The effects of population density and sociality on scent marking in the yellow mongoose

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Abstract

We investigated scent marking in the yellow mongoose *Cynictis penicillata* focusing on a low-density population where all offspring dispersed upon reaching sexual maturity. Dominant males appeared to be the main territory defenders and demarcators, with offspring foraging and marking only near the territory cores. The cheek-marking rates of dominant males increased during the breeding season and may have been involved in olfactory mate guarding. We compared our low-density population with a high-density population displaying natal philopatry. The two populations differed markedly in terms of individual contributions to territorial marking, as subordinate group members in the low-density population performed almost no territorial marking or defence, but were the primary scent-markers and territory defenders in the high-density population. We discuss scent-marking distinctions between populations in the context of ecological and social differences.

Introduction

Scent-marking forms an integral part of the communicative repertoire of many mammals (Eisenberg & Kleiman, 1974; Gorman & Trowbridge, 1989). Marking rates typically increase around the onset of puberty (e.g. Woodmansee *et al*., 1991), and many mammals are able to discriminate between individuals' scents (Swaisgood, Lindburg & Zhou, 1999; Mendl, Randle & Pope, 2002; Mateo, 2006). In solitary animals, age, gender and territory ownership appear to be the main determinants of scent-marking rates (e.g. in honey badgers *Mellivora capensis* Begg, du Toit & Mills, 2003), whereas social mammals are, additionally, affected by position in the dominance hierarchy, relative contributions to territory defence and the frequency of aggressive interactions (e.g. coyotes *Canis latrans* Gese & Ruff, 1997). Although the dominant male in a social group is usually the primary scent marker, subordinate adults often contribute substantially to territorial marking and defence (Gese & Ruff, 1997; Jordan, 2007). Additionally, males may over-mark females' scent, as a form of olfactory mate guarding (e.g. Brashares & Arcese, 1999), or other males' scents, indicating intrasexual dominance (e.g. Rich & Hurst, 1999). Within a social group, allo-marking – marking other individuals – often occurs, probably to maintain a 'familiar' group smell and tolerance between group members (e.g. in European badgers *Meles meles* Buesching, Stopka & MacDonald, 2003).

The yellow mongoose *Cynictis penicillata* dens together with conspecifics in groups ranging between two and 13 individuals in size, but individuals typically forage alone or in pairs (Rasa *et al*., 1992; Cavallini, 1993). Females are polyoestrous, occasionally giving birth to two litters per season, and young typically disperse during spring (Rasa *et al*., 1992). Similar to many mammals (Gorman & Trowbridge, 1989), the yellow mongoose is territorial and uses various forms of marking in its territory (Earlé, 1981; Wenhold & Rasa, 1994). Yellow mongooses mark vegetation and other prominent objects using anal marks, cheek marks ('cheek wipes') and body rubs ('sidewipes') (after Earlé, 1981; Wenhold & Rasa, 1994). Body rubbing appears to be a form of self-anointing with odours (including own scent marks) from the environment, rather than the actual deposition of scent, as yellow mongooses lack scent glands on their flanks (Pocock, 1916). Urination and defecation are considered secondary forms of marking (e.g. Wenhold & Rasa, 1994), and we have not included them in this study as there was no evidence of a primary communicative function (le Roux, 2007).

Scent marking in the yellow mongoose has been described in varying degrees of detail in populations of intermediate to high densities [23–26 individuals km^{-2} (Balmforth, 2004) to 133–200 individuals km^{-2} (Earlé, 1981; Wenhold & Rasa, 1994)]. Of these studies, only Wenhold & Rasa's (1994) quantified the marking behaviour of a group of mongooses ($n = 13$ group members) and tested specific hypotheses. They presented individuals' marking rates as averages over 9 months (April–December) (Wenhold & Rasa, 1994). Whereas Wenhold & Rasa (1994) showed that subordinate adults were the primary territory defenders and markers,

Earlé (1981) found in the same Big Island (BI) population in the Vaal Dam (26°52′S, 28°11′E), South Africa, that the dominant males played the main role in this respect.

