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Neither genetic nor observational data alone are sufficient for understanding sex-biased dispersal in a social-group-living species

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Abstract

Complex sex-biased dispersal patterns often characterize social-group-living species and may ultimately drive patterns of cooperation and competition within and among groups. This study investigates whether observational data or genetic data alone can elucidate the potentially complex dispersal patterns of social-group-living black and white colobus monkeys (*Colobus guereza*, 'guerezas'), or whether combining both data types provides novel insights. We employed long-term observation of eight neighbouring guereza groups in Kibale National Park, Uganda, as well as microsatellite genotyping of these and two other neighbouring groups. We created a statistical model to examine the observational data and used dyadic relatedness values within and among groups to analyse the genetic data. Analyses of observational and genetic data both supported the conclusion that males typically disperse from their natal groups and often transfer into nearby groups and probably beyond. Both data types also supported the conclusion that females are more philopatric than males but provided somewhat conflicting evidence about the extent of female philopatry. Observational data suggested that female dispersal is rare or nonexistent and transfers into neighbouring groups do not occur, but genetic data revealed numerous pairs of closely related adult females among neighbouring groups. Only by combining both data types were we able to understand the complexity of sex-biased dispersal patterns in guerezas and the processes that could explain our seemingly conflicting results. We suggest that the data are compatible with a scenario of group dissolution prior to the start of this study, followed by female transfers into different neighbouring groups.

Keywords: among-group relatedness, *Colobus guereza*, dispersal, kinship, philopatry, within-group relatedness

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Introduction

Investigating a species' dispersal pattern is important for understanding its ecology, life history, behavioural patterns, population dynamics and genetic structure. Understanding which sex disperses, the timing of dispersal and how far individuals disperse are important both for making conservation decisions and for understanding the evolutionary causes of dispersal (reviewed in Lawson Handley & Perrin 2007).

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Species that live in social groups often exhibit complex sex-biased dispersal and transfer patterns. The resulting effects on the distribution of close kin are suggested to ultimately drive patterns of cooperation and competition within and among groups (Hamilton 1964; Greenwood 1980; Sterck *et al*. 1997; reviewed in Lawson Handley & Perrin 2007; but see also West *et al*. 2002; Langergraber *et al*. 2007). A number of proximate and ultimate factors influence animals' decisions to remain in their natal groups or disperse (Greenwood 1980; reviewed in Lawson Handley & Perrin 2007). Emigration may be followed by solitary phases, same-sex groupings (e.g. bachelor groups) and/or immigration into local or far-away groups. Secondary dispersal also occurs in a number of species (Pusey &

Packer 1987). Related individuals sometimes emigrate or immigrate together, and lone individuals may immigrate into groups that do or do not contain kin (reviewed in Bradley *et al*. 2007). In social mammals, females are often philopatric, but a number of exceptions including female-biased dispersal and dispersal by both sexes occur (reviewed in Lawson Handley & Perrin 2007).

Dispersal events are relatively rare and difficult to study directly. Researchers have commonly used long-term observations, including mark-resighting or recapture techniques, to investigate dispersal in group-living species (Packer 1979; Pusey & Packer 1987; Alberts & Altmann 1995; McNutt 1996; Brockelman *et al*. 1998; Korstjens & Schippers 2003; Williams & Rabenold 2005; Ekernas & Cords 2007). Studies have also shown that sex-biased dispersal patterns can be reflected in the genetic structure of social groups (Altmann *et al*. 1996; Dobson *et al*. 1998; Gompper *et al*. 1998), leading to an interest in inferring dispersal patterns from genetic patterns, sometimes with little or no corresponding observational data on dispersal in that population (Di Fiore & Fleischer 2005; Hammond *et al*. 2006; Dechmann *et al*. 2007). Such studies typically assume that adults of the more philopatric sex will have higher mean levels of relatedness within groups and the more dispersing sex will have higher relatedness among groups. But both observational and genetic methods may provide important information that cannot necessarily be gained from the other. For example, observational data may provide information about proximate dispersal mechanisms and dispersal costs, and genetic data can provide valuable information about gene flow (reviewed in Lawson Handley & Perrin 2007).

Only a few studies on social-group-living species have used both observational and genetic data on the same individuals to investigate dispersal patterns (Temple *et al*. 2006; Huck *et al*. 2007; Nagy *et al*. 2007; Di Fiore *et al*. in press). More typically, new genetic studies add to previously derived information from observational studies. In many cases, genetic and observational studies of dispersal come to the same general conclusions (Altmann *et al*. 1996; Gompper *et al*. 1998; Temple *et al*. 2006; Huck *et al*. 2007; Nagy *et al*. 2007). Occasionally, however, their findings are somewhat contradictory (Vigilant *et al*. 2001; Möller & Beheregaray 2004; Lukas *et al*. 2005; Goossens *et al*. 2006).

Long-term observational studies of chimpanzees (*Pan troglodytes*), for example, clearly show that males are philopatric and females disperse, but genetic studies have found that average within-group relatedness usually does not differ between adult males and adult females (Vigilant *et al*. 2001; Lukas *et al*. 2005). Lukas *et al*. (2005) showed that within-group relatedness for the philopatric sex may not be significantly higher than for the dispersing sex if group size is large, most likely contributing to this finding. This explanation, however, does not suffice for other contradictions between genetic and observational data. For example, a genetic study of coastal bottlenose dolphins (*Tursiops aduncus*) that sampled relatively large numbers of individuals at two different locations found that mean relatedness among resident females was higher than among resident males, contradicting previous observational reports that both sexes are philopatric (Möller & Beheregaray 2004). Such discrepancies indicate that further studies using long-term observational and genetic data on the same individuals are needed to understand whether either method, alone, can sufficiently resolve sex-biased dispersal patterns in social-group-living species.

We used both observational and genetic data on multiple neighbouring groups of black and white colobus monkeys (*Colobus guereza*, 'guerezas') in Kibale National Park, Uganda, to test whether both data types lead to the same conclusions about sex-biased dispersal. Previous reports combined with unpublished data on this species suggest potentially complex dispersal patterns, making guerezas useful for such a test. For example, males may show natal dispersal as large juveniles, subadults or adults; they may remain in their natal groups as adults; they may become solitary or join bachelor groups; they may immigrate into other groups by joining on the periphery or staging takeovers; and they may also disperse secondarily (Marler 1972; Dunbar & Dunbar 1974; Oates 1974, 1977). Male guerezas defend high-quality feeding areas, potentially freeing females to disperse and choose the best defenders (Fashing 2001a; Harris 2005), but little has been reported about female dispersal in this species. One voluntary female dispersal event has been recorded, as well as one dispersal event as a result of group dissolution (Bocian 1997; Fashing 2007). Group fission has also been reported in Ethiopian guereza populations (Dunbar & Dunbar 1974). We examine, in turn, inferences from both observational and genetic data and ask whether they should be combined to better understand these potentially complex patterns.

