming, and
114 proximity. Analyses of social behaviour were based on 1415 hours of observations, with each of
115 the 38 males present throughout the study followed a minimum of 30 hours ($X \text{ bar} \pm SD = 37 \pm$
116 3 , range 30 – 51).

117

118 We scored male participation in coalitions, meat-sharing, and boundary patrols *ad libitum*.
119 Coalitions ($N = 709$) between two males were defined to occur whenever they directed
120 aggression together toward others (e.g. Nishida 1983; deWaal 1984; Mitani et al. 2000) Meat-
121 sharing ($N = 397$) was recorded during hunting episodes of mammalian prey (Mitani & Watts
122 1999, 2001; Watts & Mitani in press a, b). Males frequently exchange meat with the same
123 individual several times at the same hunt. To preserve statistical independence, we recorded
124 sharing between two males only once during the same hunt irrespective of the number of times
125 meat was transferred. We also recorded adult male participation in boundary patrols ($N = 56$).
126 Patrols were characterized by a unique suite of behaviours similar to those displayed by
127 chimpanzees at other sites (e.g. Goodall et al. 1979; Boesch & Boesch-Achermann 2000). During
128 patrols the Ngogo chimpanzees move silently to the periphery of their range seeking signs of

129 individuals from other communities (Watts & Mitani 2001). Such searches resulted in encounters
130 with members of other groups 39% of the time, with males from the Ngogo community killing
131 infants from neighbouring communities four times (Watts & Mitani 2000; Watts, Mitani &
132 Sherrow unpublished observations).

133

134 **Ascertainment of Ages**

135

136 We used a classification scheme originally developed and subsequently refined by Goodall
137 (1968, 1983, 1986) and divided males into five age categories (Table 1; cf. Goodall 1986;
138 Nishida et al. 1990; Boesch & Boesch-Achermann 2000). We assigned males to one of these five
139 age classes using standard morphological and behavioural criteria. We followed previous
140 convention and assigned adolescent males to one of two categories, early and late. We classified
141 adult males into three categories, young, prime, and old. We departed from convention in our
142 categorization of adults by collapsing a typically used “middle-age” class into the group of
143 “prime” males. Given the well-known anatomical and behavioural variability that exists among
144 chimpanzees (e.g. Goodall 1986), we found it especially difficult to differentiate males during
145 middle adulthood. For this reason, we took a conservative approach, adopted by others (e.g.
146 Boesch & Boesch-Achermann 2000), and pooled males at this life history stage.

147

148 Given the relatively short duration of our field observations at Ngogo, we cannot assign
149 specific ages to any of our 38 study subjects with absolute certainty. Age estimates were made
150 independently, and without consultation, by Mitani and Watts. Both were responsible for all field
151 observations, and each possesses over 22 years of experience working with a variety of primates

152 in the wild. Mitani and Watts showed remarkable congruence in their assignments, concurring on
153 37 of 38. For purposes of the following analyses, we classified the one adult male, EL, on which
154 we did not concur, as a “prime” adult male instead of an “old” adult male. Altering EL’s
155 classification, does not affect the results of any of the analyses presented below in an appreciable
156 way.

157

158 **Rank determinations**

159

160 We employed 1208 observations of pant grunts between individuals and an additional 580
161 dyadic aggressive interactions to determine dominance ranks of the 38 male study subjects. Pant
162 grunts, distinctive calls emitted by chimpanzees, are directed up the hierarchy, given by low
163 ranking individuals to higher ranking animals (Bygott 1979; deWaal 1982). We used the
164 distribution of these calls along with the outcomes of aggressive interactions to construct a 38 x
165 38 dominance matrix. We employed a scaling method developed by Batchelder, Bershad and
166 Simpson (Batchelder et al. 1992; Jameson et al. 1999) to assign dominance ranks to our 38 study
167 subjects (Table 1). For subsequent analyses (see below), we computed the absolute values of the
168 difference in rank between each male pair and classified every individual into one of four rank
169 categories, either high, middle, low or very low (Table 1). We used the distribution of the
170 number of individuals each male dominated as the basis for classification (Fig. 1). We grouped
171 the top 8 males, which dominated $\geq 60\%$ of all others, into the high-ranking class. We
172 categorized the next 12 males in the hierarchy into a middle-ranking class. These males
173 dominated $\geq 20\%$ of all other individuals. The low-ranking class consisted of the next 9 males,
174 which dominated between 14 – 24% of all others. We classified the lowest 9 males in our

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

177

178 **Genetic Analyses**

179

180 Shed hair samples were gathered in the field under CITES import (USA #US830142) and
181 export (Uganda #103) permits. All samples were collected non-invasively from subjects on the
182 ground following self-grooming episodes. Care was taken to ensure that samples were collected
183 from isolated individuals who had scratched and shed hair several metres from other
184 chimpanzees. Following collection, all samples were stored dry in sealed envelopes at ambient
185 temperature in the field and frozen at -20° C after transport to the laboratory.