We focused our research on a low-density population of yellow mongooses at the Kuruman River Reserve (KRR) in South Africa. The mated pair constituted the only adult members of each group and offspring were not involved in raising new litters but dispersed on reaching sexual maturity. Similar to other low-density populations (Cavallini, 1993), aggression between family members and neighbours was low. In contrast, groups in the BI population consisted of the mated pair, recent offspring and related adults that cooperated in the rearing of young and aggressive territory defence (Earlé, 1981; Wenhold, 1990; Wenhold & Rasa, 1994).

Here, we describe the scent marking in the KRR population and compare it with that of the BI population (Wenhold & Rasa, 1994). We predicted that, as in many mammals (Ralls, 1971), the dominant male would be the main territory defender in terms of scent marking and active defence. As territory sizes were much larger in the KRR than the BI population, the KRR population may use a hinterland-marking strategy. We did not expect adult females or offspring to show strongly territorial behaviour. We predicted that offspring would show no evidence of sexual advertisement, as they rarely encountered potential mates before dispersal, and did not stay in the natal territory as adults.

Materials and methods

We studied a habituated population of wild yellow mongooses at the KRR (28°58′S, 21°49′E), South Africa (le Roux, Cherry & Manser, in press). The study area included the dry Kuruman River bed and the surrounding dune areas, primarily covered in low shrubs, *Acacia* trees and grasses (Clutton-Brock *et al.*, 1998). The field site had a large number of bolt-holes and potential sleeping burrows (Manser & Bell, 2004) maintained and used by yellow mongooses, meerkats *Suricata suricatta* and Cape ground squirrel *Xerus inauris*. During the study period from February 2004 to March 2006, we collected data for six adult (dominant) males, 10 of their offspring (four males, six females) and one adult (dominant) female. Offspring were classified as pups (0–3 months), juveniles (3–6 months) and sub-adults (up to 12 months), and adults were older than 1 year of age. In each group, one adult animal was radio collared with collars from Sirtrack© (Havelock North, New Zealand), and non-collared individuals were identified through non-permanent, renewable dye-marks on their fur (for more details, see le Roux *et al.*, in press). We were able to follow all these habituated animals at a distance of < 5 m. We obtained the following number of sessions for individuals: adult males: 30 ± 2.9 (mean $\pm$ SE); offspring: 19 ± 6.7 and adult female: 14.

During active foraging periods, we recorded the position of focal animals at 10-min intervals and the location of all scent marks, using all-occurrence sampling, on an eTrex

Garmin® (Olathe, KS, USA) global positioning system (GPS), to an accuracy of < 10 m. Observational data were collected using a handheld computer (Psion organiser II model LZ64, Bourne End, UK). Each scent-marking act was typically preceded by sniffing the object to be marked. We described the object (or individual) marked and whether or not it was within 2 m of a bolt-hole or sleeping burrow. During morning observation sessions, we noted all marking acts from the time of emergence, but hourly marking rates were determined using only data from active foraging periods away from the sleeping burrow in the morning and afternoon. Some marking occurred at the sleeping burrow before foraging trips, and these data were included in the ArcView GIS data that we used to determine scent-mark densities.

Spatial data were analysed using ArcView GIS and its animal movements extension (Hooge, Eichenlaub & Solomon, 1999). Using all coordinates recorded at 10-min intervals, we determined home-range sizes as the 95% kernel, with least-squares cross-validation smoothing factors (Worton, 1989; Seaman *et al.*, 1999). Although autocorrelation between successive data points may reduce the accuracy of home-range estimations (Swihart & Slade, 1985), we used a data collection protocol that allowed us to retain all these data in our calculations. The effect of autocorrelation is typically addressed by subsampling the spatial dataset (e.g. Jordan, Cherry & Manser, 2007). However, de Solla, Bonduriansky & Brooks (1999) demonstrated that using the entire dataset could improve home-range estimations substantially, compared with subsampling, if data were collected with a constant sampling interval over an extended period of time. Our regular data collection spanning several months satisfied these recommendations and the number of GPS points per individual [adult males: 310 ± 64.3 (mean $\pm$ SD); offspring: 115 ± 60.2 and dominant female: 80 points] exceeded the recommended minimum of 50 points for home-range estimations (Seaman *et al.*, 1999).

