

Interspecific responses of wild African carnivores to odour of 3-mercapto-3-methylbutanol, a component of wildcat and leopard urine

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Received: 30 June 2016 / Accepted: 16 December 2016 / Published online: 23 January 2017
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Abstract The scent of 3-mercapto-3-methylbutanol (3-M-3-MB), a volatile component of leopard (*Panthera pardus*) and domestic cat (*Felis silvestris catus*) urine, released at about 10 ng/s from slow-release dispensers, elicited scent-marking from African civet (*Civettictis civetta*), small-spotted genet (*Genetta genetta*) and slender mongoose (*Galerella sanguinea*), as well as African wildcat (*F. s. cafra*). A female leopard was apparently repelled by the scent. The scent-marking and scent-rubbing by species other than African wildcats and leopards were unexpected and have important implications for the design of studies to investigate chemical communication between wild mammals and the use of camera traps to estimate animal numbers. Videos showing the behaviours referred to in this article are available at; <http://www.momo-p.com/showdetail-e.php?movieid=momo161223fs01a>; <http://www.momo-p.com/showdetail-e.php?movieid=momo161223gs01a>; <http://www.momo-p.com/showdetail-e.php?movieid=momo161223gg01a>.

Keywords Chemical communication · Pheromone · Mammal · Semiochemical · Tomcat thiol · CAS 34300-94-2 · *Felis silvestris* · *Panthera pardus*

Electronic supplementary material The online version of this article (doi:10.1007/s10164-016-0503-7) contains supplementary material, which is available to authorized users.

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Introduction

Chemical communication by scent-marking is ubiquitous among terrestrial mammals (Apps 2013; Apps et al. 2015 especially references 4–14), but work on scent-mark chemistry has been largely confined to laboratory rodents, and relatively few active constituents have been characterized from wild mammals (reviews Apps 2013; Apps et al. 2015). To begin to fill this gap, we set out to test the responses of free-ranging African wildcats (*Felis silvestris cafra*) and leopards (*Panthera pardus*) to 3-mercapto-3-methylbutanol (3-M-3-MB), the “tomcat thiol”, which is the most abundant odorous sulfur compound in domestic tomcat (*F. s. catus*) urine (Starkenmann et al. 2014) and also occurs in leopard urine (Apps et al. 2014). In cats, metabolic production of 3-M-3-MB is testosterone dependent (Hendriks et al. 1995, 2008), and its emission from urine is by a slow-release mechanism (Miyazaki et al. 2006), which suggests a role in male scent-marking. It has been asserted that it is a “pheromone”, although its biological activity has not been demonstrated. Of the species that occur in the study area, only wildcats and leopards are known to have 3-M-3-MB in their scent marks (Apps et al. 2014), so we were surprised to record scent-marking responses from other carnivores.

Heterospecific scent elicits responses in a wide range of species; American mink (*Mustela vison*) are attracted to both otter (*Lutra lutra*) and polecat (*M. putorius*) odour (Harrington et al. 2009), weasels (*M. nivalis*) avoid stoat (*M. erminea*)-scented traps but not vice versa (Erlinge and Sandell 1988), house mice (*Mus musculus*) avoid the odour of midday jirds (*Meriones meridianus*) (Krasnov and Khokhlova 1996). Both bobcats (*Lynx rufus*) and coyotes (*Canis latrans*) are attracted to bobcat and coyote faeces (Howard et al. 2002), leopards roll in gemsbok (*Oryx*

gazella) and red hartebeest (*Alcelaphus buselaphus*) urine, and on faeces and old carcasses (Bothma and Coertze 2004). Red foxes (*Vulpes vulpes*) investigate cat and dingo (*Canis dingo*) scent more than fox scent, and sometimes defaecate near it (Banks et al. 2016). In addition, a few studies mention interspecific responses in passing (Marnewick et al. 2006; Hulsman et al. 2010; Hayward and Hayward 2010).

