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Original Article

Extra-group paternity varies with proxies of relatedness in a social mammal with high inbreeding risk

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Behavioral mechanisms for avoiding inbreeding are common in the natural world and are believed to have evolved as a response to the negative consequences of inbreeding. However, despite a fundamental role in fitness, we have a limited understanding of the cues that individuals use to assess inbreeding risk, as well as the extent to which individual inbreeding behavior is repeatable. We used piecewise structural equation modeling of 24 years of data to investigate the causes and consequences of within- versus extra-group paternity in banded mongooses. This cooperatively breeding mammal lives in tight-knit social groups that often contain closely related opposite-sex breeders, so inbreeding can be avoided through extra-group mating. We used molecular parentage assignments to show that, despite extra-group paternity resulting in outbred offspring, within-group inbreeding occurs frequently, with around 16% litters being moderately or highly inbred. Additionally, extra-group paternity appears to be plastic, with females mating outside of their social group according to individual proxies (age and immigration status) and societal proxies (group size and age) of within-group inbreeding risk but not in direct response to levels of within-group relatedness. While individual repeatability in extra-group paternity was relatively low, female cobreeders showed high repeatability, suggesting a strong constraint arising from the opportunities for extra-group mating. The use of extra-group paternity as an inbreeding avoidance strategy is, therefore, limited by high costs, opportunity constraints, and the limited reliability of proxies of inbreeding risk.

Key words: **banded mongoose, behavioral plasticity, cooperative breeder, extra-group paternity, extrapair paternity, inbreeding avoidance, personality, repeatability.**

INTRODUCTION

An important selection pressure thought to shape the evolution of mating behavior is inbreeding depression (Pusey and Wolf 1996). The offspring of close relatives tend to have reduced fitness due to the expression of deleterious recessive alleles and a lack of heterozygote advantage (Charlesworth and Charlesworth 1999). This phenomenon has been shown to cause reductions in fitness traits throughout an individual's lifespan across plants and animals (Keller and Waller 2002). The widespread occurrence of inbreeding depression is believed to have been selected for individuals to mate preferentially with nonrelatives, known as inbreeding avoidance, in many species (Pusey and Wolf 1996).

Although inbreeding avoidance behaviors can produce higher-quality offspring, they may also incur a cost. If this cost is sufficient to outweigh any fitness gain, then inbreeding avoidance behaviors will not be favored (Szulkin et al. 2013). For example,

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the opportunity costs of rejecting close relatives as mates may have prevented the evolution of inbreeding avoidance in the Mandarte island song sparrow *Melospiza melodia* as unpaired individuals have substantially lower fitness than individuals that pair with a relative (Keller and Arcese 1998; Reid et al. 2015). Similarly, high costs of dispersal may have led to the evolution of inbreeding tolerance in naked mole-rats *Heterocephalus glaber* (Ingram et al. 2015). Here, dispersal is particularly constrained due to its subterranean desert habitat and the fact that movement above ground is extremely hazardous (Bennett and Faulkes 2000). Although outbreeding is generally preferred in this species (Ciszek 2000), close inbreeding is likely tolerated in colonies where one or both of the founding breeders have died (Ingram et al. 2015).

In wild systems, the cost–benefit ratio of inbreeding avoidance is unlikely to be fixed and probably varies with the prevailing social and environmental conditions. Individuals might, therefore, maximize their fitness by plastically altering their behavior according to the current cost–benefit ratio (van Hooff et al. 2005; Cohas et al. 2006; Annavi et al. 2014). In particular, when the risk of breeding with a relative is low, there is little to be gained from inbreeding avoidance compared to mating randomly with respect to relatedness (Jamieson et al. 2009). Consequently, individuals may alter their mating behavior and only pay the costs of inbreeding avoidance when the risk of inbreeding is otherwise high. For example, female European badgers *Meles meles* are more likely to produce extra-group offspring when relatedness between mothers and within-group males is high (Annavi et al. 2014).

In order to exploit the benefits of plasticity, individuals must be able to accurately identify the optimal behavior based on environmental cues (Bonamour et al. 2019). As is common in phenological examples, mate choice decisions may not always be based upon the fundamentally important variable but rather on a suitable proxy (Bonamour et al. 2019). For example, rejecting a sibling as a potential mate may be based upon familiarity instead of a direct measure of genetic relatedness (Ihle and Forstmeier 2013).

In addition to showing plasticity in behavior (Bell et al. 2009; Řežucha and Reichard 2016), animals often show individual repeatability in their behavior across time and in different contexts (Sih et al. 2004; Smith and Blumstein 2008). Repeatability is defined as the proportion of phenotypic variance that is attributable to differences among individuals (Dingemanse and Dochtermann 2013), and it can have profound fitness consequences by creating behavioral carryovers across situations that may cause individuals to deviate from the optimal behavior in a given situation (Smith and Blumstein 2008). The determinants of repeatability of mating behavior are not well understood (Bell et al. 2009) and studies have found considerable variation, even amongst the same mating behaviors in closely related species. For example, male Endler guppies *Poecilia wingei* show little repeatability in mating behavior across different social conditions in contrast to male *Poecilia reticulata* guppies (Magellan and Magurran 2007; Řežucha and Reichard 2016).

Here, we used molecular parentage data to investigate factors influencing extra-group paternity and the inbreeding status of offspring in the banded mongoose *Mungos mungo*. This small (~1–2 kg) mammal lives in cooperative social groups of approximately 20 adults plus offspring (Cant et al. 2016). Unusually among cooperatively breeding mammals, reproductive skew is relatively low as there is no single dominant breeding male or female; instead, multiple males (3–7) and females (1–5) within each social group breed several times a year (Cant et al. 2016). Breeding is synchronized within groups, with all females entering estrus during the same week and usually giving birth on the same day in an underground den (Cant et al. 2014, 2016). Pups are raised in a communal litter and receive care from multiple group members, including parents and nonbreeders (Gilchrist and Russell 2007; Hodge 2007; Cant et al. 2016). Both sexes commonly remain in their natal group for their entire lives and breed there despite the presence of close relatives (including parents, offspring, and siblings) as potential mates (Cant et al. 2013). As a consequence, within-group mating is often incestuous, with around two-thirds of offspring having nonzero inbreeding coefficients and 7% being the product of first-degree inbreeding (Nichols et al. 2014; Sanderson et al. 2015; Wells et al. 2018).

