Relatedness of matrilines, dispersing males and social groups in long-tailed macaques (*Macaca fascicularis*)

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Genealogical relatedness is thought to be an important causal factor in the evolution of cooperation. We inferred relatedness on the basis of 11 blood protein markers using the Queller and Goodnight index of relatedness in a macaque population with long-term demographic records. This estimate reflected independently determined pedigree relationships in our data set. Mean relatedness among all members of a social group was 0.10 but much higher levels of relatedness (0.30–0.47) were found among the members of matrilineal families with a high or intermediate social rank. Groups of dispersing males that had been born into the same social group were sometimes closely related (0.43 and 0.58), but they could also be less related (0.08). We found that the pattern of distribution of relatedness was associated with gene flow and differential reproduction in males, rather than with group fission and the presence of geographical barriers.

Keywords: dispersal; paternity; matriline; relatedness; macaque; geographic barrier

1. INTRODUCTION

Extensive field studies of the behaviour of long-tailed macaques (*Macaca fascicularis* Raffles 1821) have shown that related animals, particularly females, associate and cooperate (e.g. Van Schaik & Van Noordwijk 1988). Such association and cooperation among kin has been described in many primate species. Indeed the social structure of primate groups is generally thought to be based, to a large extent, on kinship relations (Moore 1992; Van Hooff & Van Schaik 1992).

In many 'female-bonded' species (Wrangham 1980), females and their offspring are organized within a group along lines of female kinship, i.e. matrilines. All members of a certain matriline are generally dominant over all members of a lower rank matriline. It is believed that such a familial division in the social hierarchy arises because members of a certain matriline support each other in conflicts (e.g. Lee 1987; Pereira 1995). Furthermore members of a matriline are also more tolerant amongst themselves in competition over resources (Walters & Seyfarth 1987). In such female-bonded species, males migrate at puberty. In contrast, in male-bonded species such as chimpanzees, it is predominantly the females who migrate, and close cooperation has been observed mostly among males, rather than among females. This cooperation has typically been explained by

the presumed high degree of genealogical relatedness among the males of a social group (Goodall 1986; De Waal 1982). Also, in species where males disperse, evidence exists that males support each other when they are related (bonnet macaques: Silk 1992) and that related cooperating males indeed have a relatively higher reproductive success (red howler monkeys: Pope 1990).

However, the underlying factors which explains the high degree of cooperativeness and seemingly altruistic behaviour among relatives are not known. The primary causal factors are thought to be kin selection (Hamilton 1964), or reciprocal altruism on the basis of familiarity (Trivers 1971; Noë 1990; Noë *et al.* 1991). Zahavi (1995) recently proposed that altruism as a handicap could yield direct benefits to the altruistic individual due to increased social status resulting from this behaviour. Here again, a correlation with kinship would result from familiarity among kin, rather than from shared genes. To be able to decide between these three alternatives we must quantify genealogical relationships in social groups.

Relatedness data is also required for a further analysis of the proximate mechanisms involved, for instance, to determine the cues used to identify close relatives.

It is not easy to analyse kinship in wild populations since pedigrees are unknown. The long life span of most primates results in the slow accumulation of demographic data. Second, dispersal and migration are common and individuals can be difficult to follow. Third, paternity is unknown unless genetic tests are performed. Relatedness estimates are, therefore, still rare in the primate literature. Therefore, the possibility to estimate genealogical relatedness from genetic data is an important new tool.

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We address the following questions in this paper. (1) Do our relatedness estimates reflect kinship as known from pedigree data? (2) How is relatedness distributed within the population (including, social groups, matrilines, age/sex classes and dispersing males)? (3) Which aspects of the demographic structure influence the pattern of relatedness (dispersal, skewed male reproduction, group fission and geographical barriers)? (4) On the basis of the distribution of relatedness, what are the expectations with respect to cooperation and kin selection?

Several studies have been published in mammals where relatedness of males and females have been estimated (e.g. chimpanzees, Morin *et al.* 1994; savannah baboons, Altmann *et al.* 1996; and African wild dog, Girman *et al.* 1997). In two of these studies relatedness differences between the two sexes were in the expected direction: chimpanzees had a higher relatedness among males, and baboons had a higher relatedness among females. In wild dogs, both sexes disperse, though at different ages, but both sexes were found to be highly related. This could only be explained if dispersing individuals migrated into groups where relatives of the same sex were already present.

For long-tailed macaques, we expected adult males to have a lower average relatedness, compared to adult females and juveniles. This is because adult males immigrate from other groups, whereas females and juveniles remain in their natal group. But adult males are expected to be related to some extent as well because our long-term data indicate that males often disperse with peers and that the males of a particular group often disperse into one particular (adjacent) group for a number of consecutive years. Such groups of dispersing peers are, therefore, expected to be related at about the level of the juveniles in a group.

