

# Subordinate male meerkats prospect for extra-group paternity: alternative reproductive tactics in a cooperative mammal

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In cooperatively breeding species, subordinates typically suffer strong constraints on within-group reproduction. While numerous studies have highlighted the additional fitness benefits that subordinates might accrue through helping, few have considered the possibility that subordinates may also seek extra-group matings to improve their chances of actually breeding. Here, we show that subordinate males in cooperative meerkat, *Suricata suricatta*, societies conduct frequent extraterritorial forays, during periods of peak female fertility, which give rise to matings with females in other groups. Genetic analyses reveal that extra-group paternity (EGP) accrued while prospecting contributes substantially to the reproductive success of subordinates: yielding the majority of their offspring (approx. 70%); significantly reducing their age at first reproduction and allowing them to breed without dispersing. We estimate that prospecting subordinates sire 20–25% of all young in the population. While recent studies on cooperative birds indicate that dominant males accrue the majority of EGP, our findings reveal that EGP can also arise from alternative reproductive tactics employed exclusively by subordinates. It is important, therefore, that future attempts to estimate the fitness of subordinate males in animal societies quantify the distribution of extra-group as well as within-group paternity, because a substantial proportion of the reproductive success of subordinates may otherwise go undetected.

**Keywords:** extra-pair paternity; reproductive skew; multi-male groups; mating system

## 1. INTRODUCTION

In cooperatively breeding species, subordinate males typically suffer strong constraints on within-group reproduction (Magrath *et al.* 2004), and so selection may strongly favour the employment of tactics to augment their fitness by other means. Numerous studies have now highlighted the fitness benefits that subordinates may accrue through helping (Cockburn 1998), but few have considered the possibility that subordinates may also attempt to improve their chances of actually breeding, by seeking extra-group reproductive opportunities. Subordinates in many cooperative societies conduct extraterritorial ‘prospecting’ forays, which are generally thought to facilitate dispersal (Stacey & Koenig 1990; Waser 1996; Young 2003; Doerr & Doerr 2005), but whether these forays also yield access to reproductive opportunities with members of other groups remains largely unexplored.

Although subordinate males prospect in a number of cooperative vertebrates, evidence that they can accrue reproductive success in the process is lacking for two main reasons. First, little is known about the behaviour of prospectors as they are typically difficult to observe, quickly covering long distances, commonly beyond the limits of study sites, and sometimes under the cover of darkness (mammals: Waser 1996; birds: Double & Cockburn 2000; Doerr & Doerr 2005). Second, although a number of recent genetic studies have reported

significant rates of extra-group paternity (EGP) in cooperative species (e.g. mammals: Goossens *et al.* 1998; Griffin *et al.* 2003; birds: Whittingham *et al.* 1997; Dunn & Cockburn 1999; Richardson *et al.* 2001; Durrant & Hughes 2005), few have identified the sires of the extra-group young. It therefore commonly remains unclear whether the EGP detected is accrued by floating individuals, subordinate males or dominant males (who may also accrue EGP either through forays of their own or because extra-group copulations actually occur during forays by females rather than males; Double & Cockburn 2000). Indeed, the two studies that have identified significant numbers of extra-group sires reveal that EGP can be accrued almost exclusively by dominant males (Richardson *et al.* 2001; Double & Cockburn 2003). To establish whether subordinate males are able to accrue EGP during their prospecting forays, it is therefore necessary to combine behavioural records of extraterritorial movements and copulations with genetic assignments of extra-group sires.

Here, we combine behavioural and genetic evidence from our long-term study of cooperative meerkats, *Suricata suricatta*, to investigate whether subordinate males accrue EGP while prospecting, and estimate the contribution of this tactic to their overall reproductive success. Meerkats are cooperatively breeding mongooses that live in groups of up to 50 individuals in the deserts of southern Africa (Clutton-Brock *et al.* 2001). Males typically remain as subordinates in their natal groups into adulthood and genetic evidence reveals that they do not breed with resident females, to whom they are

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invariably closely related (Griffin *et al.* 2003). Males generally disperse in multi-male coalitions of relatives and therefore, as only one immigrant male can assume the dominant position, commonly remain subordinates after dispersal (Young 2003). As dominant immigrant males largely monopolize within-group reproduction, subordinate immigrant males suffer low within-group breeding success too, despite having unrelated females present (Griffin *et al.* 2003). Subordinate males, both nats and immigrants, accrue some fitness benefits from helping to rear the offspring of others (direct benefits through group augmentation and indirect benefits through relatedness to the young reared; Clutton-Brock *et al.* 2001; Griffin *et al.* 2003; Young 2003), but also conduct regular extraterritorial prospecting forays (Doolan & Macdonald 1996; Young *et al.* 2005). These forays appear voluntary, not being associated in any way with aggression by other group members (Young *et al.* 2005). Although a small proportion of forays culminate in dispersal (Young 2003), it is possible that prospecting also affords males immediate access to reproductive opportunities with females in other groups (who may choose to mate extra-group for a number of reasons, e.g. if they lack unrelated males within their own group). Previous genetic analyses have found evidence of significant EGP in meerkat societies (Griffin *et al.* 2003) suggesting that it could be an important component of male reproductive success, but the extra-group sires were not identified. Here, we investigate whether subordinate males accrue this EGP while prospecting. Specifically, we (i) investigate whether prospecting forays are conducted exclusively by subordinate males, whether they are associated with periods of peak female fertility, and whether they give rise to matings with females in other groups; (ii) use paternity analyses to estimate the prevalence of EGP and to establish the extent to which it is accrued by subordinate males; and (iii) estimate the contribution that EGP makes to the overall reproductive success of subordinate male meerkats.