Methods

Study species, study area and subjects

Guerezas are medium-sized arboreal primates that occur throughout sub-Saharan Africa (Oates *et al*. 1994). They typically live in small social groups consisting of 1–5 adult males, 1–4 adult females, and their offspring (Fashing 2007). Many groups are unimale, with the resident male having virtually exclusive access to the group's females; however, in multimale–multifemale groups, females typically mate with more than one male (Harris, unpublished data). Leaves typically form a large part of the monkeys' diets, and their home ranges are relatively small (range: 8–100 ha: Fashing 2007; Harris & Chapman 2007). Males defend high-quality feeding areas against other groups, but it has

Table 1 Study group compositions and samples collected. '# individuals tracked', number of individuals observed for the first time in that group that were tracked as part of this study (i.e., they were at least large juveniles by the end of the study); A, adult; S, subadult; J, juvenile; F, female; M, male

		Group compositions										
Group		# AF	# AM	# SF	# SM	# JF	# JM	# I	Overall group size	# Individuals tracked	% Individuals tracked that were sampled	Individuals tracked but not sampled
Bat.	Min.	1	1	0	1	0	0	0	5	10	90.0	AF, died before sampled
	Max.	3	4	1	2	2	1	2	10			
Zik.	Min.	2	1	0	0	0	0	0	6	7	100.0	
	Max.	4	2	1	1	1	3	3	10			
Mug.	Min.	2	1	0	0	0	0	0	5	6	83.3	JF/SF
	Max.	4	1	2	0	3	1	2	10			
Bas.	Min.	1	1	0	0	0	0	0	4	6	83.3	AM, immigrated near
	Max.	1	2	1	1	2	1	1	6			end of study
Kas.	Min.	2	1	0	0	0	1	0	6	7	85.7	SF, disappeared beginning
	Max.	3	2	1	1	1	3	2	9			of study
Bwa.	Min.	2	1	0	0	1	0	0	8	10	70.0	AM, present only 1 subperiod;
	Max.	4	4	2	1	3	1	3	12			2 AF, one died before sampled
Mze.	Min.	3	1	0	0	0	0	0	5	9	88.9	AM, disappeared beginning
	Max.	3	6	0	0	3	1	3	10			of study
Bir.	Min.	3	1	0	0	0	2	0	7	9	100.0	
	Max.	4	2	0	2	1	3	3	12			

yet to be determined whether this strategy serves to attract females and/or to increase the females' reproductive outputs and infant survival (Fashing 2001a; Harris 2005, 2006).

We observed eight neighbouring habituated groups of guerezas at the Kanyawara research site in Kibale National Park, Uganda. Groups contained 4–10 individuals, excluding infants (Table 1). Compositions of six groups (Bas., Bat., Bwa., Kas., Mug. and Zik.) were monitored regularly (typically once or more a month) during 2002–2007 as part of a long-term behavioural ecology study, and they continue to be monitored. The compositions of the other two groups (Bir. and Mze.) were monitored regularly during 2.5 years (2005–2007) as part of the same study. We used the same age class definitions as Fashing (2001b).

All adults and most subadults and juveniles were recognizable within their groups, using facial markings, tail shape, body size and sex differences in coat colouration near the genital region. Not all individuals, however, were deemed by the observers as recognizable outside their own group (i.e. as recognizable if they dispersed to another group). Of the 21 males and seven females we tracked that disappeared from their groups, the observers deemed 13 males and three females to be recognizable outside their own groups. Of the three individuals that immigrated into one of the study groups from presumably outside the study groups, two were deemed recognizable outside of their groups. We took into account the recognizability of individuals that disappeared or that immigrated when testing the hypothesis that males and females were equally likely to disperse.

Observational data collection and analysis

We divided the study (2002–2007) into 60 subperiods of 30 days. We tracked all individuals that reached minimum dispersal stage—large juveniles—by the end of the study. Demographic information on 31 males and 33 females was collected (but note that these data were available for only 30 subperiods for the Bir. and Mze. groups). This information included the age class of each individual (infant/juvenile, subadult or adult) and their migration status (present in their group, emigrated to another group in the studied population or disappeared from the studied population). We defined the 'studied population' as the eight study groups and the neighbouring groups (about eight) that they sometimes encountered. Individuals were considered as having left their group if they were not seen in the group for more than five days, or on two consecutive observation dates separated by more than five days. When individuals died, it was generally impossible to find their bodies. Indeed, only one dead body could be found and identified during the whole study (excluding those of young infants that were not included in this study because they did not mature to dispersal age). Therefore, individuals that disappeared from the studied population may have emigrated towards unstudied groups or may have died.

Transfers of individuals between groups in the studied population could be reported only if the individuals were recognizable outside of their initial groups. Unrecognizable individuals that left their groups were considered either as having emigrated towards a group within the studied population or as having disappeared from the studied population (i.e. died or migrated to unobserved groups). Importantly, however, all animals habituated to human presence that joined study groups were recognized and all unrecognized animals that joined were unhabituated and thus unlikely to have come from study groups.

A maximum-likelihood statistical model was built to estimate the value of the following parameters: φ_i: probability that an individual belonging to the age class i remained in the studied population between two consecutive subperiods; d_i, probability that an individual belonging to the age class i migrated between two groups in the studied population between two consecutive periods. As there were three age classes (infant/juvenile, $i = 1$; subadult, $i = 2$; adult, $i = 3$), the model thus included a total of six parameters. The first step of the maximum-likelihood procedure consisted of writing the probabilities to observe each of the histories of the 64 individuals of the dataset, as a function of the parameters.

