



# Cheetah marking sites are also used by other species for communication: evidence from photographic data in a comparative setup

Sarah Edwards<sup>1,2,3</sup> · Rebekka Mueller<sup>1</sup> · Ralf Roeder<sup>1</sup> · Joerg Melzheimer<sup>1</sup> · Bettina Wachter<sup>1</sup>

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## Abstract

Many mammalian species communicate via olfactory communication placed at particular locations. The majority of these studies focused on intraspecific communication. More recently, studies have also investigated interspecific communication and recorded prey animals sniffing olfactory cues left by predators and predators investigating or counter-marking cues left by other predator species. The purpose of exchanging olfactory cues within a species community is little understood. Using a comparative study design, we investigated the behaviour of a mammalian community at cheetah marking trees and paired control trees using camera traps on Namibian farmland. We tested the predictions derived from hypotheses regarding the reasons for visits to the marking trees. Cheetah marking trees and control trees were visited 1101 times by 29 mammalian species (excluding cheetahs), with more species recorded at the marking trees than control trees. Two competitively subordinate carnivore species made more visiting and sniffing events, respectively, at cheetah marking trees than control trees, possibly to assess the time since cheetahs were in the area. Two opportunistic scavenger species sniffed more frequently at the marking trees than control trees, perhaps to feed on undigested prey remains in scats. One common prey species of cheetahs had fewer visiting events at the marking trees than control trees, likely to reduce encounters with cheetahs. Further, one species that is rarely preyed by cheetahs marked cheetah marking trees at the same frequency as control trees, suggesting it uses conspicuous sites rather for intraspecific than interspecific communication. Thus, trees used by cheetahs for marking also play an important role in olfactory communication for a variety of mammalian species.

**Keywords** *Acinonyx jubatus* · Cheetah · Camera traps · Interspecific communication · Intraspecific communication · Mammalian community · Namibia

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✉ Sarah Edwards  
sledwardsuk@gmail.com

- 1 Evolutionary Ecology, Leibniz Institute for Zoo and Wildlife Research, Berlin, Germany
- 2 Centre for Wildlife Management, University of Pretoria, Pretoria, South Africa
- 3 Capel Manor College, Bullsmoor Lane, Waltham Cross, Enfield EN1 4RQ, UK

## Introduction

Olfactory communication is an important way for animals to transfer, receive and exchange information between individuals or groups. Olfactory communication in terms of scent marks is often used by mammalian species operating in territories, such as many carnivores, to claim territory ownership (Kruuk 1972; Gosling 1982; Gorman and Mills 1984). While olfactory information is mainly directed to conspecifics, it is also used between individuals of different species (Apfelbach et al. 2005; Allen et al. 2017; Apps et al. 2019; Cornhill and Kerley 2020). The latter received increased attention with the increased use of camera traps over the last one or two decades.

Interspecific communication, i.e. communication between different species, has been mainly described between prey and predator species and between carnivore species (Roberts

and Gosling 2001). Interspecific communication often constitutes the prey animals or competitively subordinate carnivores sniffing at olfactory cues, such as scats and urine of predator/more dominant predator animals (e.g. Apfelbach et al. 2005; Wikenros et al. 2017). As a reaction, the prey animals might shift their activity pattern, foraging time and/or habitat use to reduce the chances of encountering the predator (Ward et al. 1997; Apfelbach et al. 2005; Kuijper et al. 2014; Wikenros et al. 2017; Apps et al. 2019). For example, the experimental exposure of red deers (*Cervus elaphus*) to scats of wolves (*Canis lupus*) induced an increase of vigilance and decrease in foraging time in red deers compared to control plots (Kuijper et al. 2014). In contrast, experimental exposure of a competitively subordinate carnivore, the red fox (*Vulpes vulpes*), to scats of a dominant predator, the Eurasian lynx (*Lynx lynx*), induced more visits to the scat sites by red foxes than expected, and the duration of visits was longer than at control sites (Wikenros et al. 2017). It was suggested that competitively subordinate carnivores might be attracted to scat sites to estimate their proximity to and risk of encountering the dominant predator and/or to feed on undigested prey remains in scats (King et al. 2016; Wikenros et al. 2017). Large omnivorous species, such as wild boars (*Sus scrofa*) which occasionally feed on carcasses and prey remains (Ballari and Barrios-Garcia 2014; Focardi et al. 2017), may also use scats to feed on undigested prey remains therein.

While prey species only sniff predator scent and normally do not mark at these locations, predator species might also counter-mark at them, i.e. leave a scent mark on top of (over-marking) or mark adjacent to an existing scent mark (Li et al. 2013; Apps et al. 2019). For example, red foxes over-marked scats of Eurasian lynx (Wikenros et al. 2017), wolves and coyotes (*Canis latrans*) over-marked each other's marking (Paquet 1991), and leopards (*Panthera pardus*) and lions (*P. leo*) marked at marking trees of cheetahs (*Acinonyx jubatus*; Cornhill and Kerley 2020; Verschuere et al. 2021). Interspecific communication can also occur by rubbing body parts at the marking sites of other species. Depending on the species, body rubbing is interpreted as leaving or receiving information (Allen et al. 2017). Non-prey species/dominant predator species might perform body rubbing to leave information (Cornhill and Kerley 2020; Verschuere et al. 2021), while prey species and competitively subordinate carnivore species might perform body rubbing to receive the odour of the predator/more dominant predator species (King et al. 2016). The adopted smell might have an antipredator function and reduces the risks of predation (King et al. 2016).

Counter-marking may not be related to interspecific communication when the marking sites are conspicuous and rare. It is possible that different species select easy-to-detect marking sites with similar features, and the shared marking sites do not necessarily imply that different species are responding to the

scent of one another. For example, eight carnivore species marked or rubbed body parts at a conspicuous overhanging rock on the junction of two valleys which was the main marking site of snow leopards (*P. uncia*; Li et al. 2013). The main visiting and communication activity of the different species at the overhanging rock differed between the species and was in accordance with their mating seasons or hibernation period (Li et al. 2013). Markings on conspicuous sites might, therefore, be mainly for intraspecific communication i.e. within the same species, rather than for interspecific communication.

In this study, we monitored mammalian activities at nine confirmed cheetah marking trees and nine similar looking control trees nearby on farmland in central Namibia. All the monitored trees were within the territory of a coalition of two males. We used a paired setup of marking trees and control trees to investigate whether mammalian species visit these trees for interspecific and/or intraspecific communication. Marking locations of cheetahs are conspicuous sites, mainly large single-standing trees, but also rocks, termite mounds or other structures (Caro 1994). They are located in the core area of territorial males and visited by the territorial males, and also by the non-territorial males and females to leave, receive or exchange information (Melzheimer et al. 2018; 2020). These marking trees are mainly used by cheetahs, but are also visited by other mammalian species. Here, we investigated five hypotheses (H) by testing the respective predictions. H1: prey species avoid cheetah marking trees to reduce the risks of encountering the predator. If so, we predict fewer visiting and/or sniffing events by prey species at the cheetah marking trees than control trees. H2: cheetah marking trees are used by competitively subordinate carnivore species to gain information on the more dominant predator. This hypothesis implies that cheetah marking trees are sites approached at a relatively low immediate encounter risk and provide information of perimeter to be used for roaming and foraging by the visitor species. If so, we predict more visiting and/or sniffing events of competitively subordinate carnivore species at cheetah marking trees than control trees. H3: cheetah marking trees are used by carnivorous and omnivorous species to feed on undigested prey remains in scats. If so, we predict the same as for H2, but for both carnivorous and omnivorous species. H4: cheetah marking trees are used by dominant predator species to advertise their presence. If so, we predict more visiting and/or sniffing and marking events of dominant predator species at the cheetah marking trees than control trees. H5: species use conspicuous sites for their intraspecific communication. If so, we predict similar visiting events and/or similar sniffing and marking events of these species at both the cheetah marking trees and control trees. H5 does not include potential prey species of cheetahs since we do not expect them to mark and advertise their presence at marking sites of predator species.