## 2. MATERIAL AND METHODS

The study was conducted on ranchland in the southern Kalahari desert (26°59' S, 21°50' E) from 1997 to 2002 (Clutton-Brock *et al.* 2001). Our study population comprised 15 groups that occupied contiguous home ranges, were habituated to close observation and were visited on a near-daily basis. Animals were individually identifiable (using unique haircuts) and could be weighed using electronic balances prior to each morning observation period. Males were considered to be prospecting if they were absent from their group or were sighted elsewhere. In our eight best-studied groups, their departure and return dates were generally known to the day. Litter conception dates (needed for identifying potential sires) could be backdated from accurately known birth dates (pregnancy lasts approximately 70 days), identified from a sudden change in a female's shape and weight (Griffin *et al.* 2003; Young *et al.* 2006). In each group, the 'dominant' male and female were behaviourally dominant to, and typically older and heavier than, all other same-sex group members (Griffin *et al.* 2003). All research protocols complied with the Guidelines for the Use of Animals in Research.

We refer to males of three dominance and dispersal classes: 'subordinate natal males'—prior to dispersal from

their natal group; 'subordinate immigrant males'—having dispersed into a subordinate position; and 'dominant immigrant males'—having dispersed into the dominant position (males do not become dominant breeders in their natal groups). All analyses are restricted to adult males (greater than 1 year).

Statistical analyses were conducted using GENSTAT v. 5 (Lawes Agricultural Trust). For multivariate analyses, statistical model selection was conducted using reverse stepwise elimination of fixed effects to yield a minimal model (as per Crawley 2002), and though all two-way interactions were tested, only those that were statistically significant are reported (see electronic supplementary material for further details and full tables for the statistical models).

### (a) *Patterns of extraterritorial prospecting among males*

To investigate the patterns of prospecting by males of different dominance and dispersal classes, we divided each male's tenure as an adult in a given class into a series of calendar months and calculated for each month, the number of days spent prospecting. The number of prospecting days was set as the response term in a generalized linear mixed model (GLMM) with binomial error structure, and the number of days in the month as the binomial total. The male's class (which was of primary interest) was fitted as a fixed effect, along with his age mid-month (days), his average body weight during the month (g) and average monthly temperature (°C), rainfall (mm) and female fertility. The monthly female-fertility measure was included to investigate whether males prospected more during months when they were more likely to encounter fertile females, and was calculated from our long-term data, for each calendar month, as the average probability that a dominant female would conceive during that month (conception probabilities of subordinate females are unlikely to accurately reflect seasonal variation in fertility *per se* as they commonly lack access to unrelated breeding partners; Griffin *et al.* 2003). The analysis was based on 2860 male months, for 153 subordinate natal males, 51 subordinate immigrant males and 24 dominant immigrant males from our eight best-studied groups. Repeated measures of males and groups were controlled by fitting both as random factors.

### (b) *Estimating EGP prevalence and establishing the status of extra-group sires*

Details of tissue sampling, DNA extraction and genotyping methodologies are provided in the electronic supplementary material. Of the 673 pups that emerged in our 15 study groups, 499 (74.1%) were sampled and successfully genotyped at 5–15 (median 9) polymorphic loci ( $11 \pm 4$  alleles per locus; mean  $\pm$  s.d.) using 15 microsatellite markers and are used in the genetic analyses below.

We used two methods to estimate the prevalence of EGP in our population. The exclusion method estimated EGP prevalence as the proportion of offspring for which all within-group males could be excluded as sires on the basis of mismatching the offspring at more than one locus (considering only those offspring for which all within-group adult males present at conception had been genotyped; 389 offspring in 14 groups). This should yield a conservative EGP prevalence estimate as within-group paternity is assumed even if all within-group males mismatch the offspring at one locus (genotyping error rates were low; less than 3%, as calculated from duplicate runs).

