INTERSPECIFIC SCENT MARKING: AN EXPERIMENTAL TEST OF THE INFLUENCE OF ADDED LION AND SPOTTED HYENA SCATS ON LEOPARD BEHAVIOUR IN SOUTH AFRICA

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Solitary carnivores rely strongly on scent marking to communicate, and can be attracted or repelled by the scents of conspecifics or heterospecifics. We aimed to understand the effects of intra- and interspecific olfactory interactions on *Panthera pardus* (hereinafter – leopard), and to test whether heterospecific scents could be manipulated as a tool to deter leopards. We monitored leopard scent-marking activity in the Sabi Sands Game Reserve, South Africa, by camera-trapping 43 marking sites (1450 trap nights) over a 61-day period in the 2021 dry season, of which a 38-day experimental phase used 27 sites. We addressed three objectives: (1) characterising the intraspecific communicative functions of marking; (2) evaluating the influence of dominant-competitor scents on leopard behaviour; and (3) assessing the potential of these scents as a deterrent. To simulate the presence of *Panthera leo* (hereinafter – lion) and *Crocuta crocuta* (hereinafter – spotted hyena), we added freshly collected scats to treatment sites and compared leopard visit interval, stay duration, and behaviour duration with control sites (no scats) using generalised linear mixed-effects models (GLMEMs). At the intraspecific level, 40% of consecutive visits to marking sites involved leopards of different sexes. Contrary to our prediction of male-dominated marking, females scent marked significantly more than males, suggesting that leopard scent marks serve both mating and territorial-advertisement functions. Contrary to our prediction of avoidance, leopard visit frequency was unchanged at sites with lion scats, although stay duration was significantly longer, suggesting a more complex olfactory response than simple avoidance. Our results support the prediction that leopards use scent-marking sites to gather information about neighbouring conspecifics and lions and to signal their own presence. We did not find strong evidence that lion or spotted hyena scats can deter leopards or be used as a wildlife-management tool. These findings highlight the role of olfactory communication in territorial behaviour and both its potential and its limitations for conservation.

Key words: behavioural ecology, dear enemy effect, generalised linear mixed-effects models, intraguild interactions, translocated faeces

Introduction

Scent marking is a core component of the social and spatial organisation of solitary carnivores (Wemmer & Scow, 1977; MacDonald, 1980; Rafiq et al., 2020). It usually delineates territory boundaries, prevents undesirable risky encounters with conspecifics, and facilitates desirable encounters such as mating (Wemmer & Scow, 1977; MacDonald, 1980; Apps, 2013; Allen et al., 2016a). Scent marking takes various forms, ranging from faeces and urine excretions to sprays of anal or other types of marking fluid secretions, rubbing of different body glands on a substrate, rolling, licking, scraping the ground, scratching trees, and sniffing or flehmening scents (Reiger, 1979; MacDonald, 1980; Asa, 1993). Furthermore, scent marking can elicit both behavioural and physiological responses in a receiver (Somers et al., 1990; Garvey et al., 2017; Soso & Koziel, 2017; Rafiq et al., 2020). A few studies have, therefore, suggested the potential of scent marking as a wildlife management tool, particularly in manipulating carnivore movements to reduce the incidences of human–carnivore conflict (Garvey et al., 2016; Jones et al., 2016). However, detailed descriptions and knowledge of scent-marking behaviours and their implications for interacting individuals remain relatively rare for many solitary cryptic carnivores (MacDonald, 1980; Allen et al., 2016b).

Panthera pardus Linnaeus, 1758 (hereinafter – leopards) are solitary, except during mating or when females raise cubs (Grimbeek, 1992; Bothma, 1998). The species faces multiple human-related threats (e.g. shrinking habitat, poaching, hunting of natural prey species) and is experiencing decreasing population numbers (Jacobson et al., 2016). Conservation efforts often target leopards in non-protected areas (e.g. farmlands) that regularly conflict with humans and depredate livestock, which are then occasionally killed in retaliation (Jacobson et al., 2016). Removing individuals increases the turnover rate in leopard populations and potentially attracts several nomadic individuals around the vacant territory (Balme et al., 2009, 2010; Lennox et al., 2018). Furthermore, new resident male leopards often kill cubs sired by

other males (Balme & Hunter, 2013). Thus, territorial instability and rapid turnover created by removal on farmlands place female leopards in a parenting dead-end (Balme & Hunter, 2013). The benefits of such a removal strategy are perceived to be greater to local communities than other more passive or expensive solutions, such as fencing, livestock guarding dogs, and alternative livestock husbandry practices (Eklund et al., 2017; Lennox et al., 2018). In the current Anthropocene crisis (Kennel, 2021), gaining insights into factors influencing or determining leopard distribution may help design more effective conservation plans and mitigate conflicts with humans (Jones et al., 2016). Using scent marking to manipulate leopard movements and deter them from conflict areas could help fulfil these goals (Garvey et al., 2017; Jones et al., 2016).

