THE ROYAL SOCIETY

Intracommunity relationships, dispersal pattern and paternity success in a wild living community of Bonobos (*Pan paniscus*) determined from DNA analysis of faecal samples

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Differences in social relationships among community members are often explained by differences in genetic relationships. The current techniques of DNA analysis allow explicit testing of such a hypothesis. Here, we have analysed the genetic relationships for a community of wild bonobos (*Pan paniscus*) using nuclear and mitochondrial DNA markers extracted from faecal samples. Bonobos show an opportunistic and promiscuous mating behaviour, even with mates from outside the community. Nonetheless, we find that most infants were sired by resident males and that two dominant males together attained the highest paternity success. Intriguingly, the latter males are the sons of high-ranking females, suggesting an important influence of mothers on the paternity success of their sons. The molecular data support previous inferences on female dispersal and male philopatry. We find a total of five different mitochondrial haplotypes among 15 adult females, suggesting a frequent migration of females. Moreover, for most adult and subadult males in the group we find a matching mother, while this is not the case for most females, indicating that these leave the community during adolescence. Our study demonstrates that faecal samples can be a useful source for the determination of kinship in a whole community.

Keywords: microsatellites; mitochondrial D-loop; primates; philopatry

1. INTRODUCTION

The social system of bonobos (*Pan paniscus*) is described as female-centred and egalitarian (de Waal 1995). Females were observed to transfer between communities while males are thought to be strictly philopatric (Furuichi 1989; Idani 1991). Accordingly, it is assumed that communities consist of unrelated females and closely related males (Kano 1982). Based on inclusive fitness theory (Hamilton 1963) one should expect that males show affiliative behaviour and should cooperate. In contrast, females would be expected to be less social as it is indeed observed in common chimpanzees (*Pan troglodytes*) where females often travel alone or in small family groups (Goodall 1986). However, female bonobos associate and forage in larger parties for most of the year (Kuroda 1979), share food and support each other in food defence (Hohmann & Fruth 1993, 1996). Similar bonds among bonobo males seem to be absent. Cooperation among unrelated individuals becomes beneficial if it is based on reciprocal altruism or mutualism (Trivers 1971; Noe 1990; Dugatkin 1997).

This discrepancy between observed social behaviour and inferred genetic relationships has raised speculations about the evolution of social bonding among female primates in the absence of genetic ties (Parish 1996). Yet, the genetic relationships of resident females are still unknown. A study at Wamba revealed that resident females belong to different matrilines, supporting the idea of female exogamy (Hashimoto *et al.* 1996). However, data from chimpanzees demonstrate considerable variation concerning the proportion of females emigrating from their natal community (Goodall 1986; Nishida *et al.* 1990; Boesch 1997). As a consequence, genetic relatedness among resident females and the resulting conditions for female bonding may vary between populations. The absence of data on genetic relationships prevent assessments of the role that kinship or other factors play in the cooperation and association of female bonobos.

A high degree of sociality among females should enable dominant males to control access to oestrous females and prevent mating attempts by low-ranking males and outsiders (Van Schaik 1996). However, in bonobos, mating is opportunistic, promiscuous and involves no or little aggression among male group members (Kano 1992). At the two sites where bonobos are studied in long-term

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research projects (Lomako and Wamba) oestrous females have been observed to engage in extra-community copulations even in the presence of male community members (Kano 1992; B. Fruth and G. Hohmann, unpublished data). It has been suggested that the low degree of competition between males may be related to the reproductive physiology of the females (Furuichi 1992). Female bonobos show a prolonged oestrous cycle and tumescence of the genital swelling lasts for a large proportion of their cycle (Dahl 1986). Therefore, detection of ovulation may be difficult and costs of mate guarding may be high. Under these circumstances competition for access to females may change from contest to scramble and provide the potential for sperm competition (Møller 1988; Bercovitch 1989). Unless the females are able to control fertilization (Small 1989; de Ruiter *et al*. 1994; Bercovitch 1995), one would predict that paternity will be evenly distributed among males of different rank. The high rate of matings between members of different communities could result in a decrease of paternity success of resident males and a dilution of the genetic relatedness among resident males. However, studies on macaques and chimpanzees have revealed that behavioural data alone are likely to generate wrong predictions of paternities (Inoue *et al*. 1992; de Ruiter *et al*. 1994; Morin *et al*. 1994*b*; Gagneux *et al*. 1997*b*). Therefore, genetic data are required to test the hypothesis about the reproductive success of individual males.

2. METHODS

(a) *Behavioural data*

Behavioural data were collected by two authors (B.F. and G.H.) between 1990 and 1996 from individually known members of a community of bonobos, the Eyengo community, inhabiting the Lomako forest (Democratic Republic of Congo, formerly Zaire). Composition and demography of the community are shown in figure 1 of the electronic appendix which can be found at www.pubs.royalsoc.ac.uk/publish/pro_bs/rpb1424.htm. During this time, the community consisted of up to 15 adult females, six adult males and 20 subadults and infants. Assessments of the age of individuals born before 1990 were based on body size, testes size, dentition, cyclic changes of female genital swellings and maternal behaviours (e.g. nursing, transport of immatures). Rank assessments are based on the direction and outcome of displacements and agonistic interactions (Hohmann *et al*. 1998). Calculations of male mating success are based on field records from 196 observation days during the field seasons in 1993–1995. Assessments of individual mating success refer to the number of copulations per individual per observation day.