The second method estimated EGP prevalence using likelihood-based paternity assignments. To obtain the most accurate EGP prevalence estimate, we used the program CERVUS v. 2.0 (Marshall *et al.* 1998) to assign paternity for all genotyped emergent offspring (349 offspring) conceived in our six most central groups (a contiguous cluster of six groups that were surrounded by the nine other study groups). By using only these central groups, we ensured that good life history and genetic coverage were therefore available for the males in each of the surrounding groups (i.e. the potential extra-group sires), thereby minimizing the underestimation of EGP prevalence that would otherwise result from having a poorly sampled population of extra-group candidates. Maternity could be confidently assigned for 113 of the 119 litters (95%) using observational data, exceptions being near-simultaneous births. Where maternity was unknown, we ran the analysis without this information. Candidate fathers for each litter included all adult males who were alive on the conception day, from both the conception group and all other study groups that the conception group had ever encountered during the course of our study (merely an objective means of limiting the spatial scale over which candidate fathers for a given litter are drawn; 93% of observed extraterritorial forays were between groups with such a history). This conservative approach ensured that our findings were not influenced by selective inclusion of males as paternity candidates on the basis of either their dominance rank or prospecting history. However, we did exclude previous sons of the litter's mother as candidates, as they are expected to disrupt the assignment process (Marshall *et al.* 1998) and there is good evidence that meerkats avoid such close inbreeding (females have never been observed mating with related males reared within their groups, and genetic evidence strongly suggests that they do not produce pups sired by them either; Griffin *et al.* 2003). The CERVUS simulation parameters used are detailed in the electronic supplementary material. To minimize the potential for biases arising from assignment error, we used only the strictest (greater than 95%) confidence assignments for both our EGP prevalence estimate and establishing the status of the males that accrue EGP.

### (c) *Investigating the importance of EGP to subordinate males*

To investigate the relative importance of intra- and EGP for the overall reproductive success of subordinate males, we first attempted to assign paternity for all genotyped offspring from our entire study population (499 offspring from 15 groups). Candidate father lists for this second CERVUS run were created as described above, though extra-group dominant males (who neither prospect nor accrue EGP, as revealed by the above analyses) were removed to reduce assignment complications arising from their close relatedness to many candidate subordinates. Again, the simulation parameters used are detailed in the electronic supplementary material. We then calculated the number of intra- and extra-group young assigned to each male in our eight best-studied groups during his life as an adult subordinate ( $n=174$  subordinate males; combining their subordinate natal and immigrant periods where necessary), using all greater than 80% confidence paternity assignments from this second CERVUS run (271 offspring; too few were made at greater than 95% confidence (only 93) for meaningful reproductive success calculations to be made). We used these data (i) for within-male comparisons of the extra- and intra-group

reproductive rates of subordinates ( $n=42$  subordinates who sired some offspring), and (ii) to investigate whether, during their lives as adult subordinates, males that spent a higher proportion of their time prospecting sired extra-group young at higher rates. To avoid inflating our apparent sample size with weak reproductive rate estimates resulting from short monitoring periods, only males monitored as adult subordinates for more than six months ( $n=141$  males) were used in the second analysis, though this conservative approach did not qualitatively affect our findings.

Then, to investigate whether the relative importance of intra- and extra-group reproduction differed for subordinate males before and after dispersal from their natal groups, we divided each male's time spent as an adult subordinate into natal and immigrant 'tenures' (not all males had tenures in both classes). We investigated the effect of a subordinate's dispersal class (natal or immigrant) on the probability that he sired any offspring (one or more) during his tenure in that class, using a binomial error structure in a GLMM that controlled for variation in tenure length and the average age of the male throughout his tenure (the use of a continuous error structure to analyse reproductive rates was inappropriate as most subordinates sired no offspring). To compare their probabilities of siring intra- and extra-group young, two data points were included for each male tenure (one for intra- and one for extra-group success), and the reproductive route (intra- or extra-group) was fitted as a fixed effect along with the male's dispersal status (natal or immigrant). The analysis used a dataset of 162 subordinate tenures (123 natal and 39 immigrants) for 141 males in the eight groups. Repeated measures of males and groups were controlled by fitting both as random factors.

Finally, to investigate whether prospecting afforded subordinate males access to less-related females, we compared (for natal and immigrants separately) males' relatedness to their assigned extra-group mates to (i) their relatedness to their resident dominant female (their primary within-group breeding option, as subordinate female breeding attempts are commonly disrupted; Young & Clutton-Brock 2006; Young *et al.* 2006) and (ii) their average relatedness to all resident subordinate females of breeding age (greater than nine months; Young *et al.* 2006; as some groups contained no such subordinates, sample sizes for this comparison differ slightly from those for the dominant female comparison). Estimates of relatedness were calculated with the software RELATEDNESS (Goodnight & Queller 1999), using all genetic information available from our 15 study groups to determine allele frequency distributions.