For example, we would code '1112222' the history of an individual that we observed during seven months, first as an infant (during three months, coded 1), then as a subadult (during four months, coded 2) and that did not leave his group during that period. This history includes six transitions because there are six intervals between seven elements. The first three transitions concern individuals of the age class indexed '1': 1-1, 1-1 and 1-2. The last three transitions concern individuals of the age class '2': 2-2, 2-2 and 2-2. The probability to observe that particular history is $[\varphi_1(1 - d_1)]^3 [\varphi_2(1 - d_2)]^3$. Now consider the following history: 1110022, with 0 denoting the absence of data available for the fourth and the fifth months. This individual did not leave his group during the study period, either. The probability to observe such a history is $[\varphi_1(1 - d_1)]^3[[\varphi_1(1 - d_1)]^2 + \varphi_1(1 - d_1)\varphi_2(1 - d_2) + [\varphi_2(1 - d_2)]^2]\varphi_2(1 - d_2)$. In this equation, the three terms of the sum translate the fact that the 00 sequence could be 11, 12 or 22. Lastly, consider another possible history: 3333444, with 4 denoting the disappearance of the individual. If this individual was recognizable, the probability of that history is $[\varphi_3(1 - d_3)]^3(1 - \varphi_3)$. However, if this individual was unrecognizable, this probability is $[\varphi_3(1 - d_3)]^3(1 - \varphi_3 + d_3)$. Using this method, the probabilities of each of the 64 observed histories were written as functions of the six parameters of the model. We subsequently derived the likelihood of the whole dataset by multiplying all these probabilities. The parameter values that maximize the likelihood were then sought, using the differential evolution optimization algorithm implemented in Mathematica version 5 (Wolfram Research). We computed profile-likelihood confidence intervals of these estimates using the same algorithm. Lastly, we compared estimates computed for males and females using log-likelihood ratio tests.

Sample collection and storage; DNA extraction and quantification

We noninvasively collected 322 guereza faecal samples, with most individuals sampled multiple times: 310 from individuals of all ages in the eight main study groups (nearly all individuals were sampled; Table 1), as well as 12 from subadults and adults in two unstudied neighbouring groups. Twenty-five samples were stored in plastic tubes filled with RNA Later (Ambion); 47 were stored in plastic tubes filled with silica and 272 were stored using the 2-step ethanol-silica method (Nsubuga *et al*. 2004). We extracted 227 samples (70.5% of those collected) using the QIAmp® Stool kit (Qiagen) with slight modifications (Nsubuga *et al*. 2004). We quantified the amount of DNA extracts contained using a 5′-nuclease assay targeting a highly conserved 81 bp portion of the *c-myc* proto-oncogene (Morin *et al*. 2001). Mean DNA quantities/extract ($X \pm$ SE) for samples stored in RNA later, silica, and ethanol followed by silica were 100 ± 38, 235 ± 104 and 709 ± 139 pg/2 μL, respectively.

Genotyping methods

Most of the genotyping methods are described in detail elsewhere (Arandjelovic *et al*. in press). Briefly, we attempted to amplify 15 microsatellite loci using the DNA extracted from faeces. For a majority of samples and loci [9606 polymerase chain reactions (PCRs) out of 11152], we used a 2-step multiplex PCR procedure, with both nested and un-nested primers (detailed in Arandjelovic *et al*. 2009). For a smaller subset of samples and loci (664 PCR reactions out of 11152), we modified the 2-step multiplex procedure by combining up to four differently labelled primer pairs, with differently sized products, in the second step. We attempted to combine primer pairs with similar annealing temperatures, but nearly all the combinations of primer pairs we used worked well together. Lastly, for some samples and loci (882 PCR reactions out of 11152), we used standard PCR amplification procedures, as in Bradley *et al*. (2000), with slight modifications: total volume was 20 μL, with 2 μL template, 1 × SuperTaq buffer (HT Biotechnology), 875 μM $MgCl_2$, 16 μg BSA, 125 μM dNTPs, 250 μM each forward (labelled) and reverse (unlabelled) primer, as well as 0.33 U Super Taq (HT Biotechnology) premixed 2 : 1 with TaqStart Antibody (BD Biosciences).

We electrophoresed PCR products from up to four different primer pairs, combined, using an ABI 3100 Genetic Analyser. An internal size standard (ROX labelled HD400) was added to gauge allele sizes. We used GeneMapper® Software version 3.7 (Applied Biosystems) to score alleles.

Previous analyses (Arandjelovic *et al*. 2009) using results from the 2-step multiplexing procedure and guereza sample extracts, showed that allelic dropout is infrequent (~4% of PCR reactions). Thus, we calculated that the number of successful PCR replicates necessary to assure with > 99% certainty that homozygote genotypes are authentic and not the result of allelic dropout, is: four for extracts with ≤ 25 pg DNA/reaction, three for extracts with 26–50 pg DNA/reaction, and two for extracts with > 50 pg DNA/reaction (Arandjelovic *et al*. 2009). To be conservative, we scored homozygote genotypes only if a single allele was observed in four independent PCR replicates for extracts with < 25 pg DNA/reaction, or three independent PCR replicates for extracts with > 25 pg DNA/reaction. We scored a heterozygote if we observed two alleles per locus in two or more independent PCR replicates. A single individual (T.H.) scored all genotypes.

Rates of allelic dropout and PCR success (as defined by Arandjelovic *et al*. 2009) were similar for the standard PCR procedure (on average, 91.6% of PCR reactions/extract were successful, and 9.6% of successful reactions/extract contained dropout) and the 2-step multiplexing procedure (91.4% successful, 4.9% dropout). The modified 2-step multiplexing procedure fared worse (70.6% successful, 18.7% dropout), but a higher percentage of extracts used in this procedure had < 100 pg DNA/reaction (57.1% vs. 35.7% for the unmodified 2-step multiplexing procedure and 38.6% for the standard PCR procedure). For the small set of extracts genotyped using the modified 2-step procedure, we scored homozygote genotypes only if we observed a single allele in at least five successful PCR replicates for extracts with < 50 pg DNA/reaction and three replicates for extracts with > 50 pg DNA/reaction.

We typically attempted to genotype multiple samples/individual when they were available, particularly for individuals whose genotypes could not be checked against their mother's or offspring's genotype (overall, 1.9 ± 0.1 samples/individual genotyped). We used CERVUS 3.0.3 to identify unique individuals and considered two genotypes to be from the same individual if pIDsibs for the dyad was < 0.01, or if this value was < 0.05 and we had additional information about the samples (e.g. the age/sex class and group recorded for both samples matched) that would help identify them as the same. We combined genotypes from the same individual to form consensus genotypes. We only used genotypes of adults (52 individuals) in our analyses. In this final list of genotypes, individuals were typed at 11–15 loci and genotypes were 94.7% complete. We used CERVUS 3.0.3 to calculate allele frequencies and GENEPOP (web version, genepop.curtin.edu.au/genepop_op1.html, developed from DOS version 3.3) to conduct Hardy–Weinberg exact tests. All loci were in Hardy–Weinberg equilibrium with a mean ± SD of 3.8 ± 1.5 alleles/locus (Table 2).