With respect to average relatedness within matrilines and groups, we expected larger units to be less related than smaller ones. We expected relatedness between matrilines to be higher if these were part of the same social group because they may share paternal genes. We expected matrilines in different groups to be more related if they were on one side of the river. We predicted this because groups are formed by the fission of a large group, and females and offspring, in contrast to males, were not expected to cross the large river that flowed through the study area. This expectation was confirmed with three observed group fissions.

2. MATERIAL AND METHODS

(a) *The natural macaque population at Ketambe, Sumatra*

Long-tailed macaques live in the Sumatran lowland rain forest bordering rivers. They live in stable social groups of between eight and 60 individuals. These groups contain about equal numbers of individuals from either sex and about as many juveniles as adults. Each macaque social group occupies an exclusive home range of about 50 ha. A number of these groups have been observed since 1976 (Van Noordwijk & Van Schaik 1985, 1988). Individuals could be recognized, and records have been kept on births, migrations and deaths, disappearances and the occupation of the different rank positions. For the sizes and compositions of the groups in this study, see figure 1 and De Ruiter (1992). All males, but only
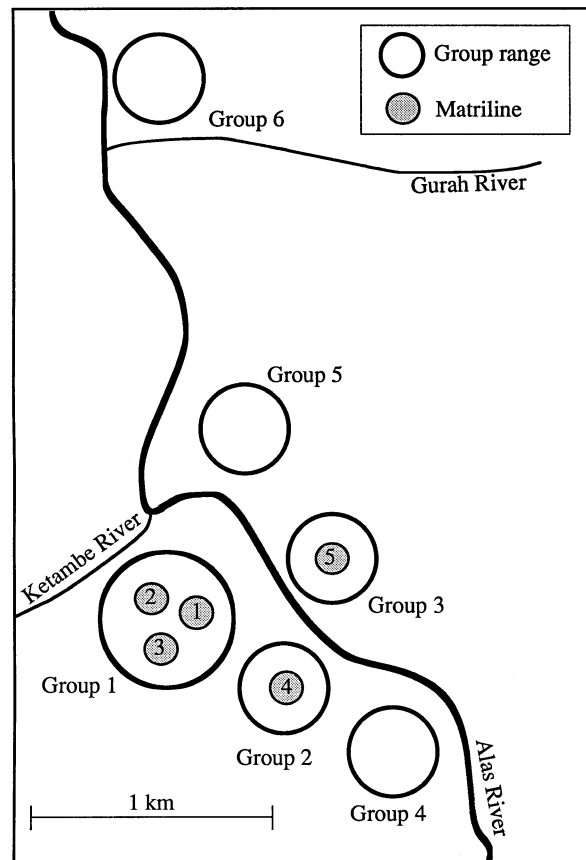

Figure 1. Map of the study area. Positions of the different social groups in relation to each other and to the rivers are indicated by open circles. Rivers contained water throughout the year and restricted ranging behaviour. However, even the Alas river, the largest river in Sumatra, was no serious impediment to dispersing males, who were able to swim across. One of the main study groups, group 1, was relatively large and could be subdivided into three maternally related families or matrilines. In the two smaller main study groups (2 and 3) the natal part, comprising all individuals except for the immigrant adult males, were considered as a single matriline (see text). Matrilines are indicated by the smaller grey circles. Group sizes were as follows: group 1, 48–53 individuals; group 2, 16–20 individuals; group 3, 16–18 individuals; group 4, 20–30 individuals; group 5, 60–70 individuals; group 6, 40–60 individuals. Groups consisted of about equal numbers of males and females, and about equal numbers of adults and juveniles.

males, migrate from their natal groups, typically into an adjacent group. A large river flowed through the study area and dispersing males have been observed to swim across this river. New groups may be formed by the fissioning of a large group. On one occasion where we could monitor this process closely this occurred along maternal family lines. In three main study groups (groups 1–3), paternity was analysed and alpha (top-ranking) males were found to sire between 50% (largest group, no.1) and 90% (smallest group, no. 3) of the offspring born into the group during their 1–5 years tenure. Most of the remaining offspring were fathered by the beta male (De Ruiter *et al.* 1992).

(b) *Genetic survey*

We trapped (De Ruiter 1992) and bled all individuals ($n=106$) from our three main study groups (groups 1–3), and

many members ($n=55$) of three more neighbouring groups (groups 4–6). Electrophoresis was carried out on 29 blood proteins (Scheffrahn *et al.* 1996), 17 of which showed polymorphism in long-tailed macaques; for 11 of these loci the polymorphisms gave reproducible results (amylase, protease inhibitor (Pi), group-specific component (Gc or DBP—vitamin D binding protein), phosphoglucomutase 1 (PGM1), phosphogluconate dehydrogenase (PGD), properdin factor B (BF), transferrin (TF), isocitrate dehydrogenase 1 (IDH), carboanhydrase 1 (CA1), carboanhydrase 2 (CA2), galactose-1-phosphate-uridyl-transferase (GALT)). Paternity could be established by means of exclusion on the basis of variability in these proteins and DNA fingerprinting (De Ruiter *et al.* 1992). The results of this paternity exclusion analysis were used to classify dyads of known kin-relatedness such as parent–offspring, siblings and half-sibs.