A key mechanism through which inbreeding is avoided in banded mongooses is extra-group paternity. Banded mongoose groups aggressively defend their territories from rival groups and violent intergroup interactions account for around 15% of deaths of known cause (Nichols et al. 2015). Despite this, around 18% of offspring are sired by extra-group males (Nichols et al. 2015). These offspring are most likely conceived during intergroup interactions when extra-group copulations have been observed and are linked to paternity outcomes (Nichols et al. 2015). Moreover, inbreeding depression has been identified for several fitness traits in this species (Sanderson et al. 2015; Mitchell et al. 2017; Wells et al. 2018) and extra-group offspring have been shown to be 5% more heterozygous, 10% heavier, and to have 27% higher survival than within-group offspring (Nichols et al. 2015). Consequently, the occurrence of two discrete possibilities (extra- and within-group paternity) with well-defined, biologically significant consequences (risk of violence and risk of inbreeding respectively) makes this system ideally suited to investigate the triggers and consequences of this binary decision.

Previous studies of banded mongooses have shown that the probability of extra-group paternity occurring within a communal litter is significantly higher in older groups (Nichols et al. 2015) and that older groups also contain more relatives (Nichols et al. 2012). Taken together, these findings are strongly suggestive of extra-group mating being a strategy for avoiding inbreeding. However, studies of this species have not previously addressed the causes and consequences of extra-group paternity at the level of the individual. Furthermore, studies of wild systems with detailed individual-based molecular parentage data have the potential to provide insights into the evolution of inbreeding avoidance and extra-group mating, which remain poorly understood in general (Arct et al. 2015).

Here, we used 24 years of detailed behavioral and genetic data from an intensively studied banded mongoose population to 1) identify factors that signify inbreeding risk, 2) investigate how individual extra-group paternity probability changes in accordance with changes in inbreeding risk factors, 3) quantify the repeatability of extra-group paternity throughout individual lifetimes and among cobreeding females, and 4) determine the consequences of extra-group and within-group paternity on offspring inbreeding levels. By addressing these questions within a single statistical framework, we were able to unravel a complex network of interacting causes and effects.

METHODS

Study system

This study was carried out on a wild but habituated population of banded mongooses on the Mweya peninsula in the Queen Elizabeth National Park, Uganda (0°12′S, 29°54′E). The population has been under continuous study since 1995 and at any one time consisted of approximately 250 individuals belonging to roughly 10 social groups. Social groups could be located to determine group composition and observe behaviors because one to two individuals per group were fitted with 27-g (±2 g) radio collars (<2% of body mass, Sirtrack Ltd, New Zealand) with 20-cm whip antennae (Biotrack Ltd, UK). Individuals within the study population could be identified on sight because adults were given a unique shave pattern in their fur and individuals under 6 months of age were marked with blonde hair dye (L'Oreal, UK). In order to maintain these identification marks, all individuals were trapped approximately every 3 months using Tomahawk traps (Tomahawk Live Trap Co., Tomahawk, WI). Once trapped, individuals were anesthetized using isoflurane as described in Hodge (2007) and Jordan et al. (2010). When individuals were trapped for the first time, at approximately 1 month old, they were given either a unique tattoo or, more recently, a subcutaneous PIT tag (TAG-P-122IJ, Wyre Micro Design Ltd, UK) to enable permanent identification. For subsequent genetic analysis, a 2-mm tissue sample was taken from the tip of the tail using sterile surgical scissors and stored in 96% ethanol. Afterward, a dilute solution of potassium permanganate was applied to the tail to minimize the risk of infection. Animals were allowed to recover from anesthetic in a covered trap with access to water and were subsequently released (on the day of capture) along with other members of their social group at the site of capture.

Ethical statement

The trapping procedure has been carried out over 8000 times and tissue samples have been collected from over 1900 individuals over the course of the project with no adverse effects. All research procedures adhere to the Association for the Study of Animal Behaviour Guidelines for the Treatment of Animals in Behavioural Research and Teaching and were approved by the Ethical Review Committee of the University of Exeter. The research was carried out under license from the Uganda National Council for Science and Technology, and all procedures were approved by the Uganda Wildlife Authority.

Genetic analysis

DNA was extracted from the tissue samples using lysis with proteinase K, followed by phenol-chloroform purification (Sambrook et al. 1989) or using DNA extraction kits (Qiagen® DNeasy blood and tissue) following the manufacturer's protocol. Over the course of over two decades of data collection, genetic technologies have improved, and our genotyping protocol was updated to take advantage of these developments. Specifically, microsatellite loci were originally genotyped individually by radioactive incorporation but latterly multiple microsatellite loci were genotyped simultaneously as multiplexes using fluorescently labeled primers. Eight of the 43 loci originally genotyped using radioactive incorporation failed to amplify consistently as part of a multiplex and so were not genotyped after 2014. The samples were, therefore, either genotyped at 35 or 43 microsatellite loci. The 35 microsatellites that could be successfully genotyped using the fluorescent approach were amplified as seven separate multiplexed PCR reactions using a Type It kit (Qiagen®) according to the manufacturer's protocol with an annealing temperature of 57 °C and a reaction volume of 12 µL. PCR products were resolved by electrophoresis on an ABI 3730xl capillary sequencer, and allele sizes were scored using Genemarker version 1.95 (SoftGenetics, PA). For full details of the multiplex genotyping, see Sanderson et al. (2015) and Wells et al. (2018) and, for the radioactive genotyping, see Nichols et al. (2010, 2012).