## 3. RESULTS

### (a) *Subordinate males prospect frequently and copulate with females in other groups*

Females were never seen leaving their group's territory unless dispersing permanently, whereas subordinate males frequently conducted extraterritorial forays throughout their adult lives (up to 11 forays per month during the conceptive season, June–January, (median 1; IQR 0–3) for 1–150 days at a time (median 1; IQR 1–2.5)). Only a small proportion of forays culminated in the male's dispersal or disappearance (3.1% of 3287 forays by males in our eight best-studied groups). Prospecting males typically approached foreign groups (witnessed for 1644 of these 3287 forays (50.0%) and could have occurred in the remainder), subject to aggressive chasing by resident males (Young *et al.* 2005), and on encountering a female usually sniffed her anogenital

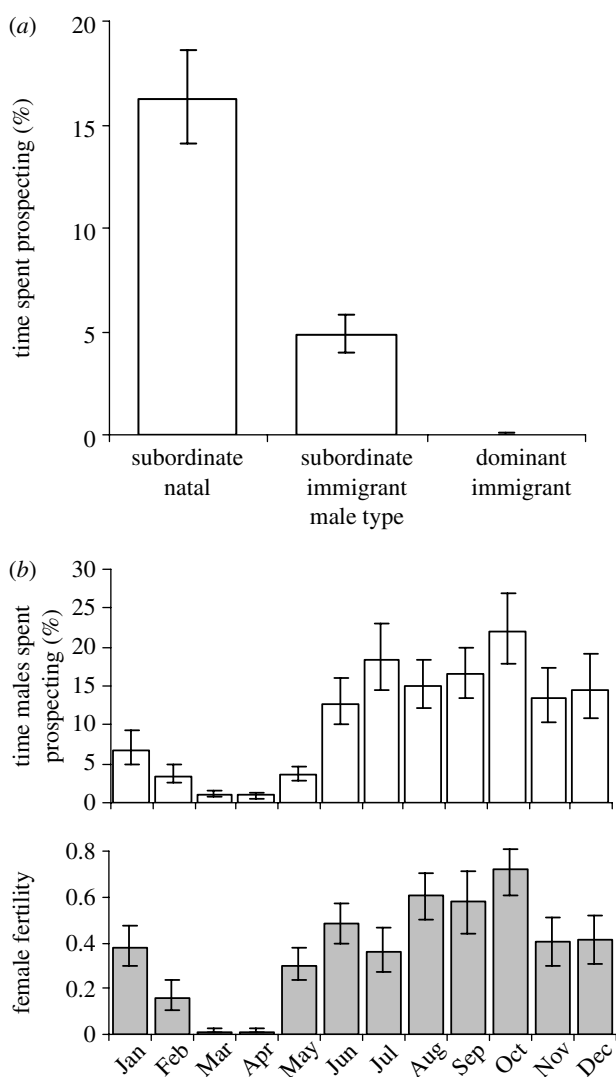


Figure 1. (a) The proportion of time spent by males prospecting in different dominance and dispersal classes. Bars present predicted means  $\pm$  s.e. from the GLMM, controlling for seasonal variables and males prospecting at higher rates as they age (see §3). (b) The seasonal variation in male prospecting closely paralleled that of female fertility. The prospecting profile presents predicted monthly means  $\pm$  s.e. for subordinate natal males (calculated by substituting calendar month in place of the female fertility variable in our prospecting-time GLMM; the profile for subordinate immigrant males was almost identical, just with lower values). The female fertility bars present monthly means  $\pm$  s.e. of dominant female conception probabilities, calculated from our historical data (see §2).

region and attempted to mount her. Females typically refused, at least initially (turning away and striking him with a paw), and were never seen copulating with extra-group males within sight of other group members. However, on 30 occasions, females were observed to move away from their group with a prospector, for 1–24 h, to mate (15 matings by six dominant females and 15 by 13 subordinate females). Females found mating extra-group typically lacked access to unrelated males within their groups (26 of the 30 matings).

Prospecting forays were conducted exclusively by subordinate males and were focused on periods of peak female fertility (figure 1). A male's dispersal and dominance class was a strong predictor of the proportion of time he spent prospecting (GLMM:  $\chi^2_2=198.42$ ;  $p<0.001$ ; figure 1a), while controlling for a strong positive effect of male age

( $\chi^2_1=331.67$ ;  $p<0.001$ ) and seasonal variables (see below). Subordinate natal males, who invariably lacked unrelated breeding partners within their groups, prospected most for their age. Subordinate immigrant males continued to prospect, despite having dispersed, but at lower rates than subordinate natal males of a comparable age. In contrast, dominant immigrant males, who largely monopolized within-group reproduction (Griffin *et al.* 2003, also this study), were never known to prospect (and any such movements are unlikely to have gone undetected as these males were often radio-collared). Time spent prospecting also showed substantial seasonal variation, being strongly positively correlated with monthly variation in female fertility ( $\chi^2=227.94$ ;  $p<0.001$ ; figure 1b) and negatively correlated with both mean monthly temperature ( $\chi^2_1=34.86$ ;  $p<0.001$ ) and rainfall ( $\chi^2_1=7.59$ ;  $p=0.006$ ). The close correlation between seasonal variation in prospecting and female fertility is unlikely to have arisen simply from correlated seasonal variation in the body condition of all individuals, as male body weight was included in the prospecting analysis ( $\chi^2_1=3.21$ ;  $p=0.073$ ; although this term was dropped from the final model owing to a lack of statistical significance, its inclusion left the statistical significance of the other terms qualitatively unaffected).