Table 2 Characteristics of fifteen microsatellite markers used in this study (adult individuals only). H_O, observed heterozygosity; H_E, expected heterozygosity

Locus	# Alleles	Allele size range (bp)	H_O	H_E	*P*-value
D13S321	5	128–160	0.765	0.667	0.219
D12S372	2	147–159	0.308	0.314	1.000
D2S442	5	190–214	0.653	0.684	0.204
D6S474	3	130–138	0.538	0.483	0.820
D6S503	3	238–258	0.216	0.263	0.074
D1S548	5	201–221	0.574	0.585	0.163
D10S611	2	143–147	0.176	0.162	1.000
D10S676	4	163–191	0.620	0.666	0.520
D6S1056	3	213–229	0.549	0.566	0.731
D2S1326	6	154–183	0.714	0.746	0.909
D10S1432	4	145–157	0.714	0.636	0.132
D1S1665	3	138–162	0.365	0.359	0.797
D11S2002	7	136–168	0.745	0.749	0.875
D4S2408	3	184–108	0.647	0.652	0.418
Fesps	2	144–148	0.176	0.162	1.000

Relatedness within and among groups

We compared average relatedness of adult males and females within groups (using group compositions from 2005 to 2006, when most samples were collected) using the 'GroupRelate' macro developed for EXCEL (www.zoo.cam.ac.uk/zoostaff/amos/#ComputerPrograms). This macro calculates dyadic relatedness using the methods of Queller & Goodnight (1989) and categorizes the results according to sex. This method compares the mean observed relatedness for each category with results from 1000 randomizations (detailed in Valsecchi *et al*. 2002). Because the macro returns *P*-values for each group, we corrected for multiple testing using the False Discovery Rate method (Benjamini & Hochberg 1995). For each dyad type (adult male–adult male, adult female–adult female and adult male–adult female), we also used Mantel tests to test whether, across all sampled groups, there was a relationship between dyadic relatedness and the location of dyads (i.e. within or among groups).

The results of GroupRelate and similar procedures are potentially biased by group size (mean within-group dyadic relatedness for the philopatric sex is only likely to be detectably higher than for the dispersing sex in small groups: Valsecchi *et al*. 2002; Lukas *et al*. 2005), so other methods for examining within- and among-group relatedness were also necessary. We did not use male and female F_{ST} values to examine sex-biased dispersal (*sensu* Dechmann *et al*. 2007) because the number of adult males and females per group were too few in most cases to reliably calculate F_{ST} and all samples came from the same study

population. Instead, we used 2×2 chi-square tests with Yates' correction to compare the observed numbers of adult male and female 'related' dyads within and among all groups, with the values we would expect if 'related' dyads were evenly distributed among all adult dyads of that sex (similar to methods used by Valsecchi *et al*. 2002). We used group compositions from 2005 to 2006 because most faecal samples were collected then. We ran the tests using two different definitions of 'related' dyads: (i) dyads with $r \geq 0.25$; and (ii) dyads with $r \geq 0.5$. All *P*-values reported are two-tailed.

Because dyadic relatedness estimates can have a high variance (Blouin 2003; Csilléry *et al*. 2006), particularly for more distant categories of relationship such as half-siblings, we also used one conservative set of criteria for defining close relatives. We determined how many pairs of groups contained among-group adult female and/or adult male dyads (using 2005–2006 group compositions) with both $r \geq 0.5$ and genotypes containing no mismatches (i.e. the dyad could be parent–offspring). We used this information on its own and in combination with the observational data to investigate whether guerezas disperse.

Results

Using only observational data

Male, but not female, dispersal was observed in the study population over 5.5 years. Both males and females (large juveniles, subadults and adults) disappeared, but a higher percentage of males did so (64.5% vs. 21.2%; Fisher's exact test: d.f. = 1, $P < 0.001$). Of individuals that disappeared, only males were later found in neighbouring groups (Table 3). Additionally, only males transferred into study groups, including three males from unstudied groups (Table 3). Lastly, seven out of eight females we first observed as juveniles in the study groups and subsequently followed for > 5 years remained in their original groups as adults (the other female disappeared). Two out of four males we followed from juveniles to adults remained in their original groups for approximately one year after being classified as adult, but both had dispersed and transferred into neighbouring groups by the end of the study.

Table 3 Summary of observational data on dispersal for the eight main study groups

	Adult males (n = 31)	Adult females (n = 33)
# Disappeared, not found	14	7
# Disappeared, found in neighboring groups	6	0
# Transferred into study groups from elsewhere	3	0

Males dispersed from their presumed natal groups as subadults and adults and, in one case, as a large juvenile. In the latter case, the juvenile male dispersed and transferred into a neighbouring group simultaneously with an adult male from his natal group. All other males that disappeared/dispersed from their groups did so alone. One adult male from the Bat. group dispersed and became a lone male, then joined a bachelor group of four adult males, and soon after joined the Bwa. group. No other bachelor groups were observed during the study.

Our statistical model supports these direct observations and, more importantly, provides quantitative estimates of male and female dispersal rates (Table 4). When comparing males and females, dispersal rates of infant/juveniles and adults, but not subadults, differ significantly (Table 4). Dispersal rates of females towards neighbouring groups are estimated to be close to zero, whereas male dispersal rates are significantly different from zero for all three age classes. Males of all age classes had values close to 0.01, indicating that, on average, they had a 1% probability to disperse toward neighbouring groups every month. So, every year, around 11% of the males in this study (i.e. all males that survived to the large juvenile stage by the end of the study) dispersed. Note that this rate does not correspond to an overall dispersal rate, since some males probably dispersed outside the study population. In our analysis, these males were considered 'disappeared' (parameters φ_i).