(b) *Sampling*

Faecal samples were collected from 36 members of the Eyengo community and from six individuals of neighbouring communities shortly after dropping, and directly transferred into ethanol (sample:ethanol, 1:3), avoiding the possibility of contamination with human DNA. All adult members of the community were sampled, but samples could not be obtained for five of the newborn animals. These are therefore not further considered here. Samples were stored under ambient temperature for up to five years. As controls, we used faecal and blood samples from 14 captive bonobos from different European zoos. Eleven of these animals were caught in the wild and are most likely unrelated.

(c) *DNA extraction*

DNA extractions of faecal samples were carried out using the diatomaceous earth protocol as described in Gerloff *et al*. (1995). During the later phase of the project, we also employed the chelex extraction method (Estoup *et al*. 1996). Usually two to five extractions were carried out per faeces sample. Up to seven samples were analysed per individual. After each extraction the presence of DNA was confirmed through a PCR amplification of part of the mitochondrial D-loop. Only extracts which produced a visible band on a 0.8% agarose gel were used for further analysis.

(d) *Mitochondrial sequence analysis*

The most variable part of the D-Loop, the hypervariable region 1, was amplified using the primers L15997 (5′-CACCATTAGCACCCAAAGCT-3′) and H16498 (5′-CCTGAAGTAGGAACCAGATG-3′; the numbers refer to the positions in the human sequence of Anderson *et al*. (1981)) and 30 cycles with 1 min each at 94, 60 and 72 °C. The amplified band was purified over an agarose gel and used for cycle sequencing employing primer L15997. Some fragments were also sequenced in the reverse direction to verify the sequence.

(e) *Microsatellite analysis*

Five unlinked CA-microsatellite loci, originally described for humans (loci D1S207, D2S141, D6S271, D16S402 and D17S791; Gyapay *et al*. 1994) and shown to be polymorphic in chimpanzees by Coote & Bruford (1996), proved to be polymorphic in bonobos as well (Gerloff *et al*. 1995). Since many extracts tended to yield poor amplification results, a prescreening procedure was routinely employed. One microlitre of each PCR reaction (set up as described in Gerloff *et al*. (1995)) was dot-blotted on to a Hybond N + membrane (Amersham) which was then UV-cross-linked and hybridized with a ^{32}P-labelled C(AC)$_7$-probe as described in Petri *et al*. (1997). Only PCR reactions which proved to contain an amplified microsatellite fragment were separated on 6% denaturing polyacrylamide gels and then blotted on to a Hybond N + membrane. Hybridizing the membrane with a ^{32}P-labelled C(AC)$_7$-repeat ensured that only the fragments containing a microsatellite were scored in the further analysis.

Because of the extremely small amount of genomic DNA in faeces samples, the amplifications from such probes are prone to contaminations and artefacts. The problems with contaminations in an early phase of the study could successfully be overcome by using a small hood for setting up the reactions (Template Tamer, Oncor–Appligene) as well as filter tips for pipetting. All humans who were in contact with the probes were also typed for all loci, to assess how far contaminations from human DNA were a problem. Since the human alleles were in most cases very distinct from the alleles found in the community typed, it was easy to decide when a human DNA contamination was present. After taking the above precautionary measures, this problem was negligible in the end. The second problem, the generation of artefacts, was more serious. When typing the individuals we have frequently encountered the problem of single allele amplification in heterozygotes (Gerloff *et al*. 1995; Taberlet *et al*. 1996; Gagneux *et al*. 1997*a*). We have therefore taken the following precautionary measures to obtain a reliable result. If only single alleles were amplified, each of them had to be

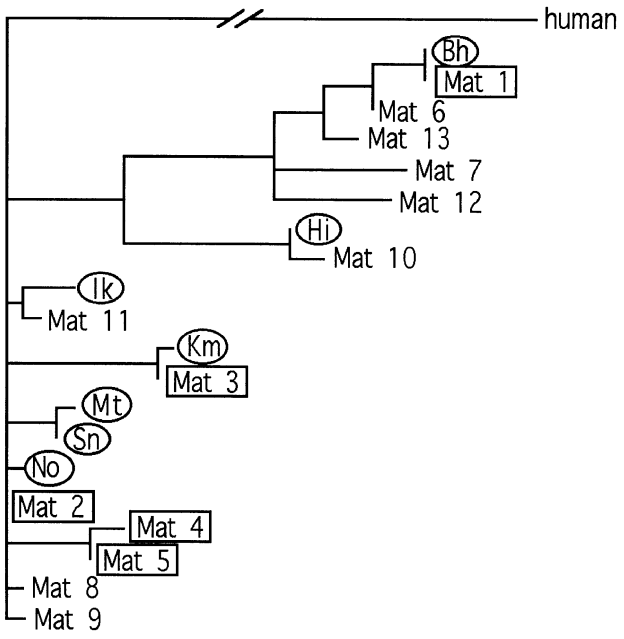

Figure 1. Parsimony phylogram of mitochondrial D-loop fragments of bonobos from Eyengo (Mat 1–Mat 5 in squares) Wamba (in ovals, abbreviations according to Hashimoto *et al.* (1996)) as well as from captive animals from European zoos. The tree is rooted with a human reference sequence (Anderson *et al.* 1981). The alignment used for creating this tree is presented in electronic Appendix C.

