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Fine-scale spatiotemporal patterns of genetic variation reflect budding dispersal coupled with strong natal philopatry in a cooperatively breeding mammal

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Abstract

The relatedness structure of animal populations is thought to be a critically important factor underlying the evolution of mating systems and social behaviours. While previous work has shown that population structure is shaped by many biological processes, few studies have investigated how these factors vary over time. Consequently, we explored the fine-scale spatiotemporal genetic structure of an intensively studied population of cooperatively breeding banded mongooses (*Mungos mungo*) over a 10-year period. Overall population structure was strong (average $F_{ST} = 0.129$) but groups with spatially overlapping territories were not more genetically similar to one another than noncontiguous groups. Instead, genetic differentiation was associated with historical group-fission (budding) events, with new groups diverging from their parent groups over time. Within groups, relatedness was high within but not between the sexes, although the latter increased over time since group formation due to group founders being replaced by philopatric young. This trend was not mirrored by a decrease in average offspring heterozygosity over time, suggesting that close inbreeding may often be avoided, even when immigration into established groups is virtually absent and opportunities for extra-group matings are rare. Fine-scale spatiotemporal population structure could have important implications in social species, where relatedness between interacting individuals is a vital component in the evolution of patterns of inbreeding avoidance, reproductive skew and kin-selected helping and harming.

Keywords: helping and harming, inbreeding, kin-selection, population genetics- empirical, social evolution, temporal

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Introduction

The relatedness structure of animal populations is thought to be a critically important factor underlying the evolution of mating systems (Lukas & Clutton-Brock 2011) and social behaviours (Gardner & West 2006; Johnstone & Cant 2008). Consequently, a current goal of evolutionary ecology is to elucidate the processes that shape the genetic structure of populations. This area of research has been made accessible through the relatively recent advent of hypervariable molecular markers such as microsatellites (Tautz 1989). A rapidly growing body of work has shown that population structure is shaped by biological processes at almost every level from social interactions and mate-choice (Höner *et al.* 2007; Archie *et al.* 2008) to dispersal (Temple *et al.* 2006; Nielsen *et al.* 2012), mating systems (Vidya *et al.* 2009; Kerth & Van Schaik 2011; Nelson-Flower *et al.* 2011), modes of reproduction (Hoffman *et al.* 2011) and environmental conditions (Nussey *et al.* 2005; Ortego *et al.* 2011).

Most studies to date have considered the genetic structure of a population to be somewhat static, either sampling a population only once, or combining samples

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collected over multiple years and assuming that patterns of genetic variation will be consistent over time (Tung *et al.* 2008). In reality, population structure is likely in many cases to be dynamic, with interactions among subpopulations changing over time as the size, spatial organization and social structure of these subpopulations vary (Nussey *et al.* 2005). For example, the degree of gene-flow among subpopulations can reflect the rates at which individuals disperse, which may in turn be dependent on environmental or social conditions (Painter *et al.* 2000; Ortego *et al.* 2011; Marsden *et al.* 2012).

Variation in relatedness structure may be particularly important for species that live in social groups. Such species often have complex social systems characterized by strong natal philopatry, limited dispersal and varying degrees of extra-group mating (Bishop *et al.* 2004; Beck *et al.* 2008; Dugdale *et al.* 2008; Brouwer *et al.* 2011; Kerth & Van Schaik 2011). Many social species also show cooperation among group members, the most striking examples coming from cooperative breeders, where some group members forego reproduction in order to help rear the offspring of others (Koenig & Dickinson 2004). Given that kin-selection is thought to have been a major evolutionary force driving cooperation, variation in relatedness structure could have implications for the evolution and maintenance of cooperative and aggressive behaviour (Hamilton 1964; Piertney *et al.* 2008). Furthermore, recent advances in kin-selection theory have highlighted the key role of demography and dispersal for the evolution of helping and harming traits in viscous groups, such as those of cooperatively breeding species (Gardner & West 2006; Johnstone & Cant 2008; Lehmann & Rousset 2010) and have suggested that temporal variation in relatedness could impact on the strength of selection for cooperative behaviour across the lifespan (Johnstone & Cant 2010).

Temporal variation in the relatedness structure of social groups may also impact on mating patterns and reproductive skew. For example, the death of one or more dominant breeders can reduce the number of unrelated breeding partners within a group. The risk of close inbreeding may trigger some group-members to disperse (Koenig *et al.* 1998; Griffin *et al.* 2003), to refrain from reproducing (Widowski *et al.* 1990; Burda 1995; Clutton-Brock *et al.* 2001) to accept immigrants (Koenig *et al.* 1998), to seek extra-group copulations (Brouwer *et al.* 2011) or alternatively to inbreed (Reeve *et al.* 1990; Keane *et al.* 1996). All of these behaviours in turn feed back into group and population structure, impacting the dynamics of the population as a whole. Despite this, few studies have explored fine-scale variation in population structure over both space and time, probably owing to a paucity of sufficiently detailed spatiotemporal data sets.

An ideal opportunity to explore both spatial and temporal variation in population structure is provided by a detailed field study of banded mongooses *Mungos mungo*. These small (<2 kg) carnivores live in groups of 10–40 adults that cooperate to care for large communal litters of pups and defend their territory from rival groups (Cant 2000). They provide an excellent natural system in which to investigate temporal aspects of population structure because they have strong but highly dynamic social and group structures where interactions both within and between groups have the potential to change over time.

Banded mongoose groups typically have a polygynandrous mating system and comprise a 'core' of breeding adults (2–5 females and 3–7 males) that reproduce on average four times per year (Bell 2010; Cant *et al.* 2010; Nichols *et al.* 2010) alongside a subset of younger individuals that breed occasionally (Nichols *et al.* 2012b). Paternity is strongly skewed towards a subset of older males that mate-guard the most fecund females (Nichols *et al.* 2010), although surreptitious copulations have also been observed with younger, subordinate males (Cant 2000). The number of breeding females within a group is highly dependent on resource availability, with dominant females suppressing subordinate reproduction when the group size is large (Cant *et al.* 2010) and when invertebrate prey is scarce (Nichols *et al.* 2012a).

New groups form when a cohort of males from one natal group fuses with a cohort of females from another natal group and establishes a territory (Cant *et al.* 2001). Group-founders are therefore likely to be closely related within but not between the sexes. Offspring of both sexes display philopatry and almost all individuals remain in their natal group beyond sexual maturity. Because banded mongooses can live to over 10 years old, offspring of the group-founders can have close relatives of both sexes present in their natal group (including parents and siblings). Despite this, however, they often breed within their natal group prior to, or instead of, dispersing (Gilchrist *et al.* 2004; Nichols *et al.* 2012a).