186

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

195

196 We extracted mtDNA from single hair follicles using the Chelex extraction protocol.
197 Following extraction, PCR amplification (Saiki et al. 1988) was carried out using Amplitaq Gold

198 at the manufacturer's recommended conditions. We amplified samples in PCR reactions using
199 primers covering a 349 bp segment corresponding to Anderson reference sequence coordinates
200 16026 - 16375 (Anderson et al. 1981). Primer pairs included 16026Ch-For (5' CTT TCA TGG
201 GGA AGC AAA TTT AAG 3') and 16375Ch-Rev (5' GGC ATC CGT GGG GAC GAG G 3'),
202 respectively. Primers were removed using Microcon 100,000MW cutoff filters, and 100 ng of
203 product was used as template for a dye-labeled dideoxy terminator cycle sequencing reaction
204 employing ABI's FS or BigDye Terminator kits. After vacuum-concentrating the samples dry,
205 they were re-hydrated in formamide/EDTA/Dextran Blue loading buffer and electrophoresed
206 through a Long Ranger Singel on an ABI 377XL automated sequencer. Sequences were aligned
207 and corrected using ABI's Sequence Navigator program. We sequenced all samples in both the
208 forward and reverse direction using the external- or internal-nested primers.

209

210 We constructed a neighbour-joining tree (Saitou & Nei 1987) to illustrate mtDNA genetic
211 relatedness between our male subjects. We used the Kimura (1981) two-parameter model, with a
212 15:1 transition:transversion ratio, to estimate mtDNA genetic distances between all pairs of
213 individuals. We implemented Felsenstein's (1993) DNADist program contained in PHYLIP
214 Version 3.5 to estimate distances and then used the Neighbor program in PHYLIP to generate the
215 neighbour-joining tree.

216

217 **Statistical Analyses**

218

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

221

222 *Matrix correlation tests*

223 For matrix correlation tests we constructed a 38 x 38 matrix of pairwise values for each
224 predictor variable: maternal kinship; age difference; and rank difference. We also constructed
225 matrices for each measure of social affinity: association; grooming; proximity; coalitions; meat-
226 sharing; and territorial behaviour. We then tested whether each predictor matrix was correlated
227 with each social affinity matrix.

228

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

233

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

235

236

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

237

238 where I_{AB} = the total number of interactions observed between individuals A and B , I_A = the total
239 number of interactions observed between individual A and all other individuals, and I_B = the total
240 number of interactions observed between individual B and all others. Here an “interaction” is
241 defined as two individuals appearing together in the same group, i.e. party, patrol and proximity
242 sample, or conventional dyadic social interaction, i.e. grooming, coalition or meat-sharing. The

243 advantage of this index over other association indices is that it factors out each individual's
244 general gregariousness or tendency to interact. Consequently, it reflects only the interaction
245 intensity that is specific to a particular dyad, rather than being generic to one or both individual's
246 behaviour (Pepper et al. 1999).

247

248 Before using the observed pairwise affinity values, we normalized them by dividing by their
249 expected values under the null hypothesis that social behaviours were generic rather than dyad-
250 specific. To generate these expected values we used the GROUPS computer program, which
251 implements the group randomisation method (Pepper et al. 1999). Here "groups" were defined in
252 terms of one of the six social behaviours we recorded. This procedure repeatedly re-shuffles the
253 membership of observed groups, while retaining both the observed number of appearances of
254 each individual and the observed distribution of group sizes. After each randomisation the
255 affinity index was calculated for each dyad, and these randomised values were averaged to
256 generate an expected value for each dyad. We performed 10,000 randomisations to generate null
257 expectations.