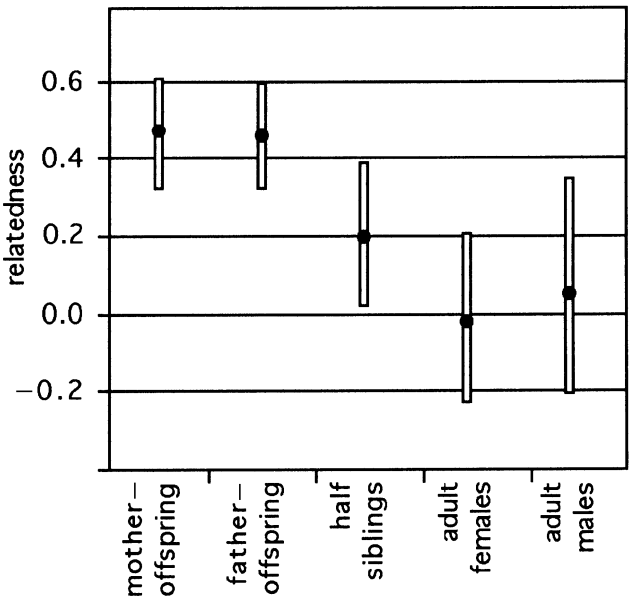

Figure 2. Comparisons of average relatedness between different subgroups. Relatedness was calculated for each pair in the respective groups and the averages over the whole group were plotted. The bars indicate the confidence interval.

present in several different independent PCRs (often from independent samples of the same individual) before a heterozygous score was accepted. In many cases this required 10–100 replicates for a certain individual at a certain locus. Alleles that were seen only once were considered to be artefactual (Foucault *et al.* 1996) and were ignored. Amplifications with a heterozygous score for a given locus were verified in at least three independent PCRs, in most cases from independent probes of the individual. The reliability of the scoring was checked by comparing the results of blood and faecal samples from zoo animals, as well as verifying known maternal relationships (see electronic Appendices A–E).

(f) *Statistics*

Parentage analysis was done with the program CERVUS (Marshall *et al.* 1998), which was also used to assess the possible occurrence of null alleles. When using the allele frequencies found within the Eyengo community, we have a total exclusion power for the combination of all five loci for the first parent of 0.92 and for the second parent of 0.99. Sampling errors in allele frequency determination do not change these values much (not shown). Relatedness values were calculated with the program KINSHIP (Queller & Goodnight 1989). Phylogeny reconstruction of the mitochondrial haplotypes was done with PAUP (Swofford 1993).

3. RESULTS

(a) *Mitochondrial haplotypes*

To get an assessment of the migration behaviour of the females, mitochondrial D-loops from 36 members of the Eyengo community, six members of neighbouring communities and 11 unrelated captive individuals were sequenced. At Lomako, we found five different haplotypes within the Eyengo community (figure 1), suggesting that there is no matrilineal organization. In the six members from neighbouring communities we found three different haplotypes, each identical to one present also within the Eyengo community. The captive individuals showed a total of nine different haplotypes, only one of which was identical to one found at Lomako. Comparing these results with a similar data set (Hashimoto *et al.* 1996) shows that only one haplotype from Wamba is identical to one from Lomako, while six others are different. A phylogenetic analysis of the haplotypes does not show a group-specific pattern of the distribution of the haplotypes (figure 1) indicating that there are no ancient splits between different populations. However, further sampling in different areas will be required to verify this inference.

(b) *Microsatellite analysis*

All adult and subadult members of the Eyengo community as well as all available infants (samples could not yet be obtained for five newborn infants) were typed for the microsatellite loci. Most individuals could be typed successfully at all five loci. Two animals (TAG and ZOR) could be typed on four loci only and the two infants GLO and UFO could be typed on three loci only. The details of the allele frequencies and the typings, both for the Eyengo community and the captive animals are provided in electronic Appendix D.