While some banded mongooses remain in their natal group for their entire lives, others disperse. Dispersers can be of either sex, but tend to be of intermediate age (between 1 and 3 years old). Dispersal happens through two distinct means. First, cohorts of same-sex individuals occasionally leave their natal group voluntarily to join dispersing individuals of the opposite sex, thereby forming new groups (Cant *et al.* 2001). Secondly and more commonly, a subset of group-members is aggressively expelled from their natal group *en masse* by older, more dominant individuals (Cant *et al.* 2010). Individuals always disperse alongside same-sex group-members and when subordinates of both sexes are evicted at the same time, they split into single-sex cohorts to disperse. Dispersing cohorts have been known to travel over 20 km, but many form territories close to their natal group (Cant *et al.* 2001).

Banded mongooses are highly territorial and frequently interact aggressively with neighbours at the borders of their home range (Cant *et al.* 2002; Müller & Manser 2007; Jordan *et al.* 2010). Neighbouring groups represent a threat to residents through competition for food and space as large groups expand their territories into those of smaller groups (Müller & Manser 2007). Encounters between groups are highly hostile and often result in the injury and death of group-members, accounting for 8% of adult mortalities where the cause of death is known (Jordan *et al.* 2010). However, copulations between members of opposing packs have also been observed during such encounters and could represent an important source of gene-flow (Rood 1975; Cant *et al.* 2002). Given the observation that group encounters are more likely to occur when females are in oestrus (Cant *et al.* 2002), it is even possible that individuals actively seek out extra-group copulations.

Here, we use a large genetic and observational data set to investigate fine-scale spatial and temporal variation in the structure of a population of over a thousand banded mongooses that has been continuously monitored and extensively sampled since 1995. The temporal component of our data set allows us to study not only the 'baseline' patterns of relatedness and population structure, but also to evaluate how group fission, fusion and extra-group mating lead to temporal variation in group and population structure. Specifically, we evaluate a number of predictions based on behavioural observations: (i) Due to the formation of groups from cohorts of relatives (budding dispersal) and the retention of philopatric offspring, overall population structure is expected to be strong; (ii) As new groups are founded by males and females from different natal groups, we expect levels of pairwise relatedness to be high within, but not between, the sexes; (iii) Although male and female founders may be unrelated, they are replaced upon death by philopatric natal individuals, predicting that average levels of relatedness between the sexes will increase over time since group formation; (iv) Extra-group paternity (EGP) and limited dispersal of cohorts when establishing new groups lead to the prediction that neighbouring groups should be more closely related than geographically distant groups; (v) Groups sharing recent common ancestry (e. g. those formed from fission of the same parent group) are expected to be genetically more similar than groups that shared ancestry longer ago, or that share no ancestry.

Materials and methods

Study population and genetic sample collection

This study was conducted on a natural population of banded mongooses, located in Queen Elizabeth National Park, Uganda (0°120′S; 27°540′E). The study site consists of ~10 km^2 of relatively low-lying savannah on and around the Mweya peninsula. Genetic and observational data were collected between 2000 and 2009 from a total of 1275 banded mongooses living in 14 social groups within the study area (Table 1). Social groups were distinct groups of individuals that forage together and defend a communal territory (temporary dispersing cohorts were therefore not considered to be social groups). Groups were habituated to the presence of human observers, allowing the collection of detailed behavioural and demographic data. Each mongoose was given a unique hair-clip or coloured plastic collar to allow individual identification in the field. To enable groups to be located, one or two adults from each group were fitted with a radio-collar weighing 27 g (representing a maximum of 2% bodyweight).

In order to fit and maintain collars and hairclips, individuals were captured every 3–6 months. On first capture, all animals were tattooed with a unique code for permanent identification and a 2 mm skin sample for genetic analysis was taken from the tip of the tail. The methods used in trapping, anaesthetization and sample-collection are described in detail elsewhere (Cant 2000; Jordan *et al.* 2010; Nichols *et al.* 2010). No mongooses died as a result of trapping or anaesthetization during the course of this study. Research was carried out under licence from the Uganda National Council for Science and Technology, and all procedures were approved by the Uganda Wildlife Authority.

Behavioural data collection

Groups were visited frequently (approximately every 4 days) to record group membership, together with dates of birth, death and dispersal (±3 days). It was usually possible to distinguish between death and dispersal as mongooses always disperse in groups (Cant *et al.* 2010) and in many cases, dispersers could be followed until they either formed a territory within the study site or dispersed away from the peninsula. While the peninsula limits the direction in which dispersers can travel, it does not prevent long-distance dispersal (at least eight dispersing cohorts left the peninsula during the course of the study). As dispersers leave their groups in large cohorts, rather than singly, we refer to the dispersal of a cohort as a group fission event. Similarly, as new groups are founded when males from one

Table 1 A summary of the banded mongoose social groups included in genetic analyses

		Year of study										Parent group	
Group	Year founded	2000	2001	2002	2003	2004	2005	2006	2007	2008	2009	Males	Females
T	<1996	p	p	p	i	p	p	p	p	p	p	N/A	N/A
B	<1996	p	p	p	p	p	p	p	p	p	p	N/A	N/A
C	1997	p	p	i	p							A	B
D	1998	p	p	p	p	p	p	p	p	p	p	B	Wild
F	1998	p	p	p	p	p	p	p	p	p	p	I	Wild
H	1999	p	p	p	p	p	p	p	p	p	p	J	B
K	2001		p	p	p	p	p					Wild	B
U	2003				p	p	p					Wild	H
G	<2004					p	p	p	p	p	p	N/A	N/A
E	2004					p	p					Wild	C
N	2004						p	p				No males	B
P	<2004				i	i	i					N/A	N/A
V	2006							p	p	p	p	K	U
S	2007								p	p	p	H	F

'p' denotes groups that were present at the study site during the year in question. Groups marked with 'i' had territories extending past the edge of the study site and/or were undergoing the process of habituation, hence it was not possible to obtain accurate recordings of group membership. Consequently, these groups are not included in calculations of *F*-statistics in these years. Where group-founders could be identified, the identities of parent groups are included (otherwise parent groups are marked as N/A). Wild group founders were unhabituated individuals originating from outside the study population. Groups A, I and J were habituated groups that no longer existed by 2000 so are not included in genetic analysis.

group join with females from a different group, we refer to the founding of a group as a fusion event.

To allow us to relate population genetic structure to incidences of mating between groups, all observed (or suspected) matings were recorded *ad libitum* during encounters between groups. Banded mongooses have not been observed leaving their group to prospect for mating opportunities (Hodge 2007), such that extra-group copulations are unlikely to occur except during inter-group encounters. Observations were recorded using hand-held Psion organizers (model LZ-64; Psion) and downloaded to a central database each evening.

