Animal Behaviour 105 (2015) 173–179

Contents lists available at ScienceDirect

Animal Behaviour

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

Handstand scent marking: height matters to dwarf mongooses

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ARTICLE INFO

Article history:
Received 7 December 2014
Initial acceptance 30 January 2015
Final acceptance 13 April 2015
Published online
MS. number: 14-00989

Keywords:
dwarf mongoose
handstand
Helogale parvula
intrasexual competition
mark height
olfactory communication
scent marking
size

Scent marking is an important means of communication in mammals and many species elevate their scent marks by depositing them on vertical objects. Traditionally, it has been assumed that marks are elevated to increase detectability, but elevated marking may have evolved to convey information about depositor size. Because the height of an elevated mark is typically dictated by the height of the marker, receivers could use the physical location of an elevated scent deposit to indirectly assess the size, and hence the competitive ability, of rivals. Considering that intrasexual competition is one of the primary motivators of mammalian scent marking, and that the ability to assess a rival indirectly would provide very real benefits (eliminating the need for potentially dangerous encounters), it would be surprising if species were not utilizing mark height in this way. Nevertheless, it remains unknown whether any mammal extracts such information from elevated scent marks. I tested whether wild dwarf mongooses, *Helogale parvula*, discriminate between handstand scent deposits of differing height. Handstand marking is an extreme form of elevated marking, with the marker balancing on its forepaws while flinging its hind legs into the air and smearing anogenital secretions one full body length above the ground. I found that females spent twice as long investigating anal-gland deposits positioned 16 cm above the ground, as compared with those at 10 cm, even though the two were swipes of the same scent deposit and presumably did not differ chemically. A faeces presentation experiment showed that females were more interested in obtaining information about same-sex than opposite-sex conspecifics. I suggest that female dwarf mongooses, which experience extreme intrasexual competition, use the height of handstand scent marks as an indicator of depositor size, allowing them to concentrate their information gathering on same-sex rivals that pose the greatest threat.

Scent marking is an important means of communication in mammals and considerable research has focused on the information that receivers can extract from the chemical composition of scent deposits (Hurst & Beynon, 2004). We know, for example, that some species can determine a depositor's identity (Porton, 1983), sex (Swaisgood, Lindburg, & Zhou, 1999), age (Linklater, Mayer, & Swaisgood, 2013), reproductive status (Converse, Carlson, Ziegler, & Snowdon, 1995), social status (Jones & Nowell, 1973), health (Zala, Potts, & Penn, 2004), quality (Charpentier, Crawford, Boulet, & Drea, 2010), kinship (Leclaire, Nielsen, Thavarajah, Manser, & Clutton-Brock, 2013) or histocompatibility (Penn & Potts, 1999). There is also considerable evidence that mark density, refreshment rate and distribution (relative to others' marks) provide critical information about a depositor's competitive ability (Ferkin, Hobbs, Ferkin, Ferkin, & Ferkin, 2011; Gosling & Roberts, 2001; Johnston, Chaing, & Tung, 1994; Rich & Hurst, 1999). However, one potentially invaluable source of information, the relative elevation of the deposit, has received virtually no scientific attention.

Many mammal species adopt marking postures that raise their scent deposits above the ground (Macdonald, 1985). Traditionally, it has been assumed that this increases the mark's detectability (e.g. Gosling & Roberts, 2001) by dispersing the scent over a wider area (Alberts, 1992). Additionally, elevated deposits are lifted clear of distracting substrate odours (Alberts, 1992) and are often conveniently located at receiver nose height (Gorman & Mills, 1984). However, the height of an elevated scent mark may also convey information about the depositor itself. In many species, the use of elevated marks is restricted to individuals of a particular sex, age or status (Macdonald, 1985). For example, leg-cocking urination in grey wolves, *Canis lupis* (Peters & Mech, 1975) and African wild dogs, *Lycaon pictus* (Jordan, Golabek, Apps, Gilfillan, & McNutt, 2013) is largely restricted to dominant individuals, while handstand urination is used only by females in bush dogs, *Speothos venaticus* (Porton, 1983) and adult males in giant pandas, *Ailuropoda melanoleuca* (White, Swaisgood, & Zhang, 2002). Under these

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http://dx.doi.org/10.1016/j.anbehav.2015.04.019
0003-3472/

circumstances, receivers can use mark height to identify the sex or status of the depositor. This has been confirmed experimentally in captive giant pandas which respond more strongly to elevated marks than those at ground level, even when the two are chemically identical (White et al., 2002).

However, elevated marks could also convey important information about the depositors' body size (Alberts, 1992). The postures adopted to elevate marks (e.g. reversing up against a vertical object with anal-gland everted, as in African civets, *Civettictis civetta*; Ewer & Wemmer, 1974) result in marks whose height directly reflects the marker's own body height. This 'honest signal' or index (Maynard Smith & Harper, 1995) of depositor size could be used by receivers to indirectly evaluate the competitive ability of their rivals, since size often determines the outcome of competitive interactions (Huntingford & Turner, 1987). The value of evaluating rivals indirectly (and thus eliminating the need for potentially dangerous encounters) is potentially huge. Mammals are known to exploit auditory cues for this purpose (Bro-Jorgensen & Dabelsteen, 2008; Fischer, Kitchen, Seyfarth, & Cheney, 2004) and scent deposits have the added advantage of being long lasting, allowing virtually risk-free information gathering. Considering that intrasexual competition is one of the primary motivators of mammalian scent marking (Gosling & Roberts, 2001; Jordan et al., 2011; Muller & Manser, 2008; Stockley, Bottell, & Hurst, 2013), it would be surprising if elevated-marking species did not utilize mark height in this manner. Yet this potentially critical function of elevated scent marking has never been scientifically evaluated.

