Potential for female kin associations in wild western gorillas despite female dispersal

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Female philopatry and male dispersal are the norm for most mammals, and females that remain in their natal region often derive foraging or social benefits from proximity to female kin. However, other factors, such as constraints on group size or a shortage of potential mates, may promote female dispersal even when female kin associations would be beneficial. In these cases, female kin associations might develop, not through female philopatry, but through female emigration to the same group. To date, little attention has been focused on the potential for kin-biased behaviour between females in female-dispersing species. Here we investigate the genetic relationships among adults in eight wild groups of unhabituated western gorillas (*Gorilla gorilla*) at the Mondika Research Center using microsatellite genotyping of DNA collected from hair and faeces. We found that almost half (40%) of adult females had an adult female relative in the same group and average within-group relatedness among females was significantly higher than that expected under a model of random dispersal. This provides the first genetic evidence that females can maintain social associations with female relatives in spite of routine natal and secondary dispersal. In addition, we show that females appear to avoid related silverback males when making dispersal decisions, suggesting that a strategy of non-random female dispersal may also function to avoid inbreeding.

Keywords: *Gorilla gorilla*; faeces; genotyping; kinship; dispersal; molecular ecology

1. INTRODUCTION

In most avian and mammalian species, one sex disperses from its natal area to reduce the genetic consequences of inbreeding. The majority of mammal species, including most Old World primates, are characterized by male-biased dispersal and female philopatry (Greenwood 1980; Pusey & Packer 1987). In these taxa, group-living females spend their lives in the company of female relatives. The reproductive success of females, unlike males, is limited primarily by nutritional constraints, and female philopatry probably confers foraging benefits on females (Greenwood 1980; Waser 1993). Current socioecological theory predicts that female philopatry will be particularly advantageous when kin-biased coalitions result in improved access to food (Wrangham 1980; van Schaik 1989; Sterck *et al.* 1997) and considerable evidence documents the link between kin-biased coalitions and greater feeding intake (Koenig 2002).

A wide variety of other benefits have been reported for female primates residing with same-sex kin. For example, in female philopatric savannah baboons (*Papio cynocephalus*), macaques and vervets, adult females spend more time near adult kin, groom them more frequently, handle their infants more often, show more tolerance towards them and lend them more coalitionary support compared with non-kin (Silk 2002), and there is a direct, demonstrable link between these social bonds and female fitness (Silk *et al.* 2003).

Surprisingly then, some female primates, including mountain and western gorillas (Harcourt 1978; Parnell 2002), chimpanzees (*Pan troglodytes*; Pusey 1979), hamadryas baboons (*Papio hamadryas*; Sigg *et al.* 1982), red (*Piliocolobus badius*) and olive (*Procolobus verus*) colobus monkeys (Starin 1994; Korstjens & Schippers 2003), capped (*Presbytis pileata*) and Thomas (*Presbytis thomasi*) langurs and Phayre's leaf monkey (*Tracypithecus phayrei*) (Stanford 1991; Sterck 1997; Borries *et al.* 2004), undergo natal, and often secondary, dispersal. This may occur because the potential benefits from dispersing, such as reduced feeding competition (Vick & Pereira 1989; Crockett & Janson 2000), inbreeding avoidance (Watts 1990; Sterck 1997; Parnell 2002) or reduced risk of infanticide, may outweigh the benefits of remaining with female kin.

It is generally assumed that the dispersing sex has limited, if any, opportunities to develop kin-biased relationships (Moore 1992; Hoelzer *et al.* 2004). However, if benefits arise from associating with same-sex kin, some form of associations may evolve through mechanisms other than philopatry. For example, non-random dispersal of males in male-dispersing species occurs through cohort dispersal, dispersal into a group containing related males or jointly migrating coalitions of males attempting group takeovers (e.g. lions (*Panthera leo*), Packer *et al.* 1991; Old World monkeys, Sugiyama 1976, Meikle & Vessey 1981, Cheney & Seyfarth 1983, van Noordwijk & van Schaik 2001; New World monkeys, Crockett & Sekulic 1984, Mitchell 1994, Jack & Fedigan 2004; lemurs, Sussman 1992, Ostner & Kappeler 2004).