(c) *Measuring relatedness*

Relatedness is a relative measure which is calibrated by the composition and the number of individuals that are present in the same population. For the purpose of investigating the role of relatedness in the evolution of social behaviour, in particular in the context of comparative analysis, one would like to have an estimator of relatedness which asymptotically equals the true degree of kinship. This requires a group of reference individuals that are unrelated to each other as well as to the individuals from which relatedness is estimated. The group of reference individuals, therefore, needs to be sufficiently large to contain mainly unrelated individuals. However, the reference individuals must be genetically different due to being unrelated only, and not because they have been sampled from a different, isolated, population which has diverged over time (Pamilo 1989). In our population, a number of kin-relationships were known due to long-term observations (mother–offspring and maternal siblings) and through paternity analysis (father–offspring and paternal siblings). For unrelated individuals we took relatedness between adult females from the large study group (group 1) with females in a group of the same continuous population 25 km to the north. These females were expected to be unrelated because females do not disperse, the distance between these groups spans a dozen or more social groups, and dispersing males who reproduce typically come from a neighbouring group.

The Queller & Goodnight (1989) index of relatedness (R) was used to estimate kinship (for applied formula, see Girman *et al.* 1997). This index may vary between -1 and $+1$, but with the proper reference population as described above we expect this value to vary between 0 and 1. Although for pairs of individuals, values are expected to greatly vary due to stochasticity. In particular when either of the individuals possesses uncommon alleles a negative R value may be expected for a pair.

We estimated the number of loci needed to adequately estimate relatedness by means of rarefaction analysis. We selected a locus at random, calculated R, selected another locus without replacement, and recalculated R based on both loci. The number of loci was increased by addition without replacement until all 11 loci were selected. We then expressed the difference between consecutive sampling in the outcome of R as a function of the number of loci drawn. We repeated this procedure 100 times and calculated mean difference values (see Altmann *et al.* 1996).

Standard errors of R were estimated by jack-knifing over all loci (Queller & Goodnight 1989).

(d) *Population structure*

We distinguished the following age classes: juveniles (aged 0–3 years); adolescents, (aged 4–6), and adults (aged 7 years and over). In our large study group, based on mother–offspring relations going back to 1976, three matrilines could be distinguished. These three matrilines, from high to low rank, contained 17, 9 and 11 individuals, respectively. These matrilines were further divided into two daughter groups or sub-matrilines and the mean relatedness within and between sub-matrilines was calculated. Standard errors for all within- and between-matriline relatedness means were calculated based on a jack-knife procedure (Queller & Goodnight 1989). In the two smaller study groups (groups 2 and 3) demographic records did not go back quite as far and not all adult females were known to be related. It is, however, likely that adult females were related. In a case where this could be documented, a group fissioned along maternal family lines as has also been documented for other macaque species (see, for instance, Chepco-Sade & Stone Sade 1979). Therefore the natal parts of these small study groups, i.e. all members except the immigrant, adult males, were considered as matrilines.

To test the prediction from sex-biased dispersal patterns (Van Noordwijk & Van Schaik 1985), we examined relatedness of age–sex categories across group borders and across a barrier (the largest river in Sumatra), by a series of randomization tests. Mean R within groups and on each side of the river for each age–sex category was compared with a random distribution generated by randomly assigning individuals to groups, keeping group sizes, sex and age ratios constant.

All comparisons between pair-wise R values of matrilines, groups and social categories were carried out by permutation tests (Manly 1994, p. 49). A permutation test has no assumptions about the distribution or interdependence of the data, and is, therefore, most appropriate for the data in hand.

3. RESULTS

The mean difference in the estimate of R values of all possible pairwise comparisons within the data generated the curve $y=1.571x^{-1.254}$ ($r^2=0.997$). The deviation strongly decreases until the point where about nine loci were included. The resolution appeared to be slightly better, compared to data for *Papio cynocephalus*, as previously reported in Altmann *et al.* (1996; $y=1.017x^{-1.108}$, $r^2=0.982$).