#### (b) EGP is relatively common and is accrued by subordinate males

Both exclusion and likelihood-based paternity assignment methods indicate that EGP is relatively common.

*Exclusion method.* Of the 389 genotyped offspring conceived in our study population at times when all potential within-group sires were genotyped, all within-group males could be excluded as sires (on the basis of mismatching the offspring at more than one locus) in 99 cases, suggesting 25.4% EGP.

*Paternity assignment method.* Of the 349 genotyped offspring conceived in our six central groups, fathers were assigned with strict (greater than 95%) confidence (from candidate males in the conception group and surrounding population) in 51 cases, 10 of which were extra-group sires, suggesting 19.6% EGP.

The latter measure is likely to be slightly conservative, as a small proportion of extra-group sires probably lie unsampled beyond our study population. The congruence of these estimates suggests that the true EGP prevalence in our population lies close to 20–25%. For the 51 offspring that were assigned sires with strict (greater than 95%) confidence, dominant males largely monopolized within-group paternity (38 of 41 offspring, 92.7%), but, in accordance with the observations of extraterritorial prospecting and copulation patterns, EGP was accrued exclusively by subordinate males (figure 2a).

#### (c) Prospecting for EGP contributes substantially to subordinate male reproductive success

Prospecting for EGP yielded the majority of the young that males sired as subordinates (approx. 70%; 69 of 108 (63.9%) greater than 80% confidence paternities and 10 of 13 (76.9%) greater than 95% confidence paternities). During the time that they were monitored as adult subordinates (combining natal and immigrant periods where necessary), males that did sire offspring sired more extra- than intra-group young (Wilcoxon signed-rank test:  $W=368$ ;  $n=42$  males;  $p=0.009$ ), and males that spent a

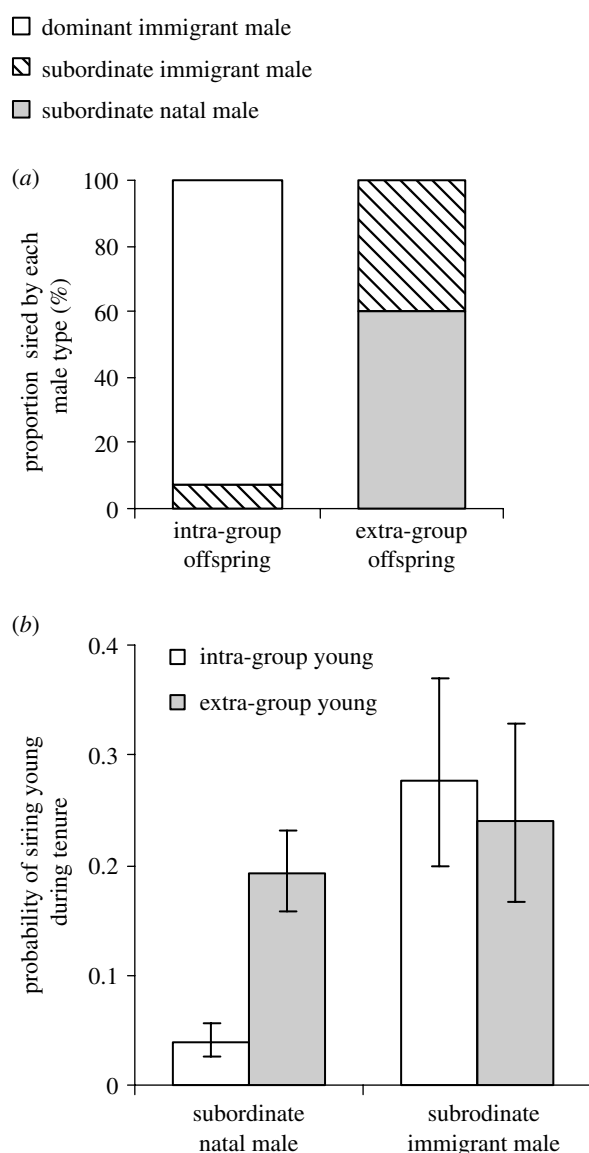


Figure 2. (a) The distribution of intra- and EGP among males of differing dominance and dispersal class (for the 51 offspring that were assigned fathers with greater than 95% confidence: 41 intra-group sirings and 10 extra-group sirings). (b) The probability that subordinate males sired intra- or extra-group offspring before and after dispersal from their natal groups. Bars represent predicted means  $\pm$  s.e. from the GLMM (using 279 offspring assigned with greater than 80% confidence), controlling for variation in each male's tenure in that dispersal class.

higher proportion of their time prospecting sired extra-group young at higher rates (Spearman rank correlation = 0.28;  $p < 0.001$ ;  $n = 141$  males).