Interspecific scent marking is also widely recorded among carnivores. Black-backed jackals (*Canis mesomelas*) defaecate on lion (*Panthera leo*) faeces (Hayward and Hayward 2010), coyotes and wolves urinate on one another's urine (Paquet 1991), honey badgers and brown hyaenas make latrines under the same trees (Begg et al. 2003), African wild dogs sniff intensively and urinate on spotted hyaena (*Crocuta crocuta*) faeces (pers. obs., BPCT unpublished, Jessica Vitale pers comm.), and slender mongooses and small-spotted genets frequent cheetah (*Acinonyx jubatus*) scent-marking trees (Jane Horgan, Cheetah Conservation Botswana pers. comm.). Six species of north American carnivore share marking sites (Allen et al. 2015) where grey foxes (*Urocyon cinereoargenteus*) cheek rub on puma (*Felis concolor*) scent scrapes (Allen et al. 2017), 14 species of mammals visit ocelot latrines in Costa Rica (King et al. 2016), and 19 species of mammals use “communication trees” in Canada (McTavish and Gibeau 2010). Certainly, there is a need for further investigation, and here we report both intra- and interspecific responses to the odour of a single component of wildcat and leopard urine, and discuss their implications for the study of chemical communication in the wild and the use of camera traps for population estimates.

Materials and methods

Study area

We worked in the savanna woodlands of the Wildlife Management Areas to the east of the Moremi Game Reserve (9°31'S, 23°37'E), which are part of the Botswana Predator Conservation Trust (BPCT) study area in northern Botswana (McNutt 1996).

Experimental odour: 3-mercapto-3-methylbutanol

Approximately 150 mg of 3-mercapto-3-methylbutanol (Sigma-Aldrich) was accurately (0.1 mg) weighed into 10-ml headspace vials capped with polytetrafluoroethylene (PTFE)-faced silicone septa (Products 20-1000 and Z20-0051ML, MicroLiter Analytical Supplies, Suwanee). To quantify release rates, the charged vials were weighed before and after deployment.

Controls: volatile acids and piperidone

As a control for responses being to the dispensers themselves or to the mere presence of a novel scent rather than to 3-M-3-MB per se, the dispensers were re-deployed with a control scent containing a mixture of volatile acids and piperidone (VA+P), which are components of carnivore faeces and urine (Apps et al. 2012). Responses that were due to the dispensers themselves or to novelty per se would be similar with the different scents. Since the polar molecules in the control do not diffuse through PTFE and silicone, the control scent was dispensed by evaporation of an aqueous solution containing the following acids: acetic (29.5 mg/g), propanoic (10.7 mg/g), 2-methylpropanoic (5.3 mg/g), *n*-butanoic (17.3 mg/g), 2-methylbutanoic (3.3 mg/g), 3-methylbutanoic (4.6 mg/g), *n*-pentanoic (5.3 mg/g), 4-methylpentanoic (5.9 mg/g), *n*-hexanoic (0.2 mg/g), and piperidone (15.4 mg/g) (all from Sigma-Aldrich) in 15 ml portions in open-topped 22-ml vials (Supelco #27004), which were refilled after 3 weeks. The composition of the control mixture approximates the highly variable relative mass fractions of these compounds in African wild dog (*Lycan pictus*) urine. In the absence of data on the emission rates of volatiles from real scent marks, the septum-capped vials of 3-M-3-MB and the VA+P solution were the outcomes of pilot trials to generate odours that were approximately as intense to the human nose as cat and wild dog urine.

Scent dispensers and camera traps

Charged vials were inserted into dispensers constructed from 25-mm galvanized pipe connectors welded to steel stems that were driven into the ground, leaving the dispenser head 20–30 cm above the ground (Fig. 1). Dispensers were placed next to game trails where African wildcats and leopards (and incidentally other species) would be expected to travel.

A camera trap was placed at each dispenser: initially a Bushnell Trophycam model 119537 (Bushnell Outdoor Products, Overland Park, KA, USA), with a Stealthcam Prowler HD (Stealth Cam, Grand Prairie TX, USA) added after 5 weeks to increase detection rates. Cameras were mounted on steel poles approximately 1.2–1.6 m above ground, and angled downwards to cover the game trail on both sides of the dispensers, which were about 3–5 m from the cameras depending on vegetation. Camera sensitivity was set to maximum. For each detection, 30 s of video was recorded, with a 1 s time-out between triggers. Daylight videos were in colour; videos taken at night used near infrared (NIR) from the cameras.

Dispenser and camera sets were approximately 2 km apart, since wildcat home ranges were expected to be about



Fig. 1 Scent dispenser used to emit 3-mercapto-3-methylbutanol (3-M-3-MB) or a mixture of volatile acids and piperidone (VA+P). A 10-ml septum-capped vial charged with scent (*inset*) or a 22-ml open-topped vial (not shown) is held within the stem of the *T-shaped head*, which is made from 25-mm pipe connectors

4 km² (Herbst 2009 p 82). Initially, five dispensers with 3-M-3-MB were put out: one on 28 October 2015, and another four on 12–14 November 2015. On 16 December 2015, these five were moved a few hundred metres to new sites, and one more set was added. All six sets were removed on 9 February 2016 after a total of 524 dispenser nights, the 3-M-3-MB vials were re-weighed, and the dispensers were cleaned. On 10 February 2016, the dispensers were put out again at new sites with the VA+P mixture and monitored for 6 weeks (252 dispenser nights). Sites were visited weekly, SD cards exchanged, batteries refreshed if required, and cameras and dispensers repositioned if they had been displaced.