258

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

266

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

272

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

282

283 Matrix correlation tests indicated that two potential predictor variables, age and rank, were
284 strongly correlated with each other ($P = 0.0002$). We therefore examined whether significant
285 relationships between predictor variables and measures of social behaviour were affected by a
286 hidden third variable using a matrix partial correlation test (Hemelrijk 1990b). In this test, the
287 association between two variables, e.g. rank and meat-sharing, is examined while controlling for
288 the effects of a third variable, e.g. age. The matrix partial correlation procedure provides a

289 multivariate version of Kendall's S statistic (τK_r) corrected for sample sizes and ties
290 (Hemelrijk 1990b).

291

292 *Re-sampling tests*

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

303

304 To generate expected values, we constructed for each predictor variable a half-matrix with 38
305 x 38 = 703 entries, one for each male dyad in the Ngogo community. Values were either 1 or 0,
306 with 1 indicating similarity, i.e. same mtDNA haplotype, age class or rank class, and 0 indicating
307 dissimilarity. We randomly selected pairs of numbers from these matrices N times, where N
308 equaled the total number of close dyads. After making these N selections, we counted the number
309 of times individuals with the same haplotype, rank or age class were selected, i.e. the number of
310 times two 1's were drawn. We used this count as a single data point and iterated this process
311 10,000 times to generate a frequency distribution of expected values. We compared observed test

312 statistics to the tails of the expected distribution to assess the null hypothesis that social affinity
313 was independent of the predictor variable. We used the sequential Bonferroni correction to adjust
314 the lengths of these tails in each test.

315

316 *Paired t-tests*

317 Both the matrix correlation tests and the resampling tests indicated that differences in age and
318 rank had significant effects on cooperative behaviour. If maternally related dyads differed more
319 in age and rank than other dyads, this might mask the direct effects of maternal relatedness. To
320 control for this potential confound, we performed a third and final set of tests in which we
321 removed the effects of age and rank before examining the relationship between maternal genetic
322 relatedness and behaviour. Here we used paired Student t-tests to compare the social behaviour
323 of related and unrelated dyads that were matched in age and rank. To ensure statistical
324 independence, we allowed each individual to appear only once in these analyses, either in a
325 related or unrelated dyad. Related dyads consisted of four of the five related pairs, and one
326 randomly drawn pair each from a quartet and sextet of related individuals (Fig. 2). Dyads
327 matched in age and rank to these related pairs were randomly selected from the remaining pool of
328 unrelated individuals. We could not use the related dyad RU – TY in this analysis because RU
329 did not match any other male in age and rank. We did not use a quartet of related individuals,
330 WY – TA – GA – RO, for similar reasons; after selecting the first six related and unrelated
331 dyads, we could not match members of this quartet with others left in the sample of non-
332 relatives. Some males that appear in these analyses did not form coalitions or share meat. We
333 therefore conducted only four tests using the other measures of social behaviour.

334

RESULTS

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Figure 2 displays the maternal relationships among the 38 male subjects as assayed by mtDNA. Matrix correlation tests revealed that at Ngogo maternal kinship, as measured by mtDNA haplotype sharing, is not a good predictor of patterns of male chimpanzee social behaviour (Table 2). In keeping with results from prior studies (Goldberg & Wrangham 1997; Mitani et al. 2000), maternal kinship was not associated with any of the six measures of social behaviour (K_r tests, $P > 0.20$ for all 6 tests). Results of the re-sampling tests reinforced this conclusion. One hundred seventy one male dyads out of 703 total associated more often than expected by chance. Of these, only six (3.5%) shared mtDNA haplotypes, a proportion that did not exceed chance expectation of 4.6% (re-sampling test, $P > 0.80$; Fig. 3a). Similar comparisons 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 (re-sampling tests, $P \geq 0.15$ for all 5 tests; Fig. 3a).

While maternal kinship had little power in predicting who affiliated and cooperated, male chimpanzees at Ngogo appeared to bias their social behaviour toward 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 (re-sampling test, coalitions: $P = 0.0001$, $\alpha' = 0.0083$; meat-sharing: $P = 0.0001$, $\alpha' = 0.0100$; patrols: $P = 0.0182$, $\alpha' = 0.0125$; Fig. 3b). Associations, grooming and proximity were not strongly affected by age, however (Fig. 3b). Matrix correlation tests revealed positive but non-significant associations between similarity

357 in age and the tendencies to form coalitions and share meat (K_r tests, $P \leq 0.02$ for both tests,
358 starting sequential Bonferroni $\alpha' = 0.0083$; Table 2).