The relative contributions of extra- and intra-group paternity to the reproductive success of subordinate males differed significantly before and after dispersal from their natal groups (figure 2b; GLMM:  $\chi^2_1 = 6.47$ ,  $p = 0.011$ ; controlling for variation in their tenure in that dispersal class:  $\chi^2_1 = 22.15$ ,  $p < 0.001$ ; there was no significant effect of male age:  $\chi^2_1 = 0.63$ ,  $p = 0.43$ ). Subordinate natal males were substantially more likely to accrue extra- than intra-group paternity, while subordinate immigrant males were equally likely to accrue intra- and EGP (figure 2b). This pattern most probably reflects inbreeding avoidance, with prospecting affording subordinate natal males access to females to whom they are less related than they are to

those within their group (the latter are usually their mother, sisters or aunts). Subordinate natal males were significantly less related to their assigned extra-group mates (median (IQR);  $r = 0.22$  (0.03–0.39)) than they were to both their within-group dominant female ( $r = 0.45$  (0.39–0.56),  $W = 509$ ,  $n = 33$  different male/extra-group mate pairings,  $p < 0.001$ ) and their within-group subordinate females ( $r = 0.35$  (0.24–0.42),  $W = 255$ ,  $n = 30$ ,  $p = 0.009$ ). In contrast, subordinate immigrant males were not less related to their extra-group mates ( $r = 0.13$  (0.03–0.22)) than they were to either their within-group dominant female ( $r = 0.15$  (0.07–0.28),  $W = 25$ ,  $n = 18$ ,  $p = 0.61$ ) or their within-group subordinate females ( $r = 0.08$  (0.03–0.25),  $W = 5$ ,  $n = 17$ ,  $p = 0.93$ ). This contrast arose because subordinate immigrant males (having already dispersed from their natal groups) were significantly less related to both their within-group dominant females and their within-group subordinate females than subordinate natal males were (Mann–Whitney  $u$ -tests:  $T = 226$ ,  $n = 18$  and  $33$ ,  $p < 0.001$ ; and  $T = 235$ ,  $n = 17$  and  $30$ ,  $p < 0.001$ , respectively). That the relatedness of males to their extra-group mates tended to be positive (i.e. above the population average) most likely reflects spatial kin structuring in the population, which will tend to leave prospectors more related on average to females in their neighbouring groups (to which they prospect) than they would be on average to any female drawn from the whole population.

The ability to prospect for extra-group reproductive opportunities allowed males to start breeding significantly earlier in life (males started siring extra-group young significantly earlier in life (median = 628 days; IQR = 473–885) than within-group young (893 days; 660–1034); Mann–Whitney:  $T = 1815$ ,  $n = 38$  and  $39$  males for which an age at first extra- and within-group reproduction were available, respectively, and  $p < 0.001$ ).

#### 4. DISCUSSION

Our behavioural analyses reveal that subordinate male meerkats, who sire few within-group young, conduct extraterritorial prospecting forays at high rates, focus their prospecting effort on periods of peak female fertility and secure extra-group matings. Our genetic analyses corroborate these findings, revealing that subordinate males alone sire extra-group young (estimated at 20–25% of all young) and that the more they prospect the more EGP they accrue. In contrast, dominant males, who largely monopolize within-group reproduction, do not prospect and do not appear to sire extra-group young. Our findings suggest that the ability to prospect for EGP contributes substantially to the reproductive success of subordinate males, yielding the majority (approx. 70%) of the young that they sire and allowing them to start breeding significantly earlier in life. As very few male meerkats attain dominance (Clutton-Brock *et al.* 2006; Spong *et al.* submitted), tactics such as prospecting, which substantially augment the meagre within-group reproductive success of subordinates, are likely to be of particular importance.

While extraterritorial prospecting afforded subordinate immigrant males additional breeding opportunities, it yielded practically all of the reproductive success of subordinate natal males (males yet to disperse from their natal groups). Subordinate natal males rarely accrue any

within-group paternity as they are invariably closely related to all within-group females (generally their mother, sisters or aunts), and genetic evidence reveals that such inbred matings are typically avoided (Griffin *et al.* 2003). Analyses based on the distribution of within-group paternity alone therefore suggest that males must first disperse if they are to breed (Griffin *et al.* 2003), but our findings reveal that natal males can circumvent this constraint by mating with females in other groups (to whom they are significantly less related). This ability to prospect for EGP from within the natal group is important, as, by allowing males to breed as well as help while awaiting a dispersal opportunity, it should strengthen selection for delayed dispersal.