We defined adult males' home ranges as territories, as these areas were defended against intruders from other groups (Maher & Lott, 1995). The undefended areas occupied by offspring and the dominant female were termed home ranges. We defined core and border areas (Fig. 1) following Jordan *et al.*'s (2007) categorization of meerkat territory areas at the same study site. The area between the 85 and 95% kernel was the 'territory border' and the 65% kernel, the 'territory core'. The area between the territory border and core was the 'kernel border'. Densities of scent marks were calculated for each of these areas and also for the whole area inside the border (i.e. the entire 85% kernel).

Owing to small sample sizes, we used mainly nonparametric statistical techniques (Siegel & Castellan, 1988), in the programme R for Microsoft Windows, version 2.3.1 (R Development Core Team, 2006). When *t*-tests were appropriate, we used unequal variance *t*-tests of the ranked data (Ruxton, 2006). Results are all presented as means $\pm$ SE unless indicated otherwise. During the summer season, we could not record all activities, for individuals were usually highly active after sunset and impossible to follow even with
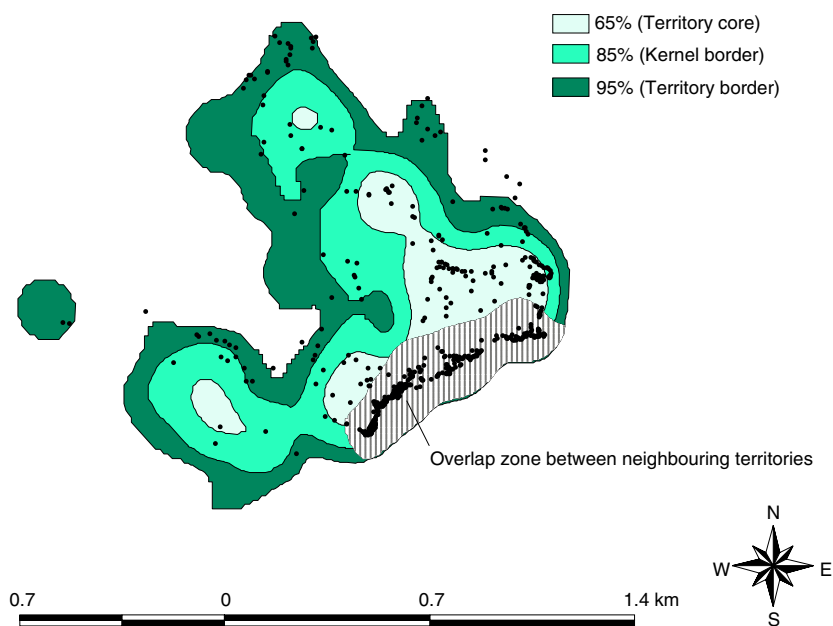
Figure 1 The main subdivisions of territory areas are shown for dominant male CM03. Anal marks are indicated by filled circles. The density of anal marks appears to be higher in the area where neighbouring territories overlapped.

night vision goggles. In summer, adults were primarily babysitting at the sleeping burrow during daylight hours and started foraging late in the afternoon, not returning from foraging and, presumably, scent marking, until after dark. Out of 201 summer observation sessions, mainly focused on habituation, we obtained eight *ad libitum* foraging sessions in total, for three adult males. This number of sessions was too small to compare statistically with the six to 14 sessions per adult male ($n = 6$) obtained for each of the other seasons.