A first test to assess migration and mating behaviour from genetic data is to compare average genetic relationships (Altmann *et al.* 1996; de Ruiter & Geffen 1998). We have employed the procedure by Queller & Goodnight (1989) for this test, using parent–offspring pairs as controls (figure 2). On average, the genetic relatedness of parent–offspring pairs was approximately 0.5 as expected, while both adult males and adult females had, on average, a genetic relatedness close to zero. Thus, this analysis does not suggest that a strong patrilineal or matrilineal group

Table 1. *Male rank, mating success and reproductive success*

(The copulation rate is the average number of copulations with adult or adolescent females per observation day.)

male (observation days)	rank category	copulation rate	number of offspring
REN (54)	1	1.29	2–4[a]
MAX (203)	1	0.58	3
PLA (207)	1	0.49	0
SAM (91)	2	0.96	2
KAR (133)	2	0.53	0–2[a]
BLA (194)	2	0.27	1
PIN (104)	3	0.27	0
VOL (207)	3	0.22	0

[a] REN and KAR are both potential fathers for UFO and LUN.

structure exists. However, it should be emphasized that because of the small number of individuals involved, these results are only tentative and have a large error margin (figure 2). Accordingly, even though there are at least three half siblings among the six adult males (see below), this has only a minor effect on the average genetic relationship among the males.

(c) *Maternity assignments*

The information from the mitochondrial and microsatellite typing was used to trace all possible mother–offspring relationships in the community. The combination of these two marker systems makes the probability of a genetic match occurring by chance smaller than 1% on average. Among all possible comparisons involving older females, we found a total of 20 genetically compatible pairs. Ten were confirmations of the relationships that were already known from the behavioural observations. Three could be excluded because of demographic reasons. The remaining seven were relationships among adult and subadult individuals, which were not evident from the field observations. Intriguingly, six of these concern mother–son pairs and only one a mother–daughter pair. This is strong evidence that adult males tend to stay in the community, while adult females tend to leave. Considering that the community consisted of eight adult and adolescent males and 18 adult and adolescent females, this is a highly significant difference ($p < 0.0008$, Fisher exact test, one-tailed).

(d) *Paternity assignments*

The identification of fathers for the juveniles for which mothers were known from the field observations was done by subtracting the respective maternal alleles and looking for a possible match among the adult males. The average probability for a chance assignment is again below 1% under these conditions. For seven out of the ten juveniles we found a single possible father within the community. UFO had two potential fathers (REN and KAR), but this can be ascribed to the fact that UFO could be typed at three loci only. For two animals (VIR and GLO), we found no matching father. Possible paternity relationships were also assessed for all adult and adolescent males in the absence of maternal information. Among all possible comparisons involving older males, we found four additional matches. Two concern the subadult female LUN, which could have been fathered by either KAR or REN. The other concern a possible father–son relationship between REN and BLA and a possible father–daughter relationship between PLA and LOR. The REN–BLA relationship holds true even when the possible maternal alleles of LOL are subtracted, making this paternity assignment likely. In contrast, the PLA–LOR relationship is unlikely to be real, since all the other evidence indicates that adult females do not normally stay in their natal group. It is therefore not further considered here.

(e) *Paternity and rank*

The field observations showed that all adult and adolescent males engaged in mating with female community members. However, mating success differed within and between rank categories (table 1). Although overt aggression was rare, two high-ranking individuals (REN and MAX) showed a strong tendency to monopolize access to tumescent females by displacing each other as well as low- and medium-ranking males. In spite of their superior status, medium-ranking males usually tolerated mating attempts by the two low-ranking individuals. Overall, the three youngest males (PIN, VOL and BLA) had the lowest mating scores. The genetic analysis shows that five to seven out of the ten infants sampled could be assigned to two males of the rank category 1, while the third male in rank category 1 (PLA) had no unequivocal paternity success. No possible offspring was found for the two youngest males, VOL and PIN (table 1).

4. DISCUSSION

This study is the first using only faeces samples to type members of a community of bonobos to assess their genetic relationships. Although the principle of the method was known before, the practical problems of getting a large set of data were greater than expected. Still, by taking a number of precautionary steps and by multiple retyping of different samples for most of the animals, it was possible to obtain reliable data. The final picture of the internal relationships of the Eyengo community is depicted in figure 3.

The data support previous inferences on female exogamy in bonobos (Kano 1982; Furuichi 1989; Idani 1991; Hashimoto *et al*. 1996). Strong evidence comes from the fact that there is a matching mother for most adult and subadult males in the group, while this is not the case for females. For one adolescent female (AMY) a matching maternal genotype was detected, but she disappeared from the community before reaching adulthood. Also the fact that five different mitochondrial haplotypes were found among 15 potentially reproductive females suggests that there is no matrilineal organization and that there must be a large exchange of females between communities. During the course of the fieldwork, several unknown females joined the Eyengo community but only one (AND) became resident. In contrast to chimpanzees, where immigrants may receive intense aggression from resident females (Pusey 1980), reactions between resident and unknown female bonobos were characterized by friendly contacts.