Home range estimation

In 2006, a Global Positioning System (GPS) survey was conducted to establish the degree of overlap between the home-ranges of all groups present within the study site. Coordinates were collected when observers first arrived at each group and at 15-min intervals during observation periods using handheld Garmin 12 GPS units (Garmin International Inc., Olathe, KS, USA). GPS coordinates were taken from the approximate centre of the foraging pack. Group home ranges were then estimated using the Animal Movement extension in ARCVIEW version 3.3 (Environmental Systems Research Institute, Redlands, CA, USA) using the 95% fixed kernel method (Worton 1989) with the least-squares cross-validation value for smoothing. Animal movement extension is third-party software produced by the United States Geological Survey, 2001. Home ranges were estimated from 764 ± 391 (±SD) coordinates per group (range: 204–1252). Estimates of areas of overlap with neighbouring groups were calculated, allowing groups to be classified as either 'neighbours' (some overlap of the 95% kernel) or 'nonneighbours' (no overlap at the 95% kernel). Calculations of home range overlap excluded group V because this group neighboured several unhabituated groups with unknown ranges (see Jordan *et al.* 2010 for further details).

DNA extraction and microsatellite genotyping

Genomic DNA was extracted from skin samples and PCR amplified as described in detail by Nichols *et al.* (2010). Individuals were genotyped at 14 microsatellite loci, previously isolated from several carnivore species (Table 2). The genotyping error rate for our data set was estimated following Hoffman & Amos (2005) by re-genotyping a random subset of 48 individuals at all loci. The resulting error rate was low, with a mean ± SE of 0.59% ± 0.17 of alleles being scored incorrectly. However, as a further guard against poor-quality genotype data, we restricted all downstream genetic analyses to individuals that successfully amplified at eight or more loci (n = 1250 of 1275 individuals sampled, 98%). Three microsatellite loci (Ss11-12, Ss7-1 and Hj35) showed significant deviations from Hardy–Weinberg Equilibrium (HWE) tested using

Table 2 Details of microsatellites used in this study, including literature sources and polymorphism characteristics for 750 banded mongooses

Locus	Species isolated from	References	Number of alleles	Polpmorphic information content
Ss11-12	Meerkat	Waldick *et al.* (2003)	9	0.626
Ss7-1	Meerkat	Griffin *et al.* (2001)	5	0.594
Ss10-4	Meerkat	Griffin *et al.* (2001)	4	0.412
Ss13-8	Meerkat	Griffin *et al.* (2001)	7	0.336
Mm5-1	Banded mongoose	Waldick *et al.* (2003)	3	0.381
Mm10-7	Banded mongoose	Waldick *et al.* (2003)	3	0.330
TGN	Banded mongoose	Waldick *et al.* (2003)	5	0.281
A248	Banded mongoose	Waldick *et al.* (2003)	3	0.230
M53	Banded mongoose	Waldick *et al.* (2003)	3	0.304
A226	Banded mongoose	Waldick *et al.* (2003)	2	0.181
AHT130	Domestic dog	Griffin *et al.* (2001)	3	0.491
Hj35	Small Indian mongoose	Thulin *et al.* (2002)	6	0.688
Ag6	Antarctic Fur seal	Hoffman *et al.* (2008)	5	0.472
Ag8	Antarctic Fur seal	Hoffman *et al.* (2008)	3	0.568

the program GENALEX (Peakall & Smouse 2006). However, when each social group was analysed separately, no locus consistently deviated from HWE, suggesting that any deviations are likely due to strong population structure and nonrandom mating within groups.

Calculation of F-statistics

F-statistics were used to assess the level of structuring present within and between subpopulations (breeding groups) in the banded mongoose population. These provide a measure of the degree of differentiation among subpopulations by comparing observed levels of heterozygosity to those that would be expected in the absence of population structure (Weir & Cockerham 1984). Three values were calculated; F_{ST}, the reduction in heterozygosity due to population subdivision, in this case indicating the degree of reproductive isolation between breeding groups; F_{IS}, the reduction in heterozygosity of individuals relative to their group, caused by nonrandom mating within groups and F_{IT}, the reduction in heterozygosity of individuals relative to the entire population. Weir & Cockerham (1984) estimators of genetic variance (CapF = F_{IT}, smallF = F_{IS}, $\theta = F_{ST}$) were calculated using FSTAT 2.9.3.2 (Goudet 1995), weighting each subpopulation by sample size. This was carried out for each year of the study and separately for all group members and pups only.

Bayesian cluster analysis

To identify genetic clusters without a priori knowledge of the group membership of individuals, we conducted a Bayesian cluster analysis of the data set using STRUCTURE version 2.3.3. (Pritchard *et al.* 2000). This program uses a maximum likelihood approach to determine both the most likely number of distinct genetic clusters in the sample (K) and which individuals are most likely to belong to each cluster (the membership of each individual is estimated as q, which varies between 0 and 1 with the latter indicating full membership). We ran five independent runs for K = 1–20 using 10^6 MCMC iterations after a burn-in of 10^5, the correlated allele frequencies model and assuming admixture. The most likely number of genetic clusters was evaluated using both the maximal average value of Ln $P(D)$, a model-choice criterion that estimates the posterior probability of the data and ΔK, an ad hoc statistic based on the second order rate of change of the likelihood function with respect to K (Evanno *et al.* 2005). Only individuals that successfully amplified at 11 or more loci, and for which the group of birth was known, were included in this analysis (n = 1082 out of 1275 individuals sampled, 85%).

One potential drawback of STRUCTURE is that the output of this program can be difficult to interpret when population structure is weak. Consequently, we also analysed our data using the LOCPRIOR model within STRUCTURE, which uses knowledge of the groups from which individuals were sampled to assist the clustering process (see Hubisz *et al.* 2009 for further details). This model essentially favours clustering solutions that correlate with group identity, while ignoring the sampling information whenever this is uninformative about the ancestry of individuals. It tends to outperform the standard model when populations are weakly differentiated, generating more accurate estimates of K together with substantially improved group membership coefficients. We ran this analysis as described above, but classifying individuals according the group they were born in and setting the option LOCPRIOR to 1.

Relatedness calculations

Mean levels of relatedness between and within the sexes were calculated using GroupRelate (Valsecchi *et al.* 2002). This program calculates pairwise relatedness values among all individuals following Queller & Goodnight (1989) and generates mean values between and within sexes for each group in each year of the study. One potential difficulty in calculating relatedness from samples containing relatives is that allele frequency estimates can be biased towards alleles found in extensively sampled clusters of kin. One way to avoid this bias is to use a set of unrelated individuals to estimate allele frequencies. However, this too can be problematic for a group-living species, as strong population structure can make it difficult to select a sufficiently large panel of unrelated individuals from which to estimate allele frequencies. Fortunately, all adults in the banded mongoose study population have been sampled and the vast majority successfully genotyped. Allele frequencies estimated from the full data set are therefore likely to closely resemble the allele frequencies present in the adult population.

Heterozygosity calculations

Multilocus heterozygosity at 14 microsatellite loci was calculated using the measure Internal Relatedness (IR; Amos *et al.* 2001). IR estimates the relatedness of an individual's parents using the extent of allele sharing relative to random expectations. When calculated across multiple loci, IR values are approximately normally distributed around zero for offspring born to random 'unrelated' parents.