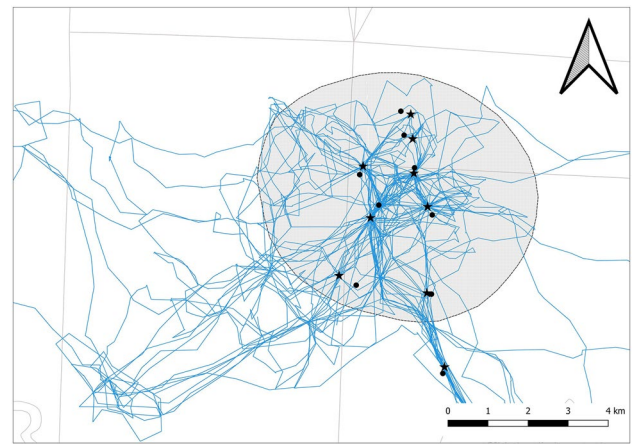
## Methods

### Study site

The study took place on a freehold farm in central Namibia, approximately 45 km east from the capital Windhoek. The farm encompassed the home range of a territorial cheetah male coalition monitored within the long-term Cheetah Research Project of the Leibniz Institute for Zoo and Wildlife Research in Berlin, Germany. For the detailed procedure of capturing, collaring and handling cheetahs, see Melzheimer et al. (2018). The farm is a commercial cattle farm with fences along the farm border and internal fences made of five-strand cattle fencing, which are easily crossable for wildlife species. Other large, more dominant carnivores, such as leopards and occasionally brown hyenas (*Parahyaena brunnea*), are also present in the study site (Hayward and Slotow 2009). The site has an average annual rainfall of 300 mm, and comprises a variety of habitats, including mountains, open plains, pans and ephemeral rivers.

### Cheetah marking trees and control trees

We identified cheetah marking trees using spatial data of the territorial coalition of two males, of which one was collared with a GPS collar (e-obs GmbH, Grünwald, Germany). The tracking data produced clusters of GPS locations at the marking trees because territorial males visit these trees frequently (Melzheimer et al. 2018). We visited the trees in the field to assess the number and freshness of scats and thus verified that they were currently used as marking sites by cheetahs (Melzheimer et al. 2018; Kusler et al. 2019). The cheetah marking trees with the most fresh cheetah scats were shortlisted. From these trees, we chose nine trees that gave the best uniform spatial coverage of the core area of the cheetah territory, where most cheetah communication occurs (Melzheimer et al. 2018; 2020). Eight trees were within the core area of the cheetah territory, and one was slightly outside (Fig. 1). We defined the core area as the 50% kernel density estimator (KDE50) of the GPS locations of the collared territorial male, i.e. the area in which 50% of all GPS locations were recorded (Melzheimer et al. 2020). We implemented a paired study design, thus selected for each of the nine marking trees one control tree. Control trees were chosen as the nearest tree to the marking tree which were most similar in size, conspicuousness and appearance. We measured the similarity in terms of trunk circumference, shade cover and number of game trails heading to the tree. We carefully screened the control trees and verified the absence of cheetah scats. Trunk circumference was measured at 1.2 m above the ground, shade cover was determined by calculating the area of the ellipse of shade on



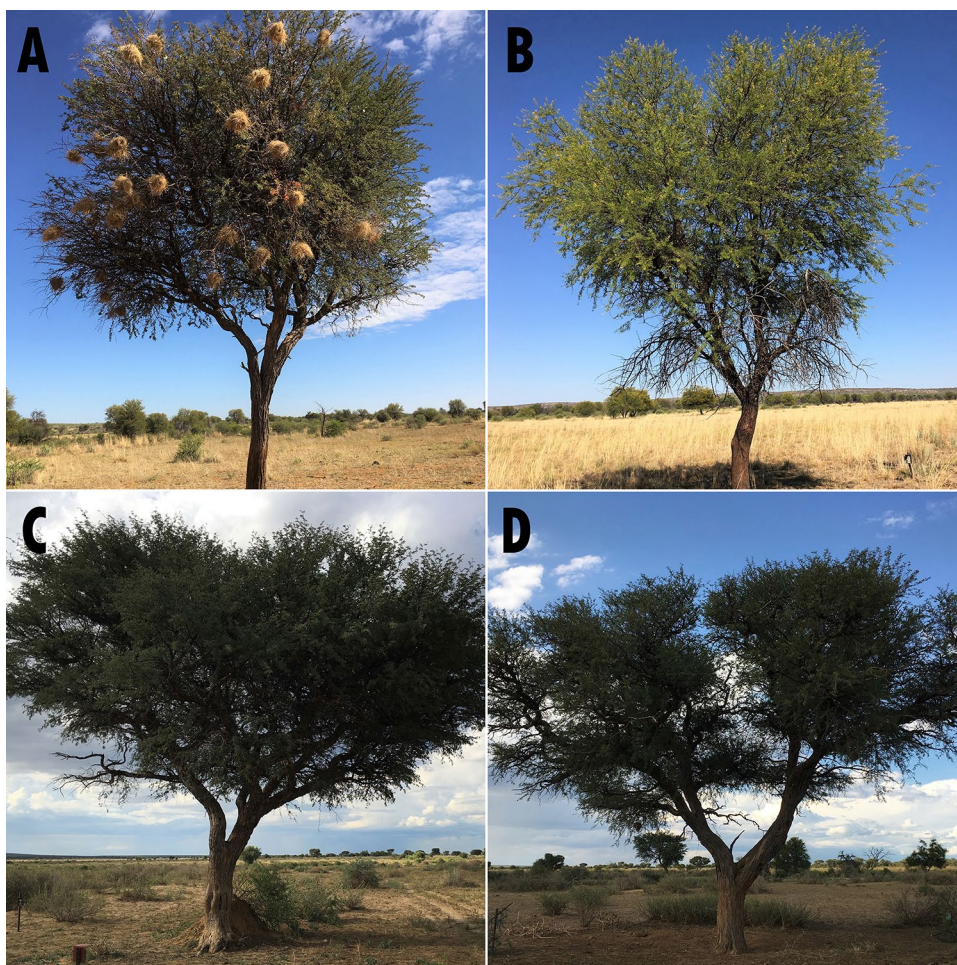
**Fig. 1** Map with movements (blue lines) of the territorial cheetah male coalition from 19th December 2017 to 25th June 2018, i.e. 2 months before the camera study started until 2 months after it ended, the cheetah marking trees (black stars) and the corresponding control trees (black dots). The grey circular area represents the 50% kernel density estimator (KDE50) of the GPS locations of the territorial males, i.e. the area in which 50% of all GPS locations of the coalition were recorded. The grey lines represent the farm borders

the ground at midday ( $\text{length}/2 * \text{width}/2 * \pi$ ) and the number of game trails heading to the tree was counted by walking around the tree one full circle. If the main trunk was separated into two or more trunks at 1.2 m above the ground, we added up the circumferences of the trunks. Cheetah marking trees comprised *Acacia erioloba* ( $n=6$ ), *A. hebeclada* ( $n=1$ ), *Searsia lancea* ( $n=1$ ), *Boscia albitrunca* ( $n=1$ ) and control trees comprised *A. erioloba* ( $n=4$ ), *A. hebeclada* ( $n=2$ ), *B. albitrunca* ( $n=1$ ), and *A. karoo* ( $n=2$ ; Fig. 2).

