

Genetic structure, relatedness and helping behaviour in the yellow mongoose in a farmland and a natural habitat

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Introduction

Mongoose (family Herpestidae) provide a unique opportunity to study the evolution of behaviour in socially living animals as their social organization ranges from being solitary to being obligatorily social (Rood, 1986). The yellow mongoose *Cynictis penicillata* is of particular interest because it is facultatively social, and appears to represent an intermediate step along the path to communal living and breeding (Balmforth, 2004). Yellow mongooses live in the open semi-arid areas of southern Africa, either solitarily or in family groups of up to four individuals, and forage solitarily or in pairs (Rasa *et al.*, 1992). However, they can also live in larger groups of up to 13 individuals on cultivated farmlands that support high densities of this species (e.g. Balmforth, 2004). Individuals in the large groups in farmland near Heidelberg in the Western Cape Province of South Africa forage together, exhibit communal

Abstract

The yellow mongoose *Cynictis penicillata* is a facultatively social species and provides an opportunity to study the evolution of social behaviour. We examined genetic structure, relatedness and helping behaviour in the yellow mongoose in natural habitat in the Kalahari Desert, where the species lives in small family groups of up to four individuals and shows no cooperative breeding; and in farmland in the Western Cape Province of South Africa, where they live in larger groups of up to 13 individuals, engage in numerous social interactions and show cooperative breeding. The farmland population showed significant inbreeding, and lower genetic variability than the desert population, but there was no evidence of a recent population bottleneck. The genetic relatedness between individuals within social groups and that between future potential helpers and pups were higher in the farmland population than in the desert population. However, based on a limited sample, helping effort (in the farmland population) was not preferentially directed towards kin. Thus, the origin of helping in the farmland population is consistent with kin selection, but in the absence of kin discrimination, future research should investigate whether long-term breeding opportunities or group augmentation contribute to maintaining cooperative breeding in this population.

vigilance and engage in a number of social interactions, although to a lesser extent than in other social mongooses, such as meerkats or dwarf mongooses (Balmforth, 2004). They also show cooperative breeding, in which non-breeding helper males and females, guard, groom and provision young that are not their own. This species, therefore, provides an opportunity to compare social and genetic structure and behaviour across different habitats.

Understanding why individuals in some social species contribute towards the rearing of young that are not their own is central to the study of cooperative breeding. Hypotheses raised to explain helping behaviour include (1) selective neutrality (in which helping is not associated with a cost and is simply a misplaced parental response: Jamieson, 1989); (2) direct benefits such as breeding experience (Solomon & Getz, 1997); (3) an increase in the probability of breeding in the group (Reyer, 1984); (4) payment of rent, in which individuals that do not help are punished (Mulder &

Langmore, 1993); (5) group augmentation, in which group productivity and recruitment increases with each additional helper (Kokko, Johnstone & Clutton-Brock, 2001); (6) kin selection (Emlen & Wrege, 1988), in which behaviours that increase the inclusive fitness of the individual that helps are selected for (Hamilton, 1964). While group augmentation explains the maintenance of cooperative breeding, one of the other factors mentioned above would be required during the initial period of its evolution (Clutton-Brock, 2002). In the obligatorily social meerkat, helping behaviour is explained by group augmentation (Clutton-Brock, 2002) and there is no relationship between helping behaviour and genetic relatedness between helper and pup (Clutton-Brock *et al.*, 2001). However, as the yellow mongoose is only facultatively social, we expected that helping would be directed towards related individuals. By combining genetic data with behavioural and demographic data, we tested the hypothesis that cooperative breeding in the yellow mongoose has arisen through kin selection. If this hypothesis were true, intra-group relatedness, as well as the relatedness between future potential helpers and pups, would be higher in the farmland population compared with the desert population. Kin discrimination would also be predicted to occur, with helping directed only towards kin, and preferentially towards more closely related kin if there is sufficient variability in helper–pup relatedness.

We also compared genetic structure of the populations in the two habitats to elucidate their population history and social structure. Using genetic data based on microsatellite markers we examined genetic diversity, tested for population bottlenecks and estimated past inbreeding, in the context of which present extra-group paternity could be explained. We discuss the possibility of kin selection in the yellow mongoose and the plausibility of other hypotheses that could explain cooperative breeding in this species.

Study area and methods

The two populations studied were in South Africa, in the Kuruman River Reserve and on farmland near Heidelberg. The Kuruman River Reserve (28°58'S, 21°49'E) is in the Kalahari Desert and has open, arid habitat classified as Kalahari Thornveld (Low & Rebelo, 1996). Predators of the yellow mongoose in the reserve included the martial eagle *Polemaetus bellicosus*, black-backed jackal *Canis mesomelas* and the Cape cobra *Naja nivea*: 2.4 ± 2.5 aerial and 0.8 ± 1.1 terrestrial predators were encountered per day (Hollén, Clutton-Brock & Manser, 2008). The density of yellow mongoose was 4–14 individuals km⁻² (depending on the season) and the mean group size was 3.7 ± 0.4 (mean ± SE) individuals (Le Roux, Cherry & Manser, 2008).