The two main theories of olfactory interactions oppose each other. The landscape of fear (Laundré et al., 2001) describes the aversive response of animals on a spatiotemporal scale. The dear enemy effect (Fisher, 1954) suggests that staying informed of the surrounding community activities, particularly of residents of high risk (predators and strong competitors capable of severe injuries), and reciprocally signalling one's presence are an anti-predator strategy that facilitates avoiding risky physical encounters (Banks et al., 2016; Garvey et al., 2016). Packs of *Lycaon pictus* Temminck, 1820 (hereinafter – African wild dog) (Jackson et al., 2012) and *Canis lupus* Linnaeus, 1758 (Ausband et al., 2013) are repelled by artificially deposited scent marks of the same species and redirected towards desired Protected Areas. However, *Vulpes vulpes* Linnaeus, 1758 spend more time in areas artificially scent marked with foreign *Vulpes vulpes* urine (Arnold et al., 2011), and *Mustela erminea* Linnaeus, 1758 are attracted to the scents of predators (*Mustela furo* Linnaeus, 1758 and *Felis catus* Linnaeus, 1758) (Garvey et al., 2016). These four studies demonstrate how the «landscape of fear» and the «dear enemy» effect theories apply in nature. They highlight the importance of researching how leopards might be affected by the scent marks of their competitors, suggesting it could be useful for managing their populations.

Here, we describe aspects of leopard scent marking behaviour in the Sabi Sands. We expected leopard behaviour to be the same as reported elsewhere (Grimbeek, 1992; Bailey, 1993; Bothma & le Riche, 1995; Bothma & Coertze, 2004). We asked what are the roles of intraspecific scent marking interactions occurring at leopard marking sites. We expected leopards to visit marking sites for i) mating purposes: 20–50-day cyclic peaks of non-pregnant females intensively scent marking over ~14 days corresponding to oestrus periods (Bothma & Coertze, 2004) and ii) territory advertising purposes for all individuals: continuous scent-marking frequencies over time. Given the high infanticide risks in leopards (ca 33% of cubs) (Balme & Hunter, 2013), we expected no females with cubs to visit (Bothma & Coertze, 2004) and a greater activity of dominant males than subadult males at scent-marking sites, as observed with *Acinonyx jubatus* Schreber, 1775 (hereinafter – cheetah) in Namibia (Melzheimer et al., 2020). Finally, we asked if interspecific olfactory interactions with *Panthera leo* Linnaeus, 1758 (hereinafter – lion) and *Crocuta crocuta* Erxleben, 1777 (hereinafter – spotted hyena) influence the behaviour of leopards at scent-marking sites. African leopards strongly compete with other members of the large carnivore guild (Palomares & Caro, 1999; Hayward & Slotow, 2009). There are risks of fatal or severe injuries occurring in confrontations with spotted hyenas and lions (Bothma, 1998; Friedmann & Traylor-Holzer, 2008; Balme et al., 2017). Therefore, we expected significant repelling effects of lions and spotted hyenas on leopards, causing a significant reduction in leopard visits and marking activities at scent-marking sites. This study also sought to determine the potential of scent marking as a wildlife management tool and to understand the effects of intra- and interspecific olfactory interactions on leopards.

To address these questions, we set three specific objectives. First, we characterised the intraspecific communicative functions of leopard scent marking, testing whether marking sites are used for mating and/or territorial advertisement and whether marking activity varies with sex and age. Second, we evaluated the influence of olfactory cues from dominant competitors by experimentally adding lion and spotted hyena scats to marking sites and comparing leopard visit interval, stay duration, and olfactory-behaviour duration with untreated control sites. Third, we assessed the efficacy of these heterospecific scats as a potential tool for deterring leopards in human–wildlife conflict contexts. Following the landscape-of-fear and dear-enemy frameworks, we predicted that both oestrus-linked female marking and continuous territorial marking would occur, that dominant males would mark more than subadult males, and that lion and spotted hyena scats would reduce leopard visitation and marking activity.