Parentage assignment

Parentage could not be assigned based on observations because mating was difficult to observe, often happening in dense shrubbery, especially when females mated with subordinate or extra-group males. Furthermore, birth was highly synchronized within groups such that multiple females frequently gave birth on the same night in the same underground den (Cant et al. 2016). Therefore, genetic parentage assignment was required to identify each parent and to determine whether they were in the same social group at the time of conception. We used the pedigree constructed in Wells et al. (2018); full details of how this was constructed are described therein. In brief, parentage was principally assigned using MasterBayes (Hadfield et al. 2006) because it can incorporate phenotypic and genetic data when calculating assignment probability. The phenotypic information supplied to MasterBayes included whether or not the candidate male was present in the group the pup was born in (i.e., incorporating extra-group paternity). This approach was also supplemented by using Colony (Jones and Wang 2010) to identify sibship groups, which allowed us to identify related founders or immigrants rather than assuming them to be unrelated. The cutoff probability for accepting parentage assignments was 0.8, and 89% of assignments were at ≥0.99 confidence. Colony assignments were only accepted if MasterBayes failed to confidently assign parentage. The final pedigree was nine generations deep and included 1547 individuals with both parents assigned and 777 of these had all four grandparents assigned.

Genetic and life-history variables

Once parentage was assigned, we determined whether pups were sired by within-group or extra-group males. Females give birth to up to six pups at a time, and we define all pups born to a single female as a result of a single breeding event as a "maternal litter" (see the key terms defined in Table 1). Multiple females in a group often give birth during a single breeding event, and we collectively refer to all of these offspring as a "communal litter," which usually contain multiple maternal litters. Ninety-seven percent of maternal litters were fathered solely by within-group or extra-group males; this indicates that the extra-group paternity status of each pup is not independent of the rest of the maternal litter's status. Consequently, each maternal litter was assigned a binary extra-group paternity status, 1 if any of the pups' fathers were extra-group and 0 if no pup in the maternal litter had an extra-group father.

A previous study found that an average of 85% of within-group reproduction is monopolized by males of the top three age ranks, who attempt to guard estrus females from rival males (Nichols et al. 2010). We, therefore, calculated a female's within-group inbreeding risk as the average pedigree relatedness of the breeding female to the top-ranking males (ranking 1–3 and over 6 months old) in her social group. A male's age rank was calculated as the number of older males in the group plus one; males born in the same communal litter were all given the same rank. Male immigrants to the study site are of unknown age and were also included when calculating relatedness as their rank could not be determined. The inbreeding coefficients (f) of pups were calculated using the inverseA function from the MCMCglmm R package (Hadfield 2010). The average inbreeding coefficient of each maternal litter (f_l) was calculated as the mean f of all pups in the maternal litter that had both parents confidently assigned (at >0.8 probability).

Table 1

Definitions of terms used in our models and throughout the paper

Term	Definition	Variable type
Maternal litter	Pups born to a single female in a single breeding event.	Categorical
Communal litter	Collective term for all pups in a group born during a single breeding event.	Categorical
Breeding event	Breeding is highly synchronized within groups. A breeding event refers to the estrus, conception, pregnancy, birth, and raising of a communal litter of pups.	Categorical
f_l	The average inbreeding coefficient of a maternal litter.	Continuous
Group age	Time between the first time the social group was observed (usually the point at which the group formed) and the time the maternal litter was conceived.	Continuous
Relatedness to top males	The average pedigree relatedness of a focal female to males of the top three age ranks (assuming that they are over 6 months old) and immigrants to the population.	Continuous
Group size	The number of individuals over 6 months old in the breeding female's group at conception.	Continuous
In natal group	Females still in the group they were born in when they conceived were said to be in their natal group.	Binary
Age	Age of the breeding female at conception.	Continuous
Extra-group mating	Pup was fathered by a male that was not in the breeding female's social group at the time of conception (in either the second or third month before birth).	Binary

Table 2

The hypothesized causal relationships that were tested as fixed effects in the structural equation model

Response variable	Explanatory variables
i. Group size	Group age
ii. Relatedness to top males	Group age Breeding female in natal group
iii. Extra-group paternity	Breeding female in natal group Group size Group age Breeding female's age
iv. Average maternal litter inbreeding coefficient	Breeding female in natal group relatedness to top males and the interaction between these two variables

Each group was visited every 1–3 days to record group and life-history variables. Because females gave birth in an underground den, births could not be directly observed. However, we were able to infer the date of parturition from a visible reduction in the size of the breeding female's abdomen, as groups with pregnant females were visited every day. From this, we estimated the date of conception by assuming a gestation period of 60 days (Cant 2000).

Statistical analysis

We were interested in 1) identifying factors that signify inbreeding risk, 2) investigating how extra-group paternity probability varies in accordance with changes in inbreeding risk factors, 3) revealing the degree to which individuals and cobreeding females show repeatability in extra-group paternity, and 4) determining the consequences of extra-group and within-group paternity on offspring inbreeding levels. We, therefore, initially constructed four separate General(ized) Linear Mixed Effect Models (GLMMs) in R to identify variables determining mating patterns. These models are described in detail below (including our reasons for including each explanatory variable) and are summarized in Table 2. Subsequently, these four models were combined into a piecewise structural equation modeling (SEM) using the R package piecewiseSEM (Lefcheck 2016).

Piecewise SEM allows us to test causal relationships in multivariate systems (Shipley 2009); the hypothesized causal relationships in our study system are described in Table 2. Relationships that were not specified in our models are believed to be biologically unimportant. These unspecified relationships are called independence claims in the context of the SEM framework, and we confirmed that they were all nonsignificant after accounting for the relationships specified in our models. These tests compare the originally specified path with one including the independent variable (see Supplementary Material SM1). Nonsignificant independence claims indicate that the variables in question are conditionally independent, that is, the relationship is not supported by our data. Multiple independence claims are a fundamental consequence of the number of variables included in our model and are philosophically different from removing nonsignificant relationships from models as we specified them as unimportant before testing (Shipley 2009). The *P*-values of these independence claims were then used collectively to calculate the Fisher's *C* statistic to test whether all of the important relationships in the data were captured by our SEM. The independence claims are reported in Supplementary Table S1.

For all models, we used the same data set of 662 maternal litters born to 180 females in 271 breeding events (each breeding event produces one communal litter) across 16 social groups. The models all included the identity of the breeding female, breeding event, and breeding female's social group at conception as random effects. All continuous variables were mean centered and standardized by their standard deviation so that effect sizes could be compared across models (Schielzeth 2010).

Identifying factors that signify inbreeding risk

The first two models (i and ii, Table 2) evaluated how social groups change through time and whether these changes alter levels of relatedness between potential breeders. Group size and relatedness to top males were fitted as response variables in separate linear mixed models using lme4 (Bates et al. 2013). Group age was analyzed as a fixed effect in both models because new groups become larger over time (Thompson, Marshall et al. 2017) and, because of limited dispersal, relatedness also increases over time (Nichols et al. 2012). Whether or not the breeding female was in her natal group was included as a fixed effect in the model of relatedness because, in a female's natal group, her father and other male relatives are potential mates. In the model of relatedness, group age was fitted as a random slope by group identity; this decision was based on data inspection and was also supported by Akaike Information Criterion (AIC). Specifically, plots of relatedness against group age suggested either a quadratic relationship or that different groups showed different relationships. Allowing groups to have separate linear relationships between group age and relatedness produced a seven AIC point improvement over specifying a quadratic relationship. The significance of fixed effects was determined through parametric bootstrapping (PB) and implemented using the R package pbkrtest (Halekoh and Højsgaard 2014).

Factors influencing extra-group paternity

Next, we investigated how variables that might signify inbreeding risk influenced within- or extra-group paternity, (model iii, Table 2). Extra-group paternity was analyzed as a binary response for each maternal litter in a binomial GLMM in lme4 (Bates et al. 2013). The age of the group was included as a continuous fixed effect, while whether or not a female bred in her natal group (or alternatively after dispersal to a new group) was included as a binary fixed effect. This was because both of these variables have previously been found to be associated with paternity outcomes in this species (Nichols et al. 2014, 2015). Group size was included in the model as females in larger groups have a wider selection of within-group potential mates (group size and the number of males are highly correlated; Sanderson et al. (2015)). The breeding female's age at conception was also included as a fixed effect in order to investigate how extra-group paternity probability changes over the lifespan. Finally, it was unclear a priori whether the relatedness of the female to the top males in her group would affect her extra-group paternity probability. Previous work found that relatedness had a nonsignificant effect after accounting for group age (Nichols et al. 2015). However, banded mongoose females do appear to express some preference for less related mates when mating within their social groups (Sanderson et al. 2015). Therefore, we tested for an effect of female relatedness to the top males in her group on her extra-group paternity probability as described in Supplementary Material SM1.

The significance of fixed effects in the extra-group paternity model could not initially be determined due to convergence errors. In other models, the significance of fixed effects was determined through PB (see Table 3). However, when bootstrapping the extra-group paternity model, a large proportion of the models fitted to simulated data failed to converge and so significance could not be accurately determined. Therefore, in order to derive accurate significance estimates, this model was refitted using Markov chain Monte Carlo GLMM using the same fixed and random effect structure as described in Supplementary Material SM2.

Repeatability of extra-group paternity

Individual breeding female, breeding attempt, and social group repeatabilities were calculated from the random effect variance estimates from the MCMCglmm models of extra-group paternity described in Table 3 and Supplementary Material SM2. Following Nakagawa and Schielzeth (2010), the random effect variances were converted into repeatabilities, conditional on the fitted fixed effects, for a logit distribution with additive overdispersion as:

$$R_{\text{logitA}} = \frac{\sigma_x^2}{\sigma^2_{\text{female}} + \sigma^2_{\text{breeding} \quad \text{attempt}} + \sigma^2_{\text{group}} + \sigma^2_e + \frac{\pi^2}{3}}$$

where σ^2_{female}, $\sigma^2_{\text{breeding} \quad \text{attempt}}$, and σ^2_{group} are the random effect variances of the breeding female, breeding attempt, and social group random effects, respectively. The random effect variance is indicated by σ_x^2 (where x indicates the random effect variance to be converted into a repeatability; $\sigma^2{}_{\text{female}}, \sigma^2{}_{\text{breeding attempt}}$, or σ^2_{group}) and the residual variance is σ_e^2. Note that, because our response variable was binary, σ_e^2 was inestimable and was, therefore, set to 1 (Nakagawa and Schielzeth 2010).

Consequences of extra-group paternity for offspring inbreeding levels

The final model in our piecewise structural equation model (iv, Table 2) focused on how extra-group paternity translated into offspring inbreeding levels. The mean inbreeding coefficient of the maternal litter (f_l) was analyzed as the response term in a linear mixed model using lme4 (Bates et al. 2013). As fixed effects, we fitted the average relatedness of the breeding female to the top-ranked males, whether or not any pups in the maternal litter were sired by extra-group males (binary extra-group paternity status), and an interaction between these two terms. The interaction was included because the relatedness between individuals within a social group is only relevant to f_l for within-group breeding.

The significance of the fixed effects in the mixed models was assessed either through PB or using MCMC methods. PB was performed using the pbkrtest package in R (Halekoh and Højsgaard 2014). A reduced model was created for each fixed effect by dropping that variable from the model, and data were simulated according to this simplified model 1000 times. The full and simplified models were compared using likelihood ratios for all

Table 3

Fixed effects and their significance in the four models that made up our piecewise structural equation model. The significance of the fixed effects was determined either by PB or using MCMC. Nonsignificant independence claims were not included in the structural equation model and are instead shown in Supplementary Table S1

Response	Fixed effect	Estimate	SE	*P*-value	Method
Model i. Group size	(Intercept)	−0.69	0.22		
	Group age	0.15	0.07	0.034	PB
Model ii. Relatedness	(Intercept)	−0.41	0.31		
	Group age	0.41	0.18	0.001	PB
	Breeding female in natal group	0.77	0.23	0.004	PB
Model iii. Extra-group paternity	(Intercept)	−6.67	0.05	0.001	MCMC
	Group age	0.77	0.01	0.040	MCMC
	Breeding female in natal group	3.42	0.04	0.004	MCMC
	Group size	−0.95	0.01	0.004	MCMC
	Age	0.9	0.01	0.001	MCMC
Model iv. Maternal litter inbreeding coefficient	(Intercept)	0.15	0.05		
	Extra-group paternity	−0.61	0.08		
	Relatedness	0.55	0.04		
	Extra-group paternity: relatedness	−0.49	0.08	0.001	PB

1000 simulated data sets. The *P*-value was calculated as the number of simulated likelihood ratios that were greater than or equal to the observed likelihood ratio. Due to convergence issues in some reduced models, but not the full model, PB was not appropriate for our model of extra-group paternity. Instead, the model was reconstructed using MCMCglmm (Hadfield 2010) as described in the Supplementary Material SM2 because accurate Bayesian *P*-values can be calculated from posterior distributions. All models were validated by checking histograms of residuals and plots of residuals against predictors. Colinearity was evaluated by calculating variance inflation factors, which were below 2 for all models.

RESULTS

Identifying factors that signify inbreeding risk

We found that group size was significantly associated with group age (group age ß = 0.15, $P = 0.034$; model i, Table 3), which is expected because newly formed groups are usually smaller than more established groups (Thompson, Marshall, et al. 2017) and become larger over time as new offspring are born and mature (although older groups can also decrease in size due to death and dispersal). We also found that the relatedness of breeding females to top-ranking males increased over time since a group was first observed (group age ß = 0.41, $P < 0.001$; Figure 1; model ii, Table 3). Levels of relatedness were low in newly founded groups, as the opposite-sex founders originate from different groups and are, therefore, unrelated (Nichols et al. 2012). However, relatedness increased over time because most mating occurs within group and the founders' offspring commonly remain in their natal group until they too become breeders (the predicted relatedness of philopatric breeding females to top males was 0.16 ten years after the group was first observed). The relatedness between breeding females and top-ranking males was significantly higher if a female stayed in her natal group (breeding female in natal group ß = 0.77, $P = 0.004$; model ii, Table 3) because the top-ranked males are likely to include her father and other male relatives.

Factors influencing extra-group paternity

Females displayed plasticity in their mating behavior such that extra-group paternity was more common when the risk of inbreeding was greater. Specifically, breeding females were more likely to have their litters sired by extra-group males when they were residing within their natal group (breeding female in natal group ß = 3.42, $P = 0.004$; Table 3) and when their group was older (group age ß = 0.77, $P = 0.040$; Figure 2A; Table 3). As described above, both of these variables are associated with increased relatedness and so should be reasonable proxies for the risk of inbreeding. However, relatedness between females and top-ranking males was not directly associated with a female's probability of obtaining extra-group paternity after accounting for other fixed effects (relatedness ß = 0.30, $P = 0.142$). Females in larger groups were less likely to obtain extra-group paternity (group size ß = −0.95, $P = 0.004$; Table 3), whereas older females were more likely to obtain extra-group paternity (age ß = 0.9, $P < 0.001$; Figure 2b; Table 3). Our long-term data set showed that changes in the frequency of extra-group paternity appeared to be driven by within-individual changes over time, rather than by differences between females in different situations, at least for the effect of female age, group age, and group size (see Supplementary Figure S3).

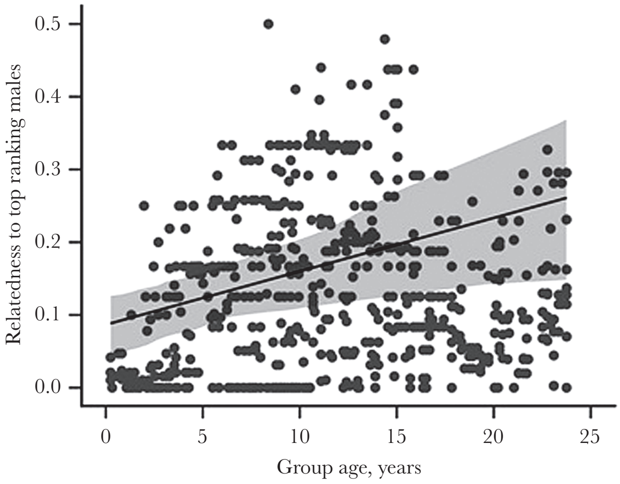

Figure 1
The relatedness of breeding females to the top-ranked males in their social group as a function of group age. The trend line shows the fitted model for females in their natal group and the shaded region shows the 95% CI.

It is possible that the selective death (prior to sampling) of inbred pups resulting from within-group matings could exaggerate or generate patterns of extra-group paternity relating to the age of the group and female. This could occur if older females or females in older groups are more likely to produce within-group inbred pups, and these pups are more likely to die prior to sampling, resulting in the appearance of an increase in the likelihood of EGP with the age of the female/group. To investigate whether older females or females in older groups were likely to be losing pups to inbreeding depression prior to genetic sampling, we investigated whether maternal litter size decreased with the age of the female or social group. We found that group age did not significantly affect litter size (β = −0.03, standard error [SE] = 0.04, $P = 0.45$) and that female age was positively correlated with litter size (β = 0.15, SE = 0.03, $P < 0.001$). This increase in litter size with female age indicates that our results are very unlikely to be caused by inbred pups dying before they are sampled.

Repeatability of extra-group paternity

We found little evidence that females displayed individual repeatability in their tendency to obtain extra-group paternity. The posterior mode of individual repeatability was 0.09 (95% CI = 0.00–0.21), indicating that only around 9% of the variance in extra- versus within-group paternity could be explained by female identity, after fixed effects had been accounted for. Although the mode of this posterior distribution was located away from zero, the 95% CI included zero (see Supplementary Material SM2), so there was insufficient evidence that repeatability was above zero. The equivalent modal repeatability for breeding event was 0.50 (95% CI = 0.30–0.67), indicating that females breeding at the same time within the same social group had similar paternity outcomes. By contrast, females in the same social group (breeding at any time point) were not alike more generally, as the modal social group repeatability was zero (95% CI = 0–0.23).

Consequences of extra-group paternity for offspring inbreeding levels

As expected, the relatedness between a female and the top-ranked males in her group was correlated with the inbreeding coefficient of her offspring (Figure 3). However, extra-group paternity successfully avoided inbreeding as indicated by a significant interaction between relatedness and extra-group breeding, whereby the

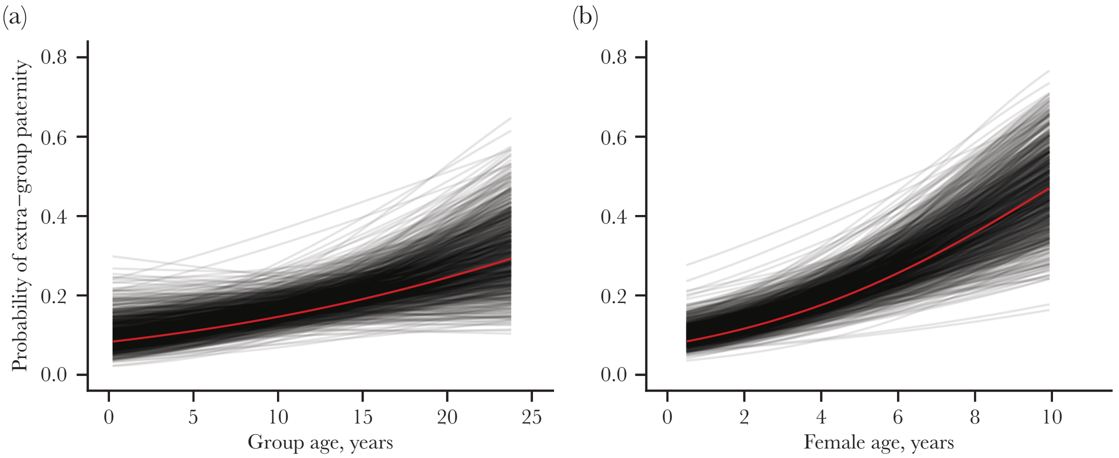

Figure 2
The probability of extra-group paternity as a function of (a) age of the social group and (b) age of the female. The red trend lines show the fitted model based on the posterior mean of all coefficients for females in their natal group with all explanatory variables fixed to their average except for that displayed on the *x* axis. Each pale gray line represents a single draw from the posterior distribution of fixed-effect coefficients.

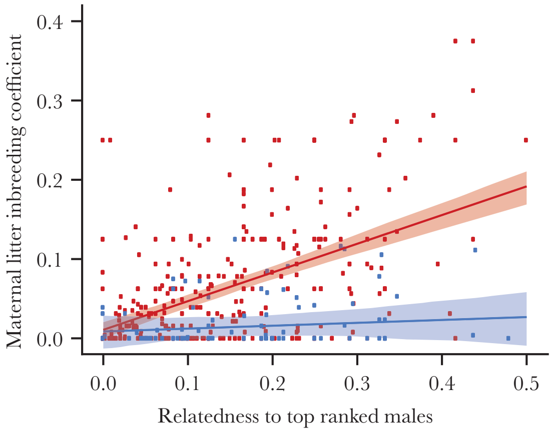

Figure 3
The average inbreeding coefficient of a maternal litter as a function of the breeding female's relatedness to the top-ranked males in her social group and whether the maternal litter resulted from within-group (dark red) or extra-group paternity (light blue). Trend lines show the fitted models and the shaded regions show the 95% CIs.

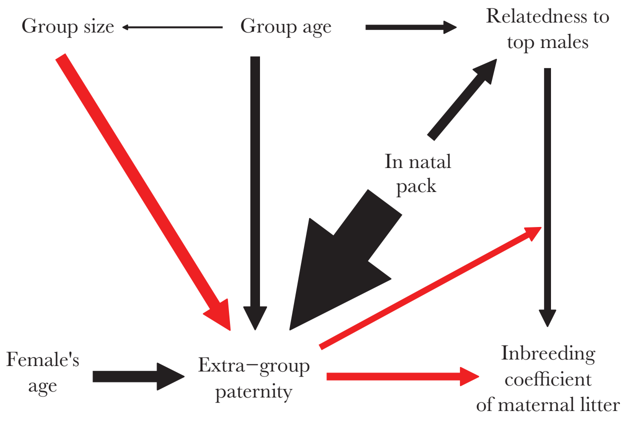

Figure 4
Path diagram representing the piecewise structural equation model. Arrows represent relationships between variables, black indicating positive effects and red indicating negative effects. The width of each arrow is proportional to the magnitude of the corresponding coefficient. Arrows directed to other arrows represent interactions.

relatedness between a female and the top males in her group had no impact on inbreeding when the female mated with an extra-group male (relatedness ß = 0.55, extra-group paternity ß = −0.61, interaction ß = −0.49, $P < 0.001$; Figure 3; Table 3). The distribution of f_i violated the assumption of normality as it was bounded at zero. However, analyses using standardized multilocus heterozygosity, a genetic marker-based measure of inbreeding, were qualitatively similar, which indicates that our results are robust to this violation (see Supplementary Material SM4). Despite high levels of inbreeding among within-group sired pups, only 18% (121/662) of maternal litters contained at least one pup with an extra-group father.

Combining our models into a single structural equation model

We created a structural equation model, which incorporated all significant effects from models i to iv (Table 3). The SEM (visualized in Figure 4) allowed us to classify the relationships between observed variables as direct or indirect and to observe the flow of causality through the system. The SEM demonstrated that the size and age of the social group, the age of the female, and whether she had dispersed from her natal group, had indirect (but not direct) effects on pup inbreeding coefficients. These indirect effects were generated through the impact of these variables on the occurrence of extra-group paternity. Female dispersal also impacted pup inbreeding coefficients indirectly through decreasing the relatedness between the female and the top-ranking males in her group. The relatedness between the female and top-ranking males had a direct impact on the inbreeding coefficients of pups, but interacted with extra-group paternity, such that relatedness only influenced the level of inbreeding of pups sired by within-group males.

In a piecewise SEM, variables with no path specified between them are assumed to be independent after accounting for the paths that are specified. All of these "independence claims" were assessed using tests of directed separation. For linear mixed models, the degrees of freedom (df) for these tests were calculated using the Kenward–Rogers approximation for the df in an *F*-test (Lefcheck 2016). The independence claim between extra-group paternity and relatedness was fitted using a GLMM and the significance was calculated using MCMCglmm (Hadfield 2010) as described in Supplementary Material SM2, with relatedness to top-ranking males included as an additional fixed effect. The results of these tests of directed separation are shown in Supplementary Table S1. As all of the independence claims were nonsignificant, we conclude that all meaningful relationships between the variables included in our data set are described by the paths specified in our piecewise SEM (see Tables 2 and 3).

The *P*-values of the independence claims were used to calculate a global goodness-of-fit measure, which indicated that all of the important relationships among variables in our data set were included in our piecewise SEM (Fisher's $C = 22.38$, df = 18, $P = 0.215$) and, therefore, that our specified relationships accurately represent the main relationships observed in our data (Lefcheck 2016). Although we cannot exclude the possibility that unmeasured variables may play a role in generating correlations among variables included in our model, we have no reason to believe that such unmeasured variables are important in our system based on an extensive body of prior knowledge.

The models that made up our piecewise SEM had considerable explanatory power, although, for some models, this was principally due to random effects (Table 4). The conditional R^2 was very high (~1) for our model of group size because females within groups gave birth on the same night and so group size was identical for all females contributing to a given communal litter. The conditional R^2 for female relatedness to top-ranking males was also very high (0.92) because a females' relatedness to the oldest males only changed when one of them died or she moved to another social group.

DISCUSSION

We show that inbreeding avoidance via extra-group paternity is a dynamic process that is influenced by a complex web of social, demographic, and individual factors. Banded mongooses display a plastic response in their paternity outcomes and show little evidence for individual repeatability; females appeared to adaptively adjust their extra-group mating levels according to within-group inbreeding risk. Interestingly, extra-group paternity patterns did not vary directly in response to female relatedness to within-group males. Instead, females were more likely to mate with extra-group males when individual and social factors indicated a high risk of inbreeding within their group. For example, extra-group paternity was more common when females were in their natal group and/or in older groups, both of which were associated with increased relatedness to breeding males. Although extra-group paternity was more common in older groups, it is unlikely that individuals born into a certain group are able to directly gauge the age of that group as those groups will always have formed prior to their birth. This may explain why female age was also predictive of extra-group paternity; the age of the natal group increases throughout the female's lifespan and, hence, may be used as a proxy for patterns of relatedness. However, other factors may contribute to this pattern as older females may be more experienced at mating extra-group, as has been shown in reed buntings *Emberiza schoeniclus* (Bouwman and Komdeur 2005). In banded mongooses, older females are preferred by high-ranking within-group males, potentially due to their higher fecundity (Nichols et al. 2010) and so older females may also be preferred by males seeking extra-group paternity.

Proxies are commonly used as cues for mating decisions, but their effectiveness depends on the strength and consistency of their relationship with the trait in question (Bonamour et al. 2019). In some species, there is evidence that individuals respond directly to relatedness, for example, through phenotype matching (Thunken et al. 2007; Leclaire et al. 2013). If banded mongooses responded directly to relatedness, instead of relying on relatively weakly correlated proxies, inbreeding avoidance could be considerably more effective. However, the degree to which banded mongooses are able to discriminate between individuals based directly on relatedness is currently unclear. Banded mongooses have been shown to vary in their response to the scent of group members based on relatedness (Mitchell et al. 2018), are more likely to evict close relatives from the social group during periods of within-group conflict (Thompson, Cant, et al. 2017), and are less likely to reproduce with closely related group members (Sanderson et al. 2015). This suggests that some degree of assessment of the relatedness of group members may be possible. However, this may be based on social or behavioral proxies of relatedness rather than on more direct measures of relatedness, such as phenotype matching (Mitchell et al. 2018). It is, therefore, possible that banded mongooses are unable to assess the relatedness of group members directly and so are constrained to rely on relatively weakly correlated proxies. Mechanisms of kin recognition in banded mongooses, including the reliability of proxies of relatedness, will be the subject of future study.

When banded mongoose females reproduced with extra-group males, they successfully avoided inbreeding as their pups had an average inbreeding coefficient of 0. By contrast, when females reproduced within their social group, 20% of maternal litters were at least moderately inbred (i.e., $f_I \geq 0.125$; the equivalent of breeding between half-siblings). Although extra-group mating was an effective way to avoid inbreeding, it was not always used; when relatedness between a female and within-group males was over 0.25, only 22% of maternal litters contained pups fathered by extra-group males. A high frequency of inbreeding likely indicates that mating

Table 4

Marginal and conditional R^2 values indicating the proportion of variance in the response terms explained by the fixed or fixed and random effects, respectively. Family is the chosen distribution underlying the model and link describes the chosen link function. For the binomial model, R^2 values were calculated using the theoretical variance associated with the link function

Response	Family	Link	Marginal R^2	Conditional R^2
Group size	Gaussian	Identity	0.02	1.00
Relatedness to top-ranked males	Gaussian	Identity	0.17	0.92
Extra-group paternity	Binomial	Logit	0.14	0.65
Maternal litter inbreeding coefficient	Gaussian	Identity	0.32	0.49

behavior is shaped in part by constraints and/or selection pressures other than inbreeding depression.

One major pressure likely to shape mating behavior is the cost of inbreeding avoidance behaviors, which will oppose their evolution (Kokko and Ots 2006; Duthie and Reid 2016). In the banded mongoose, mating with extra-group males appears to be costly as it occurs during aggressive interactions between groups (Nichols et al. 2015). Pups and adults are often injured during these interactions and 15% of deaths with a known cause can be attributed to these fights (Nichols et al. 2015). Although adult females are rarely killed during intergroup interactions, females may lose existing pups and their group may lose territory as a consequence of fights (Thompson, Marshall, et al. 2017). Within- versus extra-group mating, therefore, likely represent a trade-off between the risk of inbreeding and the risk of violence. Risk has been shown to influence paternity outcomes in other species, for example, the presence of a predator model near the nest site increases extrapair paternity in blue tits *Cyanistes caeruleus*, possibly by disrupting within-pair matings (Santema et al. 2020).

Similarly, the availability of extra-group mating opportunities may act as a constraint against inbreeding avoidance. On average, each group has an observed intergroup interaction with a rival group every 1.3 months (Nichols et al. 2015). This may not be sufficient to guarantee the availability of extra-group mating opportunities for females that are highly related to their group. The likelihood of an intergroup interaction occurring increases in older groups and when females are in estrus, suggesting that females and/or males may strategically engage in these interactions to gain outbreeding opportunities (Nichols et al. 2015). This would explain our finding that extra-group paternity increases in older groups. However, even in the oldest groups, where inbreeding is most likely, there is on average only one intergroup interaction observed during the estrus period (Nichols et al. 2015), which may be too short or chaotic for all females to gain extra-group mating opportunities. Furthermore, it is possible that within-group males may attempt to prevent extra-group males from accessing females during fights to avoid losing paternity. The limited opportunities for extra-group mating and the stochasticity of intergroup interactions are likely to explain the high level of repeatability of extra-group paternity within females cobreeding in the same group at the same time (mode 0.50, 95% CI = 0.30–0.67).

Although the cost of inbreeding avoidance appears to have shaped the evolution of breeding behavior in the banded mongoose, it is less clear how important this cost is across species. Although inbreeding depression has been investigated in a variety of species (Crnokrak and Roff 1999; Keller and Waller 2002), the costs of inbreeding avoidance have been studied less often (Forstmeier et al. 2014) despite theoretical findings implying that they should be important in determining the evolution of inbreeding behavior (Kokko and Ots 2006; Duthie and Reid 2016). Nevertheless, in the context of extra-group or extrapair paternity, studies have shown that extrapair paternity can reduce paternal care from cuckolded males (Suter et al. 2009; García-Navas et al. 2013), incite increased aggression from a female's social partner (McKibbin et al. 2011; García-Navas et al. 2013; Hoi et al. 2013), and put existing offspring at risk if they are left unattended while seeking an extrapair mate (Hoffman et al. 2007). Such costs may explain why fewer than half of the studies supported adaptive extra-group paternity in a meta-analysis (Akçay and Roughgarden 2007). Furthermore, extra-group paternity is not always associated with inbreeding avoidance and, in some species, extrapair mates are more closely related to females than their within-pair mates (Kleven et al. 2005; Wang and Lu 2011; Harrison et al. 2013). It is unclear why we find such differences between species but it is possible that broad-scale patterns relating to extra-group mating are difficult to detect as inbreeding avoidance may only be important in the subset of species where inbreeding is likely to occur when females mate within their social system (Nichols 2017), as is the case in the banded mongoose.

Identifying variables that influence individual reproductive decisions is important for understanding the factors that shape the evolution of mating behavior more generally. High levels of within-group relatedness have been reported to encourage extra-group paternity in other species, particularly when populations are viscous, leading to high average local relatedness (Cohas et al. 2006; Annavi et al. 2014). In a small number of species (e.g., resident killer whales *Orcinus orca* and long-finned pilot whales *Globicephala melas*), all paternity is extra-group. Here, both sexes are philopatric and groups contain closely related potential mates (Bigg et al. 1990; Amos et al. 1991; Pilot et al. 2010). The lack of plasticity in extra-group paternity in these toothed whales may be due to their method of forming new groups, which is thought to occur via the budding of entire matrilines (Bigg et al. 1990). As close relatives form a new group together, relatedness between the sexes remains high (Croft et al. 2017) and, hence, the relative benefits of extra- versus within-group paternity are not expected to change over time. In contrast, male and female breeders in newly formed banded mongoose groups are always unrelated (Nichols et al. 2012), which leads to marked temporal variation in the relative benefits of extra-group paternity. These patterns imply that the likelihood of encountering relatives is an important determinant of extra-group paternity across species (Jamieson et al. 2009).

We found little evidence of individual repeatability in the tendency for females to reproduce with extra-group males (mode 0.09, 95% confidence interval [CI] = 0.00–0.21). The values of repeatability estimates are difficult to compare across studies due to their reliance on the fixed effects included in the models (Wilson 2018) and so should be interpreted with caution. Nevertheless, higher individual repeatabilities have been found in other species. For example, the Mandarte island song sparrow, another species where inbreeding occurs regularly, has significant repeatability of extrapair paternity (repeatability = 0.19; Reid et al. 2011). Repeatability of this trait was also significant in tree swallows (repeatability = 0.83; Whittingham et al. 2006). The high repeatability in tree swallows could be because broods were compared within a single breeding season, whereas, in our study and in the song sparrow, broods/litters were compared across breeding seasons over several years, and repeatability often declines over time (Bell et al. 2009). However, a meta-analysis of repeatability of behavior found that mating behavior (but not the choice of specific mates) showed the highest levels of repeatability among the behaviors investigated (Bell et al. 2009). The banded mongoose may, therefore, be unusual in its low level of repeatability of extra-group paternity.

Low individual repeatability of extra-group paternity in banded mongooses could be due to constraints against females seeking extra-group paternity. For example, opportunities for extra-group mating are likely limited due to the rarity of intergroup interactions. This idea is supported by the high level of repeatability of extra-group paternity within cobreeding females, who are likely to have had similar exposure to extra-group males during intergroup interactions. Male attempts to guard estrus females may also constrain female mating behavior. Guarding males do not have complete control of females as they appear unable to force matings, and females often refuse matings, especially during their most fertile days of estrus (Cant 2000). Nevertheless, parentage outcomes are inevitably influenced by both male and female behavior, and male mating behavior has been invoked to explain patterns of extra-group paternity in cooperatively breeding white-browed sparrow weavers *Plocepasser mahali* (Harrison et al. 2013) and pied flycatchers *Ficedula hypoleuca* (Plaza et al. 2019). Alternatively, low repeatability could be due to a lack of selection for repeatability of extra-group paternity. This may occur if there are few benefits to individuals within groups developing their own micro-niches and displaying high individual repeatability (Sheppard et al. 2018).

CONCLUSION

We have shown that extra-group paternity is moderated by a complex network of social and individual factors, many of which appear to be associated with inbreeding risk. Our banded mongoose population displayed a high level of plasticity in breeding behavior, adaptively adjusting extra-group paternity in accordance with this risk and displaying low levels of individual repeatability of this trait across the lifespan. It is possible that plasticity in extra-group paternity is particularly advantageous in banded mongooses due to high temporal variation in inbreeding risk. Additionally, this form of inbreeding avoidance (and individual repeatability in it) may itself be highly constrained in the banded mongoose due to limited opportunities to engage in outbreeding and high potential costs of doing so. This may explain why banded mongooses display relatively low levels of individual-level repeatability in extra-group paternity in comparison to other species (Bell et al. 2009).

SUPPLEMENTARY MATERIAL

Supplementary data are available at *Behavioral Ecology* online.

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Data availability: Analyses reported in this article can be reproduced using the data provided by Wells et al. (2020).

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