The farmland population (34°18'S, 20°48'E) was situated near Heidelberg, ~300 km east of Cape Town and 12 km from the coast. About 20% of this study area had bushy, renosterveld habitat, 45% comprised open, grazed land and 35% was cultivated with wheat, barley or oats. Predation was not a major threat in this population: aerial predators were much less frequently seen than in the desert, jackals

had been shot out by farmers and there was no sighting of the Cape cobra in the farmland during the field study. The density of yellow mongoose was 23–26 individuals km⁻² and the mean group size was 6.3 ± 0.25 (mean ± SE) individuals (Balmforth, 2004).

Most of the detailed data on group composition and behaviour were obtained from nine focal groups in the desert population (see Le Roux, 2007) from January 2004 to July 2006 and five groups in the farmland population from January 2001 to June 2003 (see Balmforth, 2004). Mongooses were habituated by visiting their sleeping burrows daily/frequently and providing them crumbs of hard-boiled egg during the period of habituation. Individuals were identified by marking them with hair dye or tattoos. Individuals in the desert population were also implanted with IdentipetTM (Johannesburg, South Africa) microchip transponders and those in the farmland, with ear tags. Potential helpers were defined as individuals, excluding the breeding pair, that remained with the group when they were older than 4 months of age (since they reach nutritional independence at 4 months of age – Rasa *et al.*, 1992, and can help pups after that). Helping was defined as care shown by individuals towards pups that were not their own. All potential helpers in the farmland population showed helping at some point during the study and were, therefore, considered helpers. Helpers ranged in age from 4 months to over 3 years. The helping behaviours studied were babysitting (in which an individual stayed behind at the sleeping burrow with the pups instead of foraging), pup provisioning (feeding) and pup grooming. Behavioural data on helping were collected *ad libitum* and through scans. The percentage of observation time spent babysitting, frequencies of pup provisioning and grooming and quality of provisioning (based on the sizes of the food items brought) by helpers were recorded. There was no recorded instance of helping in the desert population. Mongooses in the desert population dispersed around the age of 9 months (Le Roux, 2007) and typically were not in their natal territories by the time the next litter was born.

Tissue samples were collected from individuals in both populations as the source of DNA. This was done by live-trapping animals, administering a general anaesthetic (ketamine or ketamine–dopamine mix) and taking tail tip clips. Fifty-five individuals from the Kuruman River Reserve and 100 individuals from the Heidelberg farm were sampled during this study. DNA was extracted using a phenol/chloroform/isoamyl alcohol procedure and purified using Qiagen PCR (Hilden, Germany) purification kits with the manufacturer's protocol. Nine microsatellite loci identified through cross-species amplification (T.N.C. Vidya, unpub. data) were used to genotype individuals. PCR products were electrophoresed on an ABI 3130xl Genetic Analyzer (at the University of Stellenbosch Sequencing Facility) to obtain allele sizes, which were analysed using GeneMapper Software v.3.7 (Applied Biosystems, 2004).

Population-specific F_{IS} (the inbreeding coefficient) was calculated and its statistical significance tested using Arlequin v.3.1 (Excoffier, Laval & Schneider, 2005). The

programme BOTTLENECK v.1.2.02 (Piry, Luikart & Cornuet, 1997) was used to check for recent population bottlenecks. We used the two-phase model of mutation as recommended by the authors of the programme to detect significant heterozygosity excess (under mutation–drift equilibrium) displayed by populations that have recently experienced a bottleneck (see Cornuet & Luikart, 1996). A graphical test was conducted to detect a mode-shift in the frequency distribution of allele frequencies, from rare alleles (allele frequencies of 0.001–0.01) having the highest frequency in natural populations to intermediate frequency (0.101–0.900) alleles showing high frequency in recently bottlenecked populations (Luikart *et al.*, 1998).

