

To what extent does living in a group mean living with kin?

D. LUKAS,* V. REYNOLDS,† C. BOESCH* and L. VIGILANT*

*Max Planck Institute for Evolutionary Anthropology, Deutscher Platz 6, Leipzig 04103, Germany, †Oxford University, School of Anthropology, 51, Banbury Road, Oxford OX2 6PE, United Kingdom

Abstract

Chimpanzees live in large groups featuring remarkable levels of gregariousness and cooperation among the males. Because males stay in their natal communities their entire lives and are hence expected to be living with male relatives, cooperation is therefore assumed to occur within one large 'family' group. However, we found that the average relatedness among males within several chimpanzee groups as determined by microsatellite analysis is in fact rather low, and only rarely significantly higher than average relatedness of females in the groups or of males compared across groups. To explain these findings, mathematical predictions for average relatedness according to group size, reproductive skew and sex bias in dispersal were derived. The results show that high average relatedness among the philopatric sex is only expected in very small groups, which is confirmed by a comparison with published data. Our study therefore suggests that interactions among larger number of individuals may not be primarily driven by kin relationships.

Keywords: chimpanzee, cooperation, demography, kin selection, kinship, microsatellite, relatedness

Received 24 December 2004; revision accepted 25 February 2005

Introduction

Kin selection theory has been influential in interpreting animal behaviour by offering a framework in which high relatedness among the members of a group and the resulting inclusive fitness benefits could offset the costs associated with group living and even facilitate seemingly altruistic, cooperative activities (Hamilton 1964; Wrangham 1979). For groups of social animals, philopatry in one sex could be expected to lead to higher relatedness among members of the philopatric sex as compared to the dispersing non-philopatric sex, assuming that dispersing individuals do not move in concert with relatives. For most mammals, females are the philopatric sex, while males emigrate upon maturity (Greenwood 1980) and in general, patterns of genetic relatedness in social groups of female-philopatric mammalian species often do appear to conform to the expectation of notably higher average relatedness among females than males (macaques: de Ruiter & Geffen 1998; rabbits: Surridge *et al.* 1999; sifakas: Lawler *et al.* 2003). However, some recent studies have failed to find relatedness levels in accordance with expectations (e.g. guppies: Russell *et al.* 2004; hyenas: Van Horn *et al.* 2004; wolves: Vucetich

et al. 2004). In particular, in a previous study we did not find significantly higher average relatedness of philopatric chimpanzee males as compared to females within groups (Vigilant *et al.* 2001). This was surprising because the strong social bonds between chimpanzee males within a community have previously been suggested to reflect kin associations (Morin *et al.* 1994a and references therein).

In contrast to most other Old World primates, but in common with humans (Ember 1978), in chimpanzees it is the females rather than the males that typically emigrate upon reaching maturity (Nishida & Kawanaka 1972; Pusey 1979; Boesch & Boesch-Achermann 2000). This reversal of the usual mammalian pattern implies that the intensity of competition among group females is even greater than that among group males, and/or that there exist factors that mitigate competition among the males. One such factor could be mutually supportive or affiliative behaviour among the males. Chimpanzees are territorial, and the adult and adolescent males of the community actively defend the community home range (Goodall *et al.* 1979; Boesch & Boesch-Achermann 2000; Watts & Mitani 2001). The sometimes lethal nature of the interactions between males of different communities underscores the potential costs of collective territory defense. This is notable as activities with high costs have been suggested as the most likely arena for the operation of kin-selected behaviour in primates

Correspondence: Dieter Lukas, Fax: +49-341-3550-299; E-mail: lukas@eva.mpg.de

(Chapais 2001). In order for males to gain substantial inclusive fitness benefits in these intercommunity interactions and offset costs incurred, it is expected that the average relatedness of males within communities exceed that of males compared across communities, because possible competition between relatives could reduce or remove potential inclusive fitness benefits (West *et al.* 2002).

While patterns of philopatry and dispersal create connections between groups, empirical studies have demonstrated that reproductive skew (Altmann *et al.* 1996) and group size (humans: Brown 1991; Alvard 2003; lions: Spong & Creel 2004) influence kin structure within groups. Male reproductive output in chimpanzees is influenced by the hierarchical dominance system, under which the highest-ranking male produces a disproportionate share of the offspring, with the relative shares influenced by factors such as the number of competing males and, to a lesser extent, the number of females simultaneously in oestrus (Constable *et al.* 2001). In addition, recent data show that a limited proportion of offspring are not sired by males of the community they reside in, but are the result of extra-group paternity or transfers as infants with their mothers (Vigilant *et al.* 2001). Overall, the greater the extent to which a single male dominates reproduction, the greater the number of paternally related offspring among the total number of offspring in the group. In order to understand why estimated relatedness levels within and across chimpanzee communities do not fit with pre-expectations, we need to consider in more detail the theoretical basis of the expectations and the factors influencing average relatedness levels. Early work by Altmann (1979) indicated that average within group relatedness could be low if multiple males sire offspring; however, her approach does not allow for assessment of the impact of factors like sex bias in dispersal or comparison with empirical data. Therefore, we derived here a new approach to investigate the conditions under which philopatric individuals in groups are expected to be highly related.

This study has three parts. In the first, we present a more detailed analysis of chimpanzee data in light of relatedness structure. Specifically, we employed microsatellite markers to estimate average genetic relatedness among sets of individuals in multiple wild chimpanzee communities from two separate sites in West and East Africa. Our goal was to test the following closely linked predictions: (i) adult males within a community are more related than are adult females, (ii) adult males within a community are more related than are adult males across communities, and (iii) cohorts of offspring are more related when few rather than many males achieve paternity. In the second part of this study, we compared these results to theoretical expectations derived from a mathematical model that revealed the effects of variance in lifetime reproductive success, group size and sex bias in dispersal on average relatedness levels

of a group of individuals and provided values for a 'chimpanzee' situation. Finally, by comparing the theoretically obtained as well as the empirical chimpanzee values to previously published relatedness estimates from a variety of species, we assessed the fit and the generality of our results.

Materials and methods

(a) Genetic analysis of habituated chimpanzees

Noninvasive samples, primarily faeces, were collected from habituated, individually identified chimpanzees. Three communities of West African chimpanzees (*Pan troglodytes verus*) and one community of East African chimpanzees (*Pan troglodytes schweinfurthii*) were studied. The western chimpanzees were from the North, Middle and South communities in the Tai National Park, Côte d'Ivoire (Boesch & Boesch-Achermann 2000). The eastern chimpanzees were members of the Sonso community in the Budongo Forest Reserve, Uganda (described in: Newton-Fisher 1999; Reynolds in press). After extraction and quantification of amplifiable DNA (Morin *et al.* 2001), individuals were genotyped at a total of nine highly variable microsatellite markers as previously described (Bradley *et al.* 2000; Vigilant *et al.* 2001). Multiple measures to ensure accuracy as detailed in Vigilant *et al.* (2001) were employed, the most notable being that both alleles of heterozygous genotypes were scored at least twice and depending upon template amount present in the polymerase chain reaction (PCR) (Morin *et al.* 2001), the single allele of homozygous genotypes was scored four or more times. A total of 114 western and 49 eastern chimpanzees were genotyped (Appendix I). Maternity confirmation and paternity assignment followed direct comparison of genotypes for the individuals in question. Mothers and assigned fathers each shared an allele at every locus with the offspring in question while other candidate fathers were excluded by multiple mismatches and individual paternity exclusion probabilities (Morin *et al.* 1994b) were in excess of 0.99. For all individuals, exact ages of individuals younger than 18, 6 and 8 years (Tai North, Middle and South, respectively) or 10 years (Sonso) were known while the ages of older individuals were estimates by experienced field researchers and are likely to be accurate to within 5 years. For analyses of similarly aged cohorts, individuals were classified according to age attained in full years on January 1 of the year of interest as follows: fully adult (aged 15 years and up for males, 13 and up for females); adolescent (10–14 for males, 10–12 for females); juveniles (5–9 for both sexes) and infants (0–4 years) (Boesch & Boesch-Achermann 2000). Because even young adolescent males father offspring (Constable *et al.* 2001) and take part in male affiliative activities such as hunting and boundary patrolling (Boesch

& Boesch-Achermann 2000; Mitani *et al.* 2002; Watts & Mitani 2002), they were considered as adult males for the purposes of all analyses.

The Queller and Goodnight estimator of relatedness (R) implemented in RELATEDNESS version 5.0.8 (<http://gsoft.smu.edu/GSoft.html>) was used. This particular estimator was chosen as it was designed to estimate r for the purpose of applying Hamilton's rule to natural behaviour (Queller & Goodnight 1989). Allele frequencies used in relatedness analyses of the Tai chimpanzees were based upon a subset of individuals of no known relatedness (Vigilant *et al.* 2001), and results did not vary when using allele frequencies from all individuals (data not shown). Allele frequencies from all individuals were used for the Sonso chimpanzees as the total number of individuals was too small to allow a selection of probable unrelated individuals. Thus, the relatedness values for the Sonso chimpanzees are expected to have a slight negative bias. Rarefaction analysis, whereby relatedness values were calculated after each successive inclusion of loci beginning with one locus, revealed little change in the variance of calculated relatedness values after addition of the seventh locus (data not shown). This implied that the nine loci used here were sufficient for robust estimates of relatedness in these populations. Standard errors of estimates of average R within and between groups of individuals were estimated by jackknifing across loci. Because standard errors are strongly influenced by the number of comparisons and so are not directly informative for comparisons between analyses using different sample sizes, we report instead standard deviations of R estimates as these clearly reflect the amount of scatter in the data whatever the sample sizes. However, confidence intervals cannot be directly compared because of nonindependence of data. Hence, the statistical significance of differences in average relatedness values among sets of individuals was evaluated by permutation analysis (Manly 1997). For the permutations we re-sampled individuals by pooling all individuals in the groups to be compared, and then repeatedly drawing the same number of individuals corresponding to the original group sizes and calculating average pairwise relatedness for these randomly constituted groups. All analyses were performed at the level of community-years, meaning that we compared values for each community for each of the years 1995 through 2002 (Tai Middle: 1998 through 2002). Even though the data points within the groups are not completely independent since the majority of the individuals stays the same, our approach covers a variety of demographic conditions and allows us to make statements about the general situation of chimpanzee groups. For assessing the significance of the within-group relatedness differences, in each of the 29 analyses the individuals in the group under consideration were randomly sorted into two subgroups of sizes matching the numbers of females and

males, respectively, and the difference of the average relatedness values of these random subgroups of individuals was compared to the observed difference in average female and male relatedness. The between-group analysis was performed for the three communities at Tai, whereby we pooled all males and then randomly resorted them according to the three group sizes, calculating the relatedness within and between each of the three subgroups and comparing it to the observed values. We conservatively considered results significant when the observed difference in average relatedness exceeded 95% of the values obtained in 5000 permutations.