Less is known about the potential for kin associations in female-dispersing primates. Female red colobus monkeys

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Figure 1. Minimum patterns of dyadic relatedness among adults in eight groups of western gorillas. Circles labelled with letters represent nesting sites of different social groups. Leaf symbols indicate nests that yielded insufficient DNA for analysis. The overall fraction of nests typed is noted under each nest site. Known breeding females are shaded; other females are of unknown breeding status. Dyads connected by lines were identified as related. Thin lines indicate that the dyad can be excluded as a parent–offspring pair. Position does not reflect relative location within the study site, but most groups are likely to have adjacent or overlapping home ranges.

have been documented transferring to or with female group-mates, and these individuals spent more time with each other than they spent with non-natal group-mates (Starin 1994). In mountain gorillas, when related females reside together, female relationships differentiate clearly along lines of relatedness (Watts 1994). We suggest that female kin associations in female-dispersing species may be more common and more beneficial than is currently recognized.

Here we examine the pattern of kin associations in female-dispersing western gorillas. Western gorilla groups have a single breeding silverback male (Magliocca *et al.* 1999; Parnell 2002; Gatti *et al.* 2004) and takeovers of groups by outside males have not been observed (Stokes *et al.* 2003). Although there is no evidence for long-range female-mediated gene flow in western gorillas (Douadi *et al.* 2007), females reaching reproductive age are known to disperse from their natal group (Parnell 2002; Stokes *et al.* 2003), and female secondary transfer is also common (Stokes *et al.* 2003).

Thus, at first glance, the opportunity for female kin associations appears limited. However, multi-female transfers between groups have been documented during both natal and secondary dispersals (Parnell 2002; Stokes *et al.* 2003). Although the genetic relationships of these pairs were unknown, females born in the same group are likely to be paternal sisters since group silverbacks sire most, if not all, of the offspring born during their tenure (Bradley *et al.* 2004).

Here we examine the genetic relationships among adult females and between adult females and resident silverbacks in eight unhabituated western gorilla groups to see whether adult females are able to associate with female kin despite routine dispersal.

2. MATERIAL AND METHODS

(a) Study site and sample collection

Faecal samples from wild gorillas unhabituated to human observation were collected at the Mondika Research Center, located on the border of the Central African Republic and

Republic of Congo (02°21' N, 016°16' E; see Mehlman & Doran 2002 for details about study site). The sampling area was approximately 50 km². Since, in this region, western gorilla home range size is approximately 15 km² (Doran-Sheehy *et al.* 2004), most of the sampled groups are likely to have overlapping or adjacent home ranges. Samples were collected at fresh nesting sites, which were located by tracking (Mehlman & Doran 2002). Gorillas build new nests each evening and defecate in or beside the nests the next morning, allowing for relatively complete sampling of group members at recently vacated nesting sites.

One of four age classes (infant, juvenile, adult female or blackback male and adult male silverback) could be assigned to the individual that slept in each nest based on the size of the associated dung (Schaller 1963). Fresh faeces (approx. 5 g) were placed in tubes containing 20 g silica gel beads for desiccation. Detailed methods of sample collection and storage are described in Bradley *et al.* (2004).

(b) Genotype and kinship analyses

Genomic DNA was extracted from faecal samples and typed at 10 microsatellite loci (see the electronic supplementary material for details). Because samples were collected from unhabituated gorillas that were not directly observed at the time of sample collection, individuals were identified only by their multi-locus genotypes. Probabilities of individual identity (calculated following Waits *et al.* (2001)) indicated that two samples yielding the same genotype were extremely unlikely to have come from different individuals ($P_{(ID-sibs)} = 0.000129$; see Bradley *et al.* (2004)).

Eight groups were analysed (figure 1) including samples from 8 silverbacks and 22 adult females. Of the 22 adult females, 15 were verified as breeding females based on the presence of infant dung in the same nest and/or the presence of a genetically assigned offspring at the nesting site (Bradley *et al.* 2004).

Genetic family relationships among adults were assessed conservatively using multiple criteria: (i) estimation of dyadic relatedness, (ii) likelihood analysis of hypothesized pedigree