Table 4 Results of the statistical model estimating and testing for differences in parameters φ_i and d_i for different age and sex classes. φ_i is the probability that an individual belonging to the age class i remains in the studied population between two consecutive one-month sub-periods, and d_i is the probability that an individual belonging to the age class i migrates between two groups within the study population between two consecutive periods

	Estimates [CI 95%]		Male–female difference	
Parameter	Males	Females	χ^2	*P*-value
φ_1	1.00 [0.802–1.00]	1.00 [0.995–1.00]	2.05	0.152
φ_2	0.967 [0.687–0.989]	0.987 [0.959–0.999]	2.27	0.132
φ_3	0.986 [0.973–0.994]	0.995 [0.973–0.994]	4.68	0.031
d_1	0.0159 [0.00258–0.0407]	0.00 [0.00–0.00542]	7.59	0.006
d_2	0.00857 [0.000722–0.0357]	0.00 [0.00–0.0197]	1.83	0.176
d_3	0.0113 [0.00413–0.0229]	0.00 [0.00–0.00380]	9.83	0.002

Table 5 Within-group mean relatedness (*r*) for adult males and adult females, compared to randomly generated values (using allele frequency data), using 2005–2006 group compositions. *N*, number of dyads examined. Bold text denotes cells containing *r* values that are significantly different from those generated randomly, after using the False Discovery Rate correction for multiple testing. Row 'Overall' provides results of Mantel tests correlating dyadic relatedness matrices with matrices indicating whether the dyad was located within or among groups

Group	# AM's/AF's per group	Adults not sampled	AM–AM	AF–AF	AM–AF	All
Bas.	2/1	All sampled	*r* = –0.337 *P* = 0.941 *N* = 1	N/A	*r* = –0.053 *P* = 0.590 *N* = 2	*r* = –0.147 *P* = 0.820 *N* = 3
Bat.	1/1	All sampled	N/A	N/A	*r* = –0.335 *P* = 0.942 *N* = 1	*r* = –0.335 *P* = 0.942 *N* = 1
Bir.	2/4	All sampled	*r* = 0.038 *P* = 0.433 *N* = 1	*r* = 0.057 *P* = 0.338 *N* = 6	*r* = –0.185 *P* = 0.977 *N* = 8	*r* = –0.073 *P* = 0.851 *N* = 15
Bul.	2/2	All sampled	*r* = –0.056 *P* = 0.571 *N* = 1	*r* = 0.056 *P* = 0.440 *N* = 1	*r* = 0.073 *P* = 0.396 *N* = 4	*r* = 0.049 *P* = 0.432 *N* = 6
Bwa.	3/4	All sampled	*r* = –0.080 *P* = 0.666 *N* = 3	*r* = 0.160 *P* = 0.118 *N* = 6	*r* = 0.021 *P* = 0.431 *N* = 12	*r* = 0.046 *P* = 0.299 *N* = 21
Kah.	2/3	1 AM	N/A	*r* = 0.355 *P* = 0.091 *N* = 3	*r* = –0.145 *P* = 0.801 *N* = 3	*r* = 0.105 *P* = 0.276 *N* = 6
Kas.	2/3	All sampled	***r* = 0.622** ***P* = 0.000** ***N* = 1**	*r* = 0.210 *P* = 0.041 *N* = 3	***r* = 0.356** ***P* = 0.000** ***N* = 6**	***r* = 0.338** ***P* = 0.000** ***N* = 10**
Mug.	1/4	All sampled	N/A	***r* = 0.539** ***P* = 0.000** ***N* = 6**	*r* = 0.214 *P* = 0.085 *N* = 4	*r* = 0.409 *P* = 0.001 *N* = 10
Mze.	5/3	All sampled	*r* = –0.087 *P* = 0.824 *N* = 10	*r* = 0.270 *P* = 0.036 *N* = 3	*r* = 0.063 *P* = 0.243 *N* = 15	*r* = 0.032 *P* = 0.373 *N* = 28
Zik.	2/4	All sampled	*r* = 0.488 *P* = 0.032 *N* = 1	***r* = 0.299** ***P* = 0.012** ***N* = 6**	***r* = 0.266** ***P* = 0.007** ***N* = 8**	***r* = 0.294** ***P* = 0.003** ***N* = 15**
Overall			*r* = 0.020 *P* = 0.377 *N* = 210	***r* = 0.309** ***P* = 0.000** ***N* = 406**	***r* = 0.111** ***P* = 0.000** ***N* = 609**	***r* = 0.171** ***P* = 0.000** ***N* = 1225**

Using only genetic data

Overall, adult female–adult female dyads (AF–AF), adult male–adult female dyads (AM–AF) and all adult dyads combined [but not adult male–adult male dyads alone (AM–AM)], had significantly higher relatedness (*r*) values within than among groups (Mantel test, Table 5). Only a few individual groups, however, had higher *r*-values than expected by chance based on allele frequencies for any of these categories after correcting for multiple testing (Table 5). Examining solely the distributions of 'related' dyads (using either $r \geq 0.25$ or $r \geq 0.5$ as the relatedness criterion), related AF–AF dyads occurred more often than expected within than among groups (for $r \geq 0.25$: $\chi^2 = 29.16$, d.f. = 1, $P < 0.001$; for $r \geq 0.5$: $\chi^2 = 18.00$, d.f. = 1, $P < 0.001$), whereas related AM–AM dyads were evenly distributed within and among groups (for $r \geq 0.25$: $\chi^2 = 0.04$, d.f. = 1, $P = 0.850$; for $r \geq 0.5$: $\chi^2 = 0.08$, d.f. = 1, $P = 0.775$).

Consistently, over a wide range of criteria at which dyads could be classified as closely related (*r*-values ranging from ≥ 0.3 to ≥ 0.7), a greater percentage of AF–AF than AM–AM dyads were close relatives (Fig. 1). This was the case not only for within-group but also for among-group AF–AF dyads. Moreover, these results were similar over time — using group compositions in 2002–2003 (only six groups sampled) as well as in 2005–2006 (10 groups sampled; Fig. 1).

Using the conservative criteria of dyads having both *r*-values ≥ 0.5 and no mismatches in genotype (i.e. dyads shared at least one allele at each locus), twice as many pairs