We calculated R values of dyads where kinship had been independently determined from mother–offspring associations and paternity exclusion analysis (figure 2), and found the following values: father–offspring, 0.49 ± 0.05; mother–offspring, 0.50 ± 0.06; full siblings, 0.55 ± 0.12; maternal half-sibs, 0.20 ± 0.14; paternal half-sibs, 0.35 ± 0.10. For dyads assumed to be unrelated, we found $R=-0.08\pm0.08$. R values for other dyads of unknown kinship within a social group were: adult males, -0.10 ± 0.08; adult females, 0.14 ± 0.09; male juveniles, 0.13 ± 0.06; female juveniles, 0.11 ± 0.06. Thus, males were found to be unrelated and females and juveniles were found to be related at the level of full cousins. Significant differences (permutation test) were as follows: maternal half-sibs versus mother–offspring, father–offspring and full siblings, $p<0.001$, and versus unrelated, $p=0.018$; paternal half-sibs versus mother–offspring, $p<0.006$, versus father–offspring, $p=0.017$,
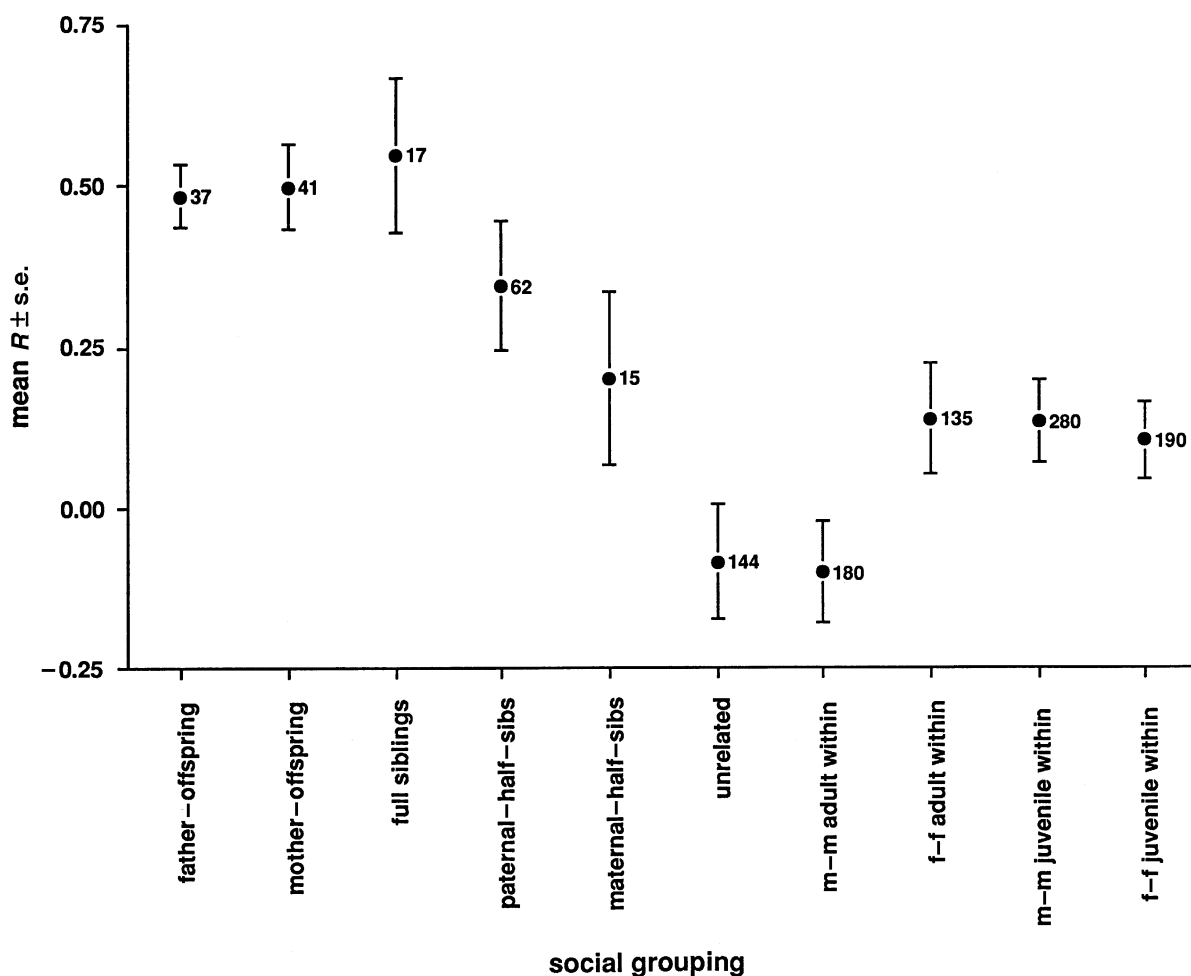
Figure 2. Mean pairwise relatedness values and standard errors of known and unknown kin relationships. Unrelated individuals were taken from a group 25 km away. Known kin relationships were independently determined by observations (mother–offspring), and by exclusion analysis. Figures besides the error bars represent the number of pairwise comparisons used.

versus unrelated, $p < 0.001$, and versus full siblings, $p = 0.01$).

The average R value for individuals of a social group was 0.067 ± 0.037. This value varied considerably from group to group (groups 1–6, respectively: 0.083, 0.091, 0.124, −0.014, −0.042, 0.166).