Table 1. Relatedness and allelic exclusions among adult females within groups of western gorillas at the Mondika Research Center. Five of six groups contain related (four groups) or potentially related (one group) dyads. (The *r*-values were not calculated for dyads compared at fewer than five loci (noted by '—'). Asterisks denote significant likelihood ratios ($p < 0.05$))

group (nesting site)	dyad	loci compared	allelic exclusions	excluded as mother–daughter?	dyadic <i>r</i> -value	likelihood analysis	relationship category
B	B6f & B4f	8	3	yes	−0.11	n.s.	not related
	B8f & B4f	7	4	yes	−0.14	n.s.	not related
	B8f & B6f	7	1	yes	0.17	*	related
J	J1f & J2f	5	3	yes	−0.42	n.s.	not related
	J1f & J7f	7	3	yes	0.03	n.s.	not related
	J1f & J8f	4	2	yes	—	—	—
	J2f & J7f	6	3	yes	−0.21	n.s.	not related
	J2f & J8f	4	1	yes	—	—	—
	J7f & J8f	6	3	yes	−0.03	n.s.	not related
M	M2f & M6f	4	0	no	—	—	—
N	N1f & N2f	6	1	yes	0.62	*	related
	N1f & N4f	5	2	yes	−0.35	n.s.	not related
	N1f & N7f	4	2	yes	—	—	—
	N2f & N4f	5	2	yes	−0.25	n.s.	not related
	N2f & N7f	4	2	yes	—	—	—
	N4f & N7f	3	1	yes	—	—	—
O	O2f & O3f	9	3	yes	0.09	n.s.	not related
	O2f & O5f	8	2	yes	−0.02	n.s.	not related
	O3f & O5f	8	0	no	0.40	*	related
P	P6f & P7f	4	1	yes	—	—	—
	P6f & P10f	5	1	yes	0.08	n.s.	not related
	P6f & P15f	4	0	no	—	—	—
	P7f & P10f	7	0	no	0.66	*	related
	P7f & P15f	4	1	yes	—	—	—
	P10f & P15f	5	1	yes	−0.13	n.s.	not related

relationships, and (iii) exclusion of parent–offspring relationships through the presence of allelic mismatches. Classifying family relationships using marked-based estimates of relatedness is difficult and prone to misinterpretation as natural populations tend to show low variance in relatedness values (Csillery *et al.* 2006). Thus, we first confirmed that our approach correctly identified dyads of known relatedness (parent–offspring pairs, half- and full-sibling pairs based on shared parentage, non-relatives based on non-shared parentage). Known related dyads had a minimum *r*-value of 0.15, and this value was used as a threshold for considering dyads potentially related in our assessment of relationships using multiple criteria (see below; Bradley *et al.* 2004).

Relatedness was estimated for all possible adult dyads using the Queller & Goodnight (1989) estimator as implemented by the computer program RELATEDNESS v. 5.0.8 (<http://gsoft.smu.edu/GSoft.html>). Dyadic relatedness values are noted here as '*r*-values', while average relatedness values across multiple dyads within a category (e.g. adult females within groups) are noted as '*R*' or 'average relatedness'. The number of loci needed for consistent estimates of dyadic relatedness was assessed by rarefaction analysis (Altmann *et al.* 1996; De Ruiter & Geffen 1998) and subsequent dyadic *r*-value calculations included only pairs that could be compared at five or more loci. The statistical significance of average relatedness estimates was evaluated by permutation analysis (Manly 1997; Lukas *et al.* 2005). Here we used a simplified model of random dispersal, in which all individuals were randomly reassigned to groups (holding group number and size constant) and average relatedness was calculated within and between groups. This was repeated 5000 times, thereby providing a distribution of average relatedness values under a simplified model of random dispersal.

Dyads were then further assessed using the program KINSHIP (Goodnight & Queller 1999) to evaluate the likelihood ratios between a hypothesized pedigree relationship (e.g. full siblings) and a null hypothesis of no relationship. Using our data, the estimated proportion of tests resulting in false rejection of the proposed hypotheses and erroneous acceptance of the null hypothesis of no relationship (i.e. type II error rates) for half siblings, full siblings and parent–offspring primary hypotheses were 0.54, 0.10 and less than 0.01 at $p = 0.05$, respectively. Therefore, it is possible that some pairs of individuals that were actually related as full or half siblings were not identified as such in the likelihood analysis. Parent–offspring pairs were required to share at least one allele at each locus.

As in our previous study on male relatedness (Bradley *et al.* 2004), here we considered dyads to be related when (i) *r*-values were greater than 0.15 and (ii) likelihood ratios were significant ($p < 0.05$) for any of three primary hypotheses of first-order relatives (full or half sibling or parent–offspring). No dyads with *r*-values below the 0.15 threshold gave significant likelihood ratios in the KINSHIP analysis. We made no further attempts to distinguish categories or degrees of relatedness, since such fine-scale relatedness assessments would require 30+ microsatellite loci (Blouin 2003; Csillery *et al.* 2006).