Results

Home-range sizes and scent-mark locations

Yellow mongoose densities in the KRR population varied between four (non-breeding season) and 14 (breeding season) individuals km^{-2}. Groups consisted of 3.7 ± 0.4 members (range: 2–7), including offspring. Dominant male territories were $0.76 \pm 0.21 \, km^2$ in size ($n = 6$), ranging between 0.17 and $1.53 \, km^2$, with a perimeter length of $5.49 \pm 0.96 \, km$. These territory sizes remained constant across seasons. Each male's territory completely encompassed the home ranges of his offspring, which were far smaller at $0.18 \pm 0.20 \, km^2$ ($n = 10$; range: $0.11–0.28 \, km^2$) with a $2.34 \pm 0.19 \, km$ perimeter length. The only dominant female that we followed had a home-range size of $0.20 \, km^2$ (perimeter length: $3.05 \, km$) near the centre of her mate's territory, which was $1.11 \, km^2$ in size. Dispersing animals established new territories $2.5 \pm 0.4 \, km$ ($n = 6$) from their natal territories.

Territorial defence

Only dominant males were observed to patrol territory borders, whereas their offspring remained within a smaller area inside the males' territories, marking at low rates (Table 1). The scent-marking rates of dominant males were significantly higher than those of their offspring (unequal variance *t*-test: anal marks: $t_{15.9} = 6.97$, $P < 0.001$; cheek marks: $t_{12.0} = 4.33$, $P < 0.001$; body rubs: $t_{10.0} = 5.60$, $P < 0.001$).

Some differences were evident in the density of dominant males' scent marks throughout their territories (Table 2). Anal marks in the territory core were denser than in the territory border as well as in the kernel border, but denser on the territory border than in the kernel border (Kruskal–Wallis ANOVA: $\chi_2^2 = 12.43$, $P = 0.002$; *post hoc* tests: $P < 0.05$). There were no differences between these areas in the densities of 'cheek mark' ($\chi_2^2 = 4.53$, $P = 0.104$) or 'body rub' ($\chi_2^2 = 4.10$, $P = 0.129$).

Sexual advertisement: seasonal changes and overmarking

There was some seasonal variation in the hourly marking rate of adult males (Fig. 2), but offspring's marking rates did not vary across seasons (Fig. 3). Dominant males' cheek-marking rates were higher during spring (pre-breeding season) than autumn (post-breeding season; Kruskal–Wallis ANOVA: $\chi_2^2 = 8$, $P = 0.018$), and body-rubbing rates differed in the same respect ($\chi_2^2 = 6.26$, $P = 0.044$). Anal-marking rate did not differ between seasons ($\chi_2^2 = 3.14$, $P = 0.208$). None of the offspring's marking rates (Fig. 3) were affected by month of the year or age.

No overmarking was observed between adults and offspring, even though they were observed foraging together. However, the area where the dominant female deposited most of her cheek marks was a location where her mate concentrated a high number of cheek marks (15 marks in a 10-m radius). Her anal marks were in an area where the male

Table 1 Average scent-marking rates (marks h^{-1}, mean ± SE) for the dominant males ($n=6$), offspring ($n=10$) and one dominant female habituated at the Kuruman River Reserve

Identity	Anal mark	Cheek mark	Body rub
Dominant males	9.11 ± 2.01	4.80 ± 1.13	1.89 ± 0.47
Offspring	1.08 ± 0.22	0.80 ± 0.56	0.28 ± 0.14
Adult female	1.02 ± 0.60	0.55 ± 0.28	0.04 ± 0.04

Dominant males had significantly higher scent-marking rates than offspring.

Table 2 Dominant male ($n=6$) scent mark densities, presented as number of marks km^{-2} (mean ± SE)

Type of mark	Territory core (65% kernel)	Kernel border (65–85%)	85% kernel	Territory border (>85% kernel)
Anal mark	1391.1 ± 784.4	145.2 ± 22.3	640.6 ± 284.4	258.8 ± 37.9
Cheek mark	881.0 ± 576.2	142.1 ± 97.5	432.0 ± 270.6	162.0 ± 63.0
Body rub	213.3 ± 91.1	24.1 ± 15.1	103.7 ± 44.3	37.5 ± 12.3

Different parts of territories are based on kernel methods (see text and Fig. 1).

also marked anally, but the closest male anal mark was 20 m from her marks.

