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
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 males 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 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 (Ge or DBP—vitamin D binding protein), phosphoglucomutase 1 (PGMI), phosphoglucone 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 Gärman 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 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 \((age 0–3 years)\); adolescents, \((age 4–6)\), and adults \((age 7 years and over)\). 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-matrilines 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, Chepko-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 \(R = -0.08 ± 0.08, R\) 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, \(p = 0.017\).
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 matriline 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 matriline ranged from 0.335 (highest ranking matriline) through 0.208 (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 matriline 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-matriline (into which a matriline could be divided) always had greater relatedness values than the lower ranking submatriline. The higher of each pair of sub-matriline had the following \( R \)'s (matriline 1 to 3, respectively): 0.44 ± 0.17 (\( n = 21 \) comparisons), 0.47 ± 0.10 (\( n = 10 \)), and 0.20 ± 0.17 (\( n = 15 \)). The mean \( R \) for the lower of each pair of sub-matriline 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-matriline was relatively low and had large standard errors (indicating a large variation in relatedness values). From matriline 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 matriline. The relatedness between matriline within a group tended to be higher than relatedness values across group boundaries. Members of matriline 1 and 2, in particular, were closely related. However, relatedness between high-ranking matriline 1, and matriline 4 and 5, were also high. Both the high relatedness between high-ranking matriline within a group and high relatedness between a high-ranking matriline and matriline in adjacent groups could result from fission processes if high-ranking matriline 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
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 \( (p < 0.025) \). The middle matriline was also found to be more related than the lower matriline with the males of groups 3 and 5 \( (p < 0.025) \).

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 \( \text{in groups of four, seven and six individuals} \) 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 \( (\text{II}) \), 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 \( (p < 0.001) \), 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 observed with microsatellites in a study on baboons \( (\text{Altmann et al. 1996}) \). 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).
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 mothers, the fathers are much less likely to be related (who are, on average, related at 0.35 for paternal sibs can also be related though their mothers). So, the 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. 1994a; 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: 0.003, 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 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.)

<table>
<thead>
<tr>
<th>relatedness between groups</th>
<th>same river bank</th>
<th>opposite river bank</th>
</tr>
</thead>
<tbody>
<tr>
<td>n</td>
<td>mean</td>
<td>p</td>
</tr>
<tr>
<td>adult males</td>
<td>668</td>
<td>−0.013</td>
</tr>
<tr>
<td>adult females</td>
<td>306</td>
<td>−0.052</td>
</tr>
<tr>
<td>juveniles</td>
<td>1095</td>
<td>0.067</td>
</tr>
</tbody>
</table>

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.)

<table>
<thead>
<tr>
<th>n</th>
<th>within groups</th>
<th>between groups</th>
<th>p</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
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<td>adult males</td>
<td>adult females</td>
</tr>
<tr>
<td>253</td>
<td>−0.119</td>
<td>−0.050</td>
<td>0.071</td>
</tr>
<tr>
<td>105</td>
<td>0.126</td>
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<td>0.003</td>
</tr>
<tr>
<td>500</td>
<td>0.164</td>
<td>0.067</td>
<td>&lt;0.001</td>
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<tr>
<td>groups 3,5,6</td>
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<td>adult females</td>
<td>juveniles</td>
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<tr>
<td>153</td>
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</tr>
<tr>
<td>101</td>
<td>0.089</td>
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<td>0.010</td>
</tr>
<tr>
<td>190</td>
<td>0.121</td>
<td>0.065</td>
<td>0.135</td>
</tr>
</tbody>
</table>

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.

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. 1994a).

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 matriline. The same was found for sub-matriline within those matriline. This does not result from differences in matrine 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 matriline. 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. 1994b). 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 matriline. The relatively high variance of $R$ found in low-ranking matriline also supports this explanation. A lower fertility of low-ranking matriline would probably not lead to this difference.

The relatedness estimates in matriline 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 matriline and groups and the influence of the river

Matriline 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 matriline 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 matriline 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 offspring of group 5). The relatedness between the high matriline and adjacent groups is, therefore, likely to result from gene flow between these groups.

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**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 to the same large group but to five different mothers and into different matriline.)

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<tr>
<td>2</td>
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<tr>
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<td>—</td>
<td>—</td>
</tr>
<tr>
<td>14</td>
<td>0.028</td>
<td>−0.266</td>
<td>−0.212</td>
<td>—</td>
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</tr>
<tr>
<td>15</td>
<td>−0.074</td>
<td>0.179</td>
<td>−0.254</td>
<td>0.215</td>
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<tr>
<td>16</td>
<td>0.117</td>
<td>−0.008</td>
<td>−0.019</td>
<td>0.396</td>
<td>0.456</td>
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<tr>
<td>mean = 0.081</td>
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</table>
The high relatedness between the two high-ranking matriline 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 true also 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 matriline. We found that relatedness within such matriline can be relatively high; R was between 0.30 and 0.47, among the members of sub-matri- lines of the two high-ranking matriline (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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