A scent mark was considered to be a response to a scent if it was deposited within 1.5 m of a dispenser after the animal had sniffed the dispenser. When videos showed the animal only as it was leaving the field of view, we took the conservative view that the animal had ignored the dispenser. All species were readily identified on video; the two species of genet were discriminated on the basis of *Genetta maculata* having large dorsal spots and a black tail

tip, and *G. genetta* having small dorsal spots and a white tail tip (Apps 2012).

The work was carried out under research permit number 8/36/4 XXIV (205) from the Department of Wildlife and National Parks of the Botswana Ministry of Environment, Wildlife and Tourism.

Results

3-Mercapto-3-methylbutanol

The mean rate of emission of 3-M-3-MB over all dispensers was 10 ng/s with maximum of 13 ng/s and minimum of 5 ng/s. Individuals of 24 mammal species, of which 17 were carnivores (Supplementary Table 1), were detected at 3-M-3-MB dispensers. Eighteen individuals of four species, all of them carnivores, scent-marked after sniffing a dispenser. One African wildcat spray-urinated against a dispenser after sniffing it (Fig. 2, frame from video 1; <http://www.momo-p.com/showdetail-e.php?movieid=momo161223fs01a>), and one spray-marked about 1.2 m from a dispenser without having been recorded sniffing it (the video begins with the cat in frame, close to the dispenser). A different cat sniffed this natural mark 2 h 20 min later and then walked past the dispenser with no response. Two cats were videoed sniffing without marking, and eight showed no response. The 3-M-3-MB attracted more interest from other carnivores than from wildcats; slender mongooses (*Galerella sanguinea*) were videoed scent-marking nine times (Fig. 3, frame from video 2;



Fig. 2 (video 1). The video opens with an adult African wildcat (*Felis silvestris cafra*) sniffing the head of a scent dispenser emitting 3-mercapto-3-methylbutanol until time stamp 02:05:12; it then walks past the dispenser, and at 02:05:15 it crouches slightly, lifts its tail, and sprays urine onto the head of the dispenser until 02:05:18, then walks away. Infrared video shot by a Bushnell Trophycam camera trap



Fig. 3 (video 2). A slender mongoose (*Galerella sanguinea*) frantically rubbing and scent-marking a 3-mercapto-3-methylbutanol dispenser. Video shot in natural light by a Bushnell Trophycam camera trap



Fig. 4 (video 3). A small-spotted genet (*Genetta genetta*) rubbing and scent-marking a 3-mercapto-3-methylbutanol dispenser, leaving briefly at time 03:12:35, and returning to rub and mark at 03:12:38 until 03:12:41. Video shot in infrared by a Bushnell Trophycam camera trap

<http://www.momo-p.com/showdetail-e.php?movieid=momo161223gs01a>), sniffing without scent-marking eight times, and showing no response six times, and small-spotted genets (*Genetta genetta*) were videoed scent-marking seven times (Fig. 4, frame from video 3; <http://www.momo-p.com/showdetail-e.php?movieid=momo161223gg01a>), sniffing without scent-marking three times, and showing no response five times. One small-spotted genet scent-marked at ground level before rubbing against the dispenser, and another sniffed and rubbed a dispenser and then sniffed a 7-hour-old wildcat spray mark 1.2 m away but did not rub on it. The difference in response between the two genet species was striking; large-

spotted genets were videoed six times, but only two of them sniffed a dispenser and none of them scent-marked (sample sizes too small to test). Two civets (*Civettictis civetta*) sniffed a 3-M-3-MB dispenser, and one of them subsequently sniffed at the ground about 1 m from it and then scent-marked. Only one leopard was videoed at a 3-M-3-MB dispenser; an adult female turned and retraced her steps when she caught the scent from the dispenser.

Volatile acids + piperidone controls

After 3 weeks, when the dispensers were recharged, the VA+P solution had nearly all evaporated and its odour had become less sharp. Individuals of 20 species were detected at VA+P dispensers. Only two individuals of two species, i.e. one slender mongoose and one black-backed jackal (*Canis mesomelas*), scent-marked the VA+P control scent.