As dominant immigrant males are able to largely monopolize within-group paternity, it is perhaps surprising that subordinate males from other groups are able to accrue a substantial proportion of paternity (estimated here at 20–25%). The opportunity for prospectors to mate with females in other groups appears to stem largely from the fact that females are frequently closely related to all of the males within their own group (with whom inbreeding is typically avoided; Griffin *et al.* 2003). Subordinate females commonly face these circumstances (having been sired by the immigrant male coalition), but dominant females sometimes do too, as they may be left with only their sons within the group if all immigrant males die. Prospecting males may often, therefore, constitute a female's only opportunity to outbreed. Indeed, our observations suggest that extra-group matings are largely restricted to females in this predicament (26 of 30 observed copulations), and the fact that all of these observed copulations arose from females moving briefly away from their groups to mate with the prospector (probably necessary for mating to occur as prospectors are chased by resident males) strongly suggests a key role for females in determining the patterns of EGP in this species. The strong kin-structuring characteristic of cooperative societies may also explain the comparatively high rates of extra-group mating in some other cooperators (Sillero-Zubiri *et al.* 1996; Durrant & Hughes 2005), though benefits of extra-group mating other than inbreeding avoidance must also be invoked if we are to explain patterns of EGP across all cooperative species (Dunn & Cockburn 1999; Richardson *et al.* 2005).

The finding that subordinate males may accrue the majority of their reproductive success in other groups poses a number of challenges for theoretical attempts to explain the distribution of reproductive success in animal groups, which typically focus on the partitioning of within-group reproduction (Magrath *et al.* 2004). First, in species where subordinate males accrue EGP, much of their reproductive success may not actually detract from that of their resident dominant. In fact, dominant males may commonly accrue inclusive fitness benefits from the extra-group success of their subordinates, through close relatedness (Young *et al.* 2005). Second, the opportunity for subordinate males to accrue EGP may be determined as much by the kin structure and/or preferences of females in neighbouring groups (see above) as by competitive interactions among males within their own group. Theoretical frameworks based on within-group reproductive conflict alone may therefore struggle to predict the distribution of reproductive success in social species with significant rates of EGP (see Westneat & Stewart 2003 for a similar argument for pair-breeding birds).

Attempts to incorporate some of the recently identified predictors of EGP prevalence (Griffith *et al.* 2002; Isvaran & Clutton-Brock 2007) into an explicit reproductive competition framework may therefore prove rewarding.

Together, our results strongly suggest that subordinate males in cooperative meerkat societies can substantially augment their limited within-group reproductive success with EGP accrued while prospecting. Our findings are important because, though a number of studies have now detected significant rates of EGP in social species (see §1), it is rarely clear how EGP arises or which males secure the paternity (owing to the difficulty in both observing extraterritorial behaviour and identifying extra-group sires). While two recent studies of cooperative birds indicate that dominant males may accrue the majority of EGP (Richardson *et al.* 2001; Double & Cockburn 2003), our study reveals that EGP can also arise from alternative reproductive tactics employed exclusively by subordinates. The finding that subordinates may actually sire most of their offspring in other groups is of particular importance, as attempts to estimate the fitness of subordinate males (or the variance in reproductive success among males) in social species may therefore fail to detect much of the reproductive success of subordinates unless they quantify the distribution of extra- as well as within-group paternity.

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## REFERENCES

- Clutton-Brock, T. H., Russell, A. F., Sharpe, L. L., Brotherton, P. N. M., McIlrath, G. M., White, S. & Cameron, E. Z. 2001 Effects of helpers on juvenile development and survival in meerkats. *Science* **293**, 2446–2449. (doi:10.1126/science.1061274)
- Clutton-Brock, T. H., Hodge, S. J., Spong, G., Russell, A. F., Jordan, N. R., Bennett, N. C., Sharpe, L. L. & Mauser, M. B. 2006 Intrasexual competition and sexual selection in cooperative mammals. *Nature* **444**, 1065–1068. (doi:10.1038/nature05386)
- Cockburn, A. 1998 Evolution of helping behavior in cooperatively breeding birds. *Annu. Rev. Ecol. Syst.* **29**, 141–177. (doi:10.1146/annurev.ecolsys.29.1.141)
- Crawley, M. J. 2002 *Statistical computing*. Chichester, UK: Wiley.
- Doerr, E. D. & Doerr, V. A. J. 2005 Dispersal range analysis: quantifying individual variation in dispersal behaviour. *Oecologia* **142**, 1–10. (doi:10.1007/s00442-004-1707-z)
- 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.
- Double, M. & Cockburn, A. 2000 Pre-dawn infidelity: females control extra-pair mating in superb fairy-wrens. *Proc. R. Soc. B* **267**, 465–470. (doi:10.1098/rspb.2000.1023)
- Double, M. C. & Cockburn, A. 2003 Subordinate superb fairy-wrens (*Malurus cyaneus*) parasitize the reproductive success of attractive dominant males. *Proc. R. Soc. B* **270**, 379–384. (doi:10.1098/rspb.2002.2261)
- Dunn, P. O. & Cockburn, A. 1999 Extrapair mate choice and honest signaling in cooperatively breeding superb fairy-wrens. *Evolution* **53**, 938–946. (doi:10.2307/2640733)