Average relatedness among members of the three matrilines in our large main study group, and among females and offspring of the two smaller study groups (2 and 3, which were of similar size and labelled matriline 4 and 5), are plotted in figure 3. Means within matrilines ranged from 0.335 (highest ranking matriline) through 0.208 (the middle ranking matriline), to 0.080 (lowest ranking matriline). Permutation tests showed that members of matriline 1 were significantly more closely related than members of matrilines 2 ($p = 0.001$), 3 ($p < 0.001$), 4 ($p = 0.036$) and 5 ($p < 0.001$). Members of matriline 2 were more closely related than those of matriline 4 ($p = 0.046$). Members of matriline 3 were less closely related than those of matriline 4 ($p = 0.049$). Furthermore, the highest ranking of a pair of sub-matrilines (into which a matriline could be divided) always had greater relatedness values than the lower ranking submatriline. The higher of each pair of sub-matrilines had the following Rs (matrilines 1 to 3, respectively): 0.44 ± 0.17 ($n = 21$ compar-

isons), 0.47 ± 0.10 ($n = 10$), and 0.20 ± 0.17 ($n = 15$). The mean R for the lower of each pair of sub-matrilines were: 0.30 ± 0.16 ($n = 70$), 0.32 ± 0.21 ($n = 20$), and 0.10 ± 0.16 ($n = 30$). The relatedness between individuals of two corresponding sub-matrilines was relatively low and had large standard errors (indicating a large variation in relatedness values). From matrilines 1–3 these values were: 0.33 ± 0.13 ($n = 45$), 0.06 ± 0.34 ($n = 6$), and 0.00 ± 0.32 ($n = 10$).

Figure 4 shows a diagram of a map with relatedness between matrilines. The relatedness between matrilines within a group tended to be higher than relatedness values across group boundaries. Members of matrilines 1 and 2, in particular, were closely related. However, relatedness between high-ranking matriline 1, and matrilines 4 and 5, were also high.

Both the high relatedness between high-ranking matrilines within a group and high relatedness between a high-ranking matriline and matrilines in adjacent groups could result from fission processes if high-ranking matrilines grow faster and fission more often. This pattern could also result from shared paternity among the high-ranking females in a group and a higher reproductive success (in adjacent groups) of males born into high matrilines. No direct data on maternal rank and male reproductive success are available. Therefore, we have tried to
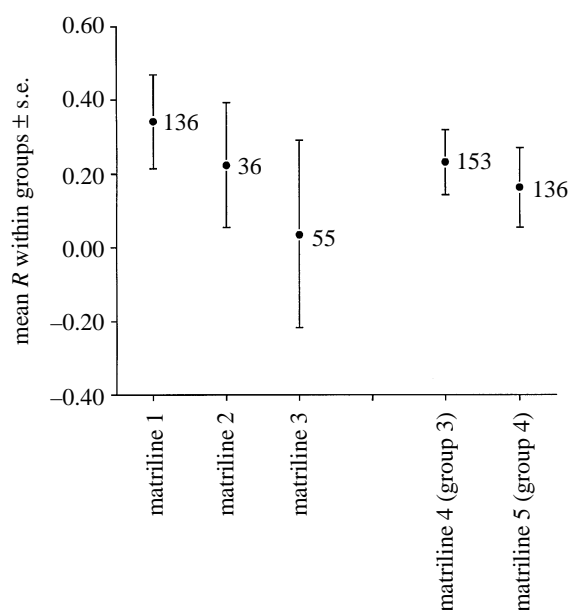
Figure 3. Mean pairwise relatedness values and standard errors among members of different matrilines. Matrilines 1, 2 and 3 were of decreasing social rank and all part of a single social group (group 1). Figures besides the error bars represent the number of pairwise comparisons used.
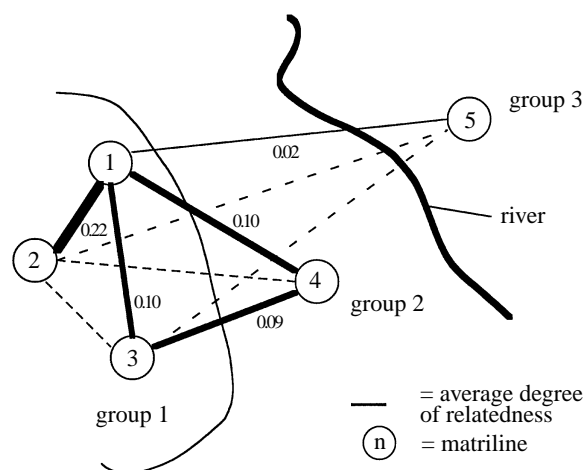

Figure 4. Schematic representation of the study area with the three main study groups in relation to each other and the river. Mean relatedness between the matrilines of the main study group (1, 2, and 3 in decreasing social rank), and between each of these matrilines and the matrilines in two other groups, are indicated by the values besides the solid connecting lines. Dashed lines indicate relatedness of zero or lower. The fine curved line represents the border for group 1.

approximate this relationship by calculating the R values between a matriline and all adult males in adjacent groups. The relatedness between the highest and middle ranking matriline and adult males in groups 3, 4, 5 and 6 was found to be significantly higher than the relatedness between the lowest ranking matriline and the males in these groups ($p \leqslant 0.025$). The middle matriline was also found to be more related than the lower matriline with the males of groups 3 and 5 ($p \leqslant 0.025$).