3. RESULTS

(a) Relationships among adult females within groups

Adult female western gorillas were likely to have an adult female relative (dyadic *r*-values greater than 0.15 and significant likelihood ratios) in their group despite routine

Table 2. Relatedness and allelic exclusions between silverbacks and adult females within groups of western gorillas at the Mondika Research Center.

group (nesting site)	silverback	female	loci compared	allelic exclusions	excluded as parent–offspring?	dyadic <i>r</i> -value	likelihood analysis	relationship category
B	B2m	B4f ^a	6	2	yes	−0.01	n.s.	not related
		B6f ^a	6	2	yes	−0.02	n.s.	not related
		B8f	6	3	yes	−0.11	n.s.	not related
D	D3m	D1f ^a	8	3	yes	−0.25	n.s.	not related
J	J3m	J1f ^a	6	2	yes	0.17	n.s.	not related
		J2f ^a	6	2	yes	−0.27	n.s.	not related
		J7f ^a	7	2	yes	−0.26	n.s.	not related
		J8f	4	0	no	—	—	potentially related
M	M5m	M2f ^a	9	3	yes	−0.13	n.s.	not related
		M6f	4	1	yes	—	—	not parent- offspring
N	N3m	N4f ^a	5	3	yes	−0.15	n.s.	not related
		N7f ^a	4	3	yes	—	—	not parent- offspring
		N1f ^a	5	2	yes	−0.10	n.s.	not related
O	O7m	N2f	5	3	yes	0.13	n.s.	not related
		O2f ^a	8	3	yes	−0.26	n.s.	not related
		O3f ^a	8	3	yes	−0.32	n.s.	not related
		O5f ^a	7	2	yes	0.04	n.s.	not related
P	P13m	P7f ^a	7	1	yes	0.01	n.s.	not related
		P6f	5	1	yes	0.12	n.s.	not related
		P10f ^a	8	0	no	0.01	n.s.	not related
		P15f	5	2	yes	−0.14	n.s.	not related
Q	Q1m	Q3f ^a	6	2	yes	−0.22	n.s.	not related

^a Breeding female.

female dispersal in this species. In the six groups for which more than one female was genotyped, 40% of females (8 of 20) had a female relative in the same group (figure 1; table 1). Of the 25 female–female dyads within groups, 16 could be compared at five or more loci and were included in the analyses of dyadic relatedness. Overall, 25% (4 of 16) of these within-group female–female dyads were identified as related. In contrast, only 9 of 231 (4%) adult female dyads compared across groups were related. Chi-square results show that significantly more dyads were related within versus between groups ($\chi^2 = 13.37$, $p = 0.0003$).

Related dyads within groups did not represent mothers with daughters that were too young to disperse from their natal group because the dyads were either directly excluded as mother–daughter pairs (B8f & B6f and N1f & N2f) or included only breeding females (O3f & O5f and P7f & P10f), and females reaching reproductive maturity disperse from and do not reproduce in their natal group (Stokes 2004; table 1; figure 1). The absence of a father–daughter genetic relationship between any of the related females and the silverback of their group (see below) further indicates that these females were not in their natal group.

This pattern of within-group female relatedness is unlikely to have occurred by chance. Permutation analyses indicated that average within-group relatedness among females ($R = 0.055 \pm 0.313$) was significantly higher than that expected under a model of random dispersal (i.e. individuals randomly assigned to groups, 5000 permutations; $p = 0.018$).

(b) Relationships between silverbacks and adult females within groups

Of the 22 adult female–silverback dyads, 19 could be compared at five or more loci and were included in the analyses of dyadic relatedness (table 2). Of these, all but one dyad (J1f & J3m) had pairwise relatedness values of less than 0.15, and all dyads had non-significant likelihood ratios, indicating that it was unlikely that these pairs represented related pairs. Furthermore, based on the allelic mismatches, the silverback was excluded as the sire of adult female group members in 20 of 22 cases within the eight groups, including one case (J1f & J3m) with an *r*-value greater than 0.15 and two cases (M6f & M5m and N7f & N3m) for which the number of comparable loci was too few for relatedness analysis (table 2). Therefore, based on allelic exclusions and/or relatedness analyses, in at least 21 of 22 cases the silverback was not the father of adult females in his group (table 2; figure 1). We considered the remaining dyad (J8f & J3m) potentially related since the silverback and female could only be compared at four loci, precluding relatedness analyses, and the pair were not excluded as father–offspring by allelic mismatch. Since J8f was not one of the 16 identified breeding females, it is possible that she had yet to undergo natal dispersal.

