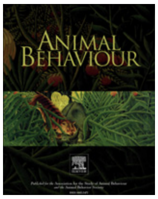
Animal Behaviour 81 (2011) 51–60

Contents lists available at ScienceDirect

Animal Behaviour

journal homepage: www.elsevier.com/locate/anbehav



Scent marking in wild banded mongooses: 3. Intrasexual overmarking in females

Neil R. Jordan[a,*], Francis Mwanguhya[a,b,1], Solomon Kyabulima[a,b,1], Peter Rüedi[c,2], Sarah J. Hodge[d,3], Michael A. Cant[d,3]

[a] *Large Animal Research Group, Department of Zoology, University of Cambridge, U.K.*
[b] *Banded Mongoose Research Project, QENP, Kasese*
[c] *Institute of Organic Chemistry, Universität Zürich*
[d] *School of Biosciences, University of Exeter (Cornwall Campus)*

A R T I C L E I N F O

Article history:
Received 20 December 2009
Initial acceptance 8 February 2010
Final acceptance 28 September 2010
Available online 13 November 2010
MS. number: 10-00014R

Keywords:
banded mongoose
communication
competition
female
intrasexual
mating success
Mungos mungo
olfactory
overmark
scent mark

In contrast to numerous studies of scent marking in male mammals, studies of female scent marking are relatively rare. We have previously shown that communally breeding female banded mongooses, *Mungos mungo*, are more likely to overmark the scent of other females. Here we describe female overmarking patterns in more detail, and discuss these results in relation to hypotheses potentially explaining such 'female intrasexual overmarking'. To our knowledge, this is the first study to investigate female overmarking in any wild mammal. First, although we found some evidence of individually distinctive scent marks in females, we found no evidence to suggest that female intrasexual overmarking was related to competition for food, as feeding competition was infrequent, and unrelated to overmarking scores. We also found no evidence to suggest that intrasexual overmarking in females was involved in reproductive suppression. Females with the highest and lowest overmarking scores in each group were mate-guarded by males for similar durations. Finally, we found little evidence to suggest that female intrasexual overmarking was involved in competition for males. Although the female with the highest overmarking score in each group tended to be mate-guarded by males in better condition than the female with the lowest overmarking score, a female's overmarking score affected neither the amount of harassment she received from males nor the frequency of mating attempts received. These results are discussed in light of these and other untested hypotheses for female overmarking.

Overmarking is the placement of a scent mark directly on top of the scent mark of another individual (Johnston et al. 1994), and individuals of some species seem to have developed specialist mechanisms to determine which individual's mark is on top (reviewed in Johnston 2005). In laboratory studies where this has been investigated, individuals showed a preferential memory for individuals whose mark was on top, regardless of the degree of scent overlap (e.g. golden hamsters, *Mesocricetus auratus*: Johnston & Bhorade 1998). This suggests a selective preference for top-scent donors rather than a masking effect (see Johnston et al. 1995; Johnston 2005). Female meadow voles, *Microtus pennsylvanicus*, seem to prefer to associate with males whose mark is on top (Johnston et al. 1997), and in some other species females even seem to mate preferentially with such top-scent males (pygmy loris, *Nycticebus pygmaeus*: Fisher et al. 2003). Like patterns of scent marking in general (reviewed in Ralls 1971; Gosling & Roberts 2001), males seem to overmark more than females in some species (e.g. meerkats, *Suricata suricatta*: Jordan 2007), and overmarking appears to be associated with the acquisition and defence of mates and mating opportunities (e.g. meadow voles: Johnston et al. 1997), although a number of other potential hypotheses have been suggested (reviewed in Ferkin & Pierce 2007). In contrast to male scent marking, studies of overmarking by females are relatively rare (but for exceptions see Johnston 1977; Hurst 1990; Wolff et al. 2002), and therefore this represents an overlooked and potentially important area of scent-marking research, particularly in the natural environment.

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* Correspondence and present address: N. R. Jordan, The Vincent Wildlife Trust, 3 & 4 Bronsil Courtyard, Eastnor, Ledbury, Herefordshire HR8 1EP, U.K.
E-mail address: neilrjordan@googlemail.com (N.R. Jordan).

[1] F. Mwanguhya and S. Kyabulima are at the Banded Mongoose Research Project, Queen Elizabeth National Park, PO Box 99, Kasese, Uganda.

[2] P. Rüedi is at the Institute of Organic Chemistry, Universität Zürich, Winterthurerstrasse 190, CH-8057 Zürich, Switzerland.

[3] S. J. Hodge and M. A. Cant are at the Centre for Ecology & Conservation, School of Biosciences, University of Exeter, Cornwall Campus, Penryn, Cornwall, TR10 9EZ, U.K.

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doi:10.1016/j.anbehav.2010.10.007

Banded mongooses, *Mungos mungo*, present an opportunity to investigate the function of female overmarking. They live in large, stable, territorial groups, within which scent marking is common (Jordan et al. 2010). Both sexes overmark frequently, preferentially overmarking the scents of same-sex individuals (Müller & Manser 2008a; Jordan et al. 2011a). Within groups, multiple males and females reproduce synchronously in each breeding attempt during oestrous periods lasting an average of 6 days (Rood 1975; Cant 2000). Males compete for access to receptive females (Cant 2000), and 83% of adult females become pregnant in each breeding attempt (Cant 2000; Gilchrist et al. 2004), giving birth to communal litters (Cant 2000). Although other functional hypotheses have been suggested for overmarking (reviewed in Ferkin & Pierce 2007), we have identified and developed three hypotheses that may be most relevant in this particular social system: (1) food competition, (2) mate competition and (3) reproductive suppression.