Genotypic differentiation between sampled communities was studied using the program MSA (Dieringer & Schlötterer 2003). This program calculates the Weir–Cockerham estimators (Weir & Cockerham 1984) of Wright's F -statistics (Wright 1951) across loci and between population pairs, and uses permutation tests with incorporation of a strict Bonferroni correction for multiple tests to estimate the probability of departure from the null hypothesis of no differentiation.

(b) Mathematical model

We derived an equation that describes average relatedness of a group of adult individuals remaining in their natal group as a function of reproductive skew, sex bias in dispersal and the number of individuals. Our approach to derive average relatedness estimates was similar to the path analysis used by Wright (1965) to derive the F -statistics and to the group-structured model by Chesser (1998) in that calculated values are relative to the average of the total population, and so they represent the inclusive fitness benefit of the interacting individuals compared to a random dyad. However, our approach more closely reflects the situation of a population of social animals by allowing analysis of the effect of manipulating different variables defining social structure.

The calculations assumed an idealized situation in which (i) all the adults are of the same generation, meaning that no reproduction via parent–offspring mating occurs; (ii) dispersal is completely sex biased, meaning all individuals of one sex leave; and (iii) these dispersing individuals join new groups randomly, so that the relatedness among the members of the immigrating sex is 0, as is their relatedness to the resident sex, which reflects the avoidance of inbreeding (for relaxation of these parameters and the general derivation see Appendix II). Under these conditions, individuals can be related either through sharing one or both parents or, if their respective parents are related. According to the third assumption above, we only have to consider relatedness through parents of the philopatric sex. A direct parent–offspring relationship has a relatedness value (R) of 0.5 and so to connect two individuals, all parent–offspring relations are counted and the value

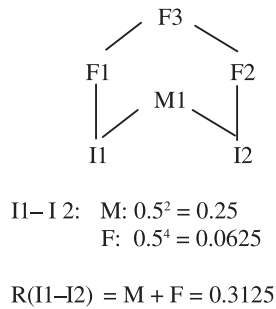


Fig. 1 This diagram illustrates how dyadic relatedness was calculated for our simulation. The numbers of steps needed to connect I1 and I2 through either the maternal or paternal side are independently counted. In this example I1 and I2 share the same mother (I1 – M1 – I2 → 2 steps), while their fathers are paternal half-sibs (I1 – F1 – F3 – F2 – I2 → 4 steps). For each path we take 0.5 to the power of the number of steps and sum the two values.

between the two individuals is 0.5 times the number of steps. To derive the R value for any given dyad, we calculate the value for the maternal side, which the two individuals may share, as their mothers can be related or unrelated, and then add the respective value from the paternal side, again analysing whether it is the same father, or their fathers are related or unrelated (Fig. 1). If one parent is shared, the relatedness value is 0.25, if the parents are related the value for the dyad is 0.25 times the relatedness of those parents and if the parents are unrelated, the relatedness value for the dyad is 0; by adding up both lines we can see that these values can range from 0 to 0.5 in the case of a full-sib dyad.

The relatedness value for a group of individuals was obtained by averaging over all dyads. The variable of lifetime reproductive skew influences the number of dyads sharing the same mother or father, while the group size variable determined the total number of dyads. Lifetime reproductive skew is expressed here for both males and females as the relative proportion of offspring of the philopatric sex per generation produced per individual (Herfindahl index, Kokko *et al.* 1999). This is incorporated in the formula as f (female reproductive skew) and m (male reproductive skew) by taking the sum of the squared percentages, and because they are given in proportions, the actual value also depends upon the group size. Group size was expressed as the number of individuals x of the philopatric sex. The values used for these factors can be interpreted as averages over a population that has been stable for some generations, so that reproductive skew indicates how many adults of a given group share the same parents.

We summarized these factors in a single formula (for details of the derivation see Appendix II):

$$R = \frac{(f + m) * x - 2}{(3 + a) * x - 4} \quad (\text{eqn 1})$$

where x , f and m are the values discussed, and a is either equivalent to f if females are philopatric or to m if males are philopatric. We used the formula in two ways. In the first, we set f and m to fixed values, by assuming a situation in which on average, 25% of the males of the parental generation sire 75% of the new individuals of the philopatric sex and the remaining 25% are sired by an additional 25% of the male parents. For the females we assumed that in each generation, 40% do not produce any offspring of the philopatric sex, 25% have one offspring, 25% have two offspring, and finally 10% of the females have three offspring of the philopatric sex during their lifetime. These numbers are based on the expectations for a species that, like most large mammals, has a limited lifetime reproductive success and an equal chance of producing a female or male offspring at each birth. The 40% of females who do not produce any offspring of the philopatric sex include all the females who only produced offspring of the dispersing sex. Under this scenario, we calculated the group size at which average relatedness drops below the level of half-sibs ($r = 0.25$) or cousins ($r = 0.125$), respectively. Second, we compared the effects of male- vs. female-biased dispersal, and their difference in degree of lifetime reproductive skew, upon the average relatedness. To facilitate comparison with our empirical results, we chose values for group size to simulate a 'chimpanzee' situation, with 12 philopatric individuals in the group and fixed female lifetime reproductive skew as in the calculations on group size in the first scenario (this gives for 12 individuals $f = 0.167$), while varying male lifetime reproductive skew.

(c) Published genetic data

We compared our chimpanzee values and the predicted values from the mathematical model with empirical data obtained from published studies. A literature search was performed in ISI Web of Science in August 2004 using as keywords 'microsatellite(s)' or 'blood protein(s)' and 'relatedness'. Data were considered relevant if the analyses were performed at the within-group level and separately for adults of each sex. If a study included analysis of more than one group, we averaged across these values to obtain one data point per publication. Group sizes were taken as reported in the methods section of the respective papers, and we tested for the influence of this demographic factor on the relatedness values. Regression analyses were performed by taking group size as the independent variable and relatedness estimates as the dependent variable by assuming either a linear (relatedness = a times group size) or an exponential relationship (relatedness = group size to the power of a), or by assuming a relationship as described in the equation 1 derived in the previous section (with female and male lifetime reproductive skew as additional parameters – to reflect a biological situation they were

restricted to range between 0 and 1). All analyses were performed in *SPSS 11.5.2* (SPSS Inc.) with iterative estimation algorithms used to derive the missing parameters.

Results

(a) Chimpanzee genetic data

Relatedness within communities of males as compared to females. We estimated average relatedness of adult males and females for a total of 29 chimpanzee community-years. The results for males and females (Table 1) contrast in two ways.

Table 1 Mean pairwise relatedness (*R*), and standard deviation (SD) estimates for adults (*n*) present each year in the four study communities. Significant *P* values for the comparison between males and females of the same group in the same year are in bold. The nd indicates the test was not done as the number of possible permutations was too few

Year	Males			Females			<i>P</i>
	<i>R</i>	SD	<i>n</i>	<i>R</i>	SD	<i>n</i>	
Tai North							
1995	-0.0697	0.1765	3	-0.0168	0.2033	10	0.636
1996	-0.0697	0.1765	3	-0.0168	0.2033	10	0.636
1997	-0.0697	0.1765	3	-0.0375	0.1491	11	0.541
1998	0.0118	0.157	2	-0.0375	0.1491	11	0.389
1999	-0.1268	0.1117	3	-0.0375	0.1491	11	0.770
2000	-0.1392	0.1558	2	-0.032	0.1045	7	0.600
2001	-0.1392	0.1558	2	-0.032	0.1045	7	0.600
2002	-0.1392	0.1558	2	-0.0484	0.1022	6	0.633
Tai Middle							
1998	0.0468	0.2361	4	-0.0849	0.1048	3	0.168
1999	0.1232	0.2667	3	-0.0849	0.1048	3	nd
2000	0.1232	0.2667	3	-0.0849	0.1048	3	nd
2001	0.1232	0.2667	3	-0.0849	0.1048	3	nd
2002	0.115	0.1978	2	-0.1213	0.1485	2	nd
Tai South							
1995	0.0944	0.3064	5	-0.0299	0.2247	20	0.040
1996	0.0944	0.3064	5	-0.0299	0.2247	20	0.040
1997	0.0944	0.3064	5	-0.0299	0.2247	20	0.040
1998	0.0676	0.2263	4	-0.0299	0.2247	20	0.116
1999	0.1311	0.1684	3	-0.0299	0.2247	20	0.053
2000	-0.0206	0.1541	4	-0.0299	0.2247	20	0.619
2001	0.0432	0.2315	5	-0.0251	0.255	19	0.099
2002	0.0166	0.256	6	-0.0244	0.2076	17	0.171
Sonso							
1995	-0.0015	0.2164	15	0.0032	0.2014	10	0.172
1996	-0.0015	0.2164	15	-0.0188	0.2074	11	0.148
1997	0.0112	0.2156	17	-0.0188	0.2074	11	0.096
1998	0.0112	0.2156	17	-0.0188	0.2074	11	0.096
1999	0.0153	0.2186	15	-0.0188	0.2074	11	0.113
2000	0.0033	0.2058	14	-0.0188	0.2074	11	0.196
2001	0.0113	0.2382	13	-0.0188	0.2074	11	0.134
2002	0.0422	0.236	12	-0.0459	0.2005	10	0.024

First, it is immediately apparent that average male relatedness levels vary greatly, with the lowest value approaching $R = -0.15$ (Table 1, Tai North) and the highest corresponding to $R = 0.123$ (Table 1, Tai Middle). Average relatedness also varied greatly within communities, as in the Tai North group that in 1 year through changes in group composition went from an average adult male relatedness of 0.0118 in 1998 to -0.1268 in 1999. In contrast, average relatedness levels of adult females did not vary as much between communities and were more consistent through time. The fluctuation in the relatedness values for males across years for the Tai communities is a function of the small number of adult males present, so that the addition or loss of a single individual had more effect upon average relatedness. Composition of the relatively larger Sonso community changed very little over the time considered, which is reflected in the stable *R* values for both males and females.

The second notable feature of the relatedness values in Table 1 is the lack of consistently higher relatedness of males as compared to females. Only rarely was the average relatedness of males significantly greater than that of the females of the same group in the same year, and the range of values largely overlaps (Table 1). The significance of the difference between male and female average *R* for 4 years in the Tai Middle community could not be tested due to a small number of individuals, but even after leaving these 4 years out, the 4 years in which significant differences were seen (Tai South 1995–1997; Sonso 2002) represent a minority of the 25 community-years considered. The average number of adult males included in the calculation for each year was 3.9, 3.0 and 4.6 for Tai North, Middle and South, respectively, and 14.8 for Sonso. The average number of females included was 11.0, 2.8, 19.5 for Tai North, Middle and South and 10.8 for Sonso. The atypically high male to female sex ratio in Sonso is attributable to lack of sampling of less-habituated females, and due to its random nature is unlikely to lead to a bias in the relatedness results.