Statistical analysis

Statistical analyses were carried out within the R package (version 2.7.2; R Development Core Team, Vienna, Austria). To examine the factors that influence the genetic distances among groups, we constructed a general linear model (GLM), looking specifically for evidence of geneflow between neighbouring groups and divergence over time between groups since fission (and any interactions). Pairwise F_{ST} between pups born in each group was fitted as the dependent variable and time since fission (in years) and whether or not the groups had neighbouring territories (0 = non-neighbouring, 1 = neighbouring) were included as explanatory variables. For 11 pairs of groups, time since fission was known exactly, but for the remaining 17 pairs the exact time since fission was not known, either because the fission event occurred before the study began, or because groups were habituated after they had formed, such that the date of formation was not known. In such cases, the minimum possible time since formation was used in the model. To compensate for nonindependence among F_{ST} values calculated from the same groups, we followed the approach of Cammen *et al.* (2011), conducting a variant of the Mantel test that allows for the fitting of interaction terms. First, the desired GLM was fitted ($F_{ST} \sim$ neighbouring vs. nonneighbouring territories + years since fission + neighbouring vs. nonneighbouring territories: years since fission). Next, significance was tested by subjecting the rows and columns of the matrix in question to 10 000 random permutations and then refitting the model with these scrambled data. Significance was determined by counting the number of times the model based on scrambled data yielded a lower AIC value compared to the original model. No model simplification was implemented during this procedure because only the component currently under investigation is affected by the randomization process, so the scrambling should only reveal a significant effect if either the component being scrambled or the interaction improves the model. This analysis was restricted to the 2006 data, for which the exact locations and degree of overlap between groups were known.

To investigate changes in group composition and relatedness structure over time, we constructed generalized linear mixed models (GLMMs). Because the data set includes groups that are sampled repeatedly across years, 'group identity' and 'year' were fitted as random factors to control for pseudoreplication. Group N was excluded from these analyses as this short-lived group contained no permanent resident males, meaning that it was not possible to investigate changes in relatedness between the sexes. Analyses were also restricted to groups where the year of formation was known ($n = 9$). Data with normal and binomial distributions were analysed in GLMMs using identity link and logit link functions, respectively. P-values were calculated by removing the term from the model and assessing whether removal caused a significant ($P < 0.05$) decrease in the explanatory power of the model, tested using ANOVA.

Results

Population structure

We genotyped 1250 banded mongooses living in 14 social groups between 2000 and 2009. Between 6 and 10 groups were present in the study site during any 1 year (Table 1). F-statistics for the banded mongoose population for each of the 10 years of the study are summarized in Table 3. F_{ST} values were consistently high (mean value for all group members = 0.129, mean value for pups = 0.143) indicating strong overall population structure corresponding to family groups. F_{IS} was significantly negative across all years when all group members were considered, and in 8 of 10 years when pups alone were considered (mean value for all group members = −0.090, mean value for pups = −0.105).

Table 3 Summary of annual *F*-statistics calculated separately for all group members and for offspring (pups) only

Year	No. groups	No. genotyped individuals	No. geontyped pups	All group members			Pups only		
				F_{IT}	F_{ST}	F_{IS}	F_{IT}	F_{ST}	F_{IS}
2000	6	161	77	0.057*	0.128*	−0.081*	0.055	0.161*	−0.126*
2001	7	271	143	0.056*	0.133*	−0.089*	0.067*	0.154*	−0.103*
2002	6	220	80	0.019	0.129*	−0.126*	0	0.155*	−0.183*
2003	7	232	95	0.042	0.130*	−0.101*	0.063	0.132*	−0.079*
2004	9	302	143	0.040	0.141*	−0.117*	0.055*	0.155*	−0.118*
2005	10	288	93	0.037	0.140*	−0.12*	0.057	0.152*	−0.112*
2006	8	273	102	0.051*	0.116*	−0.074*	0.059*	0.108*	−0.055
2007	8	241	53	0.066*	0.114*	−0.055*	0.087*	0.123*	−0.041
2008	8	285	132	0.076*	0.127*	−0.058*	0.078*	0.147*	−0.081*
2009	8	249	61	0.057	0.128*	−0.081*	0.006	0.138*	−0.153*
Mean	7.6	252.2	97.9	0.050	0.129	−0.090	0.053	0.143	−0.105

*Values that are statistically significant from zero at $P < 0.05$.

This suggests that individuals are more heterozygous than would be expected if mating within groups was random with respect to relatedness, consistent with opposite-sex group founders being unrelated. F_{IT} was found to be significantly greater than 0 in 5 of 10 years, both for all group members and pups born in the year in question (mean value for all group members = 0.050, mean value for pups = 0.053, Table 3). There were no significant positive or negative trends in global F_{ST}, F_{IS} or F_{IT} over time (GLMM; $P > 0.05$). Taken together, these results are indicative of a population that is strongly but consistently structured over time.

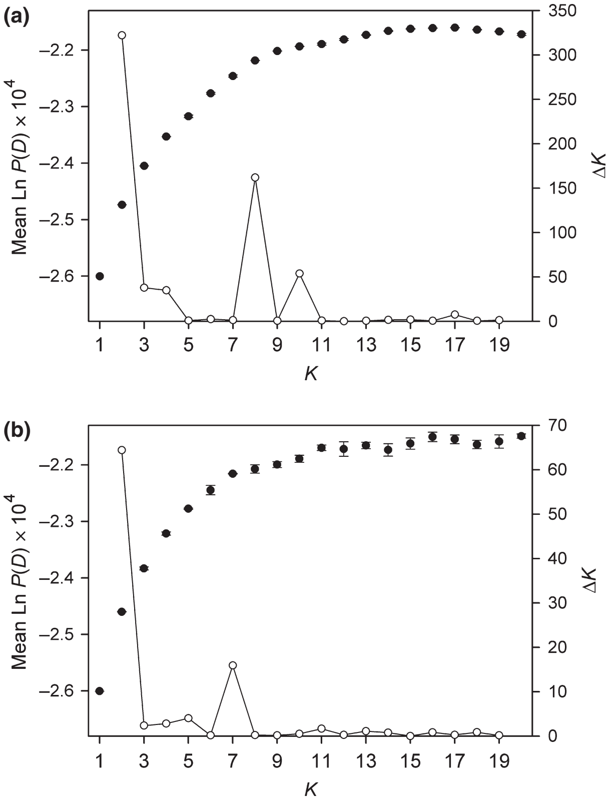

Fig. 1 Results of the STRUCTURE analysis showing mean ± standard error Ln *P*(*D*) and *Δk* values (filled and open circles, respectively) based on five replicates for each value of *k*, the hypothesized number of genetic clusters represented in the data, using (a) the standard model and (b) the LOCPRIOR model.