Genetic relatedness between individuals was calculated using Relatedness 5.0.8 (<http://www.gsoftnet.us/GSoft.html>; see Queller & Goodnight, 1989). Standard error was obtained by a jackknifing procedure across groups being analysed. Relatedness was calculated between individuals within groups in the two populations, and also between pups from one breeding event (which could have been potential helpers in the future if they had remained in the natal group) and the pups of the subsequent breeding event (separated by at least 4 months; litters within a 4-month period were considered a single litter because pups reach nutritional independence at 4 months of age and cannot help before that) in the same social group. The latter comparison potentially includes emigrants and individuals that die before the birth of the next litter, and excludes immigrants, but as there were no helpers in the desert population, we measured the relatedness between pups and future potential helpers so that the same criterion would be used in both populations. To examine helping behaviour in relation to relatedness, each pair of individuals was assigned to a relatedness class such as full-sibs, half-sibs or unrelated individuals using Kinship 1.3.1 (<http://www.gsoftnet.us/GSoft.html>; see Goodnight & Queller, 1999). Mothers identified through field observations (of abdominal swelling and lactation) and captures were confirmed using genetic data (using the Kinship software). The adult male with the highest dominance rank was designated as the breeding male or social father of the group. Using the genotypes of the mother and pups, whether or not the genetic father was present within the group was determined through exclusion. Statistical tests were carried out using Statistica version 8.0 (StatSoft Inc., 2007).

Results

Genetic relatedness within social groups, and between pups and future potential helpers

The average relatedness (mean \pm 95% CI) within social groups was 0.183 ± 0.092 (SE = 0.047; 20 group breeding events in all for 11 groups) in the desert population and 0.355 ± 0.081 (SE = 0.041; 24 group breeding events in all for 15 groups) in the farmland population (Table 1). The

Table 1 Relatedness within yellow mongoose *Cynictis penicillata* social groups in the desert and farmland populations

	Number of groups	Mean		95% CI
		intra-group relatedness	SE	
Desert				
End 2003–beginning 2004	5	0.198	0.039	0.109
End 2004–beginning 2005	6	0.297	0.054	0.139
End 2005–beginning 2006	5	0.345	0.178	0.495
End 2006–beginning 2007	4	0.104	0.038	0.121
Farmland				
End 2000–beginning 2001	7	0.275	0.052	0.128
September 2001	5	0.417	0.076	0.210
End 2001–beginning 2002	2	0.480	0.055	0.695
September 2002	6	0.392	0.080	0.206
End 2002–beginning 2003	4	0.423	0.078	0.249

Both adults and pups were included in the calculation of intra-group relatedness.

Table 2 Mixed model ANOVA of intra-group relatedness in desert and farmland populations of the yellow mongoose *Cynictis penicillata* using group as a random effect

Source	d.f.	MS	F	P value
Habitat (fixed effect)	1	2.475	67.182	<0.001
Group (random effect)	24	0.042	2.815	0.014
Error	18	0.015		

relatedness within social groups was significantly higher in the farmland population than in the desert population based on a two-sample *t*-test using average relatedness for groups with more than one breeding event ($t = -2.678$, d.f. = 24, $P = 0.013$) and a mixed model ANOVA with group as a random term (see Table 2).

The relatedness (mean \pm 95% CI) between pups and future potential helpers was 0.273 ± 0.180 (SE = 0.081, range: -0.136 to 0.470 , 11 pairwise comparisons) in the desert population and 0.445 ± 0.321 (SE = 0.101, range: 0.227 – 0.684 , four pairwise comparisons) in the farmland population. The latter was significantly higher than the relatedness between pups and future potential helpers in the desert population (Mann–Whitney *U*-test, $U = 4.0$, $Z_{adj} = -2.35$, $P = 0.019$; see Table 3 for mixed model ANOVA with group as a random term). All the pups (future potential helpers) that were recorded during the subsequent season in the farmland population showed some level of helping, although there was variation in the amount and kind of help given. In the absence of radio-collared animals, it was assumed that the individuals that were not recorded subsequently had died, although we cannot rule out the possibility of their having dispersed outside the study area.

Inbreeding, genetic diversity and population bottlenecks in the two populations

In the desert population, from 36 pups born into 21 litters, only 18 pups from nine litters were fathered by the social

Table 3 Mixed model ANOVA of relatedness between pups and future potential helpers in the desert and farmland populations using group as a random effect

Source	d.f.	MS	F	P value
Habitat (fixed effect)	1	1.207	25.748	<0.001
Group (random effect)	6	0.048	1.109	0.441
Error	7	0.043		

Table 4 Polymorphism and heterozygosity of microsatellite loci in two yellow mongoose *Cynictis penicillata* populations

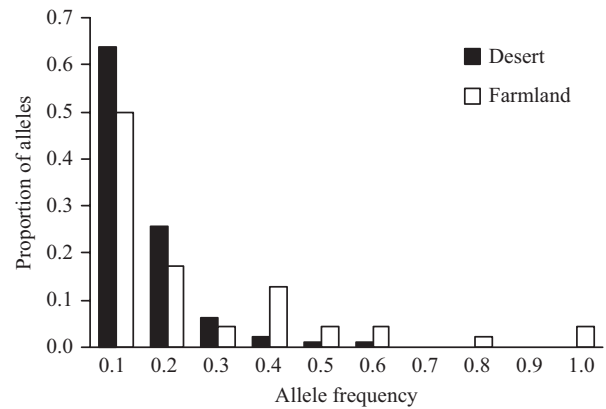
Locus	Number of alleles		Observed heterozygosity	
	Desert	Farmland	Desert	Farmland
MmAAAC5	5	2	0.545	0.040
Mm10-7	10	5	0.870	0.370
Mm18-2	8	5	0.600	0.186
Ss11.12	16	7	0.870	0.610
Ss10.1	13	5	0.873	0.550
Hj56	5	2	0.611	0.050
Mm19	14	6	0.889	0.640
Ss7.1	14	7	0.945	0.730
FCA45	12	6	0.759	0.790