Relatedness among communities. This analysis was necessarily limited to the three adjacent communities of Tai North, Middle and South. Data on this point are limited, but it is likely that emigrating females join neighbouring or at least not very distant communities (Morin *et al.* 1994a and references therein). Thus, the average relatedness of females across groups should be similar or even exceed that of within-group comparisons, because of the potential inclusion of, for example, mother to adult daughter pairs across groups. The average relatedness of males within groups should exceed that of comparisons across groups.

Results generally consistent with these expectations were found, and average relatedness of adult females across groups did tend to exceed within-group values (Fig. 2). However, average relatedness of males across the Tai communities, while lower than the values for within Tai

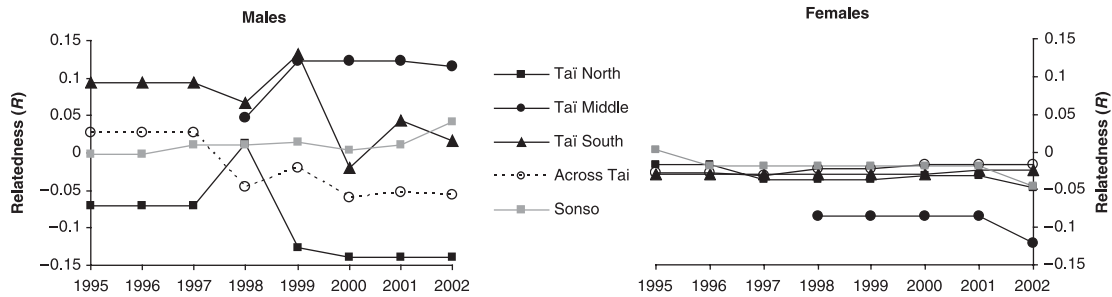


Fig. 2 Average relatedness (R) by year of the male and female chimpanzees, per each of the three groups at Tai and the Sonso group at Budongo, and the relatedness across the Tai communities comparing dyads of males or females, respectively, who are not in the same group.

Table 2 Genetic differentiation of Tai communities

Communities	F_{ST} calculated for:		
	All adults	Male adults	Female adults
North Middle	0.000394	0.000654	-0.023879
North South	0.001309	0.053211	-0.00001
Middle South	-0.007159	0.039082	-0.020769

Middle and Tai South groups, exceeded the values for most years for Tai North (Fig. 2). We evaluated whether a significant difference in average male relatedness within and among groups was present by pooling all individuals for the year in consideration, sorting them randomly into groups of the same size as observed, and calculating the average R across groups. This analysis showed that for 2 of the 8 years, 1998 and 2001, the average male R across groups was significantly lower than expected by chance ($P = 0.036$ and 0.040 , respectively).

Another way to consider the distribution of genetic variation among groups is through the use of F -statistics. We estimated genetic differentiation of the three Tai communities, using the genotypes of the adults present in 2001. We chose to use 2001 because female immigration into these habituated groups has ceased in recent years, and so a relatively recent time point might offer a greater chance to detect genetic differentiation of the groups. However, this was not the case, and the F_{ST} values for the pairwise comparisons of the communities were not significantly different from zero (Table 2). It is nonetheless interesting to note that when only females were considered, the amount of differentiation was the least and that the greatest amount of differentiation was found when considering only males, results consistent with primarily female-mediated gene flow among communities and male philopatry.

Relatedness of similarly aged offspring. We reasoned that because a particular male typically enjoys the reproductive

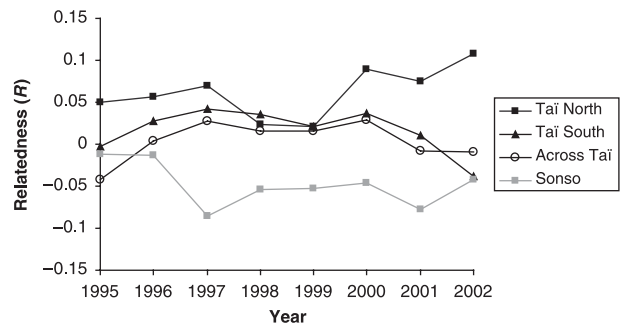


Fig. 3 Average relatedness (R) by year for offspring under 5 years of age for three study communities.

advantages of top-ranking dominance status for a limited number of consecutive years, it might be possible to detect elevated average relatedness resulting from shared paternity in cohorts of similarly aged offspring (Altmann 1979). If such a pattern was found, it would suggest that our analyses of male adults may have failed to find high average relatedness as a result of including individuals of a wide range of ages. To check this, we calculated average R for cohorts of offspring (including males and females) under 5 years of age for Tai North, Tai South, Sonso and across the Tai groups (Fig. 3). Tai Middle was not considered except for the among-group calculations as only two offspring were present. It is apparent that levels of average R in offspring did not exceed those calculated for adult males (excluding Tai Middle, Mann-Whitney U -test, $U = 258$, $P = 0.54$; Fig. 3). Closer investigation of the patterns of shared paternity among offspring cohorts in a given year revealed that, for all three communities and for all years considered, a minimum of two males fathered the offspring, in line with results showing that reproductive skew is never complete in chimpanzee groups containing multiple adult males (Vigilant *et al.* 2001). Thus, although we found that average relatedness among paternal siblings was not significantly different from the expected value of $R = 0.25$ (Vigilant *et al.* 2001), average relatedness among cohorts of offspring

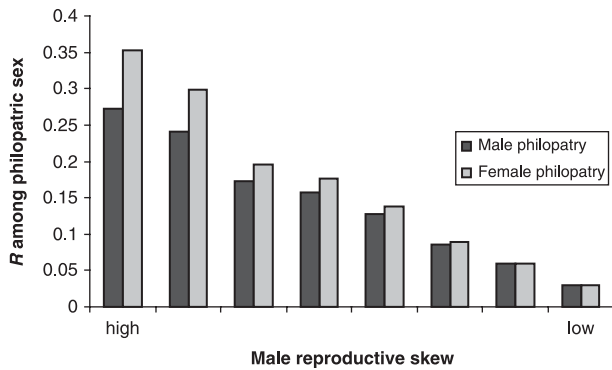


Fig. 4 Average relatedness (R) among members of the philopatric sex varies according to the identity of the dispersing sex and the level of male reproductive skew. The black bars correspond to the situation of female dispersal in chimpanzees, and thus indicate R among the males. If males disperse (grey bars), R among philopatric females is higher than it is for philopatric males (black bars) in the converse situation when females disperse and males stay. The highest category of male reproductive skew, labelled as 'high' in the figure, corresponds to one male siring all 12 offspring. The next categories are, in order: two fathers each with 1 and 11 offspring, two fathers with 8 and 4 offspring, two fathers with 6 each, three fathers with 6, 4, and 2 offspring, four fathers with three offspring each, six fathers with 2 each and finally 12 fathers each has 1 offspring (labelled 'low').

were reduced from that level, as evident in Fig. 2, because of inclusion of two or more patriline.

(b) Values from the mathematical model

We first explored the effect of group size upon relatedness by applying a situation of fixed lifetime reproductive skew as outlined in the methods and determining the group size at which the average relatedness was still above 0.125 (cousins level) or 0.25 (half-sib level). When four individuals were present per generation, average relatedness was above 0.25 under female philopatry but below 0.25 with male philopatry. When eight or more individuals were present per generation, average relatedness values dropped below 0.125 with either male or female philopatry.

In the second analysis, we contrasted the effects of male and female dispersal upon average relatedness while varying male lifetime reproductive skew and keeping group size constant. When male reproductive skew decreases towards and below the level of female skew, the average relatedness values decrease in both scenarios, as does the difference between the two (Fig. 4). If we assume a situation in which male reproductive skew is about two times greater than female, relatedness values for species with female philopatry are about 10% higher, and similarly threefold larger male skew leads to differences of about 20%.

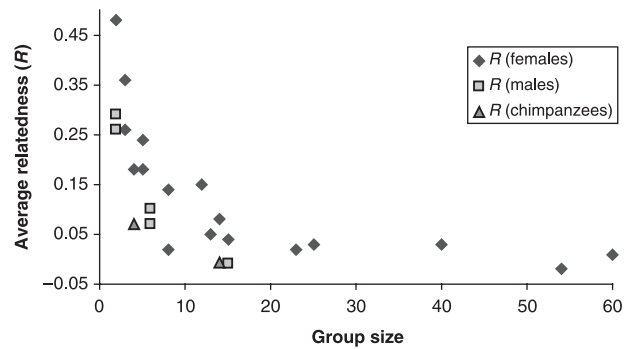


Fig. 5 The relationship between group size and average relatedness among the philopatric individuals, separated for species with female vs. male philopatry. Relatedness values drop with larger group sizes for both scenarios; however, the values for philopatric males are lower for a given group size. For details on species and publications see table 3.

Under the chimpanzee condition of male philopatry, average relatedness among the nondispersing (male) sex was below that describing half-sibs ($R = 0.25$) except for the most extreme situation in which all paternities are attributed to one male (Fig. 4). Distribution of paternity described in actual chimpanzee communities more closely resembles the situations of less extreme skew ($m < 0.35$) for which our simulated relatedness values were below 0.125 (Constable *et al.* 2001; Vigilant *et al.* 2001).

(c) Comparison with empirical data from different taxa

To compare our chimpanzee results and to assess the fit of the predicted values from the mathematical model, we used a comparative approach to assess the influence of sex-biased dispersal and group size on average relatedness values of adults of each sex in a group. Unfortunately, because most studies were limited to a small number of groups, it was not possible to use the data to make inferences about the relative degree of reproductive skew across species.