### Camera trap monitoring

We monitored the cheetah marking trees and control trees for 65 days from 19th February 2018 to 25th April 2018, with Reconyx PC900 HyperFire™ and Reconyx HC600 HyperFire Professional cameras with a passive LED infrared system (Reconyx, Holmen, Wisconsin, USA). Each tree was monitored with two cameras, set with a lateral offset to avoid flash interference, and focused towards the ‘active’ area of the marking tree. We defined the ‘active’ areas as those having urine, scats, hair and soil from the rubbing activities of various species. For the control trees, we placed the two cameras to capture a good coverage of the tree and the immediate surrounding area. The cameras were programmed to take three photos per trigger, with no delay between triggers at a photo quality of 3.1 mega-pixels on high sensitivity. We placed cameras approximately 3 m–5 m away from marking and control trees and mounted them on poles approximately 50 cm–60 cm above the ground.

**Fig. 2** Two examples of cheetah marking trees and the corresponding paired control trees. **A** and **C** were the cheetah marking trees, whereas **B** and **D** were the control trees. **A** (*Acacia erioloba*) and **B** (*A. karoo*) were 203 m apart from each other, whereas **C** (*A. erioloba*) and **D** (*A. erioloba*) were 110 m apart from each other



We included camera trap data for analysis when an animal was recorded approaching a tree rather than walking in the background. Rodent species were excluded from the analyses. We classified data into independent events when a minimum of 30 min between consecutive records passed or, for species for which individual identification is possible, when different individuals were seen. The duration between independent events was calculated by subtracting the time of the first photo of a sequence from the time of the last photo of the previous sequence. Due to the seconds not being included in the time of events at the cheetah marking trees or control trees, we allocated a default value of 30 s to any event in which less than a minute passed. We recorded the behaviours of species during independent events and classified them into two communication categories (1) ‘receiving information’, which included sniffing on the ground, vegetation and/or tree and (2) ‘leaving information’, which included scent marking in the form of urination, defecation, anal dragging, pawing/scratching the ground with the front or hind feet, tree scratching, facial rubbing and body rubbing. In this study, body rubbing was performed only by aardvark (*Orycteropus afer*) and warthog (*Phacochoerus*

*africanus*; see in the Result section), two species that are not or only rarely preyed by cheetahs (Marker et al. 2003; Hayward et al. 2006; Wachter et al. 2006). We, therefore, allocated body rubbing to ‘leaving information’, because we assumed these species did not use the predator smell as an antipredator tactic. We also conducted the analyses without body rubbing to include the option that body rubbing was not related to communication but perhaps to a comfort behaviour, i.e. scratching the body on the tree. Other behaviours such as interacting with the camera, grazing/feeding, observing the environment (vigilance), playing, jumping on the tree, grooming, resting or mating were used to count visiting events and were not allocated to one of the two defined communication categories. To acknowledge the possibility that visitors might also receive and/or leave information while performing behaviours other than sniffing and marking trees, we also used this full data set (i.e. containing all behaviours from all visits) for analyses. With this full data set, we compared the number of visits of each species at the cheetah marking and control trees, irrespective of the behaviour of the animals at the trees.

## Data analysis

We conducted the analyses in the statistical program R version 3.2.1 (R Core Development Team, 2014). The data sets used for comparing the tree characteristics of the nine cheetah marking trees and nine control trees were normally distributed (Shapiro Wilk test), thus we performed parametric paired *t* tests. Similarly, the data sets used for comparing the species diversity were normally distributed. For these data, we used the Hutcheson's test (Gardener 2012), a modified version of the *t* test to compare the Shannon diversity index (an index used to measure the diversity of a population) of two samples. In contrast, the data sets used for comparing the number of visits, number of events of 'receiving information' and number of events of 'leaving information' of each species at the nine cheetah marking trees and nine control trees deviated from normal distribution, thus we performed non-parametric paired tests (Wilcoxon signed-rank test). During a visit, an individual might display more than one behaviour within the category for 'receiving information' or 'leaving information'. In these cases, the behaviour was counted only once for the respective categories. An individual might also display both behaviour categories during one visit. In these cases, we handled 'receiving information' and 'leaving information' as independent events and counted them once for each category. We restricted the analyses to those species for which we had > 20 events in total during the survey period. The significance level was set at  $p = 0.05$ .

## Results

### Marking and control tree comparisons

Paired cheetah marking trees and control trees had a mean distance of 209.0 m (SD = 86.3, range = 110.0–350.0 m; Fig. 1). There were no differences between cheetah marking trees and control trees for tree circumference ( $Z = 25$ ,  $d.f. = 8$ ,  $p = 0.07$ ), shade cover ( $Z = 27$ ,  $d.f. = 8$ ,  $p = 0.23$ ) or the number of game trails heading to the trees ( $Z = 12$ ,  $d.f. = 8$ ,  $p = 0.23$ ; Table 1).

**Table 1** Summary of measured characteristics of the nine cheetah marking trees and nine control trees based on tree circumference measured at 1.2 m from the ground, shade cover determined as the

| Tree type    | Tree circumference (m) |     |         | Shade cover (m <sup>2</sup> ) |      |            | Number of game trails |     |       |
|--------------|------------------------|-----|---------|-------------------------------|------|------------|-----------------------|-----|-------|
|              | Mean                   | SD  | Range   | Mean                          | SD   | Range      | Mean                  | SD  | Range |
| Marking tree | 2.3                    | 1.4 | 1.1–4.5 | 88.9                          | 65.7 | 31.9–235.6 | 3.1                   | 1.2 | 2–5   |
| Control tree | 1.8                    | 1.0 | 0.7–3.6 | 76.7                          | 62.2 | 22.8–212.1 | 2.8                   | 0.7 | 2–4   |

## Number of visits and species diversity

During the 65-day survey period at the 18 trees, a total of 2567 camera trap nights were achieved with the 36 camera traps used. Three camera traps at different trees failed for eight, 12 and 13 days, respectively. During the survey period, a total of 1173 independent visits from 30 mammalian species (1101 independent visits from 29 mammalian species excluding cheetahs) were recorded, with species ranging from slender mongoose (*Galerella sanguinea*) to common eland (*Taurotragus oryx*; Table 2, Supplementary Table S1). Cheetah marking trees were visited 635 times by 27 mammal species (566 times by 26 species excluding cheetahs), whereas control trees were visited 538 times by 25 mammal species (535 times by 24 species excluding cheetahs; Table 2). These results reflected a higher diversity of species at cheetah marking trees than control trees for all species ( $t = 5.54$ ,  $d.f. = 8$ ,  $p = 0.02$ ) and for all species excluding cheetahs ( $t = 4.32$ ,  $d.f. = 8$ ,  $p = 0.01$ ).

Regarding the data set with > 20 events at the cheetah marking trees and control trees, 13 species visited the trees (Table 2). Only African wild cat (*Felis lybica*;  $Z = 35$ ,  $d.f. = 8$ ,  $p = 0.01$ ) and cheetah ( $Z = 45$ ,  $d.f. = 8$ ,  $p = 0.003$ ) visited cheetah marking trees more frequently than control trees, whereas common duiker (*Sylvicapra grimmia*;  $Z = 0$ ,  $d.f. = 8$ ,  $p = 0.03$ ) visited cheetah marking trees less frequently than control trees (Table 2).