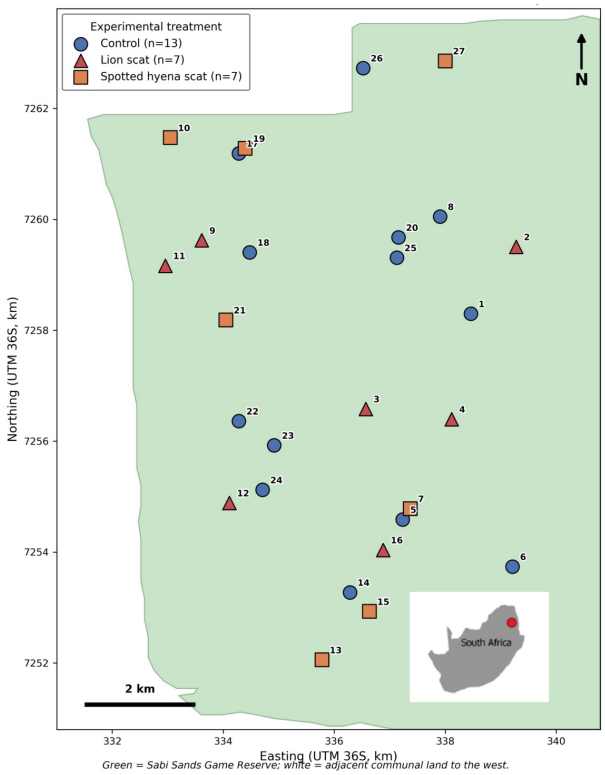


Fig. 1. The western sector of the SSGR showing the monitored leopard scent-marking sites. Symbols and colours distinguish the three experimental site types: control (n = 13), lion-scat (n = 7), and spotted hyena-scat (n = 7). Numbers are camera-trap identifiers.

Material and Methods

Study area

The Sabi Sands Game Reserve (hereinafter – SSGR) is a Protected Area conglomerate formed of 20 private game reserves covering 625 km^2 (midpoint: 31.48° E, 24.82° S) in the Mpumalanga Lowveld, South Africa (Balme et al., 2013). The study focused on six properties (ca 100 km^2) collectively forming the western sector of the SSGR: Dulini, Leopard Hills, Savanna, Inyati, Idube, and Ulusaba (Fig. 1). It is characterised by relatively flat terrains with some rocky outcrops and is dominated by a savanna ecosystem interspersed with grassland and woodland patches (Rutherford et al., 2006; Smith & Fitchett, 2020). Common vegetation includes *Diospyros mespiliformis* Hochst. ex A.DC., *Combretum* spp., *Themeda triandra* Forssk., and *Digitaria eriantha* Steud. grasses (Rutherford et al., 2006). The local climate is semi-arid, with dry winters between April and September and warm rainy summers between October and March (Fortescue, 1997). Mean annual temperatures range from 19°C to 33°C, and annual precipitation averages 650 mm (Balme et al., 2013).

The ecotourism business of the SSGR relies on 35–40 on-site lodges (Schmidtz & Willott, 2012) and multiple dirt roads throughout the Protected Area. In SSGR, animals are habituated to the presence of game drive vehicles (Pirie et al., 2014). These animals include lion, leopard, *Loxodonta africana* Blumenbach, 1797, *Syncerus caffer* Sparrman, 1779, *Diceros bicornis* Linnaeus, 1758, *Ceratotherium simum* Burchell, 1817, *Connochaetes taurinus* Burchell, 1823, *Equus quagga* Boddaert, 1785, *Aepyceros melampus* Lichtenstein, 1812, spotted hyena, *Giraffa camelopardalis* Linnaeus, 1758, cheetah, and African wild dog (Smith & Fitchett, 2020). The density of leopards is particularly high (ca 11 ind./100 km^2) (Balme et al., 2019), and knowledge of their populations (e.g. family trees, territories, diet) is detailed (Balme et al., 2013). The leopard population in this sector is male-biased (Balme & Hunter, 2013), and resident leopards occupy relatively small, overlapping home ranges typical of high-density savanna populations; individual home ranges were not quantified in the present study.

Leopard identification and monitoring

Over five months of driving in the area, we created a leopard database (06.04.2021–23.08.2021), collecting data on individuals' sex, age, kinship (mothers and cubs), territory, and flank photos to help further identify the camera trap images. During the first month, we also identified leopard marking sites through direct observations of the leopard, knowledge of rangers and trackers, and signs confirming leopard olfactory activity (tracks, scraping marks, and characteristic popcorn scent of leopard urine spray) (Apps et al., 2014). The reproductive status of females (pregnant or denning with dependent cubs) was inferred from long-term monitoring and direct field observations, including enlarged mammae, observed matings, and the presence of accompanying cubs.