In two randomization tests aimed to investigate the boundary effect of the river, we compared the observed distribution of relatedness with a random pattern, keeping group sizes, and age and sex composition constant. First, we looked at the differentiation effect of the river on mean relatedness between groups (table 1), and found that for juveniles there is a significant difference. Juveniles of different groups were more related if they were on the same side of the river. This was not true for adults. Second, we investigated how relatedness was distributed on either river bank to assess the differentiating effects of social groups. We tested for differences within and between social groups (table 2). Males were not confined to single social groups and their distribution was not distinguishable from randomness at either bank. In contrast, on either bank, related females were confined to a particular social group and not randomly distributed. Related juveniles on one bank (groups 1, 2 and 4) were confined to a particular social group, but this was not true for the other river bank (groups 3, 5 and 6).

Mean pairwise relatedness was calculated for three groups of males which dispersed during the study. The values found (in groups of four, seven and six individuals) were -0.18, 0.21, and 0.08, respectively. The values of pairwise relatedness are shown in table 3. Three males of the second group (II), numbers 5, 6 and 7, were known to

originate from the same social group; the mean relatedness of these three males was 0.47. This value is significantly higher than the relatedness of three randomly chosen individuals ($p = 0.011$; probabilities of obtaining values of a certain level of relatedness or higher for groups of 2, 3 and 4 individuals were generated with permutations, see figure 5). A fourth male who immigrated at the same time, individual 8, came from another group and was therefore unrelated. Another three dispersers (9, 10 and 11) came from the same group as 8, but at a later event. The mean relatedness of these three males was 0.43 which makes it significantly different from random ($p = 0.018$). Taken together with male 8, average relatedness of this group of four was 0.58. This differs from three randomly chosen individuals ($p = 0.001$). Males in the dispersers group III, came from the large main study group and have a relatively low average relatedness of 0.08, reflecting the observation that all but two were born to different mothers and into different matrilines. Of the first group of dispersers (I), only males 1 and 2 show a high relatedness value (table 3), and all other combinations are low. Males 1 and 2 were the only males which were known to have originated from one particular adjacent group.

4. DISCUSSION

(a) *Estimating relatedness from pairwise comparisons*

Data generated by the 11 protein-coding loci investigated here appear to be an adequate measure to estimate relatedness. The resolution obtained here is slightly better than that obtained with microsatellites in a study on baboons (Altmann *et al.* 1996). This is due to the relative high variability at these protein-coding loci and to the larger data set in this study (six groups, compared with one group of baboons).
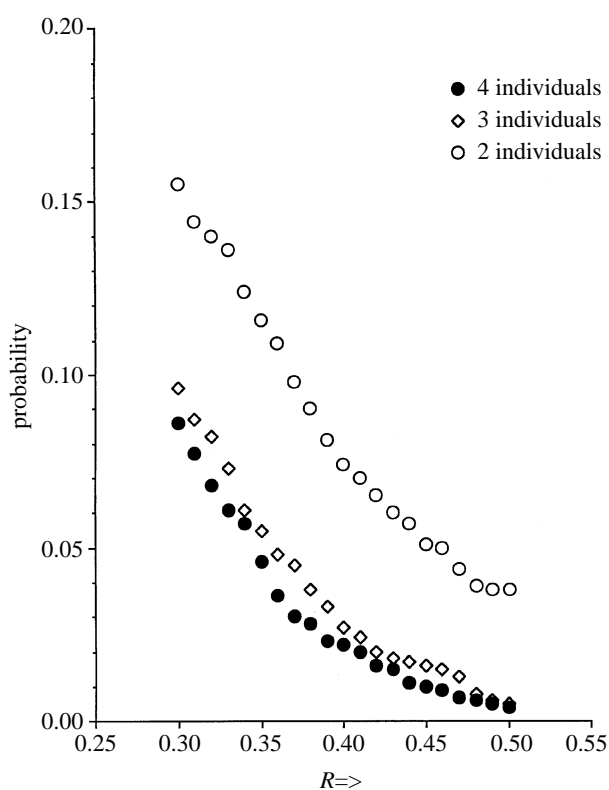
Figure 5. The probability of finding a mean R of a certain value or higher for groups of two, three and four individuals randomly selected from all adolescent males (dispersers) in the population. Groups of individuals with a mean R value with a probability lower than 0.05 are significantly different from a random sample and can, therefore, be considered as related.

A relatedness estimate reflecting kinship can only be obtained if there is a set of unrelated individuals as a reference population. Therefore, the study population must be large enough to include many unrelated individuals. For the known kin relations of parent–offspring, full-sibs and maternal half-sibs, we did find values reflecting these relationships (0.5 and 0.25, respectively). At first the value of 0.35 for paternal half-sibs seems puzzling, but since paternal sibs can also be related though their mothers (who are, on average, related at $R = 0.14$), this value also fits fairly closely with the expectation, namely: $0.25 + 1/2 \times 0.14 = 0.32$. Such elevated relatedness is not found among maternal half-sibs, because, other than the mothers, the fathers are much less likely to be related ($R = -0.10$).