## Behaviour at trees

Twenty-four species were recorded 'receiving information' at cheetah marking trees and/or control trees (Table 3). A total of 363 such events were recorded at cheetah marking trees (301 events excluding cheetah records) and 107 events were recorded at control trees (104 events excluding cheetah records; Table 3). Nine species were recorded 'receiving information' with > 20 events (Table 3). Cape porcupine (*Hystrix africae australis*;  $Z = 34$ ,  $d.f. = 8$ ,  $p = 0.03$ ), cheetah ( $Z = 45$ ,  $d.f. = 8$ ,  $p = 0.002$ ), black-backed jackal (*Canis mesomelas*;  $Z = 41$ ,  $d.f. = 8$ ,  $p = 0.03$ ) and warthog ( $Z = 25$ ,  $d.f. = 8$ ,  $p = 0.03$ ) had a higher number of events of 'receiving information' (Fig. 3) at the cheetah marking trees than control trees (Table 3). Aardvark, African wild cat, slender mongoose, greater kudu (*Tragelaphus strepsiceros*) and

ellipse of shade on the ground at midday (length/2\*width/2\* $\pi$ ) and numbers of game trails heading to the tree. SD = standard deviation

**Table 2** Mammalian species recorded at nine cheetah marking trees and nine control trees and results of Wilcoxon signed-rank tests ( $d.f. = 8$ ) on their number of independent visits. n.a. = not applicable because numbers of events were not  $> 20$ 

| Species   | Marking tree visits |        |   | Control tree visits |        |   | Wilcoxon test |        |
|---|---------------------|--------|---|---------------------|--------|---|---------------|--------|
|   | Total               | Median | 1 <sup>st</sup> ; 3 <sup>rd</sup> Quartiles | Total               | Median | 1 <sup>st</sup> ; 3 <sup>rd</sup> Quartiles | Z             | p      |
| Aardvark <i>Orycteropus afer</i>                        | 35                  | 3      | 1; 6  | 26                  | 2      | 1; 4  | 21            | 0.72   |
| Baboon <i>Papio ursinus</i>                             | 72                  | 5      | 3; 13                                       | 128                 | 9      | 4; 26                                       | 4             | 0.07   |
| Cape porcupine <i>Hystrix africaeaustralis</i>          | 36                  | 3      | 3; 4  | 21                  | 1      | 1; 2  | 34            | 0.17   |
| South African springhare <i>Pedetes capensis</i>        | 0                   | n.a.   | n.a.  | 4                   | n.a.   | n.a.  | n.a.          | n.a.   |
| South African ground squirrel <i>Xerus inauris</i>      | 0                   | n.a.   | n.a.  | 1                   | n.a.   | n.a.  | n.a.          | n.a.   |
| Scrub hare <i>Lepus saxatilis</i>                       | 12                  | n.a.   | n.a.  | 1                   | n.a.   | n.a.  | n.a.          | n.a.   |
| Cheetah <i>Acinonyx jubatus</i>                         | 69                  | 9      | 4; 11                                       | 3                   | 0      | 0; 1  | 45            | 0.003* |
| Caracal <i>Caracal caracal</i>                          | 2                   | n.a.   | n.a.  | 2                   | n.a.   | n.a.  | n.a.          | n.a.   |
| African wild cat <i>Felis lybica</i>                    | 40                  | 3      | 2; 7  | 21                  | 3      | 1; 3  | 35            | 0.01*  |
| Leopard <i>Panthera pardus</i>                          | 4                   | n.a.   | n.a.  | 2                   | n.a.   | n.a.  | n.a.          | n.a.   |
| Small spotted genet <i>Genetta genetta</i>              | 12                  | n.a.   | n.a.  | 1                   | n.a.   | n.a.  | n.a.          | n.a.   |
| Yellow mongoose <i>Cynictis penicillate</i>             | 2                   | n.a.   | n.a.  | 2                   | n.a.   | n.a.  | n.a.          | n.a.   |
| Slender mongoose <i>Galerella sanguinea</i>             | 34                  | 2      | 0; 3  | 16                  | 0      | 0; 1  | 19            | 0.62   |
| Banded mongoose <i>Mungos mungo</i>                     | 8                   | n.a.   | n.a.  | 11                  | n.a.   | n.a.  | n.a.          | n.a.   |
| Meerkat <i>Suricata suricatta</i>                       | 8                   | n.a.   | n.a.  | 4                   | n.a.   | n.a.  | n.a.          | n.a.   |
| Brown hyena <i>Parahyaena brunnea</i>                   | 1                   | n.a.   | n.a.  | 0                   | n.a.   | n.a.  | n.a.          | n.a.   |
| Aardwolf <i>Proteles cristatus</i>                      | 4                   | n.a.   | n.a.  | 3                   | n.a.   | n.a.  | n.a.          | n.a.   |
| Cape fox <i>Vulpes chama</i>                            | 0                   | n.a.   | n.a.  | 1                   | n.a.   | n.a.  | n.a.          | n.a.   |
| Black-backed jackal <i>Canis mesomelas</i>              | 128                 | 10     | 3; 16                                       | 62                  | 4      | 1; 6  | 22            | 0.25   |
| Bat-eared fox <i>Otocyon megalotis</i>                  | 17                  | 1      | 0; 1  | 4                   | 0      | 0; 0  | 18            | 0.10   |
| Honey badger <i>Mellivora capensis</i>                  | 4                   | n.a.   | n.a.  | 3                   | n.a.   | n.a.  | n.a.          | n.a.   |
| Hartmann's mountain zebra <i>Equus zebra hartmannae</i> | 1                   | n.a.   | n.a.  | 0                   | n.a.   | n.a.  | n.a.          | n.a.   |
| Warthog <i>Phacochoerus africanus</i>                   | 70                  | 7      | 3; 9  | 72                  | 5      | 4; 7  | 20            | 0.83   |
| Red hartebeest <i>Alcelaphus buselaphus</i>             | 3                   | n.a.   | n.a.  | 0                   | n.a.   | n.a.  | n.a.          | n.a.   |
| Steenbok <i>Raphicerus campestris</i>                   | 9                   | 1      | 0; 2  | 12                  | 0      | 0; 2  | 4             | 0.20   |
| Common eland <i>Taurotragus oryx</i>                    | 2                   | n.a.   | n.a.  | 0                   | n.a.   | n.a.  | n.a.          | n.a.   |
| Greater kudu <i>Tragelaphus strepsiceros</i>            | 16                  | 0      | 0; 3  | 73                  | 1      | 0; 3  | 3             | 0.28   |
| Common duiker <i>Sylvicapra grimmia</i>                 | 25                  | 1      | 1; 4  | 57                  | 2      | 2; 6  | 6             | 0.03*  |
| Gemsbok <i>Oryx gazelle</i>                             | 18                  | 1      | 1; 3  | 8                   | 1      | 0; 1  | 28            | 0.12   |
| Waterbuck <i>Kobus ellipsiprymnus</i>                   | 3                   | n.a.   | n.a.  | 0                   | n.a.   | n.a.  | n.a.          | n.a.   |
| Total   | 635 (566)           |        |   | 538 (535)           |        |   |               |        |

The sum of visits is given for all species including cheetahs and in parentheses for all species excluding cheetahs. See supplementary Table S1 for data on each species and tree

\* Indicates a significant result of  $< 0.05$

common duiker showed no difference in the number of 'receiving information' events at cheetah marking trees and control trees (Table 3).