- Durrant, K. L. & Hughes, J. M. 2005 Differing rates of extra-group paternity between two populations of the Australian magpie (*Gymnorhina tibicen*). *Behav. Ecol. Sociobiol.* **57**, 536–545. (doi:10.1007/s00265-004-0883-5)
- Goodnight, K. F. & Queller, D. C. 1999 Computer software for performing likelihood tests of pedigree relationship using genetic markers. *Mol. Ecol.* **8**, 1231–1234. (doi:10.1046/j.1365-294x.1999.00664.x)
- Goossens, B., Graziani, L., Waits, L. P., Farand, E., Magnolon, S., Coulon, J., Bel, M. C., Taberlet, P. & Allaine, D. 1998 Extra-pair paternity in the monogamous Alpine marmot revealed by nuclear DNA microsatellite analysis. *Behav. Ecol. Sociobiol.* **43**, 281–288. (doi:10.1007/s002650050492)
- Griffin, A. S., Pemberton, J. M., Brotherton, P. N. M., McIlrath, G., Gaynor, D., Kinsky, R., O'Riain, J. & Clutton-Brock, T. H. 2003 A genetic analysis of breeding success in the cooperative meerkat (*Suricata suricatta*). *Behav. Ecol.* **14**, 472–480. (doi:10.1093/beheco/arg040)
- Griffith, S. C., Owens, I. P. F. & Thuman, K. A. 2002 Extra pair paternity in birds: a review of interspecific variation and adaptive function. *Mol. Ecol.* **11**, 2195–2212. (doi:10.1046/j.1365-294x.2002.01613.x)
- Isvaran, K. & Clutton-Brock, T. H. 2007 Ecological correlates of extra-group paternity in mammals. *Proc. R. Soc. B* **274**, 219–224. (doi:10.1098/rspb.2006.3723)
- Magrath, R. D., Johnstone, R. A. & Heinsohn, R. G. 2004 Reproductive skew. In *Ecology and evolution of cooperative breeding in birds* (eds W. D. Koenig & J. L. Dickinson). Cambridge, UK: Cambridge University Press.
- Marshall, T. C., Slate, J., Kruuk, L. E. B. & Pemberton, J. M. 1998 Statistical confidence for likelihood-based paternity inference in natural populations. *Mol. Ecol.* **7**, 639–655. (doi:10.1046/j.1365-294x.1998.00374.x)
- Richardson, D. S., Jury, F. L., Blaakmeer, K., Komdeur, J. & Burke, T. 2001 Parentage assignment and extra-group paternity in a cooperative breeder: the Seychelles warbler (*Acrocephalus sechellensis*). *Mol. Ecol.* **10**, 2263–2273. (doi:10.1046/j.0962-1083.2001.01355.x)
- 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. R. Soc. B* **272**, 759–767. (doi:10.1098/rspb.2004.3028)
- Sillero-Zubiri, C., Gottelli, D. & Macdonald, D. W. 1996 Male philopatry, extra pack copulations and inbreeding avoidance in Ethiopian wolves (*Canis simensis*). *Behav. Ecol. Sociobiol.* **38**, 331–340. (doi:10.1007/s002650050249)
- Spong, G., Hodge, S. J., Young, A. J. & Clutton-Brock, T. H. Submitted. Factors affecting the reproductive success of dominant male meerkats.
- Stacey, P. B. & Koenig, W. D. (eds) 1990 *Cooperative breeding in birds*. Cambridge, UK: Cambridge University Press.
- Waser, P. M. 1996 Patterns and consequences of dispersal in gregarious carnivores. In *Carnivore behavior, ecology and evolution* (ed. J. L. Gittleman). Ithaca, NY: Cornell University Press.
- Westneat, D. F. & Stewart, I. R. K. 2003 Extra-pair paternity in birds: causes, correlates, and conflict. *Annu. Rev. Ecol. Syst.* **34**, 365–396. (doi:10.1146/annurev.ecolsys.34.011802.132439)
- Whittingham, L. A., Dunn, P. O. & Magrath, R. D. 1997 Relatedness, polyandry and extra-group paternity in the cooperatively-breeding white-browed scrubwren (*Sericornis frontalis*). *Behav. Ecol. Sociobiol.* **40**, 261–270. (doi:10.1007/s002650050341)
- Young, A. J. 2003 Subordinate tactics in cooperative meerkats: helping, breeding and dispersal. PhD thesis, University of Cambridge.
- Young, A. J. & Clutton-Brock, T. H. 2006 Infanticide by subordinates influences reproductive sharing in cooperatively breeding meerkats. *Biol. Lett.* **2**, 385–387. (doi:10.1098/rsbl.2006.0463)
- Young, A. J., Carlson, A. A. & Clutton-Brock, T. 2005 Trade-offs between extra-territorial prospecting and helping in a cooperative mammal. *Anim. Behav.* **70**, 829–837. (doi:10.1016/j.anbehav.2005.01.019)
- Young, A. J., Carlson, A. A., Monfort, S. L., Russell, A. F., Bennett, N. C. & Clutton-Brock, T. H. 2006 Stress and the suppression of subordinate reproduction in cooperatively breeding meerkats. *Proc. Natl Acad. Sci. USA* **103**, 12 005–12 010. (doi:10.1073/pnas.0510038103)