Camera trapping

We deployed 32 remote video camera traps (22 Bushnell Trophy Cam HD, Model 119537; 10 Browning Recon Force Advantage, Model BTC-7A) across the marking sites. Most sites had a single camera; at three wider sites, a second camera was added to improve coverage. For analysis, we used data from a single, optimally placed camera per site, so that the 32 cameras corresponded to the monitored sites. Both models were set to record 1-minute videos per trigger with a 30-second interval between consecutive triggers, and trigger sensitivity was set to high. Because all behavioural variables were scored visually from video, the mi-

nor differences between camera models did not affect the data extracted. Cameras were positioned approximately 40 cm above the ground, aimed at the marking object to capture leopard flanks. Camera traps were active continuously for 61 days (03.05.2021–02.07.2021); during the first approximately 20 days, cameras were rotated among a larger pool of candidate sites until the most active marking sites were identified, and data from this selection phase were used for leopard identification and site selection, but not for the comparison of treatment effects. Cameras were checked every five days to replace SD cards and batteries and to confirm they had not been disturbed by wildlife; checks were made by vehicle and kept as brief as possible. Because animals in the SSGR are habituated to vehicles (Pirie et al., 2014), we considered disturbance from these checks to be minimal, although a residual effect cannot be fully excluded (see Discussion section).

Experimental design

From the broader pool of 43 marking sites monitored during the selection phase, we retained the 27 most active sites for the scat-addition experiment. These were randomly assigned, using a random number generator, to one of three groups: control (no scats added; 13 sites), lion-scat treatment (seven sites), and spotted hyena-scat treatment (seven sites). The treatment assigned to each camera-trap site is listed in Table S1. All retained sites showed recent evidence of leopard use; we did not stratify by pre-treatment visitation rate, so that any inherent differences among sites were distributed at random across treatments. Fresh (still moist) lion and spotted hyena scats were collected opportunistically across the Protected Area using latex gloves, frozen within a few hours of collection, and stored frozen for no more than one to two weeks before use to preserve their chemical integrity. At treatment sites, scats of the corresponding species were added three times at 12-day intervals to refresh the scent stimulus as it degraded; previously added scats were not removed, to mimic the natural accumulation of marks. The experimental period lasted 38 days (approximately 23.05.2021–02.07.2021), fell within the 61-day camera-trapping period, and took place entirely within the dry season. The randomised allocation of sites to control and treatment groups follows established principles for wildlife field experiments (Morrison et al., 2008).

Data analyses

Using CameraBase software (Tobler, 2015), flank photos, and the leopard database, we sorted the camera-trap data and identified individuals from their unique rosette patterns (Sunquist & Sunquist, 2002), sexing them from conspicuous features (genitalia, swollen mammary papillae, shoulder width, dewlap size) (Balme et al., 2012). We further classed each individual as an adult or a subadult (independent but not yet territorial) from body size and proportions and from known life history in the long-term database (Balme et al., 2012). Because the analyses depended on recognising known individuals and scoring their behaviour from video, scoring could not be performed blind to the identity of the animal or the site; to maintain consistency, all footage was scored by a single observer using fixed behavioural definitions. We classified leopard behaviours as walking, olfactory activities (investigating, rubbing, spraying, scraping, rolling, urinating, or defaecating), or other (sitting, lying down, grooming); full definitions are given in the ethogram (Table S2). To ensure independence of detections, a record of the same individual at the same site within 20 minutes of its previous record was treated as part of the same detection and excluded; records of different individuals were always treated as separate detections. When quantifying sex-based interaction sequences, we considered consecutive independent visits to a site: where the same individual was recorded again after the 20-minute interval, with no other individual recorded in between, these were counted as separate consecutive visits.

The three objectives were addressed as follows: objective 1 (intraspecific communicative functions) using the descriptive and frequency analyses described here, and objectives 2 and 3 (competitor influence and deterrent potential) using the mixed-effects models. Based on the sample size meeting statistical tests' assumptions, a chi-square test was used to compare the frequencies of males and females simply walking past the marking site or performing a type of olfactory activity. We calculated the percentage of consecutive male–male, female–female, female–male, or male–female visits at a site. Two Fisher exact tests further checked for differences in male and female proportions and differences in frequencies of olfactory behaviour types between control, lion and spotted hyena treatments. Finally, a series of generalised linear models (GLMs) and generalised linear mixed effect models (GLMEMs) measured the im-