Twelve species were recorded 'leaving information' at the cheetah marking trees and/or control trees (Table 4). A total of 116 such events were recorded at cheetah marking trees (71 events excluding cheetah records) and 22 events were recorded at control trees (20 events excluding cheetah records; Table 3). Only warthogs were recorded 'leaving information' at trees with  $> 20$  events (Fig. 4) and there were

no significant differences at the cheetah marking trees versus control trees (Table 4). The result did not change when body rubbing behaviour of warthog was excluded (Table 4). In contrast, and as defined, cheetahs had significantly higher numbers of leaving information events at their marking trees than at control trees ( $Z = 45$ ,  $d.f. = 8$ ,  $p = 0.002$ ; Fig. 4, Table 4). They left scats, urine and/or scratches 45 times at cheetah marking trees, and urinated twice at control trees (Supplementary Table S1). The two control trees, although marked with urine, were not considered as cheetah marking

**Table 3** Number of events of the behaviour ‘receiving information’ recorded at cheetah marking trees and control trees by mammalian species and respective Wilcoxon signed-rank test ( $df = 8$ ) on the events. n.a. = not applicable because numbers of events were not > 20

| Species                       | Events at marking trees |        |   | Events at control trees |        |   | Wilcoxon test |        |
|-------------------------------|-------------------------|--------|---|-------------------------|--------|---|---------------|--------|
|                               | Total                   | Median | 1 <sup>st</sup> ; 3 <sup>rd</sup> Quartiles | Total                   | Median | 1 <sup>st</sup> ; 3 <sup>rd</sup> Quartiles | Z             | p      |
| Aardvark                      | 29                      | 3      | 1; 6  | 16                      | 1      | 0; 2  | 17.5          | 0.17   |
| Baboon                        | 5                       | n.a.   | n.a.  | 0                       | n.a.   | n.a.  | n.a.          | n.a.   |
| Cape porcupine                | 32                      | 3      | 2; 4  | 8                       | 1      | 0; 1  | 34            | 0.03*  |
| South African ground squirrel | 0                       | n.a.   | n.a.  | 1                       | n.a.   | n.a.  | n.a.          | n.a.   |
| Scrub hare                    | 1                       | n.a.   | n.a.  | 0                       | n.a.   | n.a.  | n.a.          | n.a.   |
| Cheetah                       | 62                      | 9      | 3; 10                                       | 3                       | 0      | 0; 1  | 45            | 0.002* |
| African wild cat              | 17                      | 1      | 0; 2  | 5                       | 0      | 0; 0  | 23.5          | 0.12   |
| Leopard                       | 4                       | n.a.   | n.a.  | 1                       | n.a.   | n.a.  | n.a.          | n.a.   |
| Small spotted genet           | 9                       | n.a.   | n.a.  | 1                       | n.a.   | n.a.  | n.a.          | n.a.   |
| Slender mongoose              | 22                      | 0      | 0; 2  | 3                       | 0      | 0; 0  | 10            | 0.11   |
| Banded mongoose               | 8                       | n.a.   | n.a.  | 6                       | n.a.   | n.a.  | n.a.          | n.a.   |
| Meerkat                       | 4                       | n.a.   | n.a.  | 0                       | n.a.   | n.a.  | n.a.          | n.a.   |
| Brown hyena                   | 1                       | n.a.   | n.a.  | 0                       | n.a.   | n.a.  | n.a.          | n.a.   |
| Aardwolf                      | 1                       | n.a.   | n.a.  | 2                       | n.a.   | n.a.  | n.a.          | n.a.   |
| Black-backed jackal           | 59                      | 5      | 1; 10                                       | 12                      | 1      | 0; 2  | 41            | 0.03*  |
| Bat-eared fox                 | 9                       | n.a.   | n.a.  | 1                       | n.a.   | n.a.  | n.a.          | n.a.   |
| Honey badger                  | 1                       | n.a.   | n.a.  | 1                       | n.a.   | n.a.  | n.a.          | n.a.   |
| Warthog                       | 52                      | 5      | 2; 7  | 15                      | 2      | 1; 2  | 25            | 0.03*  |
| Steenbok                      | 5                       | n.a.   | n.a.  | 2                       | n.a.   | n.a.  | n.a.          | n.a.   |
| Common eland                  | 1                       | n.a.   | n.a.  | 0                       | n.a.   | n.a.  | n.a.          | n.a.   |
| Greater kudu                  | 12                      | 0      | 0; 3  | 15                      | 0      | 0; 1  | 3             | 1      |
| Duiker                        | 22                      | 1      | 0; 4  | 15                      | 1      | 0; 3  | 17            | 0.32   |
| Gemsbok                       | 4                       | n.a.   | n.a.  | 0                       | n.a.   | n.a.  | n.a.          | n.a.   |
| Waterbuck                     | 3                       | n.a.   | n.a.  | 0                       | n.a.   | n.a.  | n.a.          | n.a.   |
| Total                         | 363 (301)               |        |   | 107 (104)               |        |   |               |        |

The sum of events is given for all species including cheetahs and in parentheses for all species excluding cheetahs. See supplementary Table S1 for data on each species and tree

\*Indicates a significant result of < 0.05

trees because no fresh scats were found when we visited the sites.

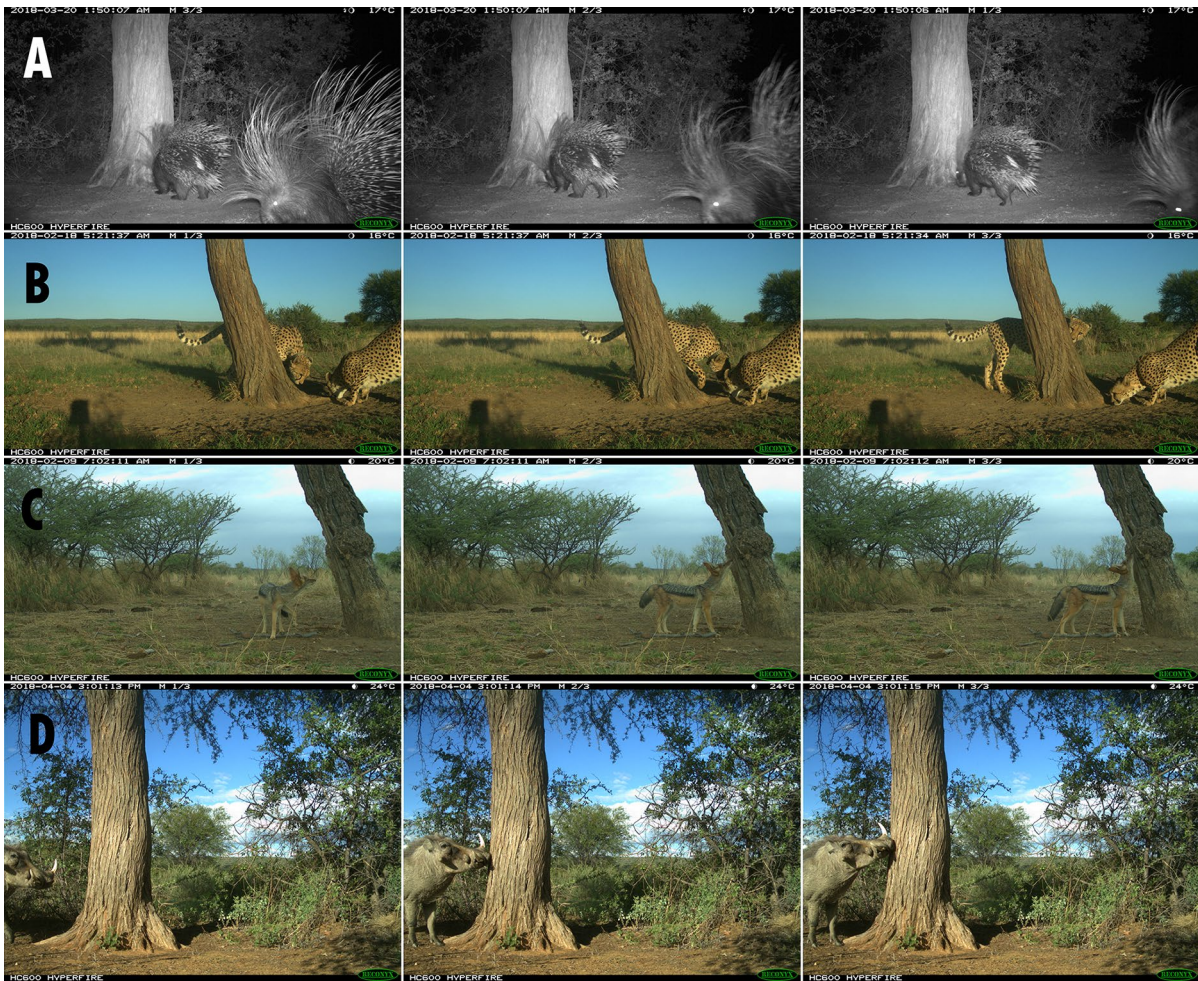
Leopards, the top predator on the study site visited the cheetah marking trees four times and the control trees twice, thus we excluded them from the analysis for species with > 20 events (Tables 2, 4). The leopard visits consisted of two adult solitary males, one adult solitary female and one female with a cub. They sniffed at the cheetah marking trees, urinated and/or did tree scratching, facial rubbing and body rubbing. They also sniffed and urinated at one of the two visited control trees (Supplementary Table S1).