When offspring dispersed (spring season), dominant-male marking rates increased (Fig. 2). However, this increase was not focused specifically in the territory core, where offspring used to mark. Although a high proportion of marks were made in the territory core (Fig. 4), the distribution of marks did not vary across seasons for anal marks (Friedman ANOVA: $\chi_2^2 = 0.4$, $P = 0.819$) or body rubs ($\chi_2^2 = 0.4$, $P = 0.819$). Cheek-mark distribution varied, however ($\chi_2^2 = 7.6$, $P = 0.022$), as winter and autumn proportions were significantly higher than spring proportions (*post hoc* tests: $P < 0.05$). Relatively more cheek marks were therefore located outside the territory core during spring.

Discussion

Territoriality

In the low-density KRR population, only the dominant males were observed to defend and mark their territories, in contrast to the high-density BI population, where especially subordinate individuals maintained the territory borders (Wenhold & Rasa, 1994). In obligate social carnivores, the dominant male is usually the main scent marker, but group members often contribute substantially to territory defence and scent marking, for example, in Ethiopian wolves *Canis simensis* (Sillero-Zubiri & MacDonald, 1998), and meerkats (Jordan *et al.*, 2007). Group defence appears to occur together with other cooperative behaviours, such as the communal rearing of young (Sillero-Zubiri & Gottelli, 1994; Clutton-Brock *et al.*, 2001). Unlike the KRR population, subordinate mongooses in the BI population not only share the mated pair's territory, but contribute to the rearing of their subsequent litters (Wenhold, 1990), which may explain why their pattern of territory defence resembles that of obligate social carnivores.
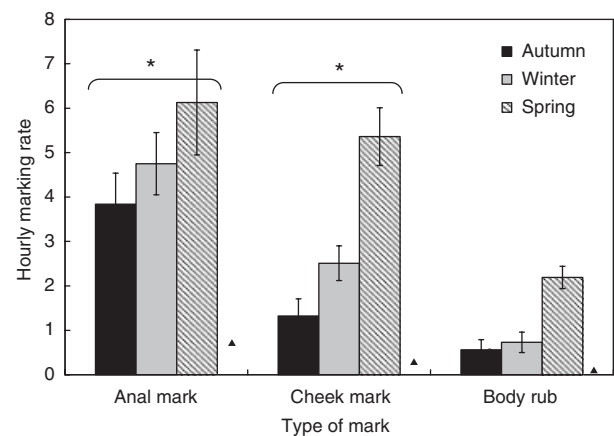
Figure 2 Dominant male scent-marking rates as affected by season (*$P < 0.05$). Filled triangles represent the average marking rates of dominant males in a high-density population, calculated across 9 months, which excluded most of the summer season (after Wenhold & Rasa, 1994). Summer marking rates are not indicated on this figure, as small sample sizes ($n=3$ males) precluded statistical comparisons. Summer marking rates were 7.1 ± 2.0 marks per hour for anal marks, 1.9 ± 0.7 for cheek marks and 2.5 ± 0.8 for body rubs.