Discussion

Responses by African wildcats and leopards

The African wildcat scent-marking after sniffing is the first record since 1980 of a carnivore overmarking an artificial scent mark (Whitten et al. 1980), and the first ever of overmarking a single compound. Although we could find no results for the rate of marking in response to whole urine, the low frequency of response suggests that the “tomcat thiol” is not particularly active alone and it is premature to refer to 3-M-3-MB as a pheromone. That a cat investigated a fresh, naturally deposited wildcat mark in preference to 3-M-3-MB is as expected; whole scents are universally more semiochemically active than their active constituents alone (Apps 2013).

Neither leopards nor wildcats paid any attention at all to the VA+P control scent, so pending a larger-scale study, their responses to 3-M-3-MB can be ascribed to the scent of the compound itself rather than to the dispensers or to olfactory novelty.

Interspecific scent-marking

In addition to African wildcats, 17 individuals of three species scent-marked after sniffing 3-M-3-MB. In contrast, the VA+P controls were scent-marked by only two individuals of two species (Fisher’s exact test for a difference in responses to the two scents, all species combined, two-tailed $P = 0.0058$), consistent with the marking responses to 3-M-3-MB not being due to the dispensers per se or to olfactory novelty. Both small-spotted genets (7 marks in 15 visits, 47%) and slender mongooses (9 marks in 23 visits, 39%) were more likely to mark dispensers than were

African wildcats (1 mark in 11 visits, 9%) (sample sizes too small to test), but interpretation of the interspecific responses is hampered by a paucity of research on most small African carnivores (Do Linh San and Somers 2013) and on interspecific responses to scent.

The behaviour of slender mongooses at the 3-M-3-MB dispensers matches descriptions in literature; males scent-mark with anal gland secretion, both sexes with urine and cheek glands, and a female in oestrus rubs her chest on other mongooses (Estes 1991; Kingdon and Hoffmann 2013). The marking of the 3-M-3-MB dispensers by small-spotted genets matches the flank-rubbing and urine-marking reported by Roeder (1980), and gas chromatography–mass spectrometry (GC–MS) analysis of deposits on the dispensers (Apps unpublished) showed the presence of urea from urine as well as free fatty acids and squalene, which are likely to be from glandular secretions. Civets did not mark the dispensers; even though they are similar to objects that civets naturally mark (Randall 1979), the odour of the marks on the two marked dispensers was warm and musky, quite unlike the rank, animalic odour of civet, and no civetone, a major component of civet, was detected by GC–MS analyses from either of the marked dispensers (Apps unpublished).

Mammals investigate and scent-mark novel objects, and small-spotted genets in captivity readily mark clean objects (Roeder 1980). Although it is possible that genets scent-marked in response to the clean outer surface of the dispenser rather than the odour of the tomcat thiol, this is unlikely given the absence of response to VA+P dispensers and the timing of the marking of 3-M-3-MB dispensers. By the time the 3-M-3-MB dispensers were moved or removed they had been at their sites for at least 5 weeks, and so were not novel. One of the dispensers was first marked 1 month after it was set up with 3-M-3-MB, and was then marked eight times in 3 days, and the other was first marked 2 weeks after it was set up and was then marked four times in 2 days. Similarly, in a small-scale study, the possibility that the difference in response to the two scents was due to their being presented at different times and in different places cannot be eliminated. Presenting both the thiol and VA+P at each camera would have confounded any attractant or repellent effects they might have had, and presenting the different scents at the same time in different places would have required more cameras than we had, and would still not have eliminated the effects of different sites.

It is not possible to be sure whether a response was to the artificial scent or to scent deposited by an earlier visitor. No marking was recorded at 7 of the 11 3M-3-MB sites, one mark was recorded at one of them, and two marks at another one. The other two sites had 9 and 11 marks, all of them from small-spotted genets and slender mongooses, strongly suggesting a positive feedback response to earlier

marks. Slender mongooses marked or rubbed only after a genet had marked. The failure of a small-spotted genet to rub on a 7-hour-old wildcat mark that it had sniffed may have been due to the mark being on a thorny bush. Captive genets overmark fresh genet scent (Roeder 1980), and it is likely that some genets were responding to conspecific scent, but this cannot apply to the first genet to mark a dispenser. Why small-spotted genets should overmark 3-M-3-MB from wildcats, and slender mongooses and genets overmark one another's scents, is uncertain. All three species are common and widespread, they have similar diets, and both genets and cats are nocturnal, while slender mongooses are diurnal. Civets which marked once are more insectivorous than the other three species.