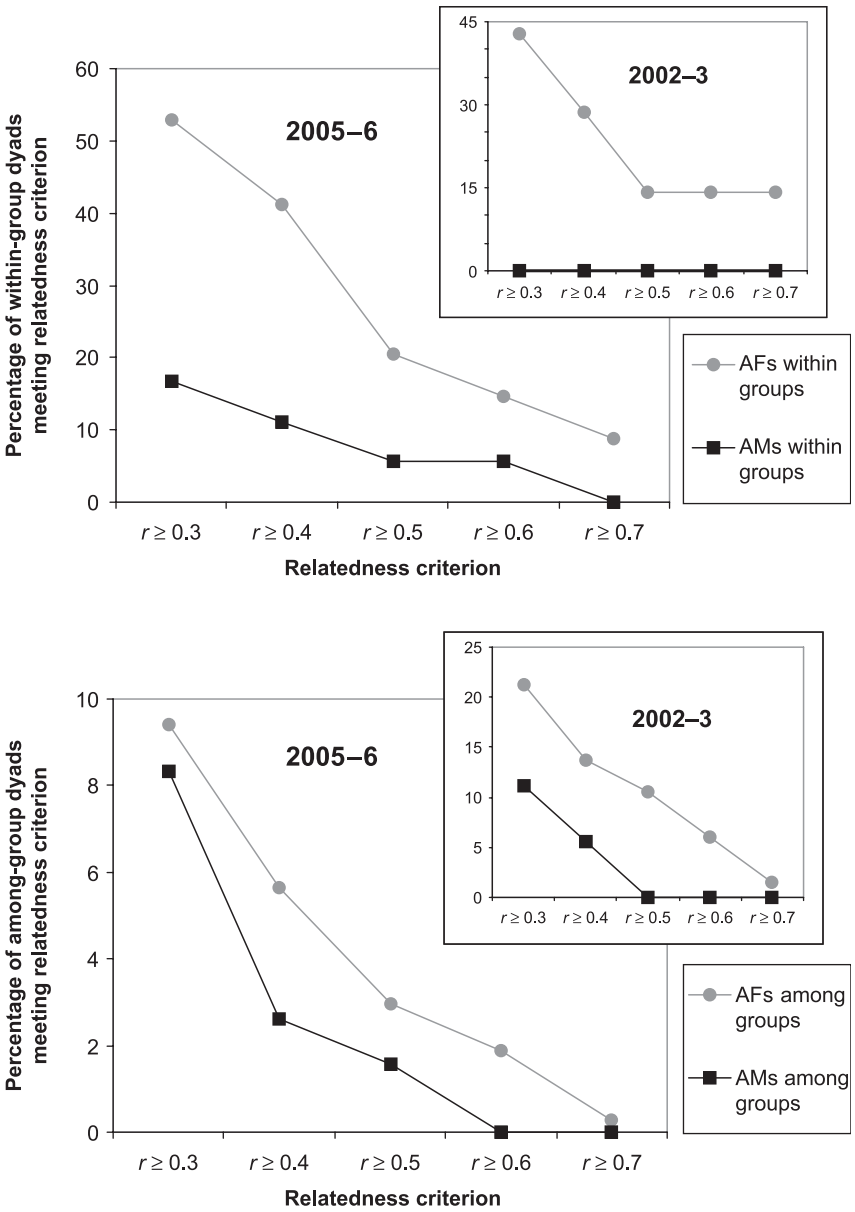


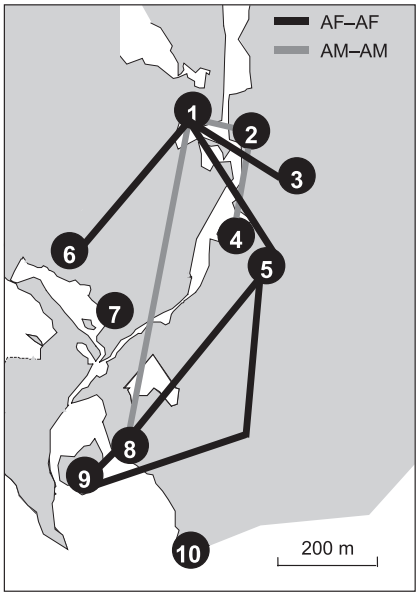
Fig. 1 Within- and among-group relatedness for adult males and females, using different relatedness criteria. Results are shown using 10 neighbouring groups' compositions from 2005 to 2006 and six of these groups from 2002 to 2003. Number of total adult female dyads within and among (shown as 'within/among') groups was 34/372 in 2005–2006 and 7/66 in 2002–2003. Number of total adult male dyads within and among groups was 19/191 in 2005–2006 and 4/36 in 2002–2003.

of groups had at least one close AF–AF among-group dyad as did pairs with at least one close AM–AM dyad (six vs. three; Fig. 2). Using these criteria, no pairs of groups had both close AM–AM dyads and AF–AF dyads (Fig. 2).

Discussion

Conclusions based on observational data

Based on long-term observational data alone, there was ample evidence that male guerezas dispersed from their natal groups and sometimes secondarily dispersed as well. Dispersing males transferred into existing groups, joined bachelor groups or became solitary. Although females sometimes disappeared from their groups, there was no evidence that they dispersed, in that no such female was ever seen subsequently. Explanations for female disappearances include death or possibly long-distance dispersal. Given that no female transferred into a study group during our long-term observations, whereas males did so, it seems unlikely that females disperse long-distance and transfer into existing groups (although this needs to be verified). Another alternative is that they disperse long-distance and form new groups by joining a solitary male. This phenomenon has not been observed in the studied population and has not been reported in the literature on guerezas. Moreover, seven of eight females we observed from juveniles to adults stayed in their original groups as



1. Mze. (5 AM, 3 AF)
2. Bir. (2 AM, 3 AF)
3. Bul. (2 AM, 2 AF)
4. Bwa. (3 AM, 4 AF)
5. Mug. (1 AM, 3 AF)
6. Bat. (1 AM, 1 AF)
7. Bas. (2 AM, 1 AF)
8. Zik. (2 AM, 4 AF)
9. Kas. (2 AM, 3 AF)
10. Kah. (2 AM, 3 AF)

Fig. 2 Spatial relationships of closely related among-group adult female (AF–AF) and adult male (AM–AM) dyads. Closely related dyads were conservatively defined as having *r*-values ≥ 0.5 and no mismatches. A line connecting two groups represents, in all cases, a single lineage (in this case, a lone individual or a mother/daughter pair) in one group related to a single lineage in another. Group locations are approximate midpoints of groups' home ranges. Map depicts continuous forest in grey and open areas or swamp in white.

adults and remained there at the end of the study. In contrast, no males that we observed from juveniles to adults had remained in their original groups at the end of the study.

The statistical model we constructed using observational data supports the conclusion that male guerezas disperse but females do not, or at least do so far less often. Male dispersal rates, for all age classes, were significantly greater than zero, whereas female dispersal rates were not. Moreover, male and female dispersal rates were significantly different for two of three age classes. That male and female subadults did not differ significantly in dispersal rates is likely due to at least two factors. First, the duration of this age class is shorter than that of the other two, so there is a relative lack of data for subadults. Subadult males also tended to disappear and not be found. In such cases, they may either have left the study population or died. Their disappearances were not factored into the dispersal 'd_2' parameter that estimates dispersal rates — only the 'φ_2' parameter that estimates the probability of remaining in the study population.