Dominant males in the low-density population had high marking rates compared with individuals in the high-density population, but groups' cumulative marking rates were similar between populations (Wenhold & Rasa, 1994). Territories in the BI population were five times smaller than those at KRR, implying a five times greater density of scent marks in BI territories. This probably allowed dominant males in the BI population to use the border-marking strategy in territory defence (*sensu* Gorman & Mills, 1984). The hinterland marking strategy (Gorman & Mills, 1984) used by dominant males in KRR territories is used by a number of carnivores such as the solitary honey badgers (Begg *et al.*, 2003) and social meerkats (Jordan *et al.*, 2007). This strategy reflects the need to protect core resources, such
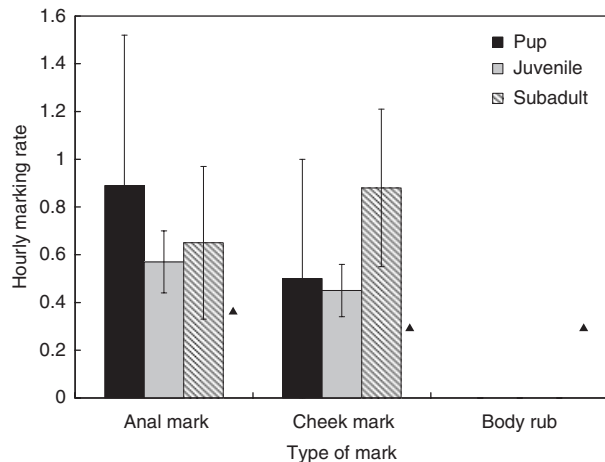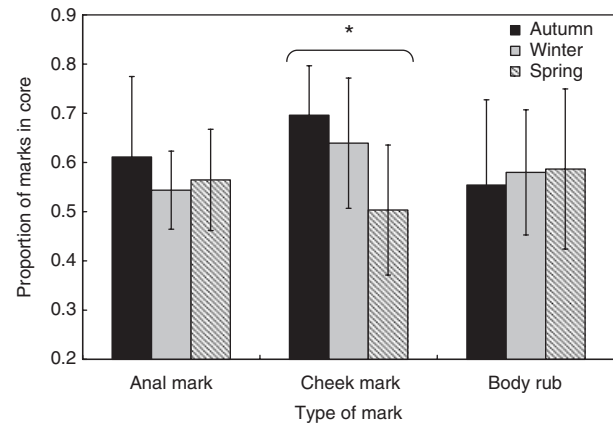
Figure 3 Offspring scent-marking rate as a function of age class. Scent-marking rates were not affected by age or season. Filled triangles indicate average marking rates for 'juvenile' (<1 year old) yellow mongooses *Cynictis penicillata* in a high-density population, calculated across 9 months, which excluded most of the summer season (after Wenhold & Rasa, 1994).

Figure 4 Proportion of dominant male scent marks that were made inside territory cores, according to season. The proportion of cheek marks inside the territory core was significantly smaller in spring than in winter and autumn (*$P<0.05$).

as sleeping burrows and feeding sites, in large territories where intruders may not come across border marks while travelling through an area (Gorman & Mills, 1984).

As with other herpestids (Rasa, 1973; Baker, 1982, 1988), anal marking was the predominant form of territorial marking in yellow mongooses. Anal gland secretions in the yellow mongoose (Apps, Viljoen & Taylor, 1989) and other herpestids function as long-lasting markers carrying information on individual identity (Rasa, 1973; Hefetz, Ben-Yaacov & Yom-Tov, 1984; Decker, Ringelberg & White, 1992). Dominant males in the KRR population increased body-rubbing rates during spring, when intruder pressure increased as dispersers attempt to find new territories. The combination of anal marking, border latrines (le Roux, 2007) and body rubbing could function as a scent-matching system of territory defence (Gosling, 1982), whereby intruders match the scent of territorial marks with the scent of the owner when encountering this individual. The scent-matching system is found in various mammals, including beavers *Castor canadensis* (Sun & Müller-Schwarze, 1998), and snow voles *Chionomys nivalis* (Luque-Larena, Lou Pez & Gosaulbez, 2001). This facilitates recognition of ownership, which in turn reduces the aggression of agonistic interactions, to the mutual advantage of intruder and owner (Gosling & McKay, 1990).