Our literature search yielded a total of 22 studies reporting, for each sex, average relatedness values within social groups, 17 of which are for female philopatric species (Table 3). In addition, we included our data from the two chimpanzee sites. The average relatedness of the dispersing sex across these species was -0.004 (range -0.19 to 0.09), with no correlation with group size, suggesting that dispersers join groups randomly. However, as predicted from the model, average relatedness values among the members of the philopatric sex showed a clear negative trend with increasing group size for both scenarios of sex-biased dispersal (Fig. 5). We assessed the significance of this trend by comparing the observed values in a regression to a linear and an exponential model, as well to a model based on

Table 3 Published relatedness data for adults of one sex within a social group. The correlation between group size and relatedness in the philopatric sex is illustrated in figure 5, there is no such correlation for the dispersing sex

Common name	Number of females	R (females)	Number of males	R (males)	Citation	Species name
Female philopatric species						
Redfronted lemur	2	0.48	3	0.086	Wimmer & Kappeler 2002	<i>Eulemur fulvus rufus</i>
Lion	3	0.26	3	0.09	Spong <i>et al.</i> 2002	<i>Panthera leo</i>
Grey mouse lemur	3	0.36			Radespiel <i>et al.</i> 2001	<i>Microcebus murinus</i>
Sifaka	4	0.18	3	0.081	Lawler <i>et al.</i> 2003	<i>Propithecus verreauxi verreauxi</i>
Rabbits	5	0.24	5	-0.069	SurrIDGE <i>et al.</i> 1999	<i>Oryctolagus cuniculus</i>
Otter	5	0.18	11	0.087	Blundell <i>et al.</i> 2002	<i>Lontra canadensis</i>
Bat	8	0.02	2	0.002	Ortega <i>et al.</i> 2003	<i>Artibeus jamaicensis</i>
Macaque	8	0.14	4	-0.1	de Ruiter & Geffen 1998	<i>Macaca fascicularis</i>
Dolphins	12	0.15	16	0.022	Moller & Beheregaray 2004	<i>Tursiops aduncus</i>
Chipmunk	13	0.05	15	-0.024	Schulte-Hostedde <i>et al.</i> 2001	<i>Tamias amoenus</i>
Wood-rats	14	0.08			Matocq & Lacey 2004	<i>Neotoma macrotis</i>
Bat	15	0.04	14	0.022	Burland <i>et al.</i> 2001	<i>Plecotus auritus</i>
Bat	23	0.02			Kerth <i>et al.</i> 2002	<i>Myotis bechsteinii</i>
Sheep	25	0.03	15	-0.005	Coltman <i>et al.</i> 2003	<i>Ovis aries</i>
Bat	40	0.03			Rossiter <i>et al.</i> 2002	<i>Rhinolophus ferrumequinum</i>
Baboon	54	-0.02	10	-0.19	Altmann <i>et al.</i> 1996	<i>Papio cynocephalus</i>
Hyenas	60	0.01	40	0.009	Van Horn <i>et al.</i> 2004	<i>Crocuta crocuta</i>
Male philopatric species						
Bell miner bird	2	-0.05	2	0.29	Painter <i>et al.</i> 2000	<i>Manorina melanophrys</i>
Shrew	8	0.05	2	0.26	Balloux <i>et al.</i> 1998	<i>Crocidura russula</i>
Chimpanzee Tai	12	-0.022	4	0.07	this study — Tai	<i>Pan troglodytes</i>
Bilby marsupial	7	0.005	6	0.1	Moritz <i>et al.</i> 1997	<i>Macrotis lagotis</i>
Bonobo	15	-0.03	6	0.07	Gerloff <i>et al.</i> 1999	<i>Pan paniscus</i>
Chimpanzee Budongo	8	-0.05	14	-0.007	this study — Budongo	<i>Pan troglodytes</i>
Red grouse	15	-0.013	15	-0.01	Piertney <i>et al.</i> 1998	<i>Lagopus lagopus scoticus</i>

eq. 1 derived above. A regression for the combined data produced a less good fit than the two individual analyses. All three gave a significant fit for the two data sets (females — linear: $F = 12.3$, $P = 0.002$; exp.: $F = 152.2$, $P < 0.001$; formula: $F = 158.2$, $P < 0.001$; males — linear: $F = 12.1$, $P = 0.02$; exp.: $F = 53.5$, $P < 0.001$; formula: $F = 62.7$, $P < 0.001$); however, the model based on our formula could explain most of the variance (for the female values the r^2 is 0.91, for the males 0.94). Consistent with expectations from the model, for a given group size the relatedness values among philopatric males were always lower than those of the philopatric females (Fig. 5).

Discussion

Hamilton's rule predicts that the sharing of genes between individuals can facilitate the evolution of cooperative activities (Hamilton 1964). Using simulations we have shown here that high average relatedness values among individuals within social groups are only obtained if groups are small and reproduction is limited to a few individuals. Even though these results are based on some simplified assumptions, such as assuming the relatedness of immigrants

to be zero, these assumptions as well as the results seem well supported by published empirical data.

In our analysis of relatedness levels in four chimpanzee groups encompassing a total of 29 community-years, we did not find consistent significantly higher average relatedness among adult community males as compared to females. This result is in contrast to that of Morin *et al.* (1994a), who used a different relatedness estimator and included individuals of all age classes (including possible parent-offspring pairs) in an examination of one community (Gombe) of chimpanzees. However, our current findings are consistent with our earlier analysis (in which age classes were also not considered) of a smaller data set on the Tai communities as well as more recent data from Gombe (Vigilant *et al.* 2001). An interesting result from the perspective of intergroup competition among chimpanzees is that we rarely detected significantly higher relatedness among males of a community as compared to males across communities. Another approach to examining patterns of genetic differentiation among groups, F_{ST} analysis, also did not reveal significant differentiation among males of the different Tai communities. However, the three communities in question were close neighbours, and additional

studies across broader spatial scales are needed. Finally, consideration of cohorts of similarly aged offspring also revealed average relatedness levels only rarely approaching that of half-sibs. The fact that we considered multiple chimpanzee communities with varying demographic characteristics and histories makes it unlikely that our results are due to particularities of certain chimpanzee groups.

Our simulations showed that the unusual system of male philopatry, a feature of two species (chimpanzees and humans) known to have extensive repertoires of cooperative group action, reduces average relatedness as compared to a female philopatric system. This seems to contradict previous results on humans stating that groups tracing descent through the male line will have higher coefficients of group relatedness (Chagnon 1979; Hughes 1988). However, those higher coefficients only reflect the fact that the time to the most recent common ancestor is reduced in the male line due to the higher reproductive skew (e.g. humans Wilder *et al.* 2004). In contrast, our analyses considered the increase in R of a given dyad as compared to a random pair of individuals in the population, and these are higher in female philopatric species. To illustrate this result, assume the most extreme situation in which reproduction in the group is limited to one male, while several females have offspring. In the case of female philopatry, these mothers are likely to be related to some degree and the offspring therefore will in addition to being paternal half-sibs as well be related maternally, while in the case of male philopatry no additional links between offspring exist. Even though our analysis assumed complete sex bias in dispersal, which has been in some exceptional chimpanzee cases observed to be less constrained (Williams *et al.* 2002), relaxation of this factor would not change the difference in relatedness between males and females. In fact, only mating between close relatives would notably increase the average relatedness, but inbreeding avoidance seems to be prevalent in animals studied thus far (Pusey & Wolf 1996).

In addition, the analyses highlight the roles of reproductive output and skew in creating a kin-group. Eusocial animals such as social insects or mole rats can be seen as enlarged families, where nonreproductive offspring and siblings help (Faulkes & Bennett 2001). As previously indicated (Altmann 1979; Chesser 1998; Aviles *et al.* 2004), the low reproductive output of mammals sets a limit to the number of potentially available partners that are kin. Our results converge with recent studies on single groups, which have suggested that kin selection is not the primary reason for animals to group together (Valsecchi *et al.* 2002; Russell *et al.* 2004; Spong & Creel 2004; Van Horn *et al.* 2004; Vucetich *et al.* 2004), and consequently that the group size of a species is not dependent on its family size.

Studies in other taxa in which males affiliate have produced contradictory results on the presence of significant relatedness among clusters of males. Although an influen-

tial work on relatedness and reproductive success among affiliative male lions has been widely taken as evidence for the benefits of kin association for males (Packer *et al.* 1991), new research on multiple prides of lions suggested that relatedness among the males is not necessary for cooperative behaviour (Spong *et al.* 2002). Results for dolphins have been contradictory (no influence of kinship: Moller *et al.* 2001; influence found: Parsons *et al.* 2003). However, a recent dolphin study found significantly higher average relatedness among pairs of individuals participating in long-term alliances consisting of six or fewer individuals as compared to random pairs of individuals, but they did not find this for larger super-alliances and subgrouping, suggesting that different male strategies might explain the apparent contradictions (Krützen *et al.* 2003).

Our study does not address the possibility that a large group of individuals might be substructured into clusters of related, cooperating individuals (e.g. long-tailed macaques, de Ruiter & Geffen 1998). Our results show that the proportion of kin vs. non-kin partners for an individual decreases with increasing group size; however, there are in all cases kin present who could be recruited as potential partners in a dyadic interaction. Some studies have highlighted the structuring of groups into matrilineal and evidence showing that social behaviours are biased accordingly to favour kin (Silk 2002). Evidence is accumulating that paternal relatedness, as indicated by age similarity (Altmann 1979), influences patterns of interaction within social groups (Widdig *et al.* 2001; Smith *et al.* 2003). More data is needed to analyse whether dyadic interactions among chimpanzee males might be influenced by relatedness. However, results thus far suggest that maternal relatives are not preferentially selected for recruitment for activities which involve only two individuals (Goldberg & Wrangham 1997; Mitani *et al.* 2002).

Direct benefits from mutualism have been proposed to play a more important role than kin selection for some cooperative actions, e.g. in the evolution of cooperative breeding in meerkats (Clutton-Brock *et al.* 2002). It is also interesting that behaviours that involve a larger number of individuals would fall into the category of complex behaviours recently suggested as less likely to be driven by kin selection, but rather to be influenced by the relative competences of the potential partners (Chapais & Berman 2004).

A high degree of male cooperation has been suggested to be a common trait of great apes and humans (Rodseth *et al.* 1991). Genetic studies on sex-biased dispersal in humans indicate that male philopatry and female dispersal seems to be the predominant system (Oota *et al.* 2001; but see Wilder *et al.* 2004), while behavioural studies indicate flexibility on the smaller scale (Alvarez 2004; Marlowe 2004). Unfortunately, there seems to be very little data from humans with which to compare our analyses. Even though sociological studies have indicated that kin selection plays a role in shaping sociality, often these analyses have

used the anthropological category of 'kin', which does not necessarily imply recent common genetic ancestry (Rodseth & Wrangham 2004). One of the best data sets on this topic stems from long-term study on the Yanomano people of South America. The most detailed study in the Yanomano population that uses genealogical information on kin in an analysis of 'ax-fight' shows positive kin bias on an interindividual level, which even overrides group membership (Chagnon & Burgos 1979). A study in Indonesia on whale hunting, which necessitates the cooperation of relatively large number of individuals per boat, found no direct choice of kin for the cooperative action, rather just a choice of individuals from the same group, and argued that 'kin selection alone cannot structure cooperation in groups larger than the nuclear family because of the ambiguous group membership it provides' (Alvard 2003). In addition, recent results from experimental economics indicate that 'biological models of self-interested cooperation' which include inclusive fitness benefits through kin selection 'are rarely plausible when they involve groups of more than a few individuals' (Gintis 2004). Instead, findings on the alternative explanation, reciprocity, converge neatly with the observation in chimpanzees, that 'cooperation within a group can make the group more lethally aggressive in its dealing with outsiders' (Seabright 2004). These results, and those presented here, suggest that indirect fitness benefits through gene sharing are not necessarily the primary mechanism driving large group actions in mammals and humans.