According to the model, at least 11% of the males we tracked dispersed yearly, compared to 0% of females. These numbers likely underestimate overall dispersal rates of males and possibly also females because they do not take into account numerous disappearances, which could represent long-distance dispersals, deaths or a combination of both.

Overall, the observational data strongly suggest that guerezas, like many other mammals and Old World primates, exhibit female philopatry and male dispersal (Greenwood 1980; Pusey & Packer 1987). Notably, however, female dispersal in other African colobine monkeys is at least occasional and sometimes even common, according to observational studies (reviewed in Fashing 2007).

Conclusions based on genetic data

The genetic data also support the conclusion that males typically disperse from their natal groups and transfer into nearby groups and probably beyond. A much lower percentage of adult male dyads, compared to adult female dyads, within groups were related (based on dyadic relatedness values); overall relatedness levels among adult males were similar within and among groups; and adult male 'relatives' (using either $r \geq 0.25$ or $r \geq 0.5$ as the relatedness criterion) were just as likely to be found within as among groups. In contrast, overall relatedness levels among adult females were higher within than among groups, and adult female 'relatives' were more likely to be found within groups, supporting the conclusion that females are more philopatric than males.

The 10 sampled groups, however, differed greatly in their relatedness patterns within groups, highlighting the potential complexity of dispersal and kinship patterns in guerezas and raising questions about the extent of female philopatry. For example, despite the overall tendency for adult females to be more related within groups, mean dyadic relatedness for adult females was higher than expected for only two out of eight groups that had multiple females, after correcting for multiple testing. These two groups were not the smallest groups, but rather had the most adult females.

The finding that a higher percentage of adult female than adult male dyads among neighbouring groups are related (over a wide range of criteria by which dyads could be considered 'related') also seems to cast doubt on the conclusion that females do not disperse. Even using very strict criteria for classifying dyads as related (dyadic $r \geq 0.5$ and no mismatches in genotype), related adult female dyads were found among six pairs of groups, compared to three for adult males. The relatively low number of related male dyads among neighbouring groups could be due to male tendencies to disperse long-distance or to higher mortality rates among males, but no data were available to evaluate these possibilities. Nevertheless, the presence of multiple related among-group adult female dyads would seem to indicate that female guerezas sometimes disperse. Although other potential explanations exist (see below), it is difficult to evaluate their likelihoods based on genetic data alone.

Combining observational and genetic data

The conclusions about dispersal derived separately from observational and genetic data generally agree for males but differ somewhat for females. How could there be so many closely related adult female dyads among groups when observational data provide no evidence of female dispersal, especially to nearby groups? Several explanations exist (Table 6), including: (i) female dispersal to nearby groups occurs, but groups were not observed long enough to detect it; (ii) male dispersal and subsequent reproduction in a nearby group results in aunt/niece and grandmother/granddaughter relationships among groups; (iii) male reproduction in multiple nearby groups results in half-sister relationships among groups; (iv) group fission splits up closely related females into two groups; and (v) group dissolution splits up closely related females—most or all of which end up in separate existing and/or new groups. These explanations can be best evaluated by combining observational and genetic data on the study groups, as well as observational data from previous guereza studies.

The likelihood that any given explanation best fits the results of this study depends on both the frequency with which the explanatory event (or series of events) occurs and the number of pairs of groups containing closely related adult females (Fig. 2) it potentially explains. The frequency with which explanatory events occur can only be estimated roughly based on existing data and reports from other study sites. All of the proposed explanations above are plausible and probably rare (Table 6). None has been definitively documented in the study population.

Explanations (i) to (iv) can only account for a single among-group link (Fig. 2) for each described event or series of events. Therefore, each rare event (or series of events) would have to have occurred multiple times to explain the multiple pairs of groups with closely related adult females (Fig. 2). Also, the theoretical average relatedness value produced by explanations (ii) and (iii) is only 0.25 and, thus, is not compatible with some of the very high levels of relatedness we found for female dyads among groups (up to 0.797; Fig. 1). Only explanation (v), group dissolution, explains multiple among-group links with a single event, as well as the high levels of dyadic relatedness among groups (c.f. white-winged choughs, *Corcorax melanorhamphos*; Beck *et al*. 2008).

A single group dissolution, occurring before 2002, could have resulted in up to five of the six among-group links depicted in Fig. 2, in that old adult females from five groups (i.e. one female from each group) all appear to be related to one another at a cousin level or greater, based on dyadic relatedness values (median $r = 0.470$; range = 0.143–0.651; $n = 10$ dyads). In this hypothetical situation, the original group would have contained these and possibly other females as adults and subadults (similar to the Mug. group's composition in 2007). This group would have dissolved upon the death of the group's resident adult male, with each female either joining an existing group or forming a new group with a male. This hypothetical situation is deemed plausible based on group compositions (prevalence of uni-male groups and number of adult and subadult females/group), within-group relatedness in the studied population, the high relatedness levels we quantified for among-group female dyads, and because the described process has been directly observed before in the nearby Ituri Forest (Bocian 1997). Also, within-group feeding competition — a factor limiting group size — appears to be influential in the studied population (TR Harris and CA Chapman, unpublished data), making it unlikely that resident females in existing groups would allow multiple females to join their groups simultaneously. Although we cannot be certain that it occurred, group dissolution is the most parsimonious of all the explanations put forth as the major factor influencing among-group adult female relatedness in this population. However, it should be emphasized that no explanation can be ruled out, and a combination of different explanations most likely resulted in the full observed pattern of relatedness.

By comparing the results of observational and genetic data on guerezas, it is clear that genetic data alone were not sufficient to infer dispersal patterns. As described in Table 6, numerous processes other than dispersal can give rise to closely related dyads among groups. Dyadic relatedness data are potentially useful when used cautiously in combination with observational data to interpret behavioural patterns such as dispersal, but clearly should not be used alone to infer them. Also evident from this study is that observational data alone were not sufficient to infer genetic structure. Even though female philopatry may be typical in guerezas, close adult female relatives were found among groups, and adult females within several groups were no more related than expected by chance. Similar results have been found in lions (*Panthera leo*), with high among-group female relatedness attributed to short-distance, nonrandom dispersal by males and/or group fissions and low within-group female relatedness attributed to genetic divergence over time resulting from persistent matrilines and multiple fathers (Spong *et al*. 2002). Another non-mutually exclusive possibility raised by this study is that female dispersal and transfer as the result of group dissolution could also result in unrelated females occupying the same group. Rare but potentially influential events such as these may not occur during long-term observational studies but leave genetic signs that can be carefully interpreted along with observational data. Whereas observational data alone provided useful information about typical sex-biased dispersal patterns in guerezas, only by adding genetic data did the potential complexity of the system become evident.