The rubbing by genets and slender mongooses was prolonged and intense, like the rubbing of other carnivores on carrion and other strongly scented materials, whose function in nearly all instances is unknown despite much speculation (Rieger 1979; Gosling and McKay 1990). They may have been anointing themselves with the scent of a dominant predator, as grey foxes do at puma scent scrapes (Allen et al. 2017) and potential prey species at ocelot latrines (King et al. 2016), but although leopards are clearly a dominant predator whose odour might enhance genet survival, it is not clear how the odour of small, nocturnal genets would enhance the survival of diurnal mongooses.

These results, and those of Allen et al. (2015, 2017) and King et al. (2016), have practical implications for studies of mammal chemical signalling. Most importantly, a scent mark sampled for chemical analysis may overlay and be contaminated by an earlier mark from a different species. After an experimental scent has been marked, any subsequent responses may be to the natural scent rather than the experimental one, and if an odourless control was marked, the mark would generate false positives by attracting further marks, which in turn will attract attention away from a nearby artificial scent. Hence our use in this study of odorous controls presented at a different time to the experimental odour.

Because they affect detection probability, responses to scent marks have implications for the use of camera trapping to estimate animal abundance and distribution. A natural scent mark in a camera's field of view (FOV) could make animals more likely to be recorded, and conversely a scent mark just outside a FOV will reduce detectability by luring animals away. Scent marks, or lures that contain components of carnivore scents (Kimball et al. 2000), might trigger cascades of multi-species counter-marking and investigation that increase detectability, and the limited lifetime of lures and scent marks will cause short-term variations in detectability at a site. These effects violate requirements of the random encounter model (Rowcliffe et al. 2013), and introduce sudden, non-linear changes in

site characteristics (MacKenzie et al. 2002) that are not easily parameterized. Fortunately, fast-triggering cameras have reduced the need for arrestant lures (Rovero et al. 2013; Newey et al. 2015), and the availability of cameras that record video as well as still images makes it possible to record scent-marking and responses to scent as well as take clear pictures for individual recognition.

The intensity of the genet and slender mongoose reactions points to the possibility of rational design of “super lures” for pest control (Linklater et al. 2013) and collecting hair samples for genetic analysis (Thomas et al. 2005). In captivity, interspecific scent-marking will provide a rational biological basis for olfactory enrichment (Coe 2004; Clark and King 2008), and extend the use of chemical signals beyond species-specific pheromones and signature mixtures (Dehnhard 2011).

Interspecific marking has now been recorded in three complex natural carnivore guilds (this study; Allen et al. 2015, 2017; King et al. 2016), and it could well be ecologically important. Sniffing, rubbing and overmarking might facilitate interspecific disease transmission. Interspecific competition among carnivores imposes temporal and spatial constraints on access to resources (e.g. Palomares and Caro 1999; Donadio and Buskirk 2006; Schuette et al. 2013; Vanak et al. 2013; Leo et al. 2015). Our study area supports 24 species of carnivore ranging in size from lions (*Panthera leo*) to dwarf mongooses (*Helogale rufula*), and interspecific scent-marking may be one means by which they mediate their interspecific interactions. A solitary animal is far more likely to encounter heterospecifics than conspecifics, and for much of the time heterospecifics may be more important than conspecifics, because among carnivores, conspecifics rarely kill one another but interspecific killing is common (Palomares and Caro 1999). Heterospecific scent marks are strong candidates as cues that enable individuals of different species to avoid conflict by keeping track of one another’s movements (Leo et al. 2015; Garvey et al. 2016), and may be important to guild and community structures and processes. Chemical signalling between mammalian species merits further attention.

Acknowledgements This work was part of the Botswana Predator Conservation Trust’s Bioboundary project, which was set up with funding from the Paul G. Allen Family Foundation. Running expenses for this work were provided by private donors through Wild Entrust International and Tusk Trust. We are grateful for permission to carry out research in Botswana granted by the Botswana Department of Wildlife and National Parks, Ministry of Environment, Wildlife and Tourism and the President’s Office under research permit number 8/36/4 XXIV (205).

Compliance with ethical standards

Ethical approval All applicable international, national, and/or institutional guidelines for the care and use of animals were followed.

Conflict of interest None of the authors declared a conflict of interest.

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