Altmann *et al.* (1996) found lower values than 0.5 for parent–offspring and full siblings. This was caused by the inclusion of too few unrelated individuals in this study, which would result in an underestimate of relatedness. Indeed, the finding that our estimates for known kin relations do, in fact, accurately reflect the degree of relatedness as known from the pedigree structure, indicates that our reference population is sufficiently large for accurate estimation of kin relationships. The relatedness value found for our reference sample of unrelated individuals was negative, which exceeds the minimal expectation of zero. This could result either if a slightly

Table 1. *Differentiating effect of the river on mean relatedness between groups*

(Number of pairwise comparisons used is indicated by *n*. Mean relatedness was calculated for all pairwise comparisons in a particular age-sex category. Randomizations were used to test whether the pattern of relatedness differed from a random distribution for a certain category.)

| | relatedness between groups | | | |
| | same river bank | | opposite river bank | |
	n	mean	mean	*p*
adult males	668	−0.013	−0.046	0.118
adult females	306	−0.052	−0.095	0.134
juveniles	1095	0.067	−0.012	0.002

Table 2. *Relatedness within and between groups on either bank of the river*

(Number of pairwise comparisons used is indicated by *n*. Mean relatedness was calculated for all pairwise comparisons in a particular age-sex category. Randomizations were used to test whether the pattern of relatedness differed from a random distribution for a certain category.)

	n	within groups	between groups	*p*
groups 1,2,4				
adult males	253	−0.119	−0.050	0.071
adult females	105	0.126	−0.057	0.003
juveniles	595	0.164	0.067	<0.001
groups 3,5,6				
adult males	153	0.002	0.075	0.088
adult females	101	0.089	−0.084	0.010
juveniles	190	0.121	0.065	0.155

high number of related individuals were included in the calculations or if the unrelated individuals selected were too distant. Because we found for the adult males in a group about the same negative value for R, the latter explanation is unlikely to be correct.

(b) ***The structure of relatedness: dispersal and paternity***

The calibration of relatedness among individuals with known pedigrees validates the estimation of the relatedness among individuals with unknown pedigree. We conclude that the relatedness within our groups is 0.068, averaged over six groups. Slightly lower, but of the same order, than the value of 0.085 ± 0.025 which was earlier obtained with the method for calculating mean group relatedness from F statistics (De Ruiter *et al.* 1994*a*; Hamilton 1972; Weir & Cockerham 1984). With the presently applied methods it was possible to document that there was a great deal of between-group variation. R values for groups 1–6 (figure 1) were: 0.083, 0.091, 0.124, −0.014, −0.042, 0.166. The values for groups 4 and 5 were much lower than for the other four groups. The reason for this may be that biased samples were taken. The individuals in groups 4 and 5 were less well habituated to

Table 3. *Pairwise relatedness values of males dispersing into a particular group*

(Integers represent individuals. Individuals 1 and 2 were known to originate from the same group but the origin of individuals 3 and 4 was unknown. From the relatedness value of 0.513 we can assert that individuals 1 and 2 were related (see figure 5). Individuals 5–7 were known to have been born into a particular small group and individuals 8–11 were known to be born into another small group. This is reflected in the high relatedness values. Mean relatedness among all immigrants is significantly reduced as a result of a high number of unrelated pair comparisons. Individuals 12–17 were all born into the same large group but to five different mothers and into different matrilines.)

dispersers group I

	1	2	3
2	0.513	—	—
3	0.054	−0.138	—
4	−0.625	−0.540	−0.362
mean = −0.183			

dispersers group II

	5	6	7	8	9	10
6	**0.188**	—	—	—	—	—
7	**0.857**	**0.370**	—	—	—	—
8	0.073	−0.256	0.018	—	—	—
9	−0.080	−0.404	−0.127	**0.906**	—	—
10	0.320	−0.330	0.240	**0.896**	**0.785**	—
11	0.030	0.020	0.227	**0.257**	**0.124**	**0.386**
mean = 0.214						

dispersers group III

	12	13	14	15	16
13	0.218	—	—	—	—
14	0.145	0.290	—	—	—
15	0.028	−0.266	−0.212	—	—
16	−0.074	0.179	−0.254	0.215	—
17	0.117	−0.008	−0.019	0.396	0.456
mean = 0.081					

human presence and, as a result, shyer age–sex categories were underrepresented in the sample (De Ruiter 1992). As a consequence, primarily adult and adolescent males were genotyped in these groups (seven of eight in group 4, and 16 of 24 in group 5). It is precisely these two categories of males who have low relatedness. Groups 1–3 were sampled completely. Group 6 was highly habituated to human disturbance (they regularly raided crops) and, as a result, juveniles and females were relatively easily trapped, whereas adult and adolescent males were underrepresented (4 of 23). This explains the high relatedness in this group. Of the groups which were completely sampled, the larger group (1) has a lower R than the two smaller groups (2 and 3), as expected. Mean relatedness in a completely sampled group was found to be around 0.10. This effect of sampling bias should be a reason for caution in comparative studies. However, data on sampling bias are not usually provided for studies reporting genetic differentiation among groups (reviews: Aoki & Nozawa 1984; De Ruiter *et al.* 1994*a*).