Aggression between familiar neighbours appeared to be low in the KRR population. During more than 100 h of observation of two habituated neighbours, we observed only five encounters, which were brief chases and fighting (<2 min in duration) that did not appear to draw blood. Adult males had almost no visible scars, and territory expansion into neighbouring territories was never observed. Preliminary experiments with fresh faeces from foreign (non-neighbouring) males (A. le Roux, unpubl. data) indi-

cated that foreign males' latrines always provoked an immediate countermarking reaction. Latrines of familiar neighbours typically evoke only sniffing (le Roux, 2007). Such a tolerance of familiar neighbours, with higher aggression against unfamiliar intruders – the 'dear enemy' effect (Fisher, 1954) – occurs in a variety of territorial species (reviewed in Temeles, 1994). This contrasts with the 'nasty neighbours' effect found in, for example, banded mongooses *Mungos mungo* (Müller & Manser, 2007), that treat neighbours more aggressively than transients because groups readily expand into neighbouring territories. In high-density populations of yellow mongooses, intergroup encounters appeared to be more violent and frequent (Wenhold & Rasa, 1994; Balmforth, 2004) and scent-mark densities were much higher than in the KRR population. This may be ascribed to the definite risk of territory reduction in areas with high territory saturation.

Sexual advertisement?

In the low-density population, there was no support for Wenhold & Rasa's (1994) hypothesis that scent marking is used as sexual advertisement by subordinate individuals. Whereas mongooses in the BI population found mating opportunities in neighbouring groups (Wenhold & Rasa, 1994), sexually mature offspring in the KRR population dispersed to new territories beyond neighbouring groups. The marks of offspring in the low-density population may, however, have functioned in intra-group communication. Allo-marking, displayed by high-density yellow mongoose populations (Earlé, 1981) and social mongooses such as the dwarf mongoose *Helogale undulata* (Rasa, 1973), was extremely rare in the KRR population. In the absence of such a 'group odour' (*sensu* Sheppard & Yoshida, 1971), familiarity could be established through scent marks regularly encountered on the substrate. In other group-living mammals, such as the collared lemming *Dicrostonyx*

groenlandicus (Huck & Banks, 1979), the familiarity of an individual's scent has been shown to reduce aggression from the dominant male. The scent marks of KRR offspring may therefore have facilitated tolerance by the dominant male during the time they shared a home range. In addition, offspring scent marks could have augmented dominant male marks around key resource areas, thereby contributing to territorial defence (e.g. Revilla & Palomares, 2002). However, dominant males did not 'compensate' for the absence of these marks once offspring dispersed.

Dominant males' cheek-marking rates increased when offspring dispersed, but this increase was primarily outside the territory core, and could have been related to higher intruder pressure during this season, rather than the decrease in the number of group members. In water mongooses *Atilax paludinosus* (Baker, 1988), and dwarf mongooses (Rasa, 1973), cheek marks appear to carry a short-lived threatening message. During fights between males, scent from cheek glands is probably exchanged, as yellow mongooses attack the face and neck of their rivals (A. L. R., pers. obs.). Yellow mongoose cheek marks were concentrated around bolt-holes, which are noticeable landmarks regularly inspected by other yellow mongooses, especially adult males. Limited data suggested that a dominant male over-marked the area that his mate cheek marked. It is therefore probable that cheek marks had a function in mate guarding (Roberts & Dunbar, 2000; Lewis, 2005), although the possibility of male sexual advertisement could not be excluded.

Conclusion

The scent-marking patterns of yellow mongooses were affected by long-term group composition. In temporary groups where the mated pair constituted the only long-term residents in a territory, marking behaviour resembled that of solitary territorial mammals, with only the dominant male appearing to defend and mark his territory. Natal philopatry in high-density populations may have implications for increased facultative cooperation that includes cooperation in scent marking and inter-group contests. Larger groups in high-density populations interact with neighbours more frequently, causing more conflict but also opportunities for mating and sexual advertisement between neighbours. Although none of these results are unexpected, considering the characteristics of the different populations, this may be the first mammalian study to show how individuals' scent-marking patterns can be affected by intra-specific fluctuations in social structure rather than just group or territory size.

Acknowledgements

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