The number of alleles and heterozygosity were significantly lower in farmland ($n=55$) compared with the desert ($n=100$) (Wilcoxon's matched pairs test, $Z=2.666$, $P=0.008$ for the difference between alleles, $Z=2.547$, $P=0.011$ for the difference in heterozygosity).

father. In the farmland population, from 15 pups born into seven litters, only five pups (33%) were fathered by the social father, and females were observed to mate with multiple males, all outside the natal group. There was genetic evidence for multiple paternity within litters in two of the seven litters analysed in the farmland population. However, genetic data showed significant inbreeding in the farmland population ($F_{IS} = 0.124$, $P < 0.001$) and no inbreeding in the desert population ($F_{IS} = 0.039$, $P = 0.081$), and genetic diversity was lower in the farmland than in the desert population (Table 4). The lower diversity had not ensued from a population bottleneck. The test for heterozygosity excess was not significant in the farmland population (Wilcoxon's one-tailed test for heterozygosity excess: $P = 0.715$) but was significant in the desert population (Wilcoxon's one-tailed test for heterozygosity excess: $P = 0.001$). Allele frequency distributions were normal with no mode-shift in either population (Fig. 1).

Kin discrimination in the farmland population

There was no helping in the desert population. We examined helping behaviour in the farmland population, in relation to the average relatedness (classified as full-sibs, half-sibs or unrelated individuals) between helpers and the pups of the litter, and found that 10 out of 15 helpers were related (as full- or half-sibs) to the pups, while five were not related.

**Figure 1** Proportion of alleles of different allele frequencies in desert and farmland populations of the yellow mongoose *Cynictis penicillata*.

Two of the five were related to the breeding females while the relatedness levels between the other three and the breeding females are not known. There was no difference in the percentage of observation time spent babysitting, the proportion of feeding or grooming events (of the total number of feeding or grooming events by all helpers during the breeding event) or the proportion of food provided (of the total quantity of food provided by all helpers during the breeding event) by helpers towards related and unrelated litters (Mann–Whitney U -test for data on babysitting: $n_{\text{related}} = 9$, $n_{\text{unrelated}} = 5$, $U = 12.0$, $P = 0.162$; Mann–Whitney U -test for data on frequency of provisioning: $n_{\text{related}} = 10$, $n_{\text{unrelated}} = 5$, $U = 11.0$, $P = 0.085$; Mann–Whitney U -test for data on quantity of provisioning: $n_{\text{related}} = 10$, $n_{\text{unrelated}} = 5$, $U = 15.0$, $P = 0.219$; Mann–Whitney U -test for grooming data: $n_{\text{related}} = 10$, $n_{\text{unrelated}} = 5$, $U = 22.0$, $P = 0.768$). There was also no difference in help provided towards full-sib and unrelated litters, based on a small sample size (Mann–Whitney U -test for data on babysitting: $n_{\text{full-sib}} = 5$, $n_{\text{unrelated}} = 5$, $U = 4.0$, $P = 0.076$; Mann–Whitney U -test for data on frequency of provisioning: $n_{\text{full-sib}} = 6$, $n_{\text{unrelated}} = 5$, $U = 10.0$, $P = 0.357$; Mann–Whitney U -test for data on quantity of provisioning: $n_{\text{full-sib}} = 6$, $n_{\text{unrelated}} = 5$, $U = 10.0$, $P = 0.357$; Mann–Whitney U -test for grooming data: $n_{\text{full-sib}} = 6$, $n_{\text{unrelated}} = 5$, $U = 13.0$, $P = 0.715$) (Fig. 2). When data were analysed by pup, neither provisioning nor grooming received by pups from unrelated helpers and from full-sib helpers was different (Wilcoxon's matched-pairs test for data on frequency of provisioning: $n = 5$ comparisons, $Z = 0.73$, $P = 0.465$; Wilcoxon's matched-pairs test for data on quantity of provisioning: $n = 5$ comparisons, $Z = 0.73$, $P = 0.465$; Wilcoxon's matched pairs test for grooming data: $n = 5$ comparisons, $Z = 0.37$, $P = 0.715$). There were only three instances in which helpers showed different categories of relatedness to pups within litters. Of these, there was a higher frequency of provisioning food for full-sibs than for unrelated pups in two instances and the reverse in the third, and a higher frequency of grooming full-sibs than unrelated pups in all three