359

360 A third set of analyses showed that rank had an equally strong effect on patterns of male
361 behaviour. Significant negative associations existed between distance in rank and three of the six
362 measures of social behaviour, proximity, coalitions, and meat-sharing (K_r tests, proximity: $P =$
363 0.0058 , $\alpha' = 0.0083$; coalitions: $P = 0.0098$, $\alpha' = 0.0100$; meat-sharing: $P = 0.0112$, $\alpha' = 0.0125$;
364 Table 2). Matrix partial correlation tests indicated that all three of these relationships still
365 persisted after controlling for the effects of age (coalitions: $P = 0.0158$, $\alpha' = 0.0167$; meat-
366 sharing: $P = 0.0236$, $\alpha' = 0.0250$; proximity: $P = 0.0298$, $\alpha' = 0.0500$). Rank showed strong, but
367 non-significant relationships with associations and patrols (K_r tests, $P = 0.03$, $\alpha' = 0.0167$; Table
368 2). Results of re-sampling tests tended to support those derived from matrix correlations. Males
369 that formed coalitions and shared meat more often than expected by chance were frequently
370 members of the same rank class (coalitions: $P = 0.00001$, $\alpha' = 0.0083$; meat-sharing: $P = 0.001$;
371 $\alpha' = 0.01$; Fig. 3c).

372

373 The preceding results indicate that both age and rank have significant effects on male
374 chimpanzee social behaviour. To remove their effects and thus discern any possible influence of
375 maternal relatedness on male behaviour, we compared the social behaviour of related and
376 unrelated dyads matched in age and rank. Results showed that maternal relatives neither
377 associated, groomed, maintained proximity nor patrolled with each other more frequently than
378 did unrelated individuals (Student's t tests, $P \geq 0.15$ for all four comparisons; Fig. 4).

379

DISCUSSION

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

396
397 If male chimpanzees do not consistently bias their affiliative and cooperative behaviour
398 toward maternal kin, what factors do play a role? Here our findings extend prior research by
399 revealing that age and rank exert important influences on structuring patterns of male
400 chimpanzee social behaviour. Both of these variables have an especially important impact on
401 behaviours that are likely to have major fitness consequences. Males preferentially formed

402 coalitions, shared meat and patrolled territorial boundaries with members of the same age and
403 rank classes.

404

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

412

413 Descriptions of alliances between presumed maternal brothers have led to the belief that male
414 chimpanzees cooperate in part to gain indirect fitness benefits (Goodall 1986). Despite this long-
415 standing assumption, our findings now indicate that demographic constraints may limit what is
416 functionally possible (cf. Sherman 1981). While it may be in the reproductive interests of male
417 chimpanzees to behave altruistically toward and cooperate with close male kin, slow female
418 reproduction may provide few opportunities for such interactions. An emerging body of theory
419 and empirical research may also be germane to our results. Here theory suggests (Frank 1998;
420 Taylor 1992; Wilson et al. 1992) and observations indicate (Dunn et al. 1995; Clutton-Brock et
421 al. 1999; Clutton-Brock et al. 2000; West et al. 2001) that limited dispersal may combine with
422 high levels of local competition to offset potential inclusive fitness benefits. These findings may
423 be especially relevant to chimpanzees, a species that displays male philopatry along with

424 extremely high levels of within-group male-male competition (Bygott 1979; Pusey 1979; Nishida
425 1983; Goodall 1986; Nishida & Kawanaka 1990; Muller in press).

426

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

436

437 Our results also highlight the tactical decisions male chimpanzees make to develop and
438 maintain alliances. Considerable evidence from the wild shows that male chimpanzees use
439 grooming, meat-sharing and decisions about associations with conspecifics as tactics to form and
440 maintain alliances (e.g., Nishida et al. 1992; Nishida & Hosaka 1996; Newton-Fisher 1999;
441 Mitani & Watts 2001). Given that the value of potential partners varies, that kin may be
442 unavailable or unsuitable as allies and that unrelated individuals make tactical decisions to
443 cooperate in other primates (e.g., bonobos: Hohmann et al. 1999; baboons: Noë 1992; red howler
444 monkeys: Pope 2000) and non-primates (e.g., dolphins: Connor et al. 2000; lions: Packer et al.
445 1991), the absence of strong maternal kinship effects on male chimpanzee social behaviour is not
446 entirely unexpected.