To test whether population structure could be detected without a priori knowledge of the groups from which each individual had been sampled, we used a Bayesian approach implemented within the program STRUCTURE (Pritchard *et al.* 2000). This program works by partitioning the data set in such a way that departures from Hardy–Weinberg and linkage equilibrium within the resulting genetic clusters are minimized. Five runs were conducted for each possible number of clusters (*K*), ranging from 1 to 20. The true number of clusters present is usually identified using the maximal value of Ln *P*(*D*), a model-choice criterion that estimates the posterior probability of the data. However, a simulation study by Evanno *et al.* (2005) found that once the true value of *K* is reached, Ln *P*(*D*) often plateaus or continues to increase slightly at larger values of *K*. Our data set yielded just such a pattern, with Ln *P*(*D*) rising steeply to around $K = 8$ and thereafter increasing gradually towards a peak at $K = 17$ before tailing off (Fig. 1a). Consequently, we calculated ΔK, an ad hoc statistic based on the second order rate of change of the likelihood function with respect to *K* that has been shown by Evanno *et al.* (2005) to be effective at detecting the uppermost hierarchical level of structure under most scenarios. This statistic peaked sharply at $K = 8$ (Fig. 1a), indicating support for eight genetic clusters. Membership coefficients for the inferred groups are summarized in Fig. 2a, where each vertical bar represents a different individual and the relative proportions

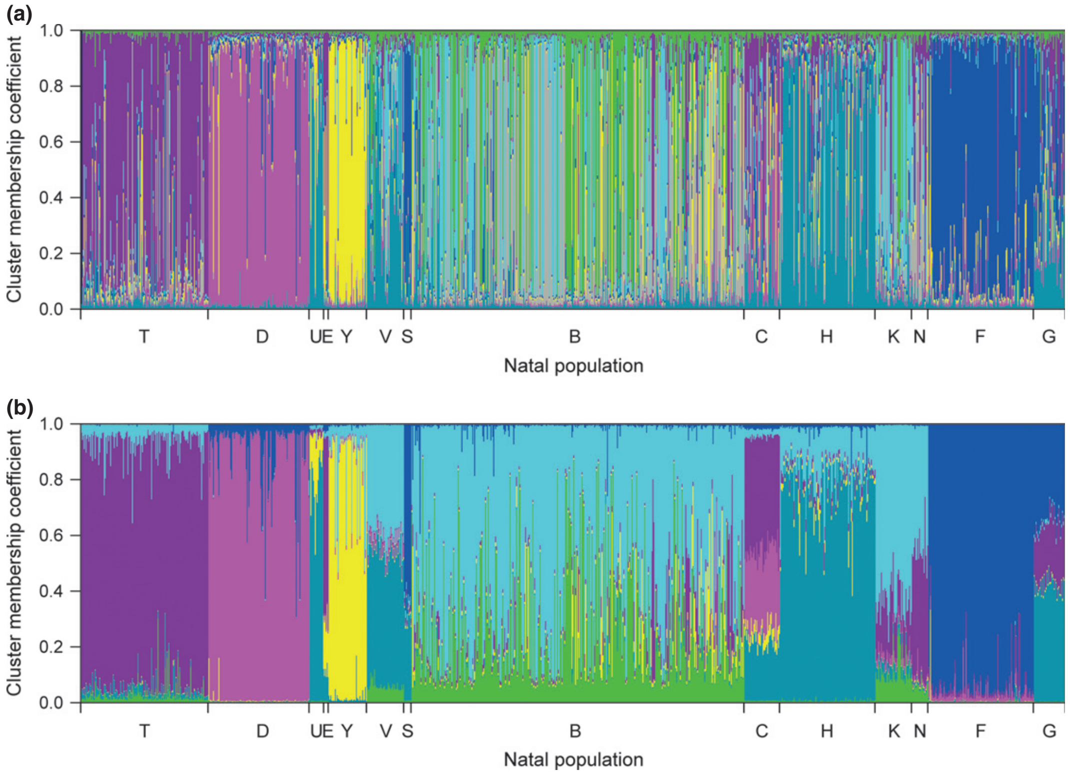

Fig. 2 Group membership coefficients derived using the program STRUCTURE for 1082 banded mongoose individuals for (a) $k = 8$ using the standard model and (b) $k = 7$ using the LOCPRIOR model. Each individual is represented by a vertical line partitioned into coloured segments, the lengths of which indicate the posterior probability of membership in each group.

of the different colours indicate the probabilities of belonging to each cluster. Classifying individuals according to their populations of birth, most groups are reasonably well defined, although others appear indistinguishable from one another (e.g. groups K and N) and considerable admixture is observed overall. Increasing K further did not substantially alter this pattern, with any additional clusters making negligible contributions other than to increase overall amount of admixture (data not shown).

Re-analysing our data set using a recently developed model within STRUCTURE that uses the sampling locations of individuals to inform cluster assignments (Hubisz *et al.* 2009), ΔK peaked at $K = 20$ and Ln $P(D)$ at $K = 7$ (Fig. 1b). Plotting individual cluster membership coefficients by natal population, the overall clustering result for $K = 7$ appears broadly similar to when the standard STRUCTURE model was used, although the overall level of admixture is reduced, making the groups more clearly defined (Fig. 2b). As found previously, the clustering result did not alter substantially when K was increased.

While some groups appear to consist of predominantly one genetic cluster (e.g. groups T, D, Y and F), others comprise several clusters (e.g. groups E, V, S and C). Furthermore, some groups share the same clusters, potentially due to their having shared ancestry. Thus, for two groups that formed from the fusion of cohorts derived from known (and genotyped) parent groups, we find substantial cluster-sharing. Group V shares light blue and green clusters with its parent group K and shares a grey cluster with parent group U. Similarly, group S shares a dark blue cluster with its parent group F and shares grey and light blue clusters with its parent group H.

Genetic distance between groups

The potential for matings between adjacent groups, combined with the limited dispersal of cohorts when establishing new groups, predicts that pups born in neighbouring groups should be more closely related than those born in more geographically distant groups. To explore this possibility, we analysed home-range data for eight groups present within our study site during 2006 (Fig. 3). These groups had a mean home range of 0.76 km^2 (range 0.1–1.52 km^2, $n = 8$) and home ranges overlapped substantially with those of neighbouring groups (mean percentage overlap = 47.16, range 17.6–87.9%, $n = 7$). To test whether genetic similarity between groups could be related to spatial proximity, we constructed a GLM with pairwise F_{ST} as the