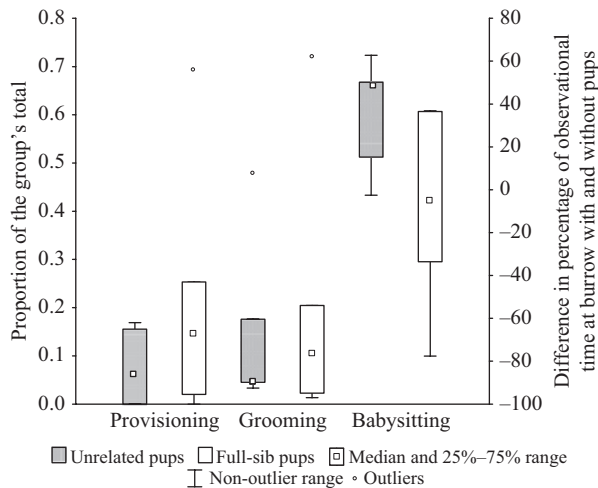


Figure 2 Proportion of the group's total provisioning and grooming provided by helpers on the left Y-axis and difference in percentage of observation time spent by helpers at burrows with and without pups on the right Y-axis. Helping towards unrelated pups is shown as hatched boxes and helping towards full-sib pups as open boxes.

instances. Babysitting data could not be analysed by pup, because all pups were present when helpers babysat at the burrow.

Discussion

Inbreeding and extra-group paternity

The lower diversity in the farmland population compared with the desert population did not result from a population bottleneck, but could have arisen from past inbreeding. We found genetic evidence of significant inbreeding in the farmland population, but during the present study, two-thirds of the fathers came from outside the pups' social groups. It is possible that such extra-group mating is a response to reduce inbreeding. Varying levels of inbreeding depression have been found in several taxa (Ralls & Ballou, 1982; see Keller & Waller, 2002) and inbreeding avoidance appears important in cooperatively breeding mammals such as prairie voles (Carter & Roberts, 1997) and callitrichid primates (French, 1997). Significant inbreeding coefficients have also been recorded in the obligatorily social dwarf mongoose *Helogale parvula* but mating continues to be largely within the group (Keane, Creel & Waser, 1996). In the facultatively social European badger *Meles meles*, extra-group paternity of about 50% is thought to serve to lower inbreeding (the F_{IS} over an 18-year period in Dugdale *et al.*'s (2007) study population was 0.08 ± 0.02 (mean \pm 95% CI); H. Dugdale, unpubl. data) and make philopatry less costly (Carpenter *et al.*, 2005; Dugdale *et al.*, 2007). In contrast, in meerkats, in which there is no reported significant inbreeding, dominant males fathered 77% of the pups (80% of litters) (Griffin *et al.*, 2003).

Kinship and helping behaviour

Intra-group relatedness was higher in the farmland population than in the desert population. This difference was not an artefact of the lower diversity or significant inbreeding coefficient in the farmland population, as relatedness was calculated taking basal population allele frequencies into account. The higher intra-group and future potential helper-pup relatedness in the farmland population point to possible kin selected benefits of helping. However, a few unrelated individuals also helped in the farmland population and there was no kin discrimination during helping, although this was based on a very small sample size. The effect of kinship on helping has been shown in cooperatively breeding species such as the brown hyaena (Owens & Owens, 1984), but the demonstration of kin discrimination in helping effort is rare. While an effect of kinship on the incidence of provisioning and kin discrimination with respect to choosing a nest to help at has been shown in some cooperatively breeding birds (Curry, 1988; Emlen & Wrege, 1988; Dickinson, Koenig & Pitelka, 1996; Russell & Hatchwell, 2001), kin discrimination in the rate of provisioning has been shown only among female Seychelles warblers *Acrocephalus sechellensis* (Komdeur, 1994; Richardson, Burke & Komdeur, 2003). However, a meta-analysis indicated that kin discrimination occurs frequently but the sample size required to reject the null hypothesis with high certainty in individual studies is very high (Griffin & West, 2003). Even if helping within social groups is indiscriminate, kin selection can operate if the mean relatedness between helpers and recipients is high enough to satisfy Hamilton's (1964) rule (Keller, 1997). Although we have not carried out a cost-benefit analysis of helping here, the average relatedness between individuals within social groups in the farmland population of yellow mongoose was high, and the same principle may apply here.