Adult females and juveniles in a group are, on average, related at the level of cousins, whereas adult males are usually unrelated. We expected higher relatedness in females due to female philopatry. A similar trend was found in baboons (Altmann *et al.* 1996), whereas the opposite trend was found in chimpanzees, in which males are philopatric (Morin *et al.* 1994). We expected adult males to be somewhat related because peers often disperse together. However, this is not what we found. The reason may be that, although groups of related adolescent males often disperse together or consecutively from their natal group, the presence of many unrelated males in their new group who immigrated previously from various other groups tends to dilute their average relatedness. The powerful effect of such a dilution was demonstrated by the addition of just one unrelated individual in the calculation of a group of three dispersers which reduced average relatedness by the expected 50%.

The relatedness within the higher ranking matriline was higher than the relatedness in lower ranking matrilines. The same was found for sub-matrilines within those matrilines. This does not result from differences in matriline size, because the highest ranking matriline was also the largest and the expectation is that smaller size results in higher relatedness. A likely explanation for this difference is a relatively high degree of shared paternity among higher ranking females compared to females from low-ranking matrilines. Behavioural observations show that the alpha male in this group mated significantly more with high-ranking than with low-ranking females during their fertile periods (De Ruiter *et al.* 1994*b*). Eight of 11 (73%) offspring of the highest ranking females were fathered by the alpha male, compared to only 5 of 10 (50%) offspring born to lower ranking females. Thus assortative mating is likely to cause the difference in relatedness between matrilines. The relatively high variance of R found in low-ranking matrilines also supports this explanation. A lower fertility of low-ranking matrilines would probably not lead to this difference.

The relatedness estimates in matrilines of free-ranging rhesus monkeys based on three loci (Olivier *et al.* 1981) were around 0.10–0.25, somewhat lower than our value for the high-ranked matriline. This may be caused by a more equal reproductive success among males, as has been found in this population (Berard *et al.* 1993).

(c) *Relatedness between matrilines and groups and the influence of the river*

Matrilines within a group were found to be somewhat related amongst each other. However, as shown in figure 4, the highest ranking matriline (1) was more closely related with segments of two neighbouring groups, than the two lower ranking matrilines were amongst each other. Therefore, it would be misleading to automatically consider the females and offspring of a social group as the typical unit of related individuals. This pattern of relatedness across group boundaries is unlikely to result from group fissions, because fissions occur along matrilineal divisions and matrilines within a group are not highly related. Group fissions may therefore have a differentiating effect, as demonstrated in free-ranging rhesus macaques (Cheverud & Dow 1985). Moreover, group 2 was known to have fissioned from another large group further to the south, and not from group 1 (whereas group 3 was an offshoot of group 5). The relatedness between the high matriline and adjacent groups is, therefore, likely to result from gene flow between these groups.

The high relatedness between the two high-ranking matrilines and adult males in all adjacent groups does suggest such gene flow.

The river is not an impediment to gene flow and does not lead to strong genetic differentiation of populations on opposite sides. The relatedness values for adults on one side of the river (different groups) are similar to values across the river (table 1). This is also true for females. Apparently no relatedness accumulates on opposite riversides as a result of females staying on one side, presumably also after group fissions. However, the finding that juveniles of different groups on the same river bank were found to be more related than juveniles on different river banks, requires an explanation. This pattern of relatedness in juveniles could be caused by subsequent group fissions on each river bank. But in that case one would expect to also find a higher relatedness among the adult females at one bank and that clearly was not the case. The higher relatedness of juveniles could be caused by higher paternal relatedness. The males of neighbouring groups on a river bank were not more related than males on opposite banks ($p = 0.13$). However, males who have reproduced may in fact have been related.

Thus, gene flow and differential reproduction in males, rather than group fission and the presence of geographical barriers, appear to be important factors responsible for genetic differentiation.

(d) *Social structure and kin selection*

The average relatedness among individuals of a social group was found to be about 0.10. The inclusive fitness benefits associated with such a value would be relatively low. Perhaps such relatedness might be high enough for the evolution of altruistic behaviour through kin selection, when the benefits are high and the costs are low. Relatedness among sub groupings could be considerably higher. Within a social group further sub-structures exist particularly according to matrilines. We found that relatedness within such matrilines can be relatively high; R was between 0.30 and 0.47, among the members of sub-matrilines of the two high-ranking matrilines (5–12 individuals). R values among adolescent males dispersing from the same natal group (3–6 individuals) could also be high (0.43 and 0.58), but could also be much lower (0.08). Relatedness among members of high-ranking matrilineal families is relatively high and kin selection may be expected with such values. Peer dispersal from a social group is not restricted to highly related individuals, however, and familiarity may contribute to the survival value of this behaviour.

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