Acknowledgements

For research in Tai, we thank the Ivorian authorities for long-term support, especially the Ministry of the Environment and Forests as well as the Ministry of Research, the directorship of the Tai National Park, and the Swiss Research Center in Abidjan. Funding for the Tai Chimpanzee Project was provided by the Swiss National Foundation and the Max Planck Society. Fieldwork at Sonso was conducted with the permission of the Uganda Council for Science and Technology, the President's Office, and the National Forest Authority, Government of Uganda. Funding for chimpanzee research at the Budongo Forest Project was provided from Norwegian support (NORAD) to Makerere University Faculty of Forestry and Nature Conservation and from the National Geographic Society. We thank the many students and field assistants at both sites for logistical support and assistance in sample collection. We thank U. D. Immel for initial attempts at laboratory analysis of the Budongo chimpanzees, and A. Abraham and H. Siedel for assistance in the laboratory. M. Lachmann, K. Langergraber, J. Manson, J. Mitani, N. Newton-Fisher and D. Stahl provided useful discussion and comments on the manuscript. The Max Planck Society also supported this research.

References

Altmann J (1979) Age cohorts as paternal sibships. *Behavioral Ecology and Sociobiology*, **6**, 161–164.

- Altmann J, Alberts SC, Haines SA *et al.* (1996) Behavior predicts genetic structure in a wild primate group. *Proceedings of the National Academy of Sciences of the United States of America*, **93**, 5797–5801.
- Alvard M (2003) Kinship, lineage, and an evolutionary perspective on cooperative hunting groups in Indonesia. *Human Nature*, **14**, 129–163.
- Alvarez H (2004) Residence groups among hunter-gatherers: a view of the claims and evidence for patrilocal bands. In: *Kinship and Behavior in Primates* (eds Chapais B, Berman C). Oxford University Press, Oxford.
- Aviles L, Fletcher J, Cutter A (2004) The kin composition of social groups: trading group size for degree of altruism. *American Naturalist*, **164**, 132–144.
- Balloux F, Goudet J, Perrin N (1998) Breeding system and genetic variance in the monogamous, semi-social shrew, *Crocidura russula*. *Evolution*, **52**, 1230–1235.
- Blundell G, Ben-David M, Groves P, Bowyer R, Geffen E (2002) Characteristics of sex-biased dispersal and gene flow in coastal river otters: implications for natural recolonization of extirpated populations. *Molecular Ecology*, **11**, 289–303.
- Boesch C, Boesch-Achermann H (2000) *The Chimpanzees of the Tai Forest: Behavioural Ecology and Evolution*. Oxford University Press, Oxford.
- Bradley B, Boesch C, Vigilant L (2000) Identification and redesign of human microsatellite markers for genotyping wild chimpanzee (*Pan troglodytes verus*) and gorilla (*Gorilla gorilla gorilla*) DNA from feces. *Conservation Genetics*, **1**, 289–292.
- Brown D (1991) *Human Universals*. McGraw-Hill, New York.
- Burland T, Barratt E, Nichols R, Racey P (2001) Mating patterns, relatedness and the basis of natal philopatry in the brown long-eared bat, *Plecotus auritus*. *Molecular Ecology*, **10**, 1309–1321.
- Chagnon N (1979) Mate competition, favoring close kin, and village fissioning among the Yanomamo Indians. In: *Evolutionary Biology and Human Social Behavior* (eds Chagnon N, Irons W). Duxbury Press, North Scituate, Massachusetts.
- Chagnon N, Burgos P (1979) Kin selection and conflict: an analysis of a Yanomamö ax fight. In: *Evolutionary Biology and Human Social Behavior* (eds Chagnon N, Irons W). Duxbury Press, North Scituate, Massachusetts.
- Chapais B (2001) Primate nepotism: what is the explanatory value of kin selection? *International Journal of Primatology*, **22**, 203–229.
- Chapais B, Berman C (2004) Variation in nepotistic regimes and kin recognition: a major area for future research. In: *Kinship and Behavior in Primates* (eds Chapais B, Berman C). Oxford University Press, Oxford.
- Chesser R (1998) Relativity of behavioral interactions in socially structured populations. *Journal of Mammalogy*, **79**, 713–724.
- Clutton-Brock T, Russell A, Sharpe L *et al.* (2002) Evolution and development of sex differences in cooperative behavior in meerkats. *Science*, **297**, 253–256.
- Coltman D, Pilkington J, Pemberton J (2003) Fine-scale genetic structure in a free-living ungulate population. *Molecular Ecology*, **12**, 733–742.
- Constable J, Ashley M, Goodall J, Pusey A (2001) Noninvasive paternity assignment in Gombe chimpanzees. *Molecular Ecology*, **10**, 1279–1300.
- Dieringer D, Schlötterer C (2003) MICROSATELLITE ANALYSER (MSA): a platform independent analysis tool for large microsatellite data sets. *Molecular Ecology Notes*, **3**, 167.
- Ember C (1978) Myths about hunter-gatherers. *Ethnology*, **17**, 439–448.

- Faulkes C, Bennett N (2001) Family values: group dynamics and social control of reproduction in African mole-rats. *Trends in Ecology & Evolution*, **16**, 184–190.
- Gerloff U, Hartung B, Fruth B, Hohmann G, Tautz D (1999) Intracommunity relationships, dispersal pattern and paternity success in a wild living community of Bonobos (*Pan paniscus*) determined from DNA analysis of faecal samples. *Proceedings of the Royal Society of London. Series B, Biological Sciences*, **266**, 1189–1195.
- Gintis H (2004) Economic interest: do strangers cooperate when they have to work together? (Book Review). *Nature*, **431**, 245–246.
- Goldberg T, Wrangham R (1997) Genetic correlates of social behaviour in wild chimpanzees: evidence from mitochondrial DNA. *Animal Behaviour*, **54**, 559–570.
- Goodall J, Bandora A, Bergmann E *et al.* (1979) Intercommunity interactions in the chimpanzee population of the Gombe National Park. In: *The Great Apes* (eds Hamburg D, McCown E). Benjamin/Cummings, Menlo Park, California.
- Greenwood P (1980) Mating systems, philopatry and dispersal in birds and mammals. *Animal Behaviour*, **28**, 1140–1162.
- Hamilton W (1964) Genetical evolution of social behaviour I. *Journal of Theoretical Biology*, **7**, 1–16.
- Hughes A (1988) *Evolution and Human Kinship*. Oxford University Press, Oxford.
- Kerth G, Safi K, König B (2002) Mean colony relatedness is a poor predictor of colony structure and female philopatry in the communally breeding Bechstein's bat (*Myotis bechsteini*). *Behavioral Ecology and Sociobiology*, **52**, 203–210.
- Kokko H, Mackenzie A, Reynolds JD, Lindström J, Sutherland WJ (1999) Measures of inequality are not equal. *American Naturalist*, **72**, 358–382.
- Krützen M, Sherwin W, Connor R *et al.* (2003) Contrasting relatedness patterns in bottlenose dolphins (*Tursiops* sp.) with different alliance strategies. *Proceedings of the Royal Society of London. Series B, Biological Sciences*, **270**, 497–502.
- Lawler R, Richard A, Riley M (2003) Genetic population structure of the white sifaka (*Propithecus verreauxi verreauxi*) at Beza Mahafaly Special Reserve, southwest Madagascar (1992–2001). *Molecular Ecology*, **12**, 2307–2317.
- Manly B (1997) *Randomization, Bootstrap and Monte Carlo Methods in Biology*. Chapman & Hall, London.
- Marlowe FW (2004) Marital residence among foragers. *Current Anthropology*, **45**, 277–284.
- Marshall TC, Slate J, Kruuk LEB, Pemberton JM (1998) Statistical confidence for likelihood-based paternity inference in natural populations. *Molecular Ecology*, **7**, 639–655.
- Matocq M, Lacey E (2004) Philopatry, kin clusters, and genetic relatedness in a population of woodrats (*Neotoma macrotis*). *Behavioral Ecology*, **15**, 647–653.
- Mitani J, Watts D, Pepper J, Merriwether D (2002) Demographic and social constraints on male chimpanzee behaviour. *Animal Behaviour*, **64**, 727–737.
- Moller L, Beheregaray L (2004) Genetic evidence for sex-biased dispersal in resident bottlenose dolphins (*Tursiops aduncus*). *Molecular Biology and Evolution*, **13**, 1607–1612.
- Moller L, Beheregaray L, Harcourt R, Krutzen M (2001) Alliance membership and kinship in wild male bottlenose dolphins (*Tursiops aduncus*) of southeastern Australia. *Proceedings of the Royal Society of London. Series B, Biological Sciences*, **268**, 1941–1947.
- Morin PA, Moore JJ, Chakraborty R *et al.* (1994a) Kin selection, social structure, gene flow, and the evolution of chimpanzees. *Science*, **265**, 1193–1201.
- Morin PA, Wallis J, Moore JJ, Woodruff DS (1994b) Paternity exclusion in a community of wild chimpanzees using hyper-variable simple sequence repeats. *Molecular Ecology*, **3**, 469–477.
- Morin P, Chambers K, Boesch C, Vigilant L (2001) Quantitative PCR analysis of DNA from noninvasive samples for accurate microsatellite genotyping of wild chimpanzees (*Pan troglodytes verus*). *Molecular Ecology*, **10**, 1835–1844.
- Moritz C, Heideman A, Geffen E, Mcrae P (1997) Genetic population structure of the greater bilby *Macrotis lagotis*, a marsupial in decline. *Molecular Ecology*, **6**, 925–936.
- Newton-Fisher N (1999) Association by male chimpanzees: a social tactic. *Behaviour*, **136**, 705–730.
- Nishida T, Kawanaka K (1972) Inter-unit-group relationships among wild chimpanzees of the Mahale Mountains. *Kyoto University African Studies*, **7**, 131–169.
- Oota H, Setheetham-Ishida W, Tiwawech D, Ishida T, Stoneking M (2001) Human mtDNA and Y-chromosome variation is correlated with matrilineal versus patrilineal residence. *Nature Genetics*, **29**, 20–21.
- Ortega J, Maldonado J, Wilkinson G, Arita H, Fleischer R (2003) Male dominance, paternity, and relatedness in the Jamaican fruit-eating bat (*Artibeus jamaicensis*). *Molecular Ecology*, **12**, 2409–2415.
- Packer C, Gilbert D, Pusey A, O'Brien S (1991) A molecular genetic analysis of kinship and cooperation in African lions. *Nature*, **351**, 562–565.
- Painter J, Crozier R, Poiani A, Robertson R, Clarke M (2000) Complex social organization reflects genetic structure and relatedness in the cooperatively breeding bell miner, *Manorina melanophrys*. *Molecular Ecology*, **9**, 1339–1347.
- Parsons K, Durban J, Claridge D *et al.* (2003) Kinship as a basis for alliance formation between male bottlenose dolphins, *Tursiops truncatus*, in the Bahamas. *Animal Behaviour*, **66**, 185–194.
- Piertney S, MacColl A, Bacon P, Dallas J (1998) Local genetic structure in red grouse (*Lagopus lagopus scoticus*): evidence from microsatellite DNA markers. *Molecular Ecology*, **7**, 1645–1654.
- Pusey A (1979) Intercommunity transfer of chimpanzees in Gombe National Park. In: *The Great Apes* (eds Hamburg D, McCown E). Benjamin/Cummings, Menlo Park, California.
- Pusey A, Wolf M (1996) Inbreeding avoidance in animals. *Trends in Ecology & Evolution*, **11**, 201–206.
- Queller D, Goodnight K (1989) Estimating relatedness using genetic markers. *Evolution*, **43**, 258–275.
- Radespiel U, Sarikaya Z, Zimmermann E, Bruford M (2001) Socio-genetic structure in a free-living nocturnal primate population: sex-specific differences in the grey mouse lemur (*Microcebus murinus*). *Behavioral Ecology and Sociobiology*, **50**, 493–502.
- Reynolds V (2005) *The Chimpanzees of the Budongo Forest: Ecology, Behaviour, and Conservation*. Oxford University Press, Oxford.
- Rodseth L, Wrangham R (2004) Human kinship: a continuation of politics by other means. In: *Kinship and Behavior in Primates* (eds Chapais B, Berman C). Oxford University Press, Oxford.
- Rodseth L, Wrangham R, Harrigan A, Smuts B (1991) The human community as a primate society. *Current Anthropology*, **32**, 221–254.
- Rossiter S, Jones G, Ransome R, Barratt E (2002) Relatedness structure and kin-biased foraging in the greater horseshoe bat (*Rhinolophus ferrumequinum*). *Behavioral Ecology and Sociobiology*, **51**, 510–518.
- de Ruiter J, Geffen E (1998) Relatedness of matrilineal, dispersing males and social groups in long-tailed macaques (*Macaca fascicularis*). *Proceedings of the Royal Society of London. Series B, Biological Sciences*, **265**, 79–87.
- Russell S, Kelley J, Graves J, Magurran A (2004) Kin structure and