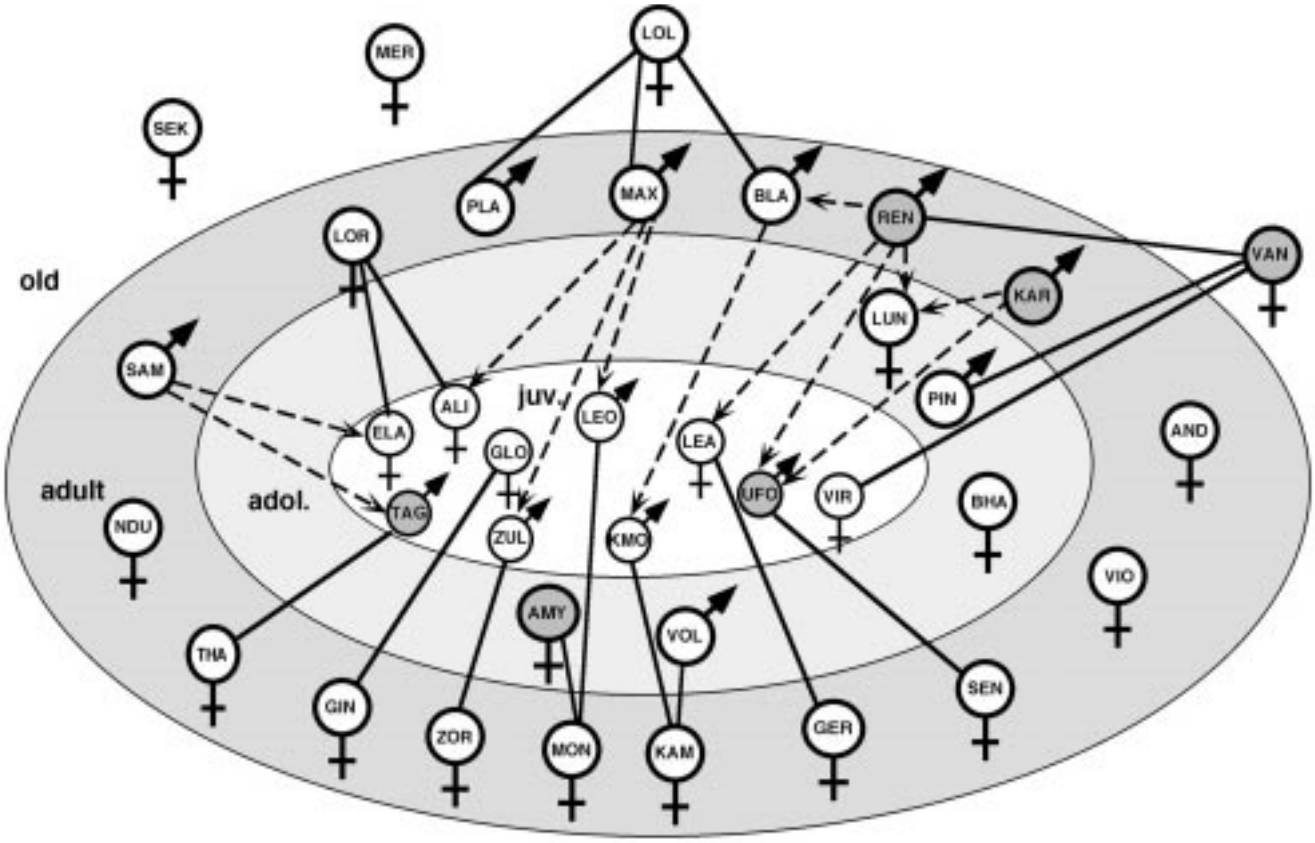

Figure 3. Genetic relationships and age structure of the Eyengo community. Solid lines indicate mother–offspring pairs, which share at least one allele at each locus and the mitochondrial haplotypes. Dashed lines indicate possible paternal relationships, which are compatible with the set of maternal alleles of the respective child. The animals were grouped into rough age classes, juveniles (up to approximately six years of age) are in the centre followed by adolescent and adult animals in successive rings. Very old animals are placed at the outer rim. Animals with grey shading have either died or have left the group.

The distribution of mitochondrial haplotypes provides some further clues about the female migration behaviour. For mitochondria, any given haplotype becomes fixed after N_e generations (N_e being the effective population size corresponding in this case roughly to the number of reproductively active adults). Thus, if exchange of females would be limited to a small number of communities (i.e. the immediate neighbourhood), N_e might not be larger than a few hundred. Thus, mitochondrial haplotypes would become locally fixed within a few hundred generations, unless new haplotypes arise by mutations from the existing ones. The fact that we find several very different, not genealogically related haplotypes in the Eyengo community argues therefore for a rather effective mixing even over longer distances. However, these considerations apply only to average effects over thousands of generations and allow little prediction of the behaviour of single females during their lifetime. A preference for joining neighbouring communities might still exist. The large number of different haplotypes found between the Eyengo and the Wamba communities, which are only approximately 150 km apart, supports the latter notion. However, in contrast to studies in chimpanzees (Morin *et al.* 1994*a*), there is no evidence for major subdivisions of bonobo populations (figure 1). Still, focused sampling of more distant areas will be required to verify this inference.