As maternal condition is likely to be an important determinant of female reproductive success (see Mousseau & Fox 1998), competition for food may drive patterns of female scent-marking behaviour, and such competition might be expected to be more frequent in the breeding season when nutritional demands are higher, or in periods of food scarcity. In many species, scent-marking sites are frequently associated with feeding sites (e.g. striped hyaena, *Hyaena hyaena*: Macdonald 1978; callitrichid primates: Lacher et al. 1981; Rylands 1985; African palm civet, *Nandinia binotata*: Charles-Dominique 1978). However, it is not yet known whether females invest disproportionately to males in scent marking food sources, nor whether defence of food sources can explain patterns of overmarking in females. Banded mongooses forage together as a group, fanning out and searching through leaf litter for small invertebrate prey (Rood 1975), but except when dependent young are fed, food items are never shared. If intrasexual overmarking in females is related to the acquisition of resources necessary to breed and rear offspring (see Clutton-Brock 2009), we might expect females that overmark more to be challenged less frequently for food items than females that overmark less.

Alternatively, in the mate competition (or mate attraction) hypothesis, females might preferentially overmark the scents of other females if this functions to signal their quality to males and allow them access to higher-quality mates. Although some authors have suggested that such a function would result in individuals overmarking the scents of opposite-sex individuals (Ferkin & Pierce 2007), in social species such as banded mongooses, placing your scent on top of that of same-sex rivals might be a form of advertising your own condition (Rich & Hurst 1998, 1999; Gosling & Roberts 2001; Jordan et al. 2011b), particularly if high-quality individuals are better able to afford the costs of continually overmarking their rivals (see Rich & Hurst 1998, 1999; Gosling & Roberts 2001). Although male mammals are generally more likely to compete for females (see Trivers 1972), in certain circumstances females may compete for mating opportunities with males (see Clutton-Brock 2009). For example, intrasexual competition between females for mates may be expected where males provide extensive parental care (e.g. Western Australian sea horse, *Hippocampus subelongatus*: Kvarnemo et al. 2007) or where the most preferred male is unable to service all females (e.g. topi, *Damaliscus korrigum*: Bro-Jørgensen 2007). In banded mongooses, both of these conditions are fulfilled, and so a degree of male mate choice and female competition for males may be expected. As oestrus is highly synchronous within groups (Cant 2000), a single male may be unable to monopolize access to all females. Additionally, males provide a high degree of paternal care by 'babysitting', 'escorting' and feeding dependent pups (Rood 1974, 1975; Cant 2003; Gilchrist 2004; Hodge 2005). In species of callitrichid primates where male care exceeds female care, rates of scent marking are strongly female biased (Heymann 2003), and intrasexual overmarking also occurs in females of these species (see Heymann 2003). Although this is unlikely to be true in all species, attracting a high-quality male may therefore be of prime importance in banded mongooses, and males might also benefit by competing for those particular females with high overmarking scores, as higher-quality females may produce more (see Gilchrist et al. 2004) or higher-quality offspring. If competition for males explains intrasexual overmarking by females, we would expect males to compete more intensively for females with higher overmarking scores, perhaps harassing them more during oestrus and attempting to mate with them more frequently. We might also expect to see females scent marking more frequently during breeding periods, as is the case for vaginal marking in golden hamsters (Johnston 1977).

A third hypothesis is that female overmarking is involved in reproductive suppression, and this may be most likely in a social species with competition over breeding. As the 'priming' effects of scents on other individuals are well known (reviewed in Brown 1985), it is possible that female overmarking might be employed as a tactic in reproductive suppression. Scents may have promotional (e.g. puberty acceleration, house mouse, *Mus musculus*: Massey & Vandenbergh 1981) or suppressive effects on recipients (e.g. puberty delay, house mouse: Massey & Vandenbergh 1980). As female scent marks placed on or in the vicinity of the scents of other females are likely to ensure that their own scent marks predominate in the environment, overmarking female scents may protect females from the primer cues produced by other females (Hurst 1990), although it is perhaps more likely to increase the efficacy of their own primer cues. If female intrasexual overmarking is a tactic employed to suppress other females, we would predict that females with higher overmarking scores might: (1) first breed at a younger age, and (2) delay their oestrus less, as there are potential fitness costs to delaying oestrus in banded mongooses. Most females give birth on the same day as each other regardless of their conception date (Cant 2000), which means that females that breed later have significantly shorter gestation periods (Cant 2000), potentially affecting pup size at emergence, which is known to have downstream fitness consequences (Hodge 2005).

We attempted to evaluate the function of scent marking in female banded mongooses, primarily by investigating the above three hypotheses. We did this by using behavioural observations of female overmarking behaviour in the field, and determining the chemical composition of multiple scent marks collected from individual females to assess whether each female has an individually recognizable scent profile. As overmarking score is likely to be correlated with other aspects of female quality likely to affect foraging challenges or breeding success, such as age and weight, we simultaneously controlled for these in our analyses. To the best of our knowledge, this study is the only evaluation of female–female overmarking in wild mammals to date, and as such it should provide a useful foundation on which future studies of female overmarking can be conducted in the natural environment.

METHODS

The general methods were identical to those described in the first paper in this series (Jordan et al. 2011a) except for the following differences and additions.

Scent Collection and Composition Analysis

To determine whether females had individually specific scents, we live-trapped 33 females from eight groups between December 2005 and October 2007, following the standard procedure (see