Qualitative evidence supporting the tenet is provided by the energetically demanding postures that some species adopt in their efforts to place their deposits as high as possible, even though such lofty marks are difficult for receivers to investigate. For example, both cervids (Schaller, 1967) and klipspringers, *Oreotragus oreotragus* (Roberts, 1997) will rear up on their hind legs to deposit facial-gland scent on otherwise unreachable twigs. Similarly, a number of carnivores, rodents and primates (see Sharpe, Jooste, & Cherry, 2012 for a species list) use handstand marking, in which an individual balances on its forepaws while flinging its hind legs up into the air and smearing urine, faeces and/or anogenital secretions as high as possible on a vertical object (Fig. 1a). Because handstand marking places the deposit one full body length above the ground, it could provide receivers with a very accurate index of the depositor's size, rather than just its height, as with other elevated marking postures.

In this study I examined whether a handstand-marking carnivore (the dwarf mongoose, *Helogale parvula*) discriminates between elevated scent deposits on the basis of height. Dwarf mongooses are small (280 g), diurnal herpestids that live in territorial groups of 6–30 individuals (Sharpe et al., 2012). They breed cooperatively with both sexes exhibiting high levels of reproductive skew (Keane et al., 1994) and fierce intrasexual competition for reproductive opportunities (Clutton-Brock et al., 2006). Groups are normally composed of an alpha pair (which largely monopolizes breeding), their adult offspring and one or two immigrant males (Rood, 1990). There are strong, intrasexual, linear dominance hierarchies within groups (Sharpe, Hill, & Cherry, 2013). Females queue for the alpha position within their natal group, although they occasionally disperse to establish new groups (they cannot join established groups that contain more than one female; Rood, 1986). Males usually disperse at 2–3 years of age (often in coalitions) to either join established groups (as subordinates or by aggressively ousting the resident males) or found new groups (Rood, 1990). It is not unusual for males to transfer between groups more than once.

Scent marking is well developed in dwarf mongooses with both sexes producing anal-gland and cheek gland secretions. Cheek marking appears to function as a dominance display during intragroup social interactions while anogenital deposits are used for territory marking (Rasa, 1973). At my study site, groups defend territories of 0.3–0.4 km^2 which include approximately 75 scent-marking sites that the group visits repeatedly, with about half located at overnight refuges (Sharpe et al., 2012). At a marking site, all group members (including pups) deposit urine and faeces on the ground and employ the handstand marking posture (Fig. 1a) to smear anal-gland secretion on vertical objects. Seventy-eight per cent of handstand marks are applied to vegetation, 16% to termite mounds and 6% to rocks (Sharpe et al., 2012). The height of female handstand marks accurately reflects depositor size, but in males the relationship is more complex because individuals that are light for their age mark higher than expected (Sharpe et al., 2012). This anomaly is consistent with 'bluffing' as predicted by models of deceptive threat communication (Adams & Mesterton-Gibbons, 1995). Males mark at three times the rate of females (Sharpe et al., 2012) and approximately 40% of handstand marks (by both sexes) are placed on top of another mark. This 'overmarking' (Johnston et al., 1994) appears to be random with regard to the sex or rank of the overmarked depositor (Jooste, 2009). Dwarf mongoose anal-gland secretion is known to be sexually dimorphic (Decker, Ringelberg, & White, 1992) and handstand marks remain detectable by the mongooses for up to 10 days (Rasa, 1973).

In this study I examined whether wild dwarf mongooses recognize small differences in handstand mark height, as would be anticipated if they are using mark height as an indicator of depositor body size. Using presentation experiments, I tested whether the mongooses exhibit a differential response to handstand deposits placed at differing heights, and examined whether this response is consistent with the tenet that they are using mark height as an indicator of depositor size.

METHODS

Study Population

I undertook the research at Phuza Moya Private Game Reserve in northeastern South Africa (24°15′S, 30°45′E; see Sharpe et al., 2012 for details of the site's vegetation) between June 2009 and June 2012, working with six groups of wild dwarf mongooses. Four of these groups were habituated to the presence of an observer walking within 2–3 m and all group members (mean group size = 16) were individually marked using Garnier 'Nutrisse' blonde hair dye (applied with a long-handled paint brush while the animals stood basking in the early morning sun at their overnight refuge). All groups had an even sex ratio, and showed little difference in the age/sex distribution of their members.

Ethical Note

All methods were approved by Stellenbosch University's ethics committee. No mongoose in the study population has ever been captured or directly handled, and none has been seen to react adversely to the hair dye used for ID marking, despite 9 years of use. The mongooses did not ingest the dye (i.e. via grooming) as they find the flavour distasteful. During the presentation experiments, I allowed only two group members to access the samples, thereby minimizing any potentially disquieting effect of exposure to another group's scent deposits.

Sample Collection

Scent-marking bouts by dwarf mongoose groups are often frenzied (with up to 90 handstand marks deposited in 10 min; Sharpe et al., 2012) and overmarking is frequent. Because it is