Average relatedness of adult female–silverback dyads within groups ($R = -0.11 \pm 0.13$) was significantly lower than that expected under our simplified model of random dispersal (5000 permutations; $p = 0.046$), suggesting that females are actively avoiding related males when making transfer decisions.

4. DISCUSSION

Our results reveal that western gorillas often maintain adult female kin associations despite routine natal and secondary dispersal. Nearly half (40%) of the adult females had an adult female relative in the same group and a quarter of adult female dyads in groups were genetically related. Since the related females were not in their natal group, female kin associations must occur as a result of choices made during dispersal, with females associating with female kin more frequently than would be expected by chance. Although western gorillas do not exhibit matrilineal associations to the same degree as some female philopatric species, our results indicate that female dispersal does not necessarily preclude female kin association, as is generally assumed.

How do these female kin associations arise? Western gorillas live in groups that contain relatively few (average 3–4) adult females with long interbirth intervals (mean = 62.3 months, $n=3$) and non-seasonal reproduction (Robbins *et al.* 2004), factors that would seemingly make natal cohort dispersal unlikely. However, groups can form abruptly as a solitary male gains several females (Stokes *et al.* 2003), and those females produce new offspring at roughly the same time. For example, in our current behavioural study of a habituated group at the site, four of six adult females gave birth within one nine-month period (D. M. Doran-Sheehy 2002–2003, unpublished observation). Offspring that are likely to be paternal siblings (Bradley *et al.* 2004) spend several years together prior to natal dispersal around the age of 8–9 years (Robbins *et al.* 2004). If group females reach reproductive maturity at similar ages, natal co-dispersal of related siblings would be possible.

Female co-transfer may also be precipitated by group disintegration following the death of the silverback. Since western gorillas have not been observed to form multi-male groups or have external takeovers of existing groups (Robbins *et al.* 2004), females and unweaned offspring must transfer to new groups when the silverback dies (Stokes *et al.* 2003).

The lack of long-term behavioural data on wild western gorillas precludes a conclusive assessment of the functions of these female kin associations. However, in the light of the growing evidence from a wide variety of species that female kin, including paternal kin (Widdig *et al.* 2001; Smith *et al.* 2003), behave preferentially towards each other and that social, as well as foraging, benefits may derive from residing with kin (Koenig 2002; Silk 2002), it seems possible that western gorilla females gain direct benefits from kin associations. In mountain gorillas, when related females reside together, they spend more time in proximity, engage in more affiliative behaviours, have wider social networks and support each other in conflicts more frequently than do non-kin (Watts 1994), behaviours that have demonstrable fitness benefits in female philopatric species such as baboons (Silk *et al.* 2003).

Female co-dispersal may also reduce the costs of transferring by reducing harassment received from conspecifics during natal transfer (Watts 1994), as has been suggested for males in male-dispersing species (Cheney & Seyfarth 1983). Similarly, it is tempting to speculate that multi-individual co-transfer might be an effective anti-infanticide strategy for females with unweaned offspring. At Mbeli Bai, in some situations involving multiple

females transferring together, expected infanticides of unweaned offspring by the new silverback did not occur (Stokes *et al.* 2003).

Our study of western gorillas demonstrates that long-term female kin associations are possible and potentially beneficial in species with routine female dispersal. This has several important implications. First, these results contribute to a growing body of evidence indicating that female social bonds may be more important in African apes than is commonly recognized (Lehmann & Boesch 2007; Townsend *et al.* 2007).

Second, in most mammalian studies, genetic relationships among group members are usually unknown, but we often assume that members of the philopatric sex will tend to be related while members of the dispersing sex will not (Altmann *et al.* 1996). Our results, along with other recent assessments of relatedness in wild populations (Lukas *et al.* 2005), indicate that this is not always the case. Dispersal patterns can be an incomplete indicator of kinship structure. Further genetic examinations of relatedness among social groups may well reveal that kin associations, and thus the potential for kin-biased social behaviours, are more common among the dispersing sex than is generally recognized.

This research met all national and international guidelines, including compliance with national animal care policies in the countries in which the research was conducted. All samples were imported/re-exported with valid CITES permits.

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