- shoal composition dynamics in the guppy, *Poecilia reticulata*. *Oikos*, **106**, 520–526.
- Schulte-Hostedde A, Gibbs H, Millar J (2001) Microgeographic genetic structure in the yellow-pine chipmunk (*Tamias amoenus*). *Molecular Ecology*, **10**, 1625–1631.
- Seabright P (2004) *The Company of Strangers: A Natural History of Economic Life*. Princeton University Press, Princeton, New Jersey.
- Silk J (2002) Kin selection in primate groups. *International Journal of Primatology*, **23**, 849–875.
- Smith K, Alberts S, Altmann J (2003) Wild female baboons bias their social behaviour towards paternal half-sisters. *Proceedings of the Royal Society of London. Series B, Biological Sciences*, **270**, 503–510.
- Spong G, Creel S (2004) Effects of kinship on territorial conflicts among groups of lions, *Panthera leo*. *Behavioral Ecology and Sociobiology*, **55**, 325–331.
- Spong G, Stone J, Creel S, Bjorklund M (2002) Genetic structure of lions (*Panthera leo* L.) in the Selous Game Reserve: implications for the evolution of sociality. *Journal of Evolutionary Biology*, **15**, 945–953.
- SurrIDGE A, Ibrahim K, Bell D *et al.* (1999) Fine-scale genetic structuring in a natural population of European wild rabbits (*Oryctolagus cuniculus*). *Molecular Ecology*, **8**, 299–307.
- Valsecchi E, Hale P, Corkeron P, Amos W (2002) Social structure in migrating humpback whales (*Megaptera novaeangliae*). *Molecular Ecology*, **11**, 507–518.
- Van Horn R, Engh A, Scribner K, Funk S, Holekamp K (2004) Behavioural structuring of relatedness in the spotted hyena (*Crocuta crocuta*) suggests direct fitness benefits of clan-level cooperation. *Molecular Ecology*, **13**, 449–458.
- Vigilant L, Hofreiter M, Siedel H, Boesch C (2001) Paternity and relatedness in wild chimpanzee communities. *Proceedings of the National Academy of Sciences of the United States of America*, **98**, 12890–12895 (published online before print 23 October 2001).
- Vucetich J, Peterson R, Waite T (2004) Raven scavenging favours group foraging in wolves. *Animal Behaviour*, **67**, 1117–1126.
- Watts D, Mitani J (2001) Boundary patrols and intergroup encounters in wild chimpanzees. *Behaviour*, **138**, 299–327.
- Watts D, Mitani J (2002) Hunting behavior of chimpanzees at Ngogo, Kibale National Park, Uganda. *International Journal of Primatology*, **23**, 1–28.
- Weir B, Cockerham C (1984) Estimating *F*-statistics for the analysis of population structure. *Evolution*, **38**, 1358–1370.
- West S, Pen I, Griffin A (2002) Cooperation and competition between relatives. *Science*, **296**, 72–75.
- Widdig A, Nurnberg P, Krawczak M, Streich W, Bercovitch F (2001) Paternal relatedness and age proximity regulate social relationships among adult female rhesus macaques. *Proceedings of the National Academy of Sciences of the United States of America*, **98**, 13769–13773.
- Wilder J, Mobasher Z, Hammer M (2004) Genetic evidence for unequal effective population sizes of human females and males. *Molecular Biology and Evolution*, **21**, 2047–2057.
- Williams J, Pusey A, Carlis J, Farm B, Goodall J (2002) Female competition and male territorial behaviour influence female chimpanzees' ranging patterns. *Animal Behaviour*, **63**, 347–360.
- Wimmer B, Kappeler P (2002) The effects of sexual selection and life history on the genetic structure of redfronted lemur, *Eulemur fulvus rufus*, groups. *Animal Behaviour*, **64**, 557–568.
- Wrangham R (1979) On the evolution of ape social systems. *Social Science Information*, **3**, 335–368.
- Wright S (1951) The genetical structure of populations. *Annals of Eugenics*, **15**, 323–354.
- Wright S (1965) The interpretation of population structure by *F*-statistics with special regard to systems of mating. *Evolution*, **19**, 395–420.

D. Lukas performed the analyses of the chimpanzee data and the mathematical derivations as part of his PhD on understanding the consequences of social structure on genetic variation. V. Reynolds and C. Boesch are field researchers interested in the behavioural ecology of chimpanzees and other primates and the use of genetic techniques to produce data relevant to the understanding of social behaviour. L. Vigilant is interested in using genetic analyses in combination with observational data to address topics such as the distribution of paternity or patterns of relatedness among individuals in primate social groups and the implications for the evolution of social behaviour.

Appendix I

List of individuals including names, sex, group, year of birth (YOB), year of death (YOD) and genotypes at nine microsatellite loci. In addition, some summary statistics for the nine loci are presented (number of alleles per loci, observed heterozygosity). The calculations were done separately for the two populations (Tai and Sonso) using *CERVUS* version 2.0 (Marshall *et al.* 1998)