In species with female exogamy, reproductive success is thought to be independent of rank (Van Schaik 1989). However, analysing long-term data from female chimpanzees, Pusey *et al.* (1997) found that infant survival increased with the rank of the mother. Moreover, daughters of high-ranking mothers reached sexual maturity earlier than those of lower-ranking females. The absence of matrilineal relationships in our community of bonobos does not permit assessments of the reproductive performance of females in relation to their rank. However, two old and high-ranking females (LOL and VAN) were found to have a particularly high maternity success (three offspring each) and two of their sons (MAX and REN) accounted for the largest number of paternities (table 1). REN was leader male when the study started and MAX became his successor. Each had an adult male half-sib living in the same community and thus, a potential ally available. Although alliances between bonobo males have been observed (Furuichi & Ihobe 1994), there is no evidence that they are used to raise their rank. Instead, it is the females that may be able to support their sons in attaining high rank. Captive studies suggest that females are sometimes able to dominate males (Parish 1996) and in the wild, groups of females were observed to defend food resources against males. Thus, a high-ranking mother may be the best ally a male can find in his natal community (compare also Boesch (1997)). During our

study at Lomako we observed several times that males received agonistic aid from their mothers in conflicts with other males and our results presented here suggest that this maternal support can have beneficial fitness effects for the mothers through the paternity success of their sons (Hohmann & Fruth 1996).

(a) *Paternity and rank*

Our data indicate that reproductive success is biased in favour of high-ranking males, even though these do not necessarily show the highest copulation rates. In chimpanzees, high-ranking males employ mating strategies that are likely to have a greater probability for fertilization than those practised by low-ranking males (Tutin 1979). Bonobos at Wamba mate almost exclusively opportunistically (Kano 1989) but in Lomako consortships have also been observed (B. Fruth and G. Hohmann, unpublished data). However, whether or not these differences affect the chance of fertilization is an open question. The interpretation of our results is problematic insofar as most of the immatures for which samples were available had been sired before 1990. Accordingly, information about the ranks of the males at the time of fertilization are unknown.

An alternative explanation for the bias in paternity distribution is the potential for female choice (Birkhead & Parker 1997; Qvarnström & Forsgren 1998). Our field data from Lomako suggest codominance between the sexes; forced matings are uncommon and males are unable to monopolize access to oestrous females for longer times. Often, oestrous females copulate in close succession with several adult males providing the potential for cryptic choice by the female among competing sperm (Eberhard 1996). The existence of female tactics to solicit mating are well-established, the precise advantages of female choice are not yet known, however. Data from macaques and baboons suggest that the proximate goal of female choice is mating with various males instead of one particular individual (de Ruiter *et al*. 1994; Bercovitch 1995) supporting the hypothesis that promiscuous mating attempts by females aim on paternity confusion (Hrdy 1988).

Although extra-community copulations are not uncommon, the proportion of infants sired by non-resident males is low. For two juveniles (GLO and VIR) no matching paternal genotype was found. GLO was already present at the time when the fieldwork started and it could be that her father has disappeared. VIR was born in 1992 when all potential fathers within the community were known and sampled. We assume therefore that VIR was sired by a male from another community. The high reproductive success of resident males is in strong contrast to a recent study of a chimpanzee group, where almost half of the infants were found to be sired by males from outside the group, although extra-community copulations were never observed (Gagneux *et al*. 1997*b*). Paternity assessments in another chimpanzee population revealed also that less than 10% of the individuals tested could be assigned to resident males (Morin *et al*. 1994*b*). However, in the latter case the authors did not ascribe the result to matings with non-resident males but suggested that pedigree relationships could not be identified because of the lack of samples from the real fathers.

5. CONCLUSION

The genetic relationships among members of the Eyengo community supports the notion that migration is female biased. Thus, the high degree of sociality and cooperation between resident females (Furuichi 1989, 1997; Hohmann & Fruth 1996; Parish 1996) cannot be ascribed to close genetic ties but is more likely the result of mutualism or reciprocity. Our data suggest that there may be a positive correlation between social dominance and reproductive success of males. However, considering the small sample size that is currently available, it is evident that more data on the reproductive success of individual males collected during periods of different rank are required to test the validity of the current result. The low degree of intrasexual aggression observed by us and reported from another field study (Furuichi & Ihobe 1994) suggests that the reproductive success of an individual male does not primarily depend on priority of access but, instead, may be also controlled by females. It seems clear that kinship relationships alone cannot explain social relationships and patterns of cooperation among bonobos, opening up the way for testing alternative models such as reciprocity or appeasement strategies (de Waal 1995).

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REFERENCES

Altmann, J. (and 12 others) 1996 Behavior predicts genetic structure in a wild primate group. *Proc. Natl Acad. Sci. USA* **93**, 5797–5801.

Anderson, S., Bankier, A. T., Barrell, B. G., De Bruijn, M. H. L., Coulson, A. R., Drouin, J., Eperon, I. C., Nierlich, D. P. & Roe, B. A. 1981 Sequence and organization of the human mitochondrial genome. *Nature* **290**, 457–465.

Bercovitch, F. 1989 Body size, sperm competition and determinants of reproductive success in male savanna baboons. *Evolution* **43**, 1507–1521.