447

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

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735

735 **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

736

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

738 Table 2. Relationships between mtDNA haplotype sharing, age and rank with social behaviour.
 739

	mtDNA					
	haplotype sharing		age		rank	
	K_r	P	K_r	P	K_r	P
association	263	0.25	838	0.12	-1707	0.03
grooming	96	0.57	553	0.13	-905	0.08
proximity	255	0.25	847	0.07	-1691	0.001
coalitions	75	0.53	740	0.02	-980	0.001
meat-sharing	87	0.44	636	0.02	-885	0.01
patrols	-10	0.99	738	0.11	-1549	0.03

740

741 K_r matrix correlation statistics and associated P values are shown. Entries highlighted in bold

742 indicate those that are less than the sequential Bonferroni criterion.

743

743 **Figure legends**

744

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

747

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

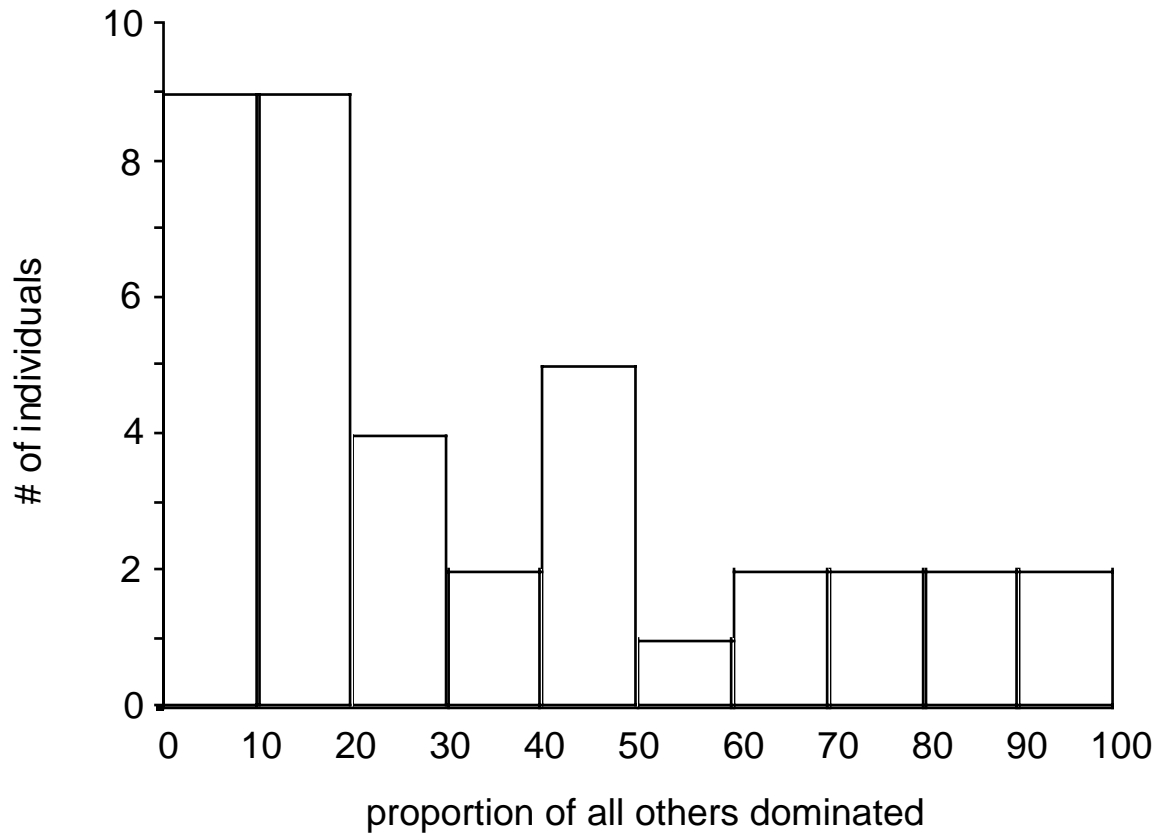
750

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

757

758 Figure 4. Comparison of the behaviour of related and unrelated male chimpanzee dyads matched
759 in age and rank. The means and standard deviations of pairwise affinity indices between related
760 and unrelated pairs are shown. $N = 6$ matched dyads.

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