Alternative hypotheses explaining helping behaviour

Alternative hypotheses explaining helping behaviour include selective neutrality, payment of rent, direct benefits (such as breeding experience or an increase in the probability of breeding in the group), group augmentation and kin selection. Social mongooses are thought to have evolved from solitary, nocturnal and forest-dwelling ancestors during the Pleistocene (Veron *et al.*, 2004; see Rood, 1986). The yellow mongoose falls within the solitary mongoose clade, and sociality in this species has originated independently and, possibly, recently (Veron *et al.*, 2004). The independent origin of helping behaviour, therefore, precludes the 'phylogenetic inertia' hypothesis (Edwards & Naeem, 1993), according to which cooperative breeding, once having arisen in a lineage, can persist in the absence of selection favouring it.

Helping has been shown to be costly in meerkats (Clutton-Brock *et al.*, 1998), banded mongooses (Hodge, 2007) and African wild dogs (Courchamp, Rasmussen & Macdonald, 2002). As yellow mongoose helpers give up food to

pups (Balmforth, 2004), helping in this species is also unlikely to be a selectively neutral behaviour that arose due to misplaced parental instinct to feed begging young. Helping as a form of payment of rent is also unlikely because there was no eviction of 'bad' helpers (Balmforth, 2004). There is nothing to suggest that breeding experience would be required in the farmland population but not in the desert population (the reverse would be more likely given lower resource availability in the desert) and, therefore, breeding experience is probably not a key factor that gives rise to cooperative breeding in this species.

Males within social groups in the farmland population fathered only one-third of the pups and those males that did father pups were not offspring from the previous year, or (for the third year of the study) from the two previous years, but were adults of older unknown ages. Both sexes dispersed at a high rate (at the age of 12–18 months), suggesting that philopatry was not a common route to breeding (Balmforth, 2004). We cannot, however, rule out the possibility that some individuals remain in their natal groups for several years and thereafter gain breeding opportunities. Of 15 group breeding events that were observed in detail in the farmland population, multiple breeding females were present in five group breeding events (three groups). In two group breeding events (from the same group), one of the three breeding females was unrelated to the other two, but in all other instances, the breeding females were related as full-sibs or mother–offspring. None of these females were offspring from the previous year or, for the breeding events during the third year of the study, from the two previous years. A long-term study would be required to evaluate the direct breeding opportunities helpers gain from remaining in the natal group for extended periods of time.

Delayed dispersal in cooperative breeders

In the desert population, individuals always dispersed by around 9 months of age (Le Roux, 2007) and became parents almost immediately after dispersal if they found a mate (Le Roux, unpubl. data). Therefore, there was no delayed dispersal. While predation killed 55% of adults and 28% of immature individuals (Le Roux, 2007) in the desert population, predation did not appear to be a major threat in the farmland population. No incident of predation was observed during the 28-month study period, and sociality was probably a response to high population density arising from increased resource availability and reduced predation pressure. Similar scenarios have been proposed for some other facultatively social species. Increased population density due to food availability and relaxation of predation pressure is thought to have fostered group formation through natal philopatry in the prairie vole *Microtus ochrogaster* (Getz *et al.*, 2006; Lucia *et al.*, 2008). Natal philopatry due to habitat saturation has also been observed in the facultatively social European badgers in pastoral landscapes in southern England (Kruuk & Parish, 1982), cooperatively breeding Florida scrub-jays *Aphelocoma coerulescens* (Woolfenden & Fitzpatrick, 1984), Galapagos

mockingbirds (Curry, 1989) and Seychelles warblers *Acrocephalus sechellensis* (Komdeur, 1992). Following delayed dispersal due to habitat saturation, the origin of helping in the farmland population of yellow mongooses is consistent with kin selection. This would not necessarily rely on the development of kin discrimination mechanisms, especially given the high level of intra-group relatedness. In meerkats, in which group augmentation is thought to maintain cooperative breeding that originated through kin selection, the overall relatedness between helpers and pups is high and there is no kin discrimination by helpers (Clutton-Brock *et al.*, 2001). It remains to be seen if group augmentation or long-term breeding opportunities additionally contribute to maintaining cooperative breeding in the farmland population of the yellow mongoose.

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References

- Applied Biosystems. (2004). *GeneMapper Software, version 3.7*. Foster City, USA: Applied Biosystems.
- Balmforth, Z.E. (2004). *The demographics, spatial structure and behaviour of the yellow mongoose, Cynictis penicillata, with emphasis on cooperative breeding*. DPhil thesis, University of Sussex at Sussex.
- Carpenter, P.J., Pope, L.C., Greig, C., Dawson, D.A., Rogers, L.M., Erven, K., Wilson, G.J., Delahay, R.J., Cheeseman, C.L. & Burke, T. (2005). Mating system of the Eurasian badger, *Meles meles*, in a high density population. *Mol. Ecol.* **14**, 273–284.
- Carter, C.S. & Roberts, R.L. (1997). The psychobiological basis of cooperative breeding in rodents. In *Cooperative breeding in mammals*: 34–75. Solomon, N.G. & French, J.A. (Eds). New York: Cambridge University Press.
- Clutton-Brock, T.H. (2002). Breeding together: kin selection and mutualism in cooperative vertebrates. *Science* **296**, 69–72.
- Clutton-Brock, T.H., Brotherton, P.N.M., O'Riain, M.J., Griffin, A.S., Gaynor, D., Kansky, R., Sharpe, L. & McIlrath, G.M. (2001). Contributions to cooperative rearing in meerkats. *Anim. Behav.* **61**, 705–710.
- Clutton-Brock, T.H., Gaynor, D., Kansky, R., MacColl, A.D.C., McIlrath, G., Chadwick, P., Brotherton, P.N.M.,