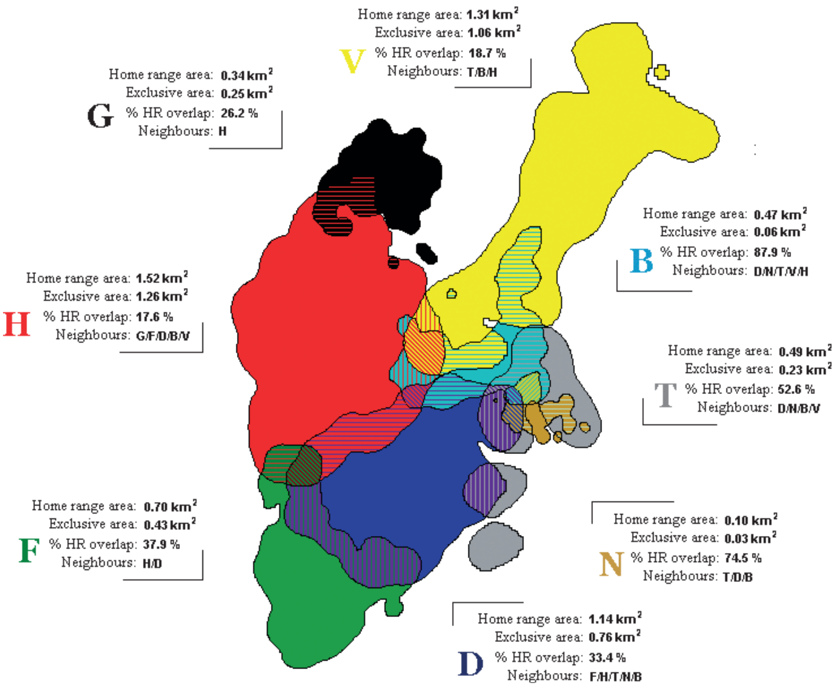

Fig. 3 Map of the study area showing home range data for all groups present in 2006.

dependent variable and whether or not groups were neighbouring and the minimum number of years since group fission as explanatory variables. The significance of each term was tested using a variant of the Mantel test (see Materials and methods for details). Contrary to our prediction, we found no relationship between pairwise F_{ST} and whether or not groups were current neighbours ($P > 0.05$). However, the frequency of copulations between neighbouring groups might be expected to increase with the area of territory overlap rather than simply depending on whether or not group territories overlap. To test this possibility, we repeated the model, replacing the term 'neighbouring vs. nonneighbouring' with the area of territory overlap (km^2), but we again found no significant relationship ($P > 0.05$). This is consistent with the fact that copulations were only observed in five and suspected in a further seven out of 325 recorded interactions between groups.

Finally, although we found no evidence of neighbouring groups being closely related to one another, pairwise F_{ST} between groups was positively correlated with the minimum time since group fission (GLM; $R^2 = 0.195$, $P = 0.034$, Fig. 4a). The exact year of fission between groups was only known in 11 of 28 cases. For the remaining 17 cases where the year of group fission was not known, the minimum possible time since fission was included in the model. As the exact time since fission should be a better measure than the minimum time, we expect the relationship to be stronger for the former. We therefore added whether or not the year of fission was known (1 = year known, 0 = year not known) into the model, along with an interaction term with the year of fission. As expected, the inclusion of this term and interaction improved the fit of the model (reduced AIC by four points) and increased the explanatory power of time since fission (GLM; $R^2 = 0.66$, $P = 0.0065$, Fig. 4b).

Group structure

A total of six new groups became established during the study period and a further four became established shortly before genetic sampling began in 2000. Once formed, these social groups remained stable, with very little migration between established groups (only three individuals were observed immigrating into existing groups over the decade of study). Groups contained a mean of 15.42 ± 0.79 (SE) adults (over 1 year old) and had a male-biased sex-ratio (1.64 ± 0.098 males per female, mean ± SE). Adult group size had a significantly quadratic relationship with time since groups were founded (GLMM; $\chi^2 = 7.30$, d.f. = 1, $P = 0.007$). The increase in group size over the first 6 years was likely to be due to a high degree of natal philopatry, with older groups becoming stable in size due to a higher probability of dispersal in large groups (GLMM; $\chi^2 = 4.20$, d.f. = 1, $P = 0.04$). The adult sex ratio of the group did not change with time since groups were founded (GLMM; $\chi^2 = 0.098$, d.f. = 1, $P = 0.75$).

As new groups arise from cohorts of males and females originating from different natal groups, we hypothesized that banded mongooses within newly established groups should be related within, but not between, the sexes. Consistent with this, relatedness within the sexes was found to be high, while relatedness between the sexes

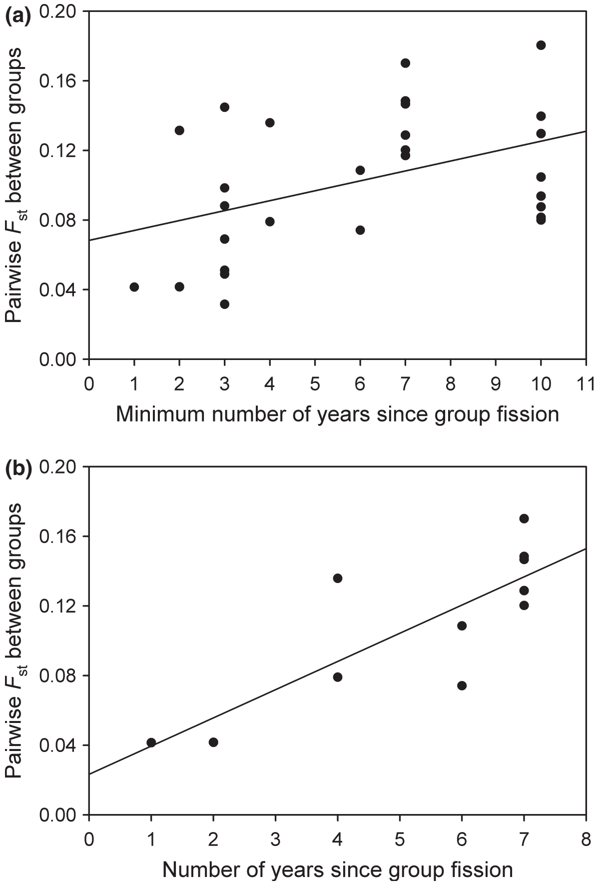

Fig. 4 The relationship between pairwise F_{ST} between groups and (a) the minimum amount of time since groups split (years), $R^2 = 0.195$, $P = 0.034$ (b) the exact time since groups split (years), excluding groups for which the exact time since splitting is not known, $R^2 = 0.6585$, $P = 0.0065$. Figures show raw data with a linear regression.

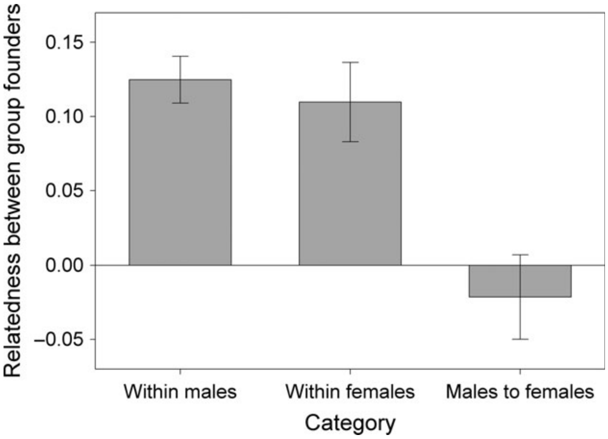

Fig. 5 Relatedness within and between the sexes in newly established groups (mean ± SE, calculated from raw data).