Indiv	Group	Sex	YOB	YOD	D2s1326	D7s817	D5s1470	D7s2204	D9s910	D2s1329	D11s200	2D12s66	vwf
Ali	North	M	1979	1992	203/203	148/136	186/174	172/164	113/107	186/178	160/152	154/150	128/124
Brutus	North	M	1951	1997	198/194	132/156	174/178	152/164	116/107	178/170	148/160	158/178	132/132
Darwin	North	M	1969	1993	203/215	156/132	190/174	168/168	113/110	186/154	168/144	154/150	136/128
Macho	North	M	1964	1999	178/182	128/136	190/182	164/160	116/110	186/178	168/148	158/158	128/124
Kendo	North	M	1969	1994	211/215	124/136	174/190	168/172	110/113	154/198	148/148	150/162	124/128
Fitz	North	M	1975	1994	194/211	124/152	178/190	168/172	116/116	178/198	148/152	154/154	124/128
Marius	North	M	1982		178/211	128/124	186/186	152/168	113/122	186/186	148/144	158/154	136/128
Nino	North	M	1988		203/207	156/128	190/178	168/168	101/113	198/154	168/152	150/150	136/132
Belle	North	F	1976		203/211	140/120	182/178	168/176	116/107	198/186	160/148	154/150	128/124
Beye	North	M	1999		211/211	128/140	178/186	168/176	116/122	186/186	160/144	154/158	128/128
Bijou	North	F	1975	1994	178/182	124/144	182/186	160/172	113/116	154/178	144/144	158/158	124/132
Bambou	North	M	1989	1991	203/182	144/156	182/190	168/172	113/116	154/178	/	154/158	124/128
Castor	North	F	1976	1999	198/203	128/120	186/186	168/168	116/116	206/202	164/148	178/150	128/128
Dilly	North	F	1978	1999	198/203	120/152	182/182	172/176	110/119	182/186	160/172	142/158	128/128
Dorry	North	F	1991	2001	198/211	120/124	182/190	172/168	110/119	182/154	148/172	142/162	128/128
Fanny	North	F	1969	1994	178/223	128/136	186/194	168/156	110/122	186/194	144/144	150/154	128/136
Manon	North	F	1987	1992	/	128/124	186/190	168/172	110/113	186/154	/	/	128/136
Fossey	North	F	1979		198/194	152/124	186/186	172/168	119/113	202/186	160/148	158/154	128/128
Fedora	North	F	1993		198/211	124/124	190/186	172/168	119/116	202/198	148/148	154/154	128/124
Faust	North	M	1999		182/194	136/152	182/186	164/172	110/119	186/178	148/148	158/158	124/128
Goma	North	F	1973	2001	174/186	148/136	186/174	164/160	116/113	186/182	160/144	154/158	128/128
Gargantu	North	M	1991	2001	186/198	156/136	186/174	164/152	116/116	186/178	160/144	158/158	132/128
Gisele	North	F	1996	2001	178/186	128/148	182/174	160/160	116/113	186/178	160/148	158/158	128/128
Gitane	North	F	1949	1994	/	124/120	182/186	168/176	116/116	/	144/164	150/158	116/124
Hector	North	M	1990	1996	203/207	136/144	170/190	156/172	/	/	148/156	162/150	124/128
Kana	North	F	1987	1998	178/190	120/136	186/190	164/172	116/119	178/182	152/168	158/158	128/136
Lefkas	North	M	1991	1999	194/215	152/136	190/174	172/156	113/116	186/154	148/148	154/150	124/124
Leonardo	North	M	1997	1999	178/194	152/136	190/174	172/164	113/110	202/178	164/148	170/158	128/124
Loukoum	North	F	1972	1999	194/198	152/148	178/174	172/156	113/116	202/186	164/148	170/154	128/124
Mystere	North	F	1975		207/215	148/140	186/182	168/164	122/107	182/154	164/148	154/146	136/124
Mognie	North	F	1990		215/215	124/140	190/182	168/168	122/113	198/182	164/148	150/146	136/128
Mozart	North	M	1995		178/215	148/136	190/182	164/164	116/107	186/154	168/148	158/146	128/124
Narcisse	North	F	1983		219/207	148/124	190/178	176/156	113/107	178/154	148/144	150/150	124/124
Noureyev	North	M	1997		178/207	128/124	190/182	160/156	110/107	186/154	168/144	158/150	124/124
Ondine	North	F	1954	1992	182/194	152/140	178/190	156/172	119/116	182/206	144/148	158/158	124/132
Sirene	North	F	1987	1999	178/194	140/128	190/182	160/156	119/110	186/182	168/148	158/158	128/124
Ovide	North	M	1992	1992	211/194	136/140	178/190	156/172	113/116	154/206	148/148	150/158	124/132
Perla	North	F	1976		178/211	152/144	174/170	172/168	113/116	182/182	152/148	158/158	128/128
Pandora	North	F	1995		178/178	152/128	186/170	172/168	122/116	186/182	148/148	158/154	128/128
Porthos	North	M	2000		178/178	128/144	174/186	168/172	113/113	182/186	148/152	154/158	128/136
Ricci	North	F	1963	1999	207/207	128/144	178/190	168/168	101/113	154/198	152/168	150/150	132/124
Roxanne	North	F	1994		194/207	128/124	190/178	168/168	113/116	198/178	168/148	154/150	128/124
Venus	North	F	1978		178/211	144/136	186/186	188/176	122/113	182/154	156/148	154/154	128/128
Volta	North	F	2002		211/211	124/144	186/186	152/176	122/122	182/186	144/148	154/154	128/136
Vanille	North	F	1991		211/211	144/136	190/186	188/172	122/110	198/182	148/148	162/154	128/128
Violetta	North	F	1997		211/211	144/128	186/186	168/176	122/113	186/182	144/148	158/154	136/128
Xeres	North	F	1970	1992	182/203	124/152	182/186	172/172	113/116	186/186	148/148	150/150	128/136
Jessica	Middle	F	1972		215/178	120/120	190/186	172/164	113/113	182/186	160/144	150/146	128/128
Joanine	Middle	F	1999		215/211	124/120	190/182	172/164	113/107	186/186	160/148	154/146	128/124
Kady	Middle	F	1966	2001	178/207	148/128	174/186	168/168	116/116	182/182	164/144	154/150	128/124
Koulo	Middle	F	1991	2002	219/207	148/128	182/186	168/156	116/116	182/154	152/144	154/158	128/128
Kassiopé	Middle	F	2000	2001	174/207	128/148	170/186	168/196	116/116	182/186	164/152	146/150	124/124
Nadesh	Middle	F	1962		203/190	128/124	174/170	172/160	116/113	186/154	152/144	158/146	136/124
Nelly	Middle	F	1989	2001	207/203	128/124	182/170	168/160	113/113	202/154	168/144	174/146	124/124
Noah	Middle	M	1995	2002	203/203	124/124	174/170	172/164	116/107	186/154	152/148	158/150	136/124
Leo	Middle	M	1983		203/174	128/124	182/170	196/160	116/113	186/154	152/152	150/146	132/124

Appendix I *Continued*

Indiv	Group	Sex	YOB	YOD	D2s1326	D7s817	D5s1470	D7s2204	D9s910	D2s1329	D11s200	2D12s66	<i>uvf</i>
Urs	Middle	M	1967	2001	211/203	156/124	182/170	168/164	107/101	186/154	152/148	154/150	124/124
Bob	Middle	M	1978		211/203	124/124	182/190	172/148	116/113	186/202	152/168	158/158	128/128
Joe	Middle	M	1977	1998	203/215	124/120	186/194	168/172	116/116	154/198	144/160	154/178	124/128
Atra	South	F	1981		178/223	124/148	174/182	164/172	107/113	154/202	148/152	154/170	124/124
Alina	South	F	1995	2001	203/223	152/148	182/182	176/172	107/113	154/202	144/148	154/158	124/128
Athena	South	F	1999		178/223	152/148	182/182	172/176	107/119	202/202	148/148	158/170	124/132
Besar	South	M	1989		178/182	120/124	190/190	160/164	107/113	154/186	148/164	154/158	124/128
Coco	South	F	1980		203/211	152/152	186/190	156/168	107/113	186/186	148/164	154/158	128/128
Celine	South	F	1995		207/211	152/144	186/190	156/164	107/119	186/186	172/164	154/158	128/128
Duna	South	F	1974		182/178	140/140	186/182	172/172	119/110	186/154	164/144	154/146	132/128
Eva	South	F	1967	2002	203/182	152/124	182/174	164/164	119/116	198/186	148/144	158/158	124/124
Endora	South	F	1991		223/182	144/124	182/170	168/164	119/119	186/186	168/144	158/158	128/124
Garuda	South	F	1975	2002	207/178	144/120	190/174	164/156	119/113	186/182	172/152	158/154	128/124
Gogol	South	M	1991		203/178	120/120	182/174	168/156	116/113	182/170	172/152	158/154	128/128
Haraka	South	F	1975	2001	194/194	124/128	174/182	172/164	107/113	182/198	144/152	158/178	128/128
Huxel	South	M	1996		194/178	128/136	174/174	172/176	107/113	182/178	144/164	158/154	128/128
Isha	South	F	1970		182/178	140/124	186/186	172/164	116/113	182/182	164/164	154/150	128/128
Inousha	South	F	1995		178/194	124/140	182/186	156/172	107/116	178/182	164/168	150/158	128/128
Ibrahim	South	M	2000		194/182	136/140	182/186	172/172	113/107	182/202	164/164	154/154	128/128
Julia	South	F	1970		190/203	124/152	170/186	168/168	113/113	154/190	152/152	150/178	132/136
Jacobo	South	M	1998		190/211	124/124	170/174	168/172	101/113	198/190	152/152	150/170	128/136
Kabisha	South	F	1977	2002	203/219	120/156	174/182	168/168	101/107	154/182	144/152	150/154	128/128
Kinshasa	South	F	1990		219/219	152/120	186/174	172/168	113/107	182/154	164/144	158/154	128/128
Kuba	South	M	1996		219/194	152/120	174/174	168/176	107/107	178/154	164/152	154/150	128/128
Louise	South	F	1980		211/207	152/124	182/178	168/168	116/107	186/154	164/144	182/158	136/128
Linus	South	M	1993		182/207	140/152	178/186	164/168	107/116	182/186	144/168	154/158	128/136
Lukas	South	M	1998	2002	207/207	144/152	170/182	164/168	119/116	154/186	144/172	158/158	128/128
Mandy	South	F	1967	2001	215/178	152/148	190/182	172/152	116/113	202/154	152/144	174/154	132/132
Max	South	M	1995	2001	178/207	128/152	190/186	172/172	116/119	202/186	152/148	158/154	128/132
Margot	South	F	1975	2002	182/203	152/152	174/190	168/168	107/113	182/186	160/168	150/158	124/128
Mustapha	South	M	1995		203/182	152/148	190/182	176/168	113/107	202/182	160/144	158/158	128/128
Olivia	South	F	1973		174/190	124/152	182/170	172/172	107/113	154/186	152/148	146/154	124/136
Olduvai	South	M	1994	2002	190/198	152/128	170/182	172/164	116/113	182/154	148/148	154/146	124/124
Oreste	South	M	1998		174/211	128/152	182/182	172/176	116/107	154/198	148/152	170/154	124/128
Rubra	South	F	1970		182/203	124/128	186/190	164/168	107/116	178/190	144/152	150/162	128/128
Rebecca	South	F	1995		182/182	124/128	178/190	164/168	107/116	178/182	152/168	154/162	128/128
Romario	South	M	1999		182/207	124/144	170/186	164/164	107/107	186/190	144/172	150/158	128/128
Sumatra	South	F	1965		203/215	140/136	182/186	156/168	113/116	178/198	168/164	150/158	124/132
Sagu	South	M	1989		215/182	136/144	186/182	172/156	116/116	186/178	164/168	158/150	124/124
Settut	South	F	1996		203/207	128/136	170/186	168/172	107/116	178/186	148/164	158/158	124/128
Tita	South	F	1975	2000	194/178	144/128	174/178	164/168	116/116	186/186	148/160	158/150	136/128
Taboo	South	M	1992		194/178	152/128	182/178	176/168	116/107	186/182	168/160	158/150	136/128
Totem	South	M	1992	1999	215/203	140/136	190/182	188/164	116/107	186/186	164/164	154/150	128/128
Utan	South	M	1994		211/194	124/120	174/174	168/164	116/110	198/154	164/160	158/150	132/128
Virunga	South	F	1965		194/194	148/144	186/170	168/156	113/113	198/186	168/160	178/154	128/128
Voltaire	South	M	1999		194/215	144/136	182/186	156/156	113/116	186/178	164/168	154/150	124/128
Wapi	South	F	1970		178/203	136/124	186/186	164/176	107/116	154/198	164/152	150/158	144/144
Woodstoc	South	M	1994		178/194	136/152	186/186	164/176	107/116	154/202	164/168	158/158	144/128
Yucca	South	F	1970		198/178	136/120	198/178	172/172	122/113	198/186	152/144	158/150	128/124
Yoghiti	South	M	1990	2002	203/198	136/120	198/190	160/172	113/107	198/186	164/152	158/158	128/124
Yao	South	M	1995		194/198	152/136	182/178	172/176	113/119	178/186	148/144	158/158	132/128
Zita	South	F	1996	2001	203/194	136/124	190/174	172/168	107/107	186/178	148/144	154/150	132/124
Zora	South	F	1957		203/203	152/124	190/174	172/168	113/107	186/154	168/144	158/150	124/136
Zyon	South	M	1964		178/194	152/136	174/182	176/172	119/107	202/178	148/164	158/154	128/132
Rafiki	South	M	1979	1998	211/182	128/120	182/174	172/156	116/113	186/170	148/144	150/150	128/128
Kaos	South	M	1977		207/207	144/128	186/170	172/164	119/107	186/186	172/148	158/158	128/128
Mkubwa	South	M	1959	1999	223/207	144/128	186/170	168/168	119/116	202/186	168/156	150/158	128/128
Natan	South	M	1960	1997	178/203	120/124	182/182	168/168	116/116	186/186	148/160	154/158	128/128
Black	Sonso	M	1975		203/203	120/124	178/182	144/168	104/110	182/186	148/156	146/154	116/116
Bwoya	Sonso	M	1967	2001	190/215	120/140	174/178	144/184	104/107	182/190	152/152	138/154	120/140