- O'Riain, J.M., Manser, M. & Skinner, J.D. (1998). Costs of cooperative behaviour in suricates (*Suricata suricatta*). *Proc. Roy. Soc. Lond. Ser. B Biol. Sci.* **265**, 185–190.
- Cornuet, J.-M. & Luikart, G. (1996). Description and power analysis of two tests for detecting recent population bottlenecks from allele frequency data. *Genetics* **144**, 2001–2014.
- Courchamp, F., Rasmussen, G.S.A. & Macdonald, D.W. (2002). Small pack size imposes a trade-off between hunting and pup-guarding in the painted hunting dog *Lycaon pictus*. *Behav. Ecol.* **13**, 20–27.
- Curry, R.L. (1988). Influence of kinship on helping behaviour in Galapagos mockingbirds. *Behav. Ecol. Sociobiol.* **22**, 141–152.
- Curry, R.L. (1989). Geographic variation in social organization of Galápagos mockingbirds: ecological correlates of group territoriality and cooperative breeding. *Behav. Ecol. Sociobiol.* **25**, 147–160.
- Dickinson, J.L., Koenig, W.D. & Pitelka, F.A. (1996). The fitness consequences of helping behavior in the western bluebird. *Behav. Ecol.* **7**, 168–177.
- Dugdale, H.L., Macdonald, D.W., Pope, L.C. & Burke, T. (2007). Polygynandry, extra-group paternity and multiple-paternity litters in European badger (*Meles meles*) social groups. *Mol. Ecol.* **16**, 5294–5306.
- Edwards, S.V. & Naem, S. (1993). The phylogenetic component of cooperative breeding in perching birds. *Am. Nat.* **141**, 754–789.
- Emlen, S.T. & Wrege, P.H. (1988). The role of kinship in helping decisions among white-fronted bee-eaters. *Behav. Ecol. Sociobiol.* **23**, 305–315.
- Excoffier, L., Laval, G. & Schneider, S. (2005). Arlequin ver. 3.0: an integrated software package for population genetics data analysis. *Evol. Bioinform. Online* **1**, 47–50.
- French, J.A. (1997). Regulation of singular breeding in callitrichid primates. In *Cooperative breeding in mammals*: 34–75. Solomon, N.G. & French, J.A. (Eds). New York: Cambridge University Press.
- Getz, L.L., Oli, M.K., Hofmann, J.E. & McGuire, B. (2006). Vole population fluctuations: factors that initiate and determine intervals between them in *Microtus ochrogaster*. *J. Mammal.* **87**, 387–393.
- Goodnight, K.F. & Queller, D.C. (1999). Computer software for performing likelihood tests of pedigree relationship using genetic markers. *Mol. Ecol.* **8**, 1231–1234.
- Griffin, A.S., Pemberton, J.M., Brotherton, P.N.M., McIlrath, G., Gaynor, D., Kansky, 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.
- Griffin, A.S. & West, S.A. (2003). Kin discrimination and the benefit of helping in cooperatively breeding vertebrates. *Science* **302**, 634–636.
- Hamilton, W.D. (1964). The evolution of altruistic behaviour. *Am. Nat.* **97**, 354–356.
- Hodge, S.J. (2007). Counting the costs: the evolution of male-biased care in the cooperative breeding banded mongoose. *Anim. Behav.* **74**, 911–919.
- Hollén, L.I., Clutton-Brock, T. & Manser, M.B. (2008). Ontogenetic changes in alarm-call production and usage in meerkats (*Suricata suricatta*): adaptations or constraints? *Behav. Ecol. Sociobiol.* **62**, 821–829.
- Jamieson, I.G. (1989). 'Behavioural heterochrony and the evolution of birds' helping at the nest: an unselected consequence of communal breeding. *Am. Nat.* **133**, 394–406.
- Keane, B., Creel, S.R. & Waser, P.M. (1996). No evidence of inbreeding avoidance or inbreeding depression in a social carnivore. *Behav. Ecol.* **7**, 480–489.
- Keller, L. (1997). Indiscriminate altruism: unduly nice parents and siblings. *Trends Ecol. Evol.* **12**, 99–103.
- Keller, L.F. & Waller, D.M. (2002). Inbreeding effects in wild populations. *Trends Ecol. Evol.* **17**, 230–241.
- Kokko, H., Johnstone, R.A. & Clutton-Brock, T.H. (2001). The evolution of cooperative breeding through group augmentation. *Proc. Roy. Soc. Lond. Ser. B Biol. Sci.* **268**, 187–196.
- Komdeur, J. (1992). Importance of habitat saturation and territory quality for evolution of cooperative breeding in the Seychelles warbler. *Nature* **358**, 493–495.
- Komdeur, J. (1994). The effect of kinship on helping in the cooperative breeding Seychelles warbler (*Acrocephalus sechellensis*). *Proc. Roy. Soc. Lond. Ser. B Biol. Sci.* **256**, 47–52.
- Kruuk, H.H. & Parish, T. (1982). Factors affecting population density, group size and territory size of the European badger, *Meles meles*. *J. Zool. (Lond.)* **196**, 31–39.
- Le Roux, A. (2007). *Communication in the yellow mongoose, Cynictis penicillata*. PhD thesis, Stellenbosch University at Stellenbosch.
- Le Roux, A., Cherry, M.I. & Manser, M.B. (2008). The effect of population density and sociality on scent marking in the yellow mongoose. *J. Zool. (Lond.)* **275**, 33–40.
- Low, A.B. & Rebelo, A.G. (1996). *Vegetation of Southern Africa, Lesotho and Swaziland*. Pretoria: Department of Environmental Affairs and Tourism.
- Lucia, K.E., Keane, B., Hayes, L.D., Lin, Y.K., Schaefer, R.L. & Solomon, N.G. (2008). Philopatry in prairie voles: an evaluation of the habitat saturation hypothesis. *Behav. Ecol.* **19**, 774–783.
- Luikart, G., Allendorf, F., Cornuet, J.-M. & Sherwin, W. (1998). Distortion of allele frequency distributions provides a test for recent population bottlenecks. *J. Hered.* **89**, 238–247.
- Mulder, R.A. & Langmore, N.E. (1993). Dominant males punish helpers for temporary defection in superb fairy-wrens. *Anim. Behav.* **45**, 830–833.
- Owens, D.D. & Owens, M.J. (1984). Helping behaviour in brown hyenas. *Nature* **308**, 843–845.
- Piry, S., Luikart, G. & Cornuet, J.-M. (1997). *BOTTLE-NECK A program for detecting recent effective population*