Bercovitch, F. 1995 Female cooperation, consortship maintenance, and male mating success in savanna baboons. *Anim. Behav.* **50**, 137–149.

Birkhead, T. R. & Parker, G. A. 1997 Sperm competition and mating systems. In *Behavioral ecology* (ed. J. R. Krebs & N. B. Davies), pp. 121–145. Oxford: Blackwell Science.

Boesch, C. 1997 Evidence for dominant wild female chimpanzees investing more in sons. *Anim. Behav.* **54**, 811–815.

Coote, T. & Bruford, M. W. 1996 Human microsatellites applicable for analysis of genetic variation in apes and old world monkeys. *J. Hered.* **87**, 406–410.

Dahl, J. F. 1986 Cyclic perineal swelling during the intermenstrual intervals of captive female pygmy chimpanzees (*Pan paniscus*). *J. Hum. Evol.* **15**, 369–385.

de Ruiter, J. R. & Geffen, E. 1998 Relatedness of matrilines, dispersing males and social groups in long-tailed macaques (*Macaca fascicularis*). *Proc. R. Soc. Lond.* B **265**, 79–87.

de Ruiter, J. R., Van Hooff, J. A. R. A. M. & Scheffrahn, W. 1994 Social and genetic aspects of paternity in wild long-tailed macaques (*Macaca fascicularis*). *Behaviour* **129**, 203–224.

de Waal, F. B. M. 1995 Bonobo sex and society. *Sci. Am.* **272**, 82–88.

Dugatkin, L. A. 1997 *Cooperation among animals.* New York: Oxford University Press.

Eberhard, W. G. 1996 *Female control: sexual selection by cryptic female choice.* Princeton University Press.

Estoup, A., Largiader, C. R., Perrot, E. & Chourrout, D. 1996 Rapid one-tube DNA extraction for reliable PCR detection of fish polymorphic markers and transgenes. *Mol. Mar. Biol. Biotechnol.* **5**, 295–298.

Foucault, F., Praz, F., Jaulin, C. & Amor-Gueret, M. 1996 Experimental limits of PCR analysis of (CA)n repeat alterations. *Trends Genet.* **12**, 450–452.

Furuichi, T. 1989 Social interactions and the life history of female *Pan paniscus* in Wamba, Zaire. *Int. J. Primatol.* **10**, 173–197.

Furuichi, T. 1992 The prolonged estrus of females and factors influencing mating in wild group of bonobos (*Pan paniscus*) in Wamba, Zaire. In *Topics in primatology.* 2. *Behavior, ecology, and conservation* (ed. N. Itoigawa, Y. Sugiyama, G. P. Sackett & R. K. R. Thompson), pp. 179–190. University of Tokyo Press.

Furuichi, T. 1997 Agonistic interactions and matrifocal dominance rank of wild bonobos (*Pan paniscus*) at Wamba. *Int. J. Primatol.* **18**, 855–875.

Furuichi, T. & Ihobe, H. 1994 Variation in male relationships in bonobos and chimpanzees. *Behaviour* **130**, 211–228.

Gagneux, P., Boesch, C. & Woodruff, D. S. 1997*a* Microsatellite scoring errors associated with noninvasive genotyping based on nuclear DNA amplified from shed hair. *Mol. Ecol.* **6**, 861–868.

Gagneux, P., Woodruff, D. S. & Boesch, C. 1997*b* Furtive mating in female chimpanzees. *Nature* **387**, 348–350.

Gerloff, U., Schlötterer, C., Rassmann, K., Rambold, I., Hohmann, G., Fruth, B. & Tautz, D. 1995 Amplification of hypervariable simple sequence repeats (microsatellites) from excremental DNA of wild living Bonobos (*Pan paniscus*). *Mol. Ecol.* **4**, 515–518.

Goodall, J. 1986 *The chimpanzees of Gombe.* Cambridge, MA: The Belknap Press of Harvard University Press.

Gyapay, G., Morissette, J., Vignal, A., Dib, C., Fizames, C., Millasseau, P., Marc, S., Bernardi, G., Lathrop, M. & Weissenbach, J. 1994 The 1993–94 Généthon human genetic linkage map. *Nature Genet.* **7**, 246–339.

Hamilton, W. D. 1963 The evolution of altruistic behavior. *Am. Nat.* **97**, 354–356.

Hashimoto, C., Furuichi, T. & Takenaka, O. 1996 Matrilineal kin relationship and social behaviour of wild bonobos (*Pan paniscus*): sequencing the D-Loop region of mitochondrial DNA. *Primates* **37**, 305–318.

Hohmann, G. & Fruth, B. 1993 Field observations on meat sharing among bonobos (*Pan paniscus*). *Folia Primatol.* **60**, 225–229.

Hohmann, G. & Fruth, B. 1996 Food sharing and status in unprovisioned bonobos. In *Food and the status quest* (ed. P. Wiessner & W. Schiefenhoevel), pp. 47–67. Providence and Oxford, UK: Berghahn Books.