Table 6 Potential explanations for occurrence of closely related adult female dyads among groups (as shown in Fig. 2)

Potential explanation	Frequency or likelihood of occurrence	# Among-group links (Fig. 2) explained by a single occurrence of the 'explanation'	Reasons for/against this explanation as the major factor underlying among-group AF–AF relatedness
Females do disperse and transfer into nearby groups, but the study groups were not observed long enough to detect it.	Would have to be rare if it was not observed over a > 5 year period*; but at least one case of female dispersal in guerezas has been reported†.	One	Unlikely, because a single occurrence is likely rare and only explains a single among-group link.
Male-mediated aunt/niece and grandmother/granddaughter relationships: Males disperse from natal groups, leaving mothers and sisters behind. They transfer into neighbouring groups and sire daughters there. Daughters survive to adulthood and are the nieces and granddaughters of females surviving in males' natal groups.	Male dispersal from natal groups occurs relatively often‡. They sometimes transfer to neighbouring groups, but many do not*. Most that do so, join as peripheral males and sire relatively few offspring‡. For those that reproduce, the likelihood that any offspring is female is 0.5. Also, infant and juvenile mortality averages 37%‡, so many females do not survive to adulthood. Overall, therefore, the entire series of events is probably rare and has never been documented.	One	Unlikely, because the full series of events is probably rare and only explains a single among-group link.
Male-mediated half-sister relationships: Males reproduce in multiple neighbouring groups, resulting in half-sister relationships among groups (explanation assumes nothing about the females in males' natal groups).	Extra-group paternity is rare in this population‡; typically only males that join groups sire offspring‡. Secondary male dispersal is infrequent and occurs mostly when males are old or when they are deposed in takeovers‡. If a male sired offspring in two groups, the probability of both being female is only 0.25. With infant and juvenile mortality averaging 37%‡, many females do not survive to adulthood. Overall, therefore, the entire series of events is probably rare and has never been documented.	One initially (i.e. for the first two groups a male mates in)	Unlikely, because the full event is both rare and only explains a single among-group link.
Group fission (i.e., a group splits in two); assumes some females in the original group are closely related.	Rare but has been observed in this species elsewhere§.	One	Unlikely, because a single occurrence is both rare and only explains a single among-group link.
Group dissolution (i.e., a group dissolves, with most individuals joining existing groups or forming new groups); assumes some females in the original group are closely related.	Rare, but has been observed in this species elsewhere; many groups are uni-male; groups presumably dissolve if their only male dies, as was observed in the Ituri Forest¶.	Multiple, depending upon # closely related females (potentially subadults + adults) in original group and subsequent # groups into which they transfer or which they start with a new male.	Most likely; event is rare but likely to occur at some point if many groups are uni-male. A single event occurring before the study began could explain up to five of the six among-group AF–AF links.

*This study.
†Fashing 2007.
‡TR Harris, unpublished data.
§Dunbar & Dunbar 1976.
¶Bocian 1997.

The perplexing nature of female philopatry in guerezas

The high level of female philopatry we discovered for guerezas at Kanyawara, in the absence of events such as group dissolution, is particularly surprising given that a high proportion of groups contain only one adult male or two closely related adult males (4/6 and 5/8 of the study groups, at the beginning and end of this study, respectively), and adult male tenures are typically long (see below). Mammals with these characteristics often exhibit dispersal by both sexes (e.g. *Equus zebra zebra*: Lloyd & Rasa 1989; *Procolobus verus*: Korstjens & Schippers 2003; *Lophostoma silvicolum*: Dechmann *et al*. 2007), presumably because females would otherwise face inbreeding in their natal groups.

Of the six adult males that were both resident and dominant when the study began, three still retained these positions at the end of our more than five-year study, two remained in their groups but were no longer dominant and one disappeared after more than four years as the resident, dominant male in his group. These males' daughters (some of which were born before this study began; parentage confirmed through paternity analysis, unpublished data) matured to adulthood in approximately four years. Thus, by combining genetic and observational data, we can confirm that at least four females in three groups remained in their natal groups as adults despite having only their fathers and brothers as potential mates (three females born in the Bwa. group also remained there as adults but had access to unrelated adult males in their group). These females were not observed to mate either within or outside of their groups.

Why would these females remain in their natal groups and forego reproduction? Why would they not disperse to find mates and avoid inbreeding and/or competing for resources with kin? We propose that for an individual female guereza, waiting a few years as an adult for an unrelated male to take over or join her natal group may be less costly than dispersing and transferring into a group of females to which she is unrelated or has unknown relatedness. Within-group feeding competition in this high-density population (Harris 2005; TR Harris and CA Chapman, unpublished data) presumably imposes costs for females remaining in their natal groups (ensuring local resource competition with kin), while simultaneously imposing restrictions on their ability to disperse and transfer (increasing resistance by resident females in other groups to immigration). But females may also accrue inclusive fitness benefits by remaining and cooperating with kin (cf. Le Galliard *et al*. 2006). In guerezas, such benefits likely come from the extensive care natal females give to their infant siblings (Oates 1977; TR Harris, unpublished data), raising the intriguing idea that guerezas may be facultative cooperative breeders. Natal female guerezas may also gain benefits by participating with kin in intergroup encounters that function to defend their groups' core feeding areas (Harris 2006).

Conclusions

This study highlights the potential importance of combining observational and genetic data on the same individuals to understand complex sex-biased dispersal patterns in social-group-living species. Using only observational data, we would have concluded that male guerezas disperse but females do not. In contrast, using only genetic data, we would have concluded that females are more philopatric than males, but that they probably also sometimes disperse to neighbouring groups. Only by combining both data types were we able to notice a discrepancy and better understand the complexity of dispersal and kinship patterns in guerezas. Using observational and genetic data on the same individuals was also important because it allowed us to control for external factors that could have influenced dispersal patterns (e.g. conducting observational and genetic studies during different time periods or on different sets of individuals). Not all studies that collect both data types on the same individuals have found, or will find, discrepancies (Temple *et al*. 2006; Huck *et al*. 2007; Nagy *et al*. 2007), but conclusions based on only a single data type could clearly be overlooking valuable information about dispersal. This is all the more important, considering that our understanding of the factors influencing cooperation and competition in a given taxon may depend, at least in part, on the extent to which we understand the complexities of sex-biased dispersal and its effects on kin distribution.

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