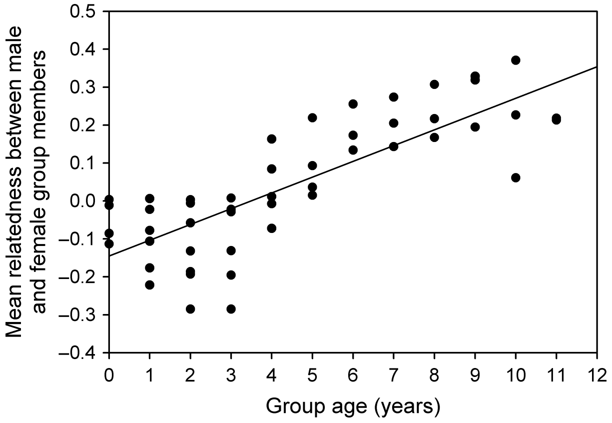

Fig. 6 Relatedness between sexually mature male and female group members (adults over 2 years old) over time since groups were founded. The graph shows mean values per group-year, with the line indicating a linear regression fitted to the data.

was not significantly different from zero (Fig. 5). Average levels of relatedness within the sexes did not change over time since group formation (GLMM females; $\chi^2 = 0.0022$, d.f. = 1, $P = 0.96$, males; $\chi^2 = 0.27$, d.f. = 1, $P = 0.60$). However, relatedness between the sexes increased significantly over time, both considering all adults over 1 year old (GLMM; $\chi^2 = 10.81$, d.f. = 1, $P = 0.0015$) and restricting the analysis to the individuals most likely to breed (at least 2 years old, GLMM; $\chi^2 = 35.02$, d.f. = 1, $P < 0.0001$, Fig. 6). This is probably due to the mortality of founding group members and the recruitment of their offspring into the breeding population.

Inbreeding and inbreeding avoidance

Groups often persisted beyond the point at which all the group founders of at least one sex had died. Of nine groups with known founders of both sexes, three were monitored until all founders of one sex had died, and a further two until all founders of both sexes had died. None of the groups dissolved upon the death of one or more founders and none accepted immigrant breeders. As relatedness between opposite-sex adult group-members increases over time and groups do not dissolve or accept immigrant breeders, the potential for inbreeding within groups may increase over time if breeding is random with regards to relatedness.

Groups with closely related breeders may inbreed, or alternatively could employ mechanisms to avoid inbreeding, such as mating with individuals from other groups. Due to the rarity of observations of extra-group mating (only five observations in 10 years) and the difficulty of establishing the identity of mates during fights between groups, it was not possible to investigate whether extra-group mating was more likely to occur after the death of founders. However, if inbreeding occurs, we would expect pups to become increasingly homozygous as average relatedness between breeders increases. In contrast to this prediction, we found no evidence that pup heterozygosity decreased either with time since group formation (GLMM; $\chi^2 = 1.77$, d.f. = 1, $P = 0.18$) or with relatedness between potential breeders (GLMM; $\chi^2 = 0.17$, d.f. = 1, $P = 0.68$).

As an alternative to extra-group mating, banded mongooses could potentially avoid inbreeding by mating with the least related individuals present in their natal groups. While relatedness between breeders in established groups is, on average, high (Fig. 6), females often have access to males of low genetic relatedness from within the group. In the three groups known to be 10 or more years old in 2009, all females that were likely to breed (at least 2 years of age) had access to at least one male with $R < 0.125$ within the group. However, males of $R > 0.25$ and even $R > 0.5$ were almost always amongst the pool of males available to breeding females (mean relatedness between opposite sex breeders over 2 years old was 0.20, range −0.42 to 0.80). Inbreeding avoidance in older groups would therefore require nonrandom mating with respect to relatedness (e.g. pre or postcopulatory mate choice).

Discussion

This study investigated the fine-scale spatial and temporal genetic structure of an intensively studied population of cooperatively breeding banded mongooses. We find that population structure is shaped by behavioural interactions within and between groups. Budding dispersal combined with the retention of philopatric young results in a highly structured population corresponding to social groups, whereby historical relationships between groups can be traced through genetic similarity. Somewhat surprisingly, neighbouring groups were no more genetically similar to one another than non-neighbouring groups, suggesting that extra-group paternity (EGP) occurs relatively infrequently. In recently founded groups, individuals were found to be closely related within the sexes but not between the sexes, corresponding with behavioural observations that male and female group founders originate from different natal groups. However due to strong natal philopatry of both sexes, relatedness between sexually-mature opposite-sex adults increases over time since group formation. Despite the presence of close relatives, we found little evidence of habitual inbreeding in older groups.

Overall strength of population structure

The banded mongoose population was highly structured, with relatively strong genetic differentiation among breeding groups considering the close spatial proximity and considerable overlap of many of the territories ($F_{ST} = 0.129$ for all group-members and 0.143 for pups). This is likely due to the combination of natal philopatry of both sexes and low gene-flow among groups. A similar level of structuring is seen in cooperatively breeding apostle birds, where both males and females often remain in their natal groups [mean $F_{ST} = 0.18$, Woxvold *et al.* (2006)].

The overall strength of population structure varied little over time, with F_{ST} being significantly positive in all years, suggesting that the banded mongoose population dynamics have not undergone any directional changes in the past 10 years. This is in contrast to studies of red deer (Nussey *et al.* 2005), African wild dogs (Marsden *et al.* 2012) and prairie chickens (Johnson *et al.* 2004), although the trends reported for these species are largely attributable to changes in management practices or increasing habitat fragmentation. As banded mongooses are not hunted or managed by humans in Queen Elizabeth National Park, the lack of directional change is probably a consequence of the relatively stable environment and overall population size.

In line with high F_{ST} values, the program STRUCTURE was able to uncover most of the groups in the absence of a priori information on group membership, although clustering was improved when the LOCPRIOR model was implemented. For the two groups for which both parental populations had been genotyped, considerable admixture was observed, with these groups sharing clusters present at high frequencies within the parental groups from which the founders were derived. This suggests that in systems with strong group structure such as the banded mongoose, STRUCTURE could provide a powerful tool for exploring shared ancestry, even in the absence of detailed observational data. In species with higher levels of dispersal between groups, and genetic mixing across social boundaries through EGP, population structure may be much weaker. Here, alternative approaches to exploring spatio-temporal genetic variation may be more appropriate. For example, genetic relatedness networks in combination with behavioural data may help to reveal temporal patterns in group structure and dispersal (Rolins *et al.* 2012).

Genetic distance between groups

To our initial surprise, geographically adjacent social groups were not more similar to one another than relatively distant groups, as would be expected under an isolation-by-distance pattern. This suggests that rates of extra group parentage and immigration between neighbouring groups are probably low. This is in contrast to many other social species, in which physical and genetic distances are strongly correlated (e.g. white-winged choughs; Beck *et al.* (2008), African lions; Spong *et al.*(2002); spotted hyenas; Holecamp *et al.* (2012), white-breasted thrasher; Temple *et al.* (2006)). However, because our study covered a relatively small geographic range (~10 km^2), we cannot discount the possibility that isolation by distance could exist over a wider scale.