Hohmann, G., Gerloff, U., Tautz, D. & Fruth, B. 1998 Social bonds and genetic ties: kinship, association and affiliation in a community of bonobos (*Pan paniscus*). *Behaviour.* (In the press.)

Hrdy, S. B. 1988 The primate origins of human sexuality. In *The evolution of sex* (ed. R. Bellig & G. Stevens), pp. 101–136. New York: Harper & Row.

Idani, G. 1991 Social relationships between immigrant and resident bonobo (*Pan paniscus*) females at Wamba. *Folia Primatol.* **57**, 83–95.

Inoue, M., Mitsunaga, F., Ohsawa, H., Takenaka, A., Sugiyama, Y., Soumah, A. G. & Takenaka, O. 1992 Paternity testing in captive Japanese macaques (*Macaca fuscata*) using DNA fingerprinting. In *Paternity in primates: genetic tests and theories* (ed. R. D. Martin, A. F. Dixson & E. J. Wickings), pp. 131–140. Basel: Karger.

Kano, T. 1982 The social group of pygmy chimpanzees (*Pan paniscus*) of Wamba. *Primates* **23**, 171–188.

Kano, T. 1989 The sexual behavior of pygmy chimpanzees. In *Understanding chimpanzees* (ed. G. Heltne & L. A. Marquardt), pp. 176–183. Cambridge, MA: Harvard University Press.

Kano, T. 1992 *The last ape: pygmy chimpanzee behaviour and ecology.* Cambridge, MA: Stanford University Press.

Kuroda, S. 1979 Grouping of the pygmy chimpanzees. *Primates* **20**, 161–183.

Marshall, T. C., Slate, J., Kruuk, L. & Pemberton, J. L. 1998 Statistical confidence for likelihood-based paternity inference in natural populations. *Mol. Ecol.* **7**, 639–655.

Møller, A. P. 1988 Ejaculate quality, testes size and sperm competition in primates. *J. Hum. Evol.* **17**, 479–488.

Morin, P. A., Moore, J. J., Chakraborty, R., Jin, L., Goodall, J. & Woodruff, D. S. 1994*a* Kin selection, social structure, gene flow, and the evolution of chimpanzees. *Science* **265**, 1193–1201.

Morin, P. A., Wallis, J., Moore, J. J. & Woodruff, D. S. 1994*b* Paternity exclusion in a community of wild chimpanzees using hypervariable simple sequence repeats. *Mol. Ecol.* **3**, 469–478.

Nishida, T., Takasaki, H. & Takahata, Y. 1990 Demography and reproductive profiles. In *The chimpanzees of Mahale mountains* (ed. T. Nishida), pp. 63–97. Tokyo University Press.

Noe, R. 1990 A veto game played by baboons: a challenge to Prisoner's Dilemma as a paradigm for reciprocity and cooperation. *Anim. Behav.* **39**, 78–90.

Parish, A. R. 1996 Female relationships in bonobos (*Pan paniscus*). Evidence for bonding, cooperation, and female dominance in a male-philopatric species. *Hum. Nat.* **7**, 61–96.

Petri, B., Pääbo, S., Von Haeseler, A. & Tautz, D. 1997 Paternity assessment and population subdivision in a natural population of the larger mouse-eared bat *Myotis myotis*. *Mol. Ecol.* **6**, 235–242.

Pusey, A. E. 1980 Inbreeding avoidance in chimpanzees. *Anim. Behav.* **28**, 543–552.

Pusey, A., Williams, J. & Goodall, J. 1997 The influence of dominance rank on the reproductive success of female chimpanzees. *Science* **277**, 828–830.

Queller, D. C. & Goodnight, K. F. 1989 Estimating relatedness using genetic markers. *Evolution* **43**, 258–275.

Qvarnström, A. & Forsgren, E. 1998 Should females prefer dominant males? *Trends Ecol. Evol.* **13**, 498–501.

Small, M. 1989 Female choice in nonhuman primates. *Yb. Phys. Anthropol.* **32**, 103–127.

Swofford, D. L. 1993 Phylogenetic Analysis Using Parsimony, 3.4.1. Illinois Natural History Survey.

Taberlet, P., Griffin, S., Goossens, B., Questiau, S., Manceau, V., Escaravage, N., Waits, L. P. & Bouvet, J. 1996 Reliable genotyping of samples with very low DNA quantities using PCR. *Nucl. Acids Res.* **24**, 3189–3194.

Trivers, R. 1971 The evolution of reciprocal altruism. *Q. Rev. Biol.* **46**, 35–57.

Tutin, C. E. G. 1979 Mating patterns and reproductive strategies in a community of wild chimpanzees (*Pan troglodytes schweinfurthii*). *Behav. Ecol. Sociobiol.* **6**, 29–38.

Van Schaik, C. P. 1989 The ecology of social relationships amongst female primates. In *Comparative socioecology* (ed. V. Standen & R. A. Foley), pp. 195–218. Oxford: Blackwell.

Van Schaik, C. P. 1996 Social evolution in primates: the role of ecological factors and male behaviour. *Proc. Br. Acad.* **88**, 9–31.

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