Appendix I *Continued*

Indiv	Group	Sex	YOB	YOD	D2s1326	D7s817	D5s1470	D7s2204	D9s910	D2s1329	D11s200	2D12s66	<i>vwf</i>
Duane	Sonso	M	1965		203/203	124/124	174/186	180/184	116/116	182/186	144/152	146/158	116/140
Jambo	Sonso	M	1975		194/203	124/124	178/194	176/184	116/119	182/182	144/160	142/154	116/120
Maani	Sonso	M	1960		203/211	120/124	178/182	168/184	116/116	178/186	140/144	142/142	116/128
Muga	Sonso	M	1976	2000	190/207	112/124	174/182	144/172	110/116	178/186	144/152	154/154	116/128
Nkojo	Sonso	M	1970		190/190	124/124	178/186	176/180	116/116	186/186	144/152	142/142	116/116
Tinka	Sonso	M	1959		198/211	120/124	174/186	184/184	116/116	186/186	144/152	150/158	116/120
Vernon	Sonso	M	1967	1999	198/203	116/124	178/190	168/184	116/116	174/182	144/148	158/158	116/116
Kikunku	Sonso	M	1977	1998	194/211	124/140	178/182	144/184	/	178/182	148/152	142/142	140/144
Magosi	Sonso	M	1972	1999	203/207	120/124	182/194	144/180	104/116	186/186	/	142/154	116/120
Zesta	Sonso	M	1981	1998	211/211	124/140	174/182	144/164	116/116	178/186	144/148	142/142	116/136
Nambi	Sonso	F	1965		/	112/120	174/194	172/176	110/116	178/186	152/148	142/154	140/128
Andy	Sonso	M	1985	2000	190/211	120/124	174/178	172/172	110/116	178/182	144/152	142/142	120/140
Nora	Sonso	F	1995		190/203	112/120	182/194	168/172	104/110	182/186	148/148	142/154	116/128
Musa	Sonso	M	1994		190/207	112/120	174/182	144/176	104/110	186/186	148/152	142/142	116/140
Kalema	Sonso	F	1982		194/215	116/140	174/178	144/144	104/116	182/186	152/152	142/154	136/140
Bahati	Sonso	F	1994		203/215	120/140	174/182	144/168	104/116	182/186	152/156	146/154	116/136
Kumi	Sonso	M	1999		194/203	124/140	174/178	144/184	116/116	182/186	152/152	142/146	136/140
Zefa	Sonso	M	1983		190/203	124/136	174/186	176/180	110/116	186/186	144/152	142/142	116/136
Shida	Sonso	F	1990		203/203	124/136	174/190	180/180	110/116	182/186	144/148	142/146	116/116
Hawa	Sonso	M	1994		203/211	120/124	178/182	180/184	116/116	174/178	148/148	142/142	140/140
Kigere	Sonso	F	1966		190/203	116/120	182/190	176/176	116/116	174/178	148/152	158/158	140/140
Keti	Sonso	F	1998		190/203	116/124	174/190	176/180	116/116	174/182	148/152	146/158	116/140
Kutu	Sonso	F	1982		203/207	116/124	182/198	144/172	116/116	182/182	152/152	138/142	116/136
Kato	Sonso	M	1993		207/211	116/124	178/198	144/172	116/116	182/182	144/152	138/142	116/116
Kana	Sonso	F	1998		203/207	116/124	182/198	144/144	104/116	182/182	152/156	142/154	116/136
Kwera	Sonso	F	1975		198/203	112/124	178/182	168/180	116/116	174/182	144/148	142/146	116/116
Kwezi	Sonso	M	1995		203/207	112/124	174/182	168/172	116/116	/	144/144	142/154	116/128
Karo	Sonso	F	2000		198/211	112/120	178/182	168/168	116/116	178/182	144/148	142/142	116/116
Ruda	Sonso	F	1966	2001	203/211	120/124	178/182	172/180	116/116	178/182	152/152	154/158	116/128
Bob	Sonso	M	1990		203/198	120/124	182/182	172/184	116/116	182/182	144/152	146/154	128/144
Rachel	Sonso	F	1997	2001	190/211	120/124	182/186	176/180	116/116	182/186	144/152	142/158	116/128
Ruhara	Sonso	F	1962		203/203	120/124	178/182	180/180	116/116	178/178	148/152	150/154	116/120
Rose	Sonso	F	1997		203/203	124/124	174/178	180/180	116/116	178/182	144/148	150/158	116/116
Nick	Sonso	M	1986		203/207	120/124	178/182	144/180	104/116	178/186	152/152	142/150	120/120
Zana	Sonso	F	1962		207/219	116/120	178/186	176/184	116/116	178/186	152/152	150/158	116/120
Zalu	Sonso	M	1995		207/211	116/124	174/186	176/184	116/116	178/182	148/152	142/150	116/120
Zimba	Sonso	F	1966		190/203	112/120	182/190	144/172	110/116	182/186	148/152	150/178	116/120
Gonza	Sonso	F	1989		203/207	120/120	182/194	144/144	104/116	182/186	152/152	142/150	116/120
Zig	Sonso	M	1997		190/207	120/120	190/194	144/144	104/110	182/186	148/152	142/150	116/120
Kewaya	Sonso	F	1983		190/211	120/124	174/190	172/172	110/116	182/186	144/148	142/178	116/116
Katia	Sonso	F	1998		211/211	120/140	174/182	172/184	110/116	178/182	144/152	142/142	116/140
Mukwano	Sonso	F	1969		207/211	116/120	182/194	144/184	116/116	178/186	152/156	142/178	136/140
Gershom	Sonso	M	1983		190/203	120/124	178/186	144/180	116/116	186/190	148/152	142/142	116/116
Emma	Sonso	F	1990	2001	203/211	120/124	174/174	144/176	116/116	182/182	144/152	142/142	116/120
Bwoba	Sonso	M	1986		207/211	116/120	174/194	144/168	104/116	174/186	152/152	142/142	116/140
Mark	Sonso	M	2000		194/203	112/124	190/190	144/172	110/110	174/186	152/156	154/178	124/140
Janet	Sonso	F	1998		203/207	120/124	174/182	180/180	116/116	182/186	152/152	142/158	116/124

Summary statistics for the nine loci

	Average	D2s1326	D7s817	D5s1470	D7s2204	D9s910	D2s1329	D11s200	2D12s66	<i>vwf</i>
Number of alleles per locus										
Tai	10.33	13	12	8	13	8	11	9	11	8
Sonso	6.44	8	6	7	7	5	5	6	7	7
Observed heterozygosity										
Tai	0.786	0.844	0.908	0.871	0.773	0.702	0.831	0.806	0.722	0.620
Sonso	0.746	0.833	0.878	0.939	0.735	0.438	0.750	0.729	0.673	0.735

Appendix II

Here we illustrate how we derived the average relatedness within one group of individuals. These calculations only consider the relationship between individuals within one generation.

The formula aims at deriving average relatedness in a group of individuals, so the basic approach is to analyse how many of the pairwise relationships between any two individuals in the group have a specific value.

First, individuals can be related by sharing the same parent. Per set of n siblings we obtain $n \times (n-1)/2$ links. For the whole group we have to sum all these pairs n, m, \dots and divide by the total number of possible dyads $n + m + \dots = x$

$$\begin{aligned} & \rightarrow \frac{\frac{n \times (n-1)}{2} + \frac{m \times (m-1)}{2} + \dots}{\frac{x \times (x-1)}{2}} \\ & = \frac{n^2 - n + m^2 - m + \dots}{x \times (x-1)} = \frac{n^2 + m^2 + \dots - x}{x \times (x-1)} \end{aligned}$$

To simplify, the actual number of siblings for each parent is replaced by his relative share

$$\begin{aligned} n &= i \times x, m = j \times x, \dots; 0 < i, j < 1; i + j + \dots = 1 \\ & \rightarrow \frac{(i \times x)^2 + (j \times x)^2 + \dots - x}{x \times (x-1)} = \frac{(i^2 + j^2 + \dots) \times x - 1}{x-1} \end{aligned}$$

For the calculation, we assume the simplifying situation in which the incoming, dispersing individuals are not related among each other or to the philopatric individuals. We can then simplify the formula by summing up over all philopatrics (where reproductive success now is summarized by taking $p = i^2 + j^2 + \dots; 0 < p < 1$) and for dispersers

($d = a^2 + b^2 + \dots, 0 < d < 1$). If there is complete sex bias in dispersal, as assumed in the paper, p and d can be replaced by the values for the females and the males, respectively. In addition however, individuals who do not share a parent can be related if their respective parents are related. With the assumption as before, this can only occur among philopatric individuals. We therefore have to add only one term, where we take all the dyads that are not sharing the same parent and the average relatedness

$$\left[1 - \frac{(i^2 + j^2 + \dots) \times x - 1}{x-1} \right] \times R$$

To obtain actual relatedness values, all of the three terms have to be multiplied by 0.25, the value for half-sibs.

$$\begin{aligned} \rightarrow R &= \frac{p \times x - 1}{x-1} \times 0.25 + \frac{d \times x - 1}{x-1} \times 0.25 \\ &+ \left(1 - \frac{p \times x - 1}{x-1} \right) \times R \times 0.25 \end{aligned}$$

Since the R over generations is recursive, the formula is just solved for R :

$$4R - \left(1 - \frac{d \times x - 1}{x-1} \right) \times R = \frac{p \times x - 1}{x-1} + \frac{d \times x - 1}{x-1} \Leftrightarrow$$

$$R \times \left(3 + \frac{d \times x - 1}{x-1} \right) = \frac{(p+d) \times x - 2}{x-1} \Leftrightarrow$$

$$R \times \left(\frac{3 \times x - 3 + d \times x - 1}{x-1} \right) = \frac{(p+d) \times x - 2}{x-1} \Leftrightarrow$$

$$R = \frac{(p+d) \times x - 2}{(3+d) \times x - 4}$$