In contrast, we found that genetic distance between groups (pairwise F_{ST}) was highly correlated with time since group-fission. This is the first time to our knowledge that such a relationship has been reported. Differentiation between groups over time may occur due to genetic drift, which can occur relatively quickly in small, reproductively isolated populations (Frankham *et al.* 2002; Ortego *et al.* 2011). While few studies appear to have linked relationships among social groups to historical dispersal events, this kind of effect could be common in species where dispersal occurs through group-fission or 'budding', and hence relatives disperse together. Examples of such species include African elephants (Archie *et al.* 2008) and primates such as rhesus macaques (Widdig *et al.* 2006).

Relatedness structure of social groups

In recently founded groups, individuals were found to be closely related within the sexes but not between the sexes. This is concordant with observational data, which reveal that male and female group-founders originate from the different natal packs. Even when males and females are evicted from their natal group simultaneously, they split into single sex cohorts to disperse (Cant *et al.* 2001). This almost certainly serves to avoid breeding with close relatives. A similar pattern is observed in other cooperatively breeding species such as meerkats (Griffin *et al.* 2003; Nielsen *et al.* 2012) pied babblers (Nelson-Flower *et al.* 2011) and mole-rats (Ciszek 2000; Burland *et al.* 2002), where breeders in new groups are unrelated.

Within banded mongoose groups, average relatedness between sexually mature males and females increased over time since groups were founded. Although the generality of this finding remains to be explored, similarly high levels of relatedness between breeding adults have been observed in dwarf mongooses, naked mole-rats and Damaraland mole-rats, where natals often inherit breeding positions upon the death of group founders (Reeve *et al.* 1990; Keane *et al.* 1996; Burland *et al.* 2002). However, it seems unlikely that pairwise relatedness will increase over time in the majority of cooperatively breeding species, where groups dissolve or accept immigrants on the death of dominant breeders (Koenig *et al.* 1998; Daniels & Walters 2000; Koenig & Haydock 2004). Although it is currently unclear why species differ in group-stability after the death of breeders, a lack of migration between groups could be related to ecological constraints on dispersal (Burland *et al.* 2002).

Inbreeding and inbreeding avoidance

Despite average relatedness between opposite-sex breeding adults increasing over time within groups, we found no concurrent decrease in the average heterozygosity of pups over the same period. We also found no significant association between offspring heterozygosity and mean relatedness between adult breeders, as would be expected if mating within groups was random with respect to relatedness. By implication, frequent close inbreeding may be avoided within long-established groups. In many social mammals, inbreeding is avoided through the dispersal of one sex prior to breeding (Lukas & Clutton-Brock 2011). However, the banded mongoose appears to be an exception; male group-founders were still alive up to 9 years after groups formed, while females began to breed in their natal group at 1 year old (Cant 2000; Gilchrist *et al.* 2004). In some species that live in groups containing closely related breeders, EGP may represent an important means of inbreeding avoidance (e.g. pilot whales; Amos *et al.* (1991) and fairy-wrens; Brouwer *et al.*(2011)). While there is some evidence that banded mongooses may seek out extra-group copulations during interactions between neighbouring groups (Cant *et al.* 2002), matings are in fact rarely observed. Furthermore, extensive EGP among neighbouring groups would be expected to undermine population structure (Kerth & Van Schaik 2011).

Inbreeding within older groups could potentially be avoided by pre-copulatory or post-copulatory mate choice (Tregenza & Weddell 2002; Höner *et al.* 2007; Perry *et al.* 2008). The former is potentially supported by the observation that mate-guarding males are often incapable of preventing females from mating with others (Nichols *et al.* 2010). Females could therefore evade a closely related mate-guard in order to mate with a lesser relative from within the group. Alternatively, inbreeding may occur but be difficult to detect using proxy measures of heterozygosity at a small number of microsatellites (Balloux *et al.* 2004). To explore these possibilities would require a detailed paternity analysis. However, due to the presence of relatives, the large number of potential fathers and the fact that pups are born into communal litters, many more genetic markers will be required to provide adequate resolution.

Implications for kin-selected helping and harming behaviour

The banded mongoose has a breeding system at the boundaries of cooperative and communal breeding. As in cooperatively breeding species, nonbreeding helpers contribute to care of the communal litter (Hodge 2007; Nichols *et al.* 2012a). However reproductive skew is low, such that helpers are only temporarily nonbreeding, and breeders contribute highly to offspring care (Gilchrist & Russell 2007; Nichols *et al.* 2012b), more akin to communal breeders. This mixture of characteristics may be due to the banded mongoose having evolved from a monogamous, cooperatively breeding ancestor, while the majority of communal breeders appear to have evolved from plural-breeders with a polygynous mating system (Lukas & Clutton-Brock 2012). Although monogamy is likely to be important in the evolution of cooperative breeding as it leads to a high level of relatedness between breeders and helpers (Lukas & Clutton-Brock 2012), monogamy is unlikely to be involved in the maintenance of cooperation in the banded mongoose as reproductive skew is low and both sexes are promiscuous (Nichols *et al.* 2010). A high level of relatedness between banded mongoose group members could instead result from the method by which banded mongooses disperse and form new groups. Such 'budding dispersal' is conducive to the evolution of helping behaviour because it decouples the positive and negative consequences of dispersal: extra offspring produced as a result of cooperation can disperse away from their parents (so avoiding competition with kin) but still form groups in which relatedness is high (Gardner & West 2006; Cant in press). However, direct fitness benefits resulting from cooperation are also likely to contribute to the maintenance of cooperative breeding in this system as group augmentation is likely to increase the survival and reproductive success of group-members (Kokko *et al.* 2001; Müller & Manser 2007).

Finally, temporal variation in within-group relatedness over time raises the possibility that helping and harming behaviour within groups could also vary over time. For example, contributions to pup care could increase with relatedness to the litter (Clutton-Brock *et al.* 2002) and dominants may be more tolerant of subordinate reproduction when they are closely related (Clutton-Brock *et al.* 2010). Similarly, changes in relatedness structure may have implications for interactions between groups. For example, we might expect greater numbers of aggressive interactions between more distantly related groups than those that split more recently, at least if individuals are able to recognize kin. These questions should provide fruitful avenues for future research.

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H.J.N's research interests center on understanding the evolution of animal societies, using a combination of molecular and behavioural techniques. N.R.J.'s main interests lie in scent communication and its potential application for conservation. His previous work investigated the function(s) of scent marking in wild carnivores and involved a combination of behavioural observations, field experiments and laboratory analyses of scent marks. G.A.J is interested in evolutionary genetics. M.A. C. studies the evolution of social behaviour and life history in animal societies. J.I.H. is interested in the application of molecular markers to questions relating to vertebrate mating systems and population structure.

Data accessibility

DNA sequences: Genbank accessions AF271115, AF271117, AF271118, AF271120, AY142693, AY142694, AY142696, AY142697, AY142700, AY142703, AY155580, AY090498, EU045417, EU045419.

Behavioural data and genotypes: DRYAD entry doi: 10.5061/dryad.hj4t4.