## Discussion

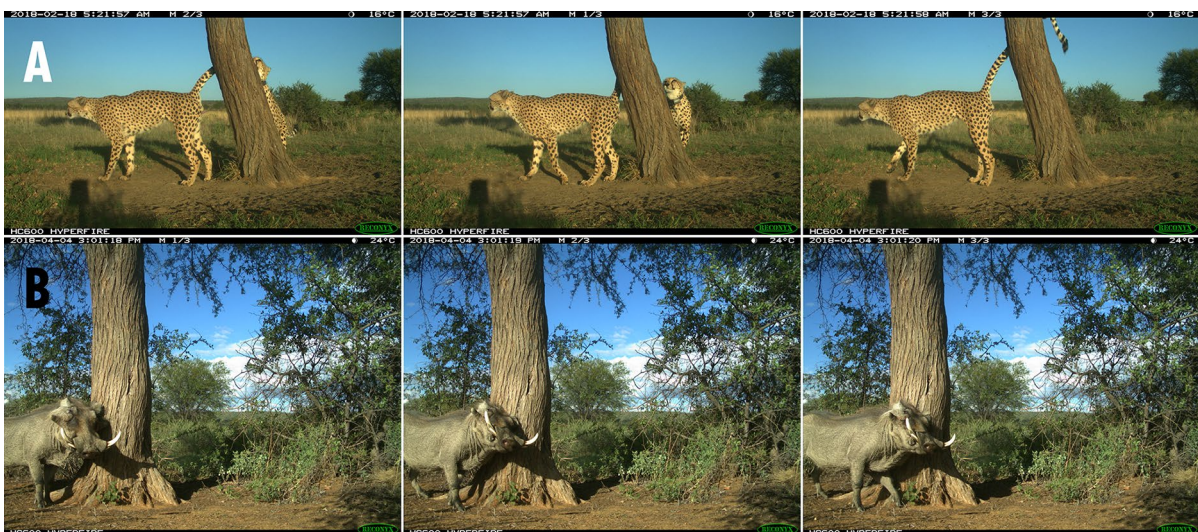
Marking sites of large carnivores being visited by a number of species within the wider mammalian wildlife community is an emerging topic that holds the potential of uncovering

a complex network of communication between different mammalian species. A number of previous studies have recorded visits by mammals to the marking sites belonging to a variety of predatory species, including snow leopard (Li et al. 2013), ocelot (*Leopardus pardalis*; King et al. 2016), puma (*Puma concolor*; Allen et al. 2017), North American river otter (*Lontra canadensis*; Wagnon and Serfass 2016) and cheetah (Cornhill and Kerley 2020). Given the potential cascading influences of large carnivores on mammalian communities (Shurin et al. 2002), the community members may gain fitness benefits from accessing olfactory information produced by large carnivores. As such, their marking sites may provide opportunities for prey species and competitively subordinate carnivore species to ‘eavesdrop’ on the olfactory information left by dominant carnivores.

Visiting species can be repelled or attracted by the scents of a predator/more dominant predator, depending on whether the visiting species is a potential prey species or not (Ward



**Fig. 3** Series of three consecutive pictures of the four species that had higher number of events in the behaviour of ‘receiving information’, i.e. sniffing at cheetah marking trees, than control trees. **A** Cape porcupine, **B** cheetah, **C** black-backed jackal, **D** warthog



**Fig. 4** Series of three consecutive pictures of the two species that showed the behaviour of ‘leaving information’ at cheetah marking trees with > 20 events in total. **A** A cheetah scent marking the tree with urine, **B** A warthog rubbing its facial gland on the tree



**Table 4** Number of events of the behaviour 'leaving information' recorded at cheetah marking trees and control trees by mammalian species and respective Wilcoxon signed-rank tests (*d.f.* = 8) on the events

| Species                | Events at marking trees |        |   | Events at control trees |        |   | Wilcoxon test |        |
|------------------------|-------------------------|--------|---|-------------------------|--------|---|---------------|--------|
|                        | Total                   | Median | 1 <sup>st</sup> , 3 <sup>rd</sup> Quartiles | Total                   | Median | 1 <sup>st</sup> , 3 <sup>rd</sup> Quartiles | Z             | p      |
| Aardvark, including BR | 11                      | n.a    | n.a   | 3                       | n.a    | n.a   | n.a           | n.a    |
| Aardvark, excluding BR | 9                       | n.a    | n.a   | 3                       | n.a    | n.a   | n.a           | n.a    |
| Cape porcupine         | 11                      | n.a    | n.a   | 0                       | n.a    | n.a   | n.a           | n.a    |
| Cheetah                | 45                      | 6      | 3; 7  | 2                       | 0      | 0; 0  | 45            | 0.002* |
| African wild cat       | 5                       | n.a    | n.a   | 4                       | n.a    | n.a   | n.a           | n.a    |
| Leopard                | 4                       | n.a    | n.a   | 1                       | n.a    | n.a   | n.a           | n.a    |
| Banded mongoose        | 1                       | n.a    | n.a   | 0                       | n.a    | n.a   | n.a           | n.a    |
| Meerkat                | 3                       | n.a    | n.a   | 0                       | n.a    | n.a   | n.a           | n.a    |
| Aardwolf               | 0                       | n.a    | n.a   | 1                       | n.a    | n.a   | n.a           | n.a    |
| Black-backed jackal    | 8                       | n.a    | n.a   | 0                       | n.a    | n.a   | n.a           | n.a    |
| Warthog, including BR  | 25                      | 1      | 0; 3  | 10                      | 1      | 0; 2  | 15            | 0.41   |
| Warthog, excluding BR  | 18                      | 1      | 0; 2  | 3                       | 0      | 0; 1  | 15            | 0.40   |
| Common eland           | 1                       | n.a    | n.a   | 0                       | n.a    | n.a   | n.a           | n.a    |
| Greater kudu           | 2                       | n.a    | n.a   | 1                       | n.a    | n.a   | n.a           | n.a    |
| Total, including BR    | 116 (71)                |        |   | 22 (20)                 |        |   |               |        |
| Total, excluding BR    | 107 (62)                |        |   | 15 (13)                 |        |   |               |        |

Results for aardvark and warthog are given with and without the behaviour 'body rubbing' (BR), see method section for explanation. n.a. = not applicable because numbers of events were not > 20. The sum of events is given for all species including cheetahs and in parentheses for all species excluding cheetahs. See supplementary Table S1 for data on each species and tree

\* Indicates a significant result of < 0.05

et al. 1997; Apfelbach et al. 2005; Kuijper et al. 2014; Wikenros et al. 2017). We found that common duikers visited cheetah marking trees less frequently than control trees. Based on direct observations of cheetah hunts and analyses of prey remains in cheetah scats, common duikers were an important prey species of cheetahs (Hayward et al. 2006). Thus, it is likely that common duikers avoided cheetah marking trees to reduce their risk of encounters with cheetahs (see H1).