pact of lion's and spotted hyena's scats on the visit duration of leopards at marking sites, the duration of olfactory activities, and the visit interval of individual leopards at a marking site (Table 1). Models were fitted using a gamma family and a log link function (Zuur et al., 2009; Bates et al., 2015). Duration (number of seconds a leopard remained at a site) was taken as a response variable, and treatments as the fixed effects, and for the GLMEMs, the identity (sex and adult or subadult) of previous and current leopard visitors as the random effects, as done in Cornhill & Kerley (2020a). Models 1b and 2b were generalised linear models and therefore included no random effect; sample sizes for each model are given in the Results. The model fit for the data was checked using QQplots, residuals vs. fitted plots, and AIC values (Bolker et al., 2009). Finally, models were compared based on AIC values, and the most parsimonious models were selected. Post hoc Tukey tests were used for pairwise comparisons within the models. All statistical analyses were performed in R (R Core Team, 2017) using lme4 package (Bates et al., 2015). Statistical significance was assessed at an alpha level of 0.05.

This study was approved by the Sabi Sands Wildtuin, managers of the western sector of the Sabi Sands Game Reserve. The study was also approved by the Animal Ethics Committee of the University of Pretoria (NAS007/2021) and the Mpumalanga Tourism and Parks Agency (MPB 5685).

Results

A total of 15 individually identified leopards were detected over 122 independent detection events. Seven females, including one subadult, were each detected one to 17 times, totalling 57 detections (Table 2). Eight males, including three subadults and a new individual for the area, were each detected one to 22 times, totalling 65 detections (Table 2). We could not identify six additional leopards (at least three males) due to poor image quality, and recorded one cub of unknown sex. These unidentified individuals and the cub were excluded from the statistical models, which were restricted to identified adults and subadults. Of the resident females, five were denning with cubs or pregnant at some point during the study period. We also directly observed at least two cases of infanticide by resident males during the study period.

Table 1. Models computed to test the effects of lion and spotted hyena scat treatments on the total visit duration, olfactory activity duration, and visit interval of leopards at marking sites

Model	Type	Response variable	Independent variable	Random effect
1a	Glmer	TD	Treatment	Current visitor, previous visitor
1b	Glm	TD	Treatment	–
1c	Glmer	TD	Treatment	Current visitor
1d	Glmer	TD	Treatment	Previous visitor
2a	Glmer	OD	Treatment	Current visitor, previous visitor
2b	Glm	OD	Treatment	–
3a	Glmer	Visit interval	Treatment	Previous visitor
3b	Glmer	Visit interval	Treatment	Current visitor, previous visitor

Note: «TD» – total visit duration (in seconds), «OD» – olfactory activity duration (in seconds).

Table 2. Total detections and independent recaptures (20 min intervals) of independent leopard individuals (> 18 months old) at 43 marking sites in the western sector of the SSGR in 03.05.2021–02.07.2021

Leopard ID	Sex	Age category	Detections	Independent recaptures
M1	Male	Subadult	3	2
M2	Male	Adult	1	0
M3	Male	Subadult	5	4
M4	Male	Adult	12	11
M5	Male	Adult	22	21
M6	Male	Adult	15	14
M7	Male	Adult	6	5
M8	Male	Subadult	1	0
F9	Female	Adult	9	8
F10	Female	Adult	4	3
F11	Female	Adult	7	6
F12	Female	Subadult	9	8
F13	Female	Adult	1	0
F14	Female	Adult	17	16
F15	Female	Adult	10	9

Intraspecific scent marking

Based on long-term observations of leopard dynamics by rangers, all traps were within the territorial reach of five individuals (adults and subadults) on average. Of the 43 sites monitored during the selection phase, 17 detected no leopards and were not among the 27 sites carried forward to the experiment. Nine sites detected only one individual, whereas all others detected two or more individuals. Overall, 38% of the sites were shared by individuals of both sexes, 35% by males, and 27% by females. Twenty-eight per cent of consecutive visits were female–female interactions (after a female leopard visited the site, the next individual was also a female, either the same or a different individual), 32% were male–male interactions (either the same or a different individual), and 40% were male–female or female–male interactions (Fig. 2).

Overall, leopards simply walked past the sites in 64% of all detection events and performed olfactory activities in 36% of the detections (Table 3), but there was a significant difference in leopard behaviour between sexes ($X^2 = 11.04$, df = 1, $p < 0.05$, N = 116 sexed detections). When detected, females undertook olfactory activities approximately half the time (50.9%), whereas males walked past the marking place in approximately 77% of observations (Table 3).

Leