

Mating strategies in dominant meerkats: evidence for extra-pair paternity in relation to genetic relatedness between pair mates

S. LECLAIRE*†, J. F. NIELSEN‡§, S. P. SHARP*† & T. H. CLUTTON-BROCK*†

*Department of Zoology, University of Cambridge, Cambridge, UK

†Kalahari Meerkat Project, Kuruman River Reserve, Northern Cape, South Africa

‡Institute of Evolutionary Biology, School of Biological Sciences, University of Edinburgh, Edinburgh, UK

§Institute of Zoology, Zoological Society of London, London, UK

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Abstract

Rates of extra-pair paternity (EPP) have frequently been associated with genetic relatedness between social mates in socially monogamous birds. However, evidence is limited in mammals. Here, we investigate whether dominant females use divorce or extra-pair paternity as a strategy to avoid the negative effects of inbreeding when paired with a related male in meerkats *Suricata suricatta*, a species where inbreeding depression is evident for several traits. We show that dominant breeding pairs seldom divorce, but that rates of EPP are associated with genetic similarity between mates. Although extra-pair males are no more distantly related to the female than social males, they are more heterozygous. Nevertheless, extra-pair pups are not more heterozygous than within-pair pups. Whether females benefit from EPP in terms of increased fitness of the offspring, such as enhanced survival or growth, requires further investigations.

Introduction

Inbreeding occurs when relatives mate and can lead to a decline in offspring fitness, known as inbreeding depression (Lynch & Walsh, 1998). When inbreeding depression is substantial, theory predicts the evolution of inbreeding avoidance mechanisms (Charlesworth & Charlesworth, 1987; Pusey & Wolf, 1996), including dispersal and active choice of unrelated mates (Charlesworth & Charlesworth, 1987). Mate choice is, however, a competitive process that takes place over a limited time, and individuals may often be paired to a suboptimal partner. Therefore, alternative mating strategies may have evolved to modify initial mate choice and adjust mate acquisition (Blomqvist *et al.*, 2002; Dubois & Cézilly, 2002), including extra-pair copulation (EPC) and mate change (i.e. divorce) (McNamara & Forslund, 1996; Kempenaers *et al.*, 1997; Blomqvist *et al.*, 2002).

In birds, rates of EPC and, to a smaller extent, divorce have often been shown to be related to genetic

relatedness between pair mates (Kempenaers *et al.*, 1998; Blomqvist *et al.*, 2002; Freeman-Gallant *et al.*, 2003; Van de Castele *et al.*, 2003; Tarvin *et al.*, 2005). In mammals, although some studies have shown that nonmonogamous females preferentially choose unrelated partners (Hoffman *et al.*, 2007), very few studies have investigated the relationship between within-pair relatedness and rates of EPC in socially monogamous species (Cohas *et al.*, 2008; Driller *et al.*, 2009). To the best of our knowledge, studies are limited to Alpine marmots *Marmota marmota* and Lariang tarsiers *Tarsius lariang*, where extra-pair young (EPY) are more frequent when pairs exhibit close relationships (Cohas *et al.*, 2008; Driller *et al.*, 2009).

In this study, we investigated whether rates of EPY and divorce are associated with genetic relatedness within pairs in meerkats *Suricata suricatta* where dominants monopolize breeding (Griffin *et al.*, 2003; Spong *et al.*, 2008). Groups of meerkats consist of a dominant breeding pair and their offspring, which remain in their natal group past sexual maturity and help rear subsequent litters. Resident breeding males are usually immigrants, but individuals often disperse over short distances (Doolan & Macdonald, 1996), so that the probability of encounters between closely related

Correspondence: Sarah Leclaire, Université Paris 6, Laboratoire Ecologie et Evolution, 7 quai Saint-Bernard 75252 Paris Cedex 05, France.
Tel.: +33 (0)1 44 27 32 94; fax: +33 (0)1 44 27 35 16;
e-mail: sarah.leclaire@free.fr

individuals of opposite sexes can be high. Accordingly, a number of breeding events between related individuals have been detected in our study population (Nielsen *et al.*, 2012). Inbreeding depression is evident for several early life traits, including mass at emergence and juvenile survival (Nielsen *et al.*, 2012), and would be expected to favour the evolution of increased rates of EPC or divorce where pairs are related. We consequently investigated whether causes of mate change, length of pair tenure and frequency of EPY by females varied with genetic relatedness between dominant mates, whether extra-pair males were less related to females and more heterozygous than within-pair males and whether EPY were more heterozygous than within-pair young (WPY).

Methods

Study site

This study was conducted on a wild population of meerkats at the Kalahari Meerkat Project in the Kuru-man River Reserve (26°58'S, 21°49'E) on ranchland in the South African Kalahari desert. Data were collected from October 1993 to December 2010. Around 2000 individuals living in more than 40 social groups were closely monitored, most of whom were habituated to observation from <2 m. In addition, more than 95% of individuals were trained to climb onto an electronic balance and could be weighed most mornings before they went foraging (Russell *et al.*, 2002). Further details of the habitat and climate of the study system are provided elsewhere (Clutton-Brock *et al.*, 1999; Russell *et al.*, 2002). Most individuals were marked with subcutaneous transponder chips, and all were recognizable in the field by unique dye marks applied to their fur. Each group was visited approximately once every 3 days to record all key life-history events and changes in group composition, including births, deaths, eviction of subordinate females from the group and changes in pregnancy or dominance status. Pregnancy in meerkats lasts for approximately 70 days and could be identified at about 30 days by swelling of the abdomen and an increase in body mass. Birth dates could be accurately determined by a sudden change in the female's weight and body shape. As there were rarely behavioural signs of oestrous, conception dates were estimated by backdating 70 days from birth (Russell *et al.*, 2002). Following a change in dominance, or after formation of a new group, the identity of the new dominant could be determined through behavioural observations of dominance assertion (Kutsukake & Clutton-Brock, 2006). Changes in dominance, often preceded by a short period (hours to days) of intense hostility, were accompanied by dramatic changes in behaviour in the contesting individuals and hence were immediately recognizable.

Individuals were recorded as having assumed the dominant position if all other adults in the group responded submissively to dominance assertion behaviours for at least 1 week.

All research protocols were approved by the University of Pretoria Ethics committee and conform to the Association for the Study of Animal Behaviour guidelines for the use of animals in research.

Dominant pair tenure

Male meerkats may acquire the dominant position in two ways. First, they may occasionally inherit the dominant position within their natal group, generally after the death of the dominant male. As these philopatric dominant males are usually related to all within-group females, they never breed within the group, and their breeding opportunities are restricted to extra-group females that they may encounter during extra-territorial forays (Young *et al.*, 2007). Second, after dispersal at the age of 2–4, males may acquire a dominant breeding position by defeating the dominant male after integrating a new group or by forming a new group with a coalition of unfamiliar females. Females may also acquire the dominant position by inheriting it within their natal group or by forming a new group with unfamiliar males after forced dispersal at the age of 2–4 (Hodge *et al.*, 2008). Pairs that do not breed together, that is, pairs with a philopatric dominant male, or pairs in which the female has just inherited the dominant position in her natal group and in which the dominant male is thus potentially her father were excluded from our study ($n = 48$ pairs excluded). Over the course of this study, we obtained data on 117 dominant breeding pairs formed by individuals that were not born in the same group and had no known contact early in life. We excluded dominant pairs formed of founder individuals, as the status of the dominant male (philopatric or immigrant) was unknown ($n = 7$ pairs). Furthermore, to be sure to retain only true dominant breeding pairs, we excluded dominance tenures shorter than a month ($n = 18$ pairs).

For each dominant pair, we determined its length of tenure as the number of days the male and female behaved as dominant together. Seven pairs that disrupted and re-paired at a later stage (mean: 12 months later; range: 2–35 months) were excluded from the analyses.

For each dominant pair, we determined the cause of mate change (i.e. end of tenure). Mate change can be due to (i) the death of one member when this individual is found dead during its dominance tenure, (ii) the displacement of one member when another individual challenges it and becomes the new dominant, (iii) emigration when one member is seen roving in the study site after leaving the group where it was dominant and (iv) an unknown reason when either member disappears from the study site.

Genetic analyses

To date, the most precise and reliable estimates of individual relatedness and inbreeding appear to be those derived from accurate genetically validated multigenerational pedigrees (Pemberton, 2004, 2008; Taylor *et al.*, 2010). In contrast, estimates of genome-wide heterozygosity that are based on only a small panel of microsatellite markers are often only weakly correlated with inbreeding coefficient calculated from a pedigree (Balloux *et al.*, 2004) and have been suggested to be imprecise because of sampling noise. Furthermore, the use of microsatellite loci to determine both paternity and individual heterozygosity may produce biases in terms of an increase in results supporting the idea that heterozygous males have an advantage in siring extra-pair offspring (Wetzel & Westneat, 2009). However, reconstructing pedigrees for wild populations can be difficult (Pemberton, 2008), and it has been suggested that marker-based estimates may be more accurate when only shallow pedigrees are available (Csillery *et al.*, 2006). In our study, 43% of dominant males come from nonstudied groups, and as for classical pedigree construction, they were assumed as unrelated and outbred. It is therefore very likely that pedigree data are not accurate for many of the studied individuals. Pedigree and marker-based data were thus both used in our study, but the results obtained with microsatellites were emphasized in the presentation of the results.

We used two indices of pairwise relatedness: pedigree relatedness (R) and identity index (ID) based on genetic similarity at neutral markers (Mathieu *et al.*, 1990; Belkhir *et al.*, 2002). Full details on DNA extraction, genotyping and pedigree methods are described in Nielsen *et al.* (2012). In brief, DNA was extracted from tail tip samples and genotyped at up to 18 variable microsatellite loci. A combination of genetic data and behavioural records and two programs, MASTERBAYES v.2.47 (Hadfield *et al.*, 2006) and COLONY2 v.2.0.1.1 (Wang, 2004), was used to infer parentage for the whole population from the study's inception in 1993

until late 2011. Candidate fathers were any males alive in any group during the 2-week window surrounding conception (i.e. 63–77 days prior to pup birth), and for mixed maternity litters, candidate mothers were any females known to have given birth in the group at pup birth. The combined average parentage assignment confidence from both programs was 95.57% (minimum confidence interval: 80%), and the resulting categorical pedigree spanned eight generations. Founders and immigrants to the population were assumed to be unrelated. Based on the pedigree relationships, a matrix of pairwise coefficients of relatedness (R) (i.e. the percentage of genes shared by common descent) was calculated for the whole population in PEDANTICS (Morrissey & Wilson, 2010). In our study, R ranged from 0 to 0.375 and averaged 0.09 (Fig. 1a), whereas in the whole population, R ranged from 0 and 0.75 and averaged 0.05.

ID was calculated using the software IDENTIX (Belkhir *et al.*, 2002) from data on the 18 microsatellites (Nielsen *et al.*, 2012). ID has been validated as a good estimator of the consanguinity of offspring in cases where identical alleles are likely to be identical by descent, something especially relevant when we are interested in the fitness consequences of consanguineous mating (Belkhir *et al.*, 2002). ID ranges theoretically from 0 (all loci are expected to be heterozygous in the offspring) to 1 (all loci are expected to be homozygous in the offspring). In our study, ID ranged from 0.24 to 0.70 and averaged 0.42 (Fig. 1b), whereas in the whole population, ID ranged from 0.02 to 1.00 and averaged 0.41. ID was correlated with R (in dominant individuals: Spearman's correlation: $r = 0.56$, $P < 0.0001$; in the whole population: Mantel test with 5000 permutations: $P = 0.0002$).

To estimate the genetic diversity of extra-pair and within-pair males and offspring, we used standardized heterozygosity (Hst) measured at 18 microsatellites (Nielsen *et al.*, 2012) and inbreeding coefficient based on pedigree relationships (F). Hst was calculated using the software NAUSICAA (Mulard *et al.*, 2009), and F was calculated as described in Nielsen *et al.* (2012). In our

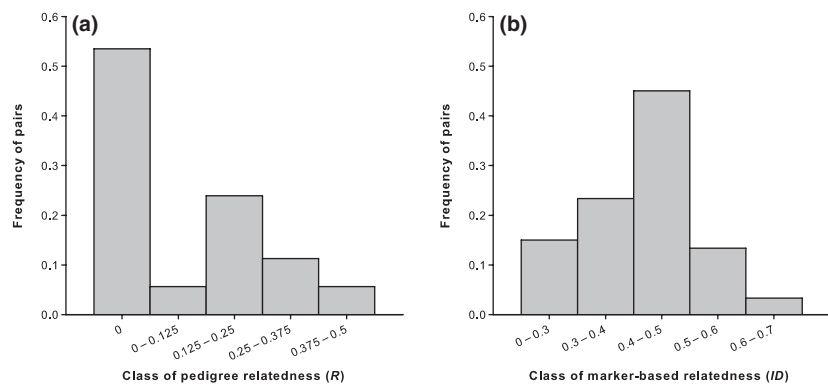


Fig. 1 Distribution of (a) pedigree relatedness (R) and (b) identity index (ID) in dominant breeding pairs.

study, *Hst* and *F* ranged from 0.31 to 0.96 and from 0 to 0.19, respectively, and averaged 0.69 and 0.03, respectively, whereas in the whole population, *Hst* and *F* ranged from 0.26 to 1.00 and from 0.00 to 0.22, respectively, and averaged 0.67 and 0.03, respectively. *Hst* was weakly correlated with *F* in the studied pups (Pearson's correlation: $r = -0.18$, $P < 0.0001$) and in the whole population (Pearson's correlation: $r = -0.14$, $P < 0.0001$). However, *Hst* was not correlated with *F* in cuckolds and cuckolders (Spearman's correlation: $r = -0.01$, $P = 0.94$), probably because we lacked accurate pedigree information for most of these males.

Statistical analyses

To test for a relationship between length of dominance tenure and pairwise relatedness, we used linear mixed models (LMM), with box-cox transformed length of tenure ($\lambda = 0.25$) as the dependent variable and pairwise relatedness as a fixed effect (*ID* or *R*). Weight, age at start of tenure and group size may affect survival and therefore the length of dominance tenure (Clutton-Brock *et al.*, 1999; Hodge *et al.*, 2008; Spong *et al.*, 2008). Female weight and age (in days) at start of tenure were thus included in the model (87% of females were regularly weighed and 93% of females had known age). Female weight was calculated as the mean morning weight (in grams) during the tenure excluding measurements made during pregnancy. Equivalent values for males could not be fitted as 42% of dominant males came from nonhabituated groups, and therefore, they could not be weighed regularly and were of unknown age. Group size included all individuals present in the group and was calculated as the mean daily group size during tenure. To avoid pseudoreplication, female and group identities were included in the model as random factors.

To test for a relationship between the proportion of EPY and pairwise relatedness, we used a generalized linear mixed model (GLMM) with binomial error structure. The number of EPY mothered by the dominant female was fitted as the response term, and the total number of pups with paternity assigned and mothered by the dominant female during the tenure was fitted as the binomial total. To only retain pups potentially sired by the dominant male, we focused on litters born at least 75 days after the start of pair tenure. Pairwise relatedness, group size, female weight and female age were included as fixed effects. Female and group identities were included as random factors.

To compare, for each pair, the heterozygosity of EPY and WPY, we used LMMs with within-group centring (Van de Pol & Wright, 2009). Centred average *Hst* was the dependent variable, pup status (EPY or WPY) was the fixed effect, and female identity and pair identity nested in female identity were the random factors. To compare the inbreeding coefficient of EPY and WPY for

each pair, we used a Wilcoxon signed rank sum tests as inbreeding coefficients were not normally distributed.

To compare, for each litter, the heterozygosity (*Hst*) of extra-pair (EP) and within-pair (WP) males and the relatedness (*ID*) between the female and EP and WP males, we used LMMs with within-group centring (Van de Pol & Wright, 2009). Centred *ID* or *Hst* was the dependent factor, male status (EP or WP male) was the fixed factor, and female identity and litter identity nested in female identity were the random factors. Averaged values of EP males were obtained in litters with more than one identified EP sire ($n = 2$ L). To compare, for each litter, the inbreeding coefficient values (*F*) of EP and WP males and the pedigree relatedness (*R*) between the female and EP and WP males, we used Wilcoxon signed rank sum tests as *R* and *F* were not normally distributed.

All analyses were conducted within SAS version 9.1. All predictors were centred and standardized (Schieletzeth, 2010). Prior to model selection, collinearity between all explanatory variables was assessed by calculating variance inflation factors (VIFs) (Zuur *et al.*, 2009). All variables were included in the initial models because pairwise correlations were weak ($r < 0.5$ in all cases) and no variable had a VIF of >2 . All biologically meaningful first-order interactions were fitted. Model selection was performed by backward dropping nonsignificant terms (unless they appeared in higher-order interaction terms) using a stepwise elimination procedure. When the minimal model was obtained, each removed term was then put back into the minimal model to assess the level of nonsignificance and to ensure that significant terms had not been inappropriately dropped. The final model was validated by plotting the distribution of the residuals, residuals vs. fitted values and residuals vs. each of the covariates. Overdispersion was assessed using variance of Pearson's residuals (Littell *et al.*, 2006). We used 2-tailed type-3 tests for fixed effects with a significance level set to $\alpha = 0.05$, and the Satterthwaite correction for the calculation of fixed effects degrees of freedom (Littell *et al.*, 2006). Values are expressed as mean \pm SE throughout.

Results

Mate change and length of pair tenure

Dominant breeding pairs had a mean tenure of 402 ± 42 days (range: 33–1869 days), and divorce (i.e. mate changes when both mates were known to be alive) was only observed in four cases (4% of mate changes). Most mate changes were caused by the death of females or males (see Table 1).

Length of pair tenure was negatively related to identity index (*ID*) (Table 2 and Fig. 2) and pedigree relatedness (*R*; $F_{1,57} = 5.18$, $P = 0.027$, Table S1 and Fig. S1 in Supporting Information), but pairwise relatedness did

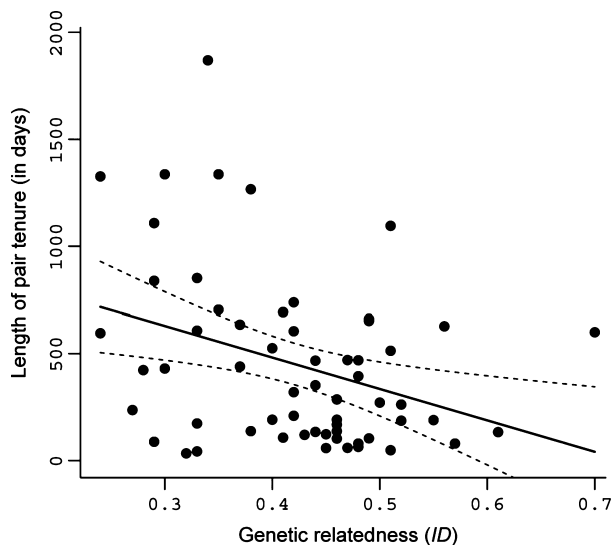
Table 1 Percentage of mate changes due to the death, displacement, or emigration of either mate or to unknown reason.

Percentage	Death, %	Displacement, %	Emigration, %	Unknown, %
Female (Total: 40%)	67	12	3	18
Male (Total: 60%)	47	31	6	16

Table 2 Linear mixed model testing for an effect of pairwise relatedness on duration of tenure. Sample sizes vary between the analyses because of missing values for some pairs.

Random effects	Length of pair tenure		
	Estimate ± SE	Wald Z	P
Female identity	0		
Group	0.79 ± 2.03	0.39	0.35
Fixed effects	Estimates ± SE	F _{df}	P
Genetic relatedness (<i>ID</i>)	-1.50 ± 0.72	4.33 _{1,50}	0.043
Group size	0.85 ± 0.55	1.82 _{1,55}	0.18
Female age	-1.93 ± 2.19	0.77 _{1,53}	0.38
Female weight	-0.35 ± 0.60	0.33 _{1,49}	0.57

Terms retained in the final model are highlighted in bold.

**Fig. 2** Duration of pair tenure according to pairwise relatedness (*ID*) in dominant breeding pairs. Lines show GLM prediction and 95% confidence bands.

not differ between pairs where mate change was caused by death, displacement or emigration of either mate (*ID*: ANOVA: $F_{2,49} = 0.56$, $P = 0.58$; death: 0.42 ± 0.02 ; displacement: 0.41 ± 0.03 ; and emigration:

0.48 ± 0.02 ; *R*: ANOVA on ranks: $H_2 = 5.50$, $P = 0.06$; death: 0.08 ± 0.02 ; displacement: 0.16 ± 0.04 ; and emigration: 0.02 ± 0.02).

Extra-pair young

Of the 537 pups produced by dominant females, 11.5% of pups ($n = 24$ litters) were sired by extra-pair (EP) males. The proportion of EPY produced by dominant females was higher in more related pairs (*ID*: Table 3 and Fig. 3; *R*: $F_{1,36} = 4.30$, $P = 0.045$, Table S2 and Fig. S2 in Supporting information) and in smaller groups (Tables 3 and S2).

The standardized heterozygosity (*Hst*) and the inbreeding coefficient (*F*) of pups ranged from 0.31 to 0.96 (mean: 0.70 ± 0.00) and from 0 to 0.19 (mean: 0.03 ± 0.00 ; 64% of pups had $F = 0$), respectively. In breeding pairs with EPY, the mean heterozygosity and inbreeding coefficient of EPY were not different from the mean heterozygosity and inbreeding coefficient of WPY (difference in *Hst* between WPY and EPY: 0.034 ± 0.046 ; $F_{1,20} = 0.69$, $P = 0.42$; difference in *F* between WPY and EPY: 0.015 ± 0.011 ; $W = 2.5$, $P = 0.63$). Results were similar when focusing on EPY born from within-group males only or on EPY born from outside-group males only.

Extra-pair vs. within-pair males

55% of extra-pair (EP) fathers were members of the same group as the dominant female and the dominant male, but none were born into the group, and all had immigrated into the group at the same time as the dominant male. These EP males were thus closely related to the dominant male (*ID* and *R* between within-group EP males and WPY: 0.51 ± 0.03 and 0.32 ± 0.05). The remaining EP fathers were males

Table 3 Generalized linear mixed model testing for an effect of pairwise relatedness (*ID*) on the proportion of EPY. Sample sizes vary between the analyses because of missing values for some pairs.

Random effects	Number of EPY/total number of young		
	Estimate ± SE	Wald Z	P
Female identity	0.00		
Group	3.34 ± 1.92	1.74	0.04
Fixed effects	Estimates ± SE	F _{df}	P
Genetic relatedness (<i>ID</i>)	1.19 ± 0.35	11.89 _{1,29}	0.002
Group size	-1.26 ± 0.41	9.42 _{1,29}	0.005
Female age	0.09 ± 0.34	0.07 _{1,27}	0.79
Female weight	-0.02 ± 0.49	0.00 _{1,28}	0.96

Fixed terms retained in the final model are highlighted in bold.

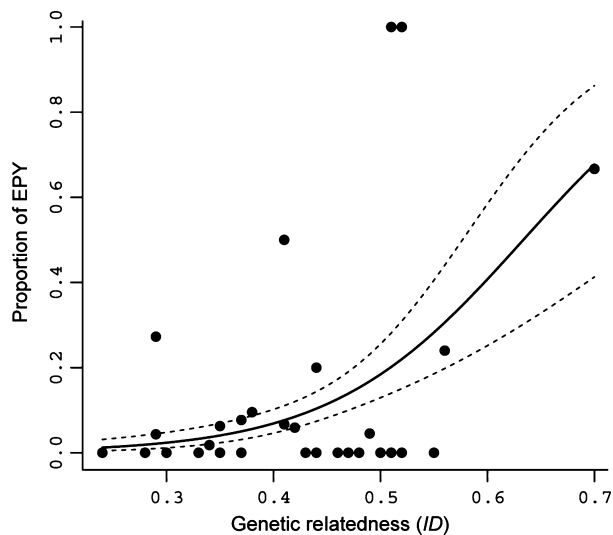


Fig. 3 Proportion of EPY per dominant breeding pair (i.e. number of EPY/total number of young) according to pairwise relatedness (ID). Lines show GLM prediction for average daily group size and 95% confidence bands.

from outside groups and were less related to the dominant male (ID and R between extra-group EP males and WP males: 0.32 ± 0.09 and 0.04 ± 0.03). EP males were no less related to the female than WP males (differences in ID between WP and EP males: -0.02 ± 0.03 , $F_{1,30} = 1.19$, $P = 0.28$, Fig. 4a; difference in R between WP and EP males: -0.02 ± 0.04 , $W = 0.00$, $P = 1.00$).

Hst and F of EP and WP males ranged from 0.54 to 0.95 (mean: 0.72 ± 0.02) and from 0 to 0.125 (mean: 0.01 ± 0.00 ; 76% of males had $F = 0$), respectively. EP males were more heterozygous than WP males (differences in Hst between WP and EP males: -0.11 ± 0.04 ; $F_{1,30} = 15.22$, $P = 0.0005$; Fig. 4b), but they were not more outbred (differences in F between WP and EP males: -0.004 ± 0.004 , $W = 6$, $P = 0.38$).

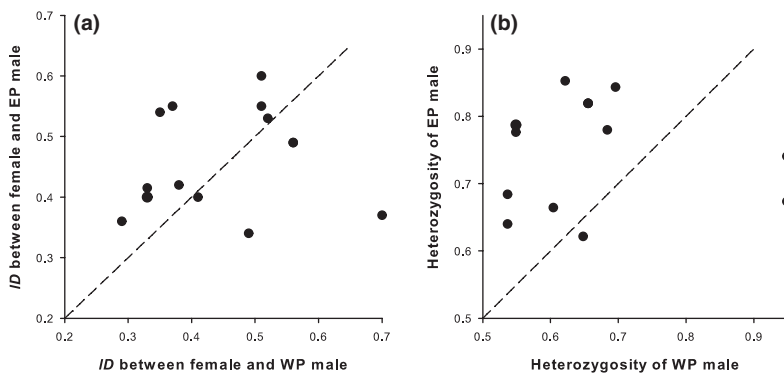


Fig. 4 Comparison of (a) genetic relatedness to female (ID) between EP and WP males and (b) heterozygosity (Hst). The size of the dot is proportional to the number of litters ($n = 16 L$). The dashed line indicates identical values in WP and EP males.

Discussion

In meerkats, only dominants generally breed successfully (Griffin *et al.*, 2003), and dispersal is costly (Clutton-Brock *et al.*, 1999; Young *et al.*, 2005). The benefits of being dominant and maintaining the dominance position are therefore expected to outweigh the costs of producing inbred pups. Accordingly, our results indicate that dominant breeding pairs seldom divorce, and mate changes are mainly due to the death of either mate.

Although dominant females that are related to their mate do not use divorce to adjust initial mate choice, they sire more EPY. In monogamous birds, extra-pair paternity (EPP) has often been linked to genetic relatedness between social pair mates (e.g. Blomqvist *et al.*, 2002; Stapleton *et al.*, 2007; Suter *et al.*, 2007; Varian-Ramos & Webster, 2012), but evidence in monogamous mammals is limited. Combined with evidence from studies of other monogamous species including Alpine marmots *Marmota marmota* and Lariang tarsiers *Tarsus lariang* (Cohas *et al.*, 2008; Driller *et al.*, 2009), our results suggest that, like birds, female mammals may use extra-pair mating when paired with a related male.

Several proximate mechanisms may explain the tendency for EPY to increase in related pairs. First, females may copulate more often with EP males when they are more related to their own mate. Meerkats have been shown to discriminate between unfamiliar kin and unfamiliar nonkin based on olfactory cues (Leclaire *et al.*, 2013), and females may therefore assess their genetic similarity to their social mates using kin discrimination. Second, as in many species (Kempnaers *et al.*, 1996; Taylor *et al.*, 2010), the offspring of related meerkats are less likely to survive than outbred embryos or pups (Nielsen *et al.*, 2012). After several failed breeding attempts, females of related pairs may seek better breeding opportunities beyond their social mate without relying on kin discrimination. Alternatively, the rate of EPC may be independent of partners' relatedness, but EPC may translate into EPY only when social partners are related to each other.

Although relatedness affects the proportion of EPY, the benefits of EP matings are not clear. Mating with immigrant males other than the dominant may have few benefits as males commonly emigrate into a new group as a cohort of relatives (Doolan & Macdonald, 1996) and cuckolds and cuckolders are similarly related to the female. Several studies of monogamous vertebrates have also failed to find benefits from EPP. For instance, in reed buntings *Emberiza schoeniclus*, EPY are not more heterozygous than WPY (Kleven & Lifjeld, 2005); in tree swallows *Tachycineta bicolor*, they do not have higher immune response (Dunn *et al.*, 2009); and in coal tits *Parus ater*, they do not have higher local recruitment rate (Schmoll *et al.*, 2003; review in Schmoll, 2011). Moreover, in wandering albatrosses *Diomedea exulans* and Alpine marmots, although EPP seems to be higher when pair mates are genetically related, EPY and WPY show similar levels of heterozygosity (Cohas *et al.*, 2007, 2008; Jouventin *et al.*, 2007). However, extra-pair mating may have other benefits (Aguirre & Marshall, 2012). For instance, multiple paternities may promote genetic diversity within litters, as in Alpine marmots (Cohas *et al.*, 2007) or Brandt's voles *Lasiopodomys brandtii* (Huo *et al.*, 2010), and hence buffer against environmental uncertainty (genetic bet-hedging, Yasui, 1998) or reduce the likelihood of disease (Zhu *et al.*, 2000). Given that EPY are rare, it is also possible that we lack statistical power to detect genetic benefits to females as a result of insufficient sample size. Nonexclusively, EPP may provide benefits in terms of increased pup heterozygosity at particular loci, such as the major histocompatibility complex (MHC) (Richardson *et al.*, 2005).

Although EP males are not more distantly related to the female than WP males, they are more heterozygous. Heterozygosity is commonly associated with higher fitness (Asa *et al.*, 2007; Forstmeier *et al.*, 2012; Nielsen *et al.*, 2012), and a correlation between parental and offspring heterozygosity has been reported in several species (Cothran *et al.*, 1983; Mitton *et al.*, 1993; Hoffman *et al.*, 2007). However, EPY were not found to be more heterozygous than WPY suggesting that in meerkats, EP males do not provide indirect benefits to females in terms of increased heterozygosity of the pups. Moreover, EP males do not usually care for EPY and do not contribute to new territory access or protection for the female. More heterozygous males may, however, have sperm with higher fertilizing success (Asa *et al.*, 2007), thus providing direct benefits to the female. As inbreeding has negative consequence on mass and skeletal size at emergence and early growth (Nielsen *et al.*, 2012), it is possible that females can assess the heterozygosity of their potential partners through body condition, size or competitive ability, as suggested in other species (e.g. Danzmann *et al.*, 1988; Valimaki *et al.*, 2007). Alternatively, more heterozygous males may be more successful in forcing copula-

tions and therefore sire more offspring than more homozygous males.

More closely related pairs had shorter tenures which often end through the death or disappearance of either mate and they had probably therefore lower reproductive success. The relationship between pairwise relatedness and length of tenure may occur by several mechanisms. First, the production of inbred pups could have physiological costs associated with spontaneous abortion (Hussain, 1998) or compensatory allocation (i.e. allocating more resources or care to expected lower-quality offspring, Harris & Uller, 2009). Alternatively, poor-quality individuals with lower survival may be more likely to breed with related individuals. In several species, competitive ability, body size or fat reserves correlate with dispersal propensity (Ims & Hjermann, 2001). In meerkats, poor-quality males may disperse at shorter distance than higher-quality males, as found in roe deer *Capreolus capreolus* (Debeffe *et al.*, 2012), and may therefore be more likely to breed with closely related females. Effects of this kind may reflect state-dependent variation in the costs and benefits of inbreeding avoidance (Reid *et al.*, 2008), the cost of inbreeding being less than the cost of long-distance dispersal for low-quality individuals.

In conclusion, we found that EPPs are more frequent when females are paired with a related partner. However, females do not seem to benefit from this strategy in terms of increased heterozygosity of their offspring. Understanding whether females gain other benefits from EPP, including higher pup growth rate, immunocompetence or survival as found in other species (Johnsen *et al.*, 2000; Charmantier *et al.*, 2004), is now needed.

Acknowledgments

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References

- Aguirre, J.D. & Marshall, D.J. 2012. Does genetic diversity reduce sibling competition? *Evolution* **66**: 94–102.
- Asa, C., Miller, P., Agnew, M., Rebolledo, J.A.R., Lindsey, S.L., Callahan, M. *et al.* 2007. Relationship of inbreeding with sperm quality and reproductive success in Mexican gray wolves. *Anim. Conserv.* **10**: 326–331.

- Balloux, F., Amos, W. & Coulson, T. 2004. Does heterozygosity estimate inbreeding in real populations? *Mol. Ecol.* **13**: 3021–3031.
- Belkhir, K., Castric, V. & Bonhomme, F. 2002. IDENTIX, a software to test for relatedness in a population using permutation methods. *Mol. Ecol. Notes* **2**: 611–614.
- Blomqvist, D., Andersson, M., Kupper, C., Cuthill, I.C., Kis, J., Lanctot, R.B. *et al.* 2002. Genetic similarity between mates and extra-pair parentage in three species of shorebirds. *Nature* **419**: 613–615.
- Charlesworth, D. & Charlesworth, B. 1987. Inbreeding depression and its evolutionary consequences. *Annu. Rev. Ecol. Syst.* **18**: 237–268.
- Charmantier, A., Blondel, J., Perret, P. & Lambrechts, M.M. 2004. Do extra-pair paternities provide genetic benefits for female blue tits *Parus caeruleus*? *J. Avian Biol.* **35**: 524–532.
- Clutton-Brock, T.H., Gaynor, D., McIlrath, G.M., Maccoll, A.D.C., Kansky, R., Chadwick, P. *et al.* 1999. Predation, group size and mortality in a cooperative mongoose, *Suricata suricatta*. *J. Anim. Ecol.* **68**: 672–683.
- Cohas, A., Yoccoz, N.G. & Allaine, D. 2007. Extra-pair paternity in alpine marmots, *Marmota marmota*: genetic quality and genetic diversity effects. *Behav. Ecol. Sociobiol.* **61**: 1081–1092.
- Cohas, A., Yoccoz, N.G., Bonenfant, C., Goossens, B., Genton, C., Galan, M. *et al.* 2008. The genetic similarity between pair members influences the frequency of extrapair paternity in alpine marmots. *Anim. Behav.* **76**: 87–95.
- Cothran, E.G., Chesser, R.K., Smith, M.H. & Johns, P.E. 1983. Influence of genetic-variability and maternal factors on fetal growth in white-tailed deer. *Evolution* **37**: 282–291.
- Csillery, K., Johnson, T., Beraldi, D., Clutton-Brock, T., Coltman, D., Hansson, B. *et al.* 2006. Performance of marker-based relatedness estimators in natural populations of outbred vertebrates. *Genetics* **173**: 2091–2101.
- Danzmann, R.G., Ferguson, M.M. & Allendorf, F.W. 1988. Heterozygosity and components of fitness in a strain of rainbow trout. *Biol. J. Linn. Soc.* **33**: 285–304.
- Debeffe, L., Morellet, N., Cargnelutti, B., Lourtet, B., Bon, R., Gaillard, J.-M. *et al.* 2012. Condition-dependent natal dispersal in a large herbivore: heavier animals show a greater propensity to disperse and travel further. *J. Anim. Ecol.* **81**: 1327–1327.
- Doolan, S.P. & Macdonald, D.W. 1996. Dispersal and extra-territorial prospecting by slender-tailed meerkats (*Suricata suricatta*) in the south-western Kalahari. *J. Zool.* **240**: 59–73.
- Driller, C., Perwitasari-Farajallah, D., Zischler, H. & Merker, S. 2009. The social system of Lariang tarsiers (*Tarsius lariang*) as revealed by genetic analyses. *Int. J. Primatol.* **30**: 267–281.
- Dubois, F. & Cézilly, F. 2002. Breeding success and mate retention in birds: a meta-analysis. *Behav. Ecol. Sociobiol.* **52**: 357–364.
- Dunn, P.O., Lifjeld, J.T. & Whittingham, L.A. 2009. Multiple paternity and offspring quality in tree swallows. *Behav. Ecol. Sociobiol.* **63**: 911–922.
- Forstmeier, W., Schielzeth, H., Mueller, J.C., Ellegren, H. & Kempenaers, B. 2012. Heterozygosity–fitness correlations in zebra finches: microsatellite markers can be better than their reputation. *Mol. Ecol.* **21**: 3237–3249.
- Freeman-Gallant, C.R., Meguerdichian, M., Wheelwright, N.T. & Sollecito, S.V. 2003. Social pairing and female mating fidelity predicted by restriction fragment length polymorphism similarity at the major histocompatibility complex in a songbird. *Mol. Ecol.* **12**: 3077–3083.
- Griffin, A.S., Pemberton, J.M., Brotherton, P.N.M., McIlrath, G., Gaynor, D., Kansky, R. *et al.* 2003. A genetic analysis of breeding success in the cooperative meerkat (*Suricata suricatta*). *Behav. Ecol.* **14**: 472–480.
- Hadfield, J.D., Richardson, D.S. & Burke, T. 2006. Towards unbiased parentage assignment: combining genetic, behavioural and spatial data in a Bayesian framework. *Mol. Ecol.* **15**: 3715–3730.
- Harris, W.E. & Uller, T. 2009. Reproductive investment when mate quality varies: differential allocation versus reproductive compensation. *Phil. Trans. R. Soc. B* **364**: 1039–1048.
- Hodge, S.J., Manica, A., Flower, T.P. & Clutton-Brock, T.H. 2008. Determinants of reproductive success in dominant female meerkats. *J. Anim. Ecol.* **77**: 92–102.
- Hoffman, J.I., Forcada, J., Trathan, P.N. & Amos, W. 2007. Female fur seals show active choice for males that are heterozygous and unrelated. *Nature* **445**: 912–914.
- Huo, Y.J., Wan, X.R., Wolff, J.O., Wang, G.M., Thomas, S., Iglay, R.B. *et al.* 2010. Multiple paternities increase genetic diversity of offspring in Brandt's voles. *Behav. Processes* **84**: 745–749.
- Hussain, R. 1998. The role of consanguinity and inbreeding as a determinant of spontaneous abortion in Karachi, Pakistan. *Ann. Hum. Genet.* **62**: 147–157.
- Ims, R.A. & Hjernann, D.O. 2001. Condition-dependent dispersal. In: *Dispersal* (J. Clobert, E. Danchin, A.A. Dhondt & J.D. Nichols, eds.), pp. 203–216. Oxford University Press, Oxford.
- Johnsen, A., Andersen, V., Sunding, C. & Lifjeld, J.T. 2000. Female bluethroats enhance offspring immunocompetence through extra-pair copulations. *Nature* **406**: 296–299.
- Jouventin, P., Charmantier, A., Dubois, M.P., Jarne, P. & Bried, J. 2007. Extra-pair paternity in the strongly monogamous Wandering Albatross *Diomedea exulans* has no apparent benefits for females. *Ibis* **149**: 67–78.
- Kempenaers, B., Adriaensens, F., van Noordwijk, A.J. & Dhondt, A.A. 1996. Genetic similarity, inbreeding and hatching failure in blue tits: are unhatched eggs infertile? *Proc. R. Soc. Lond. B* **263**: 179–185.
- Kempenaers, B., Verheyren, G.R. & Dhondt, A.A. 1997. Extra-pair paternity in the blue tit (*Parus caeruleus*): female choice, male characteristics, and offspring quality. *Behav. Ecol.* **8**: 481–492.
- Kempenaers, B., Adriaensens, F. & Dhondt, A.A. 1998. Inbreeding and divorce in blue and great tits. *Anim. Behav.* **56**: 737–740.
- Kleven, O. & Lifjeld, J.T. 2005. No evidence for increased offspring heterozygosity from extrapair mating in the reed bunting (*Emberiza schoeniclus*). *Behav. Ecol.* **16**: 561–565.
- Kutsukake, N. & Clutton-Brock, T.H. 2006. Social functions of allogrooming in cooperatively breeding meerkats. *Anim. Behav.* **72**: 1059–1068.
- Leclaire, S., Nielsen, J.F., Thavarajah, N.K., Manser, M. & Clutton-Brock, T.H. 2013. Odour-based kin discrimination in the cooperatively breeding meerkat. *Biol. Lett.* **9**: 20121054.
- Littell, R.C., Milliken, G.A., Stroup, W.W., Wolfinger, R.D. & Schabenberger, O. 2006. *SAS for Mixed Models*, 2nd edn. SAS institute Inc., Cary, NC.
- Lynch, M. & Walsh, B. 1998. *Genetics and Analysis of Quantitative Traits*. Sunderland, MA.

- Mathieu, E., Autem, M., Roux, M. & Bonhomme, F. 1990. Épreuves de la validation dans l'analyse de structures génétiques multivariées: comment tester l'équilibre panmixique? *Rev. Stat. Appl.* **38**: 47–66.
- McNamara, J.M. & Forslund, P. 1996. Divorce rates in birds: predictions from an optimization model. *Am. Nat.* **147**: 609–640.
- Mitton, J.B., Schuster, W.S.F., Cothran, E.G. & Defries, J.C. 1993. Correlation between the individual heterozygosity of parents and their offspring. *Heredity* **71**: 59–63.
- Morrissey, M.B. & Wilson, A.J. 2010. pedantics: an R package for pedigree-based genetic simulation and pedigree manipulation, characterization and viewing. *Mol. Ecol. Resour.* **10**: 711–719.
- Mulard, H., Danchin, E., Talbot, S.L., Ramey, A.M., Hatch, S.A., White, J.F. *et al.* 2009. Evidence that pairing with genetically similar mates is maladaptive in a monogamous bird. *BMC Evol. Biol.* **9**: 147.
- Nielsen, J., English, S., Goodall-Copstake, W., Wang, J., Walling, C., Bateman, A.W. *et al.* 2012. Inbreeding and inbreeding depression of early life traits in a cooperative mammal. *Mol. Ecol.* **21**: 2788–2804.
- Pemberton, J. 2004. Measuring inbreeding depression in the wild: the old ways are the best. *Trends Ecol. Evol.* **19**: 613–615.
- Pemberton, J.M. 2008. Wild pedigrees: the way forward. *Proc. R. Soc. Lond. B* **275**: 613–621.
- Pusey, A. & Wolf, M. 1996. Inbreeding avoidance in animals. *Trends Ecol. Evol.* **11**: 201–206.
- Reid, J.M., Arcese, P. & Keller, L.F. 2008. Individual phenotype, kinship, and the occurrence of inbreeding in song sparrows. *Evolution* **62**: 887–899.
- Richardson, D.S., Komdeur, J., Burke, T. & von Schantz, T. 2005. MHC-based patterns of social and extra-pair mate choice in the Seychelles warbler. *Proc. Biol. Sci.* **272**: 759–767.
- Russell, A.F., Clutton-Brock, T.H., Brotherton, P.N.M., Sharpe, L.L., McClrath, G.M., Dalerum, F.D. *et al.* 2002. Factors affecting pup growth and survival in co-operatively breeding meerkats *Suricata suricatta*. *J. Anim. Ecol.* **71**: 700–709.
- Schielzeth, H. 2010. Simple means to improve the interpretability of regression coefficients. *Methods Ecol. Evol.* **1**: 103–113.
- Schmoll, T. 2011. A review and perspective on context-dependent genetic effects of extra-pair mating in birds. *J. Ornithol.* **152**: 265–277.
- Schmoll, T., Dietrich, V., Winkel, W., Eppel, J.T. & Lubjuhn, T. 2003. Long-term fitness consequences of female extra-pair matings in a socially monogamous passerine. *Proc. R. Soc. Lond. B* **270**: 259–264.
- Spong, G.F., Hodge, S.J., Young, A.J. & Clutton-Brock, T.H. 2008. Factors affecting the reproductive success of dominant male meerkats. *Mol. Ecol.* **17**: 2287–2299.
- Stapleton, M., Kleven, O., Lifjeld, J. & Robertson, R. 2007. Female tree swallows (*Tachycineta bicolor*) increase offspring heterozygosity through extrapair mating. *Behav. Ecol. Sociobiol.* **61**: 1725–1733.
- Suter, S.M., Keiser, M., Feignoux, R. & Meyer, D.R. 2007. Reed bunting females increase fitness through extra-pair mating with genetically dissimilar males. *Proc. R. Soc. Lond. B* **274**: 2865–2871.
- Tarvin, K.A., Webster, M.S., Tuttle, E.M. & Pruett-Jones, S. 2005. Genetic similarity of social mates predicts the level of extrapair paternity in splendid fairy-wrens. *Anim. Behav.* **70**: 945–955.
- Taylor, S.S., Sardell, R.J., Reid, J.M., Bucher, T., Taylor, N.G., Arcese, P. *et al.* 2010. Inbreeding coefficient and heterozygosity-fitness correlations in unhatched and hatched song sparrow nestmates. *Mol. Ecol.* **19**: 4454–4461.
- Valimaki, K., Hinten, G. & Hanski, I. 2007. Inbreeding and competitive ability in the common shrew (*Sorex araneus*). *Behav. Ecol. Sociobiol.* **61**: 997–1005.
- Van de Castele, T., Galbusera, P., Schenck, T. & Matthysen, E. 2003. Seasonal and lifetime reproductive consequences of inbreeding in the great tit *Parus major*. *Behav. Ecol.* **14**: 165–174.
- Van de Pol, M. & Wright, J. 2009. A simple method for distinguishing within- versus between-subject effects using mixed models. *Anim. Behav.* **77**: 753–758.
- Varian-Ramos, C.W. & Webster, M.S. 2012. Extrapair copulations reduce inbreeding for female red-backed fairy-wrens, *Malurus melanocephalus*. *Anim. Behav.* **83**: 857–864.
- Wang, J. 2004. Sibship reconstruction from genetic data with typing errors. *Genetics* **166**: 1963–1979.
- Wetzel, D.P. & Westneat, D.F. 2009. Heterozygosity and extra-pair paternity: biased tests result from the use of shared markers. *Mol. Ecol.* **18**: 2010–2021.
- Yasui, Y. 1998. The 'genetic benefits' of female multiple mating reconsidered. *Trends Ecol. Evol.* **13**: 246–250.
- Young, A.J., Carlson, A.A. & Clutton-Brock, T. 2005. Trade-offs between extraterritorial prospecting and helping in a cooperative mammal. *Anim. Behav.* **70**: 829–837.
- Young, A.J., Spong, G. & Clutton-Brock, T. 2007. Subordinate male meerkats prospect for extra-group paternity: alternative reproductive tactics in a cooperative mammal. *Proc. R. Soc. Lond. B* **274**: 1603–1609.
- Zhu, Y., Chen, H., Fan, J., Wang, Y., Li, Y., Chen, J. *et al.* 2000. Genetic diversity and disease control in rice. *Nature* **406**: 718–722.
- Zuur, A., Ieno, E., NJ, W., AA, S. & GM, S. 2009. *Mixed Effects Models and Extensions in Ecology with R*. Springer, New York.

Supporting information

Additional Supporting Information may be found in the online version of this article:

Table S1 Linear mixed model testing for an effect of pairwise relatedness (R) on duration of tenure.

Table S2 Generalized linear mixed model testing for an effect of pairwise relatedness (R) on the proportion of EPY.

Figure S1 Duration of pair tenure according to pairwise relatedness (R) in dominant breeding pairs.

Figure S2 Proportion of EPY per dominant breeding pair (i.e. number of EPY/total number of young) according to pairwise relatedness (R).

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