African wild cats visited cheetah marking trees more frequently than control trees and black-backed jackals sniffed more frequently at cheetah marking trees than control trees. These species might have used the scent information of cheetahs to assess the time since cheetahs were in the area to avoid an encounter with them (see H2). This explanation was also made for red foxes visiting sites with scats of Eurasian lynx, a dominant predator, more often than control sites (Wikenros et al. 2017). Subordinate carnivore species might also feed on scats or on the insects gathering at scats, as was documented for subordinate species feeding on scats and insects at ocelot latrines (King et al. 2016). Thus, African wild cats and black-backed jackals may also feed on cheetah scats or prey on other species attracted to the sites (see H3). Further, warthogs sniffed more frequently at cheetah marking trees than control trees. Warthogs are not an important prey species of cheetahs (Hayward et al. 2006). They are omnivorous and opportunistic scavengers (Skinner

and Chimimba 2005) and thus might also feed on undigested prey remains in scats (see H3). This detailed feeding behaviour can be documented by video recording which we might have missed using still photographs.

Leopards, as the top predator species in the study site, visited the cheetah marking trees four times. Two males and a mother with her offspring sniffed, urinated, scratched and/or rubbed their face or body on the trees. One additional female visited two control trees and urinated on one. Although these few observations cannot be tested statistically, they suggest that leopards use large, single-standing and conspicuous trees for olfactory communication. Marking at cheetah marking trees might also be used for interspecific communication and demonstrate their presence towards cheetahs (see H4). This explanation would be in line with other camera trap studies which were conducted at cheetah marking sites and demonstrated urinating, tree scratching, rubbing and defecating of leopards (Cornhill & Kerley 2020; Verschueren et al. 2021).

Warthogs left information in the form of scats, facial rubbing and body rubbing at both the cheetah marking trees and control trees. They marked the cheetah marking trees at the same frequency as the control trees. Warthogs mark particular sites within their home ranges, allowing individual to exchange olfactory information (Corbert

and Van Aarde 1996; Skinner and Chimimba 2005). They might have chosen these conspicuous, single-standing trees (cheetah marked or not) to maximize the detectability of their scent marks by conspecifics. This suggests that warthogs use conspicuous sites for intraspecific rather than interspecific communication (see H5; Kleiman 1966; Apps et al. 2019). And not surprising, warthogs are rarely preyed on by cheetahs (Hayward et al. 2006), allowing them to leave olfactory information at, otherwise dangerous, cheetah marking sites.

By using a comparative approach with paired survey design, we demonstrated for several species significant differences in the number of visits and number of behaviour events at cheetah marking trees compared to control trees. This paired setup helped to distinguish whether the observed behaviour was likely to be interspecific communication or rather intraspecific communication. Our study was conducted during the Namibian rainy season, thus visitation and marking events might differ in other seasons.

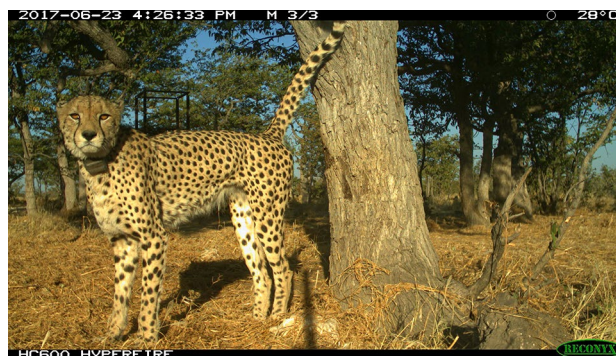
Territories of cheetah males are distributed in a regular pattern across the landscape and are stable over time but are not contiguous with each other (Melzheimer et al. 2020). This results in marking tree clusters in the core areas of territories being approximately 23 km apart from each other and a surrounding matrix without cheetah marking trees (Melzheimer et al. 2020). This spatial pattern results in cheetah marking trees being at predictable locations not only for cheetahs but also for other species. Thus, cheetah marking trees could play a predestinated role in communication within and between various species. It is unknown whether individuals of visiting species have home ranges overlapping with the core area of a cheetah territory or whether they make an excursion to visit cheetah marking trees. Studies covering several cheetah territories, in different habitats, and of other species will help to better understand the role of cheetah and predator marking trees, in general, in olfactory communication for the wider mammalian community. Cheetah marking trees might hold environmental cues that are not apparent for researchers but affect scent marking behaviour of cheetahs and other species. A treatment–control study design in which cheetah scats are placed at randomly selected conspicuous trees could further help to clarify the motivation of species to visit cheetah marking trees and other trees for olfactory communication.

Individuals of a species can gain important information from sympatric individuals of other mammalian species. Thus, it is likely that mammals maintain communication networks across species. These networks might be laid out along cheetah marking trees and also along communication locations of other species such as latrines of brown hyenas, spotted hyenas (*Crocuta crocuta*), ocelots

or river otters (Kruuk 1972; Gorman and Mills 1984; King et al. 2016; Wagnon and Serfass 2016), middens of white rhinoceros (*Ceratotherium simum*; Marneweck et al. 2018), marking sites of Eurasian lynx or pumas (Vogt et al. 2014; Allen et al. 2017), or scraping trees of brown bears (*Ursus arctos*) or giant anteaters (*Myrmecophaga tridactyla*; Braga et al. 2010; Clapham et al. 2013). Studies on the interspecific communication of various species in different populations and ecosystems will likely uncover more details on the complexities of communication networks.

## Appendix

See Appendix Fig A1



**Fig. A1** A territorial cheetah male scent marking with urine a cheetah marking tree. Our study suggests that sites used by cheetahs for marking also play an important role in olfactory communication for a variety of mammalian species

**Supplementary Information** The online version contains supplementary material available at <https://doi.org/10.1007/s42991-022-00284-w>.

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**Author contributions** Conceived the study: SE, JM, BW. Designed the experiments: SE, JM, RM. Performed the experiments and collected the data: RM, RR. Analyzed the data: SE, BW. Wrote the paper: SE, BW. Commented on the manuscript: JM, RM.

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**Data availability** The datasets analyzed during the current study are available in the supplementary Table S1.

**Code availability** The codes supporting the current study are available from the corresponding author on request.

## Declarations

**Conflict of interest** The authors declare that they have no conflict of interest.

**Ethics approval** The methods applied and the study design were approved by the Ministry of Environment, Forestry and Tourism, Namibia, and the Namibia Commission of Research, Science and Technology.

**Consent to participate** All authors agreed to participate to this manuscript and all have contributed to its content and current version.

**Consent for publication** All authors agreed to submit this manuscript to the Special Issue of Mammalian Biology for publication.