- size reductions from allele frequency data*. Montpellier: Laboratoire de Modélisation et Biologie Evolutive.
- Queller, D.C. & Goodnight, K.F. (1989). Estimating relatedness using genetic markers. *Evolution* **43**, 258–275.
- Ralls, K. & Ballou, J. (1982). Effects of inbreeding on infant mortality in captive primates. *Int. J. Primatol.* **3**, 491–505.
- Rasa, O.A.E., Wenhold, B.A., Howard, P., Marais, A. & Pallett, J. (1992). Reproduction in the yellow mongoose revisited. *S. Afr. J. Zool.* **27**, 192–195.
- Reyer, H.-U. (1984). Investment and relatedness: a cost/benefit analysis of breeding and helping in the pied kingfisher (*Ceryle rudis*). *Anim. Behav.* **32**, 1163–1178.
- Richardson, D.S., Burke, T. & Komdeur, J. (2003). Sex-specific associative learning cues and inclusive fitness benefits in the Seychelles warbler. *J. Evol. Biol.* **16**, 854–861.
- Rood, J.P. (1986). Ecology and social evolution in the mongooses. In *Ecological aspects of social evolution*: 131–152. Rubenstein, D.I. & Wrangham, R.W. (Eds). Princeton: Princeton University Press.
- Russell, A.F. & Hatchwell, B.J. (2001). Experimental evidence for kin-biased helping in a cooperatively breeding vertebrate. *Proc. Roy. Soc. Lond. Ser. B Biol. Sci.* **268**, 2169–2174.
- Solomon, N.G. & Getz, L.L. (1997). Examination of alternative hypotheses for cooperative breeding in rodents. In *Cooperative breeding in mammals*: 199–230. Solomon, N.G. & French, J.A. (Eds). Cambridge: Cambridge University Press.
- StatSoft Inc. (2007). Statistica (data analysis software system), version 8.0. <http://www.statsoft.com>
- Veron, G., Colyn, M., Dunham, A.E., Taylor, P. & Gaubert, P. (2004). Molecular systematics and origin of sociality in mongooses (Herpestidae, Carnivora). *Mol. Phylogenet. Evol.* **30**, 582–598.
- Woolfenden, E. & Fitzpatrick, J.W. (1984). *The Florida scrub jay: demography of a cooperative breeding bird*. Princeton: Princeton University Press.