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## References

- Allen ML, Gunther MS, Wilmers CC (2017) The scent of your enemy is my friend? The acquisition of large carnivore scent by a smaller carnivore. *J Ethol* 35:13–19. <https://doi.org/10.1007/s10164-016-0492-6>
- Apfelbach R, Blanchard CD, Blanchard RJ, Hayes RA, McGregor IS (2005) The effects of predator odors in mammalian prey species: a review of field and laboratory studies. *Neurosci Biobehav Rev* 29:1123–1144. <https://doi.org/10.1016/j.neubiorev.2005.05.005>
- Apps P, Rafiq K, McNutt WJ (2019) Do carnivores have a world wide web of interspecific scent signals? In: Buesching CB (ed) *Chemical signals in vertebrates 14*. Springer, Cham Switzerland, pp 182–202
- Ballari SA, Barrios-Garcia MN (2014) A review of wild boar *Sus scrofa* diet and factors affecting food selection in native and introduced ranges. *Mamm Rev* 44:124–134
- Braga FG, Santos REF, Batista AC (2010) Marking behavior of the giant anteater *Myrmecophaga tridactyla* (Mammalia: Myrmecophagidae) in Southern Brazil. *Zoologia* 27(7):12
- Caro T (1994) *Cheetahs of the Serengeti Plains: group living in an asocial species*. University of Chicago Press, Chicago
- Clapham M, Nevin OT, Ramsey AD, Rosell F (2013) The function of strategic tree selectivity in the chemical signaling of brown bears. *Anim Behav* 85:1351–1357
- Corbet NU, Van Aarde RJ (1996) Social organization and space use in the Cape porcupine in a Southern African savanna. *Afr J Ecol* 34:1–14. <https://doi.org/10.1111/j.1365-2028.1996.tb00589.x>
- Cornhill KL, Kerley GIH (2020) Cheetah behaviour at scent-marking sites indicates differential use by sex and social rank. *Afr J Ecol* 126:976–986. <https://doi.org/10.1111/eth.13071>
- Focardi S, Materassi M, Innocenti G, Berzi D (2017) Kleptoparasitism and scavenging can stabilize ecosystem dynamics. *Am Nat* 190:398–409. <https://doi.org/10.1086/692798>
- Gardener M (2012) *Statistics for ecologists using R and Excel. Data collection, exploration, analysis and presentation*. Pelagic Publishing, USA.
- Gorman ML, Mills MGL (1984) Scent marking strategies in hyaenas (Mammalia). *J Zool* 202:535–547
- Gosling L (1982) A reassessment of the function of scent marking in territories. *Ethology* 60:89–118. <https://doi.org/10.1111/j.1439-0310.1982.tb00492.x>
- Hayward MW, Slotow R (2009) Temporal partitioning of activity in large African carnivores: test of multiple hypotheses. *S Afr J Wildl Res* 39:109–125
- Hayward MW, Hofmeyr M, O'Brien J, Kerley GIH (2006) Prey preferences of the cheetah (*Acinonyx jubatus*) (Felidae: Carnivora): morphological limitations or the need capture rapidly consumable prey before kleptoparasites arrive? *J Zool* 270:615–627. <https://doi.org/10.1111/j.1469-7998.2006.00184.x>
- King TW, Salom-Perez R, Shipley LA, Quigley HB, Thornton DH (2016) Ocelot latrines: communication centers for Neotropical mammals. *J Mammal* 98:106–113. <https://doi.org/10.1093/jmammal/gyw174>
- Kleiman DG (1966) Scent marking in the canidae. *Symp Zool Soc Lond* 18:167–177
- Kruuk H (1972) *The Spotted Hyena*. University of Chicago Press, Chicago
- Kuijper DPJ, Verwijmeren M, Churski M, Zbyryt A, Schmidt K, Jedrzejska B, Smit C, Smit C (2014) What cues do ungulates use to assess predation risk in dense temperate forests? *PLoS ONE* 9(1):e84607. <https://doi.org/10.1371/journal.pone.0084607>
- Kusler A, Jordan NR, McNutt JW, Broekhuis F (2019) Cheetah marking trees: distribution, visitation and behavior. *Afr J Ecol* 57:419–422. <https://doi.org/10.1111/aje.12602>
- Li J, Schaller GB, McCarthy TM, Wang D, Jiagong Z, Cai P, Basang L, Lu Z (2013) A communal sign post of snow leopards (*Panthera uncia*) and other species on the Tibetan Plateau, China. *Int J Biodiv*: 370905. <https://doi.org/10.1155/2013/370905>
- Marker LL, Muntifering JR, Dickman AJ, Mills MGL, Macdonald DW (2003) Quantifying prey preference of free-ranging Namibian cheetahs. *S Afr J Wildl Res* 33:43–53
- Marneweck C, Jürgens A, Shrader AM (2018) The role of middens in white rhino olfactory communication. *Anim Behav* 140:7–18
- Melzheimer J, Streif S, Wasiolka B, Fischer M, Thalwitzer S, Heinrich SK, Weigold A, Hofer H, Wächter B (2018) Queuing, takeovers, and becoming a fat cat: Long-term data reveal two distinct male spatial tactics at different life-history stages in Namibian cheetahs. *Ecosphere* 9(6):e02308. <https://doi.org/10.1002/ecs2.2308>
- Melzheimer J, Heinrich SK, Wasiolka B, Mueller R, Thalwitzer S, Palmegiani I, Weigold A, Portas R, Roeder R, Krofel M, Hofer H, Wächter B (2020) Communication hubs of an asocial cat are the source of a human-carnivore conflict and key to its solution. *Proc Natl Acad Sci USA* <https://doi.org/10.1073/pnas.2002487117>
- Paquet PC (1991) Scent-marking behavior of sympatric wolves (*Canis lupus*) and coyotes (*C. latrans*) in Riding Mountain National Park. *Can J Zool* 69:1721–1727
- R Development Core Team (2014) *R: a language and environment for statistical computing; Version 3.5.5*. R Foundation for Statistical Computing, Vienna.

- Roberts SC, Gosling LM (2001) Economic consequences of advertising scent mark location on territories. In: Marchlewska-Koj A, Lepri JJ, Miiller-Schwarze D (eds) Chemical signals in vertebrates. Springer, New York, New York, USA, pp 11–17
- Shurin JB, Borer ET, Seabloom EW, Anderson K, Blanchette CA, Broitman B, Cooper SD, Halpern BS (2002) A cross-ecosystem comparison of the strength of trophic cascades. *Ecol Lett* 5:785–791
- Skinner JD, Chimimba CT (2005) The mammals of the southern Africa subregion. Cambridge University Press, Cambridge
- Verschueren S, Briers-Louw WD, Cristescu B, Fabiano E, Nghikembua M, Torres-Uribe C, Walker EH, Marker L (2021) Spatiotemporal sharing and partitioning of scent-marking sites by cheetahs and leopards in north-central Namibia. *Afr J Ecol* 59:605–613. <https://doi.org/10.1111/aje.12878>
- Vogt K, Zimmermann F, Kölliker M, Breitenmoser U (2014) Scent-marking behaviour and social dynamics in a wild population of Eurasian lynx *Lynx lynx*. *Behav Processes* 106:98–106
- Wachter B, Jauernig O, Breitenmoser U (2006) Determination of prey hair in faeces of free-ranging Namibian cheetahs with a simple method. *Cat News* 44:8–9
- Wagon CJ, Serfass TL (2016) Camera traps at northern river otter latrines enhance carnivore detectability along riparian areas in eastern North America. *Glob Ecol Conserv* 8:138–143. <https://doi.org/10.1016/j.gecco.2016.08.010>
- Ward JF, Macdonald DM, Doncaster CP (1997) Responses of foraging hedgehogs to badger odor. *Anim Behav* 53:709–720
- Wikenros C, Jarnemo A, Frisen M, Kuijper DPJ, Schmidt K (2017) Mesopredator behavioral response to olfactory signals of an apex predator. *J Ethol* 35:161–168. <https://doi.org/10.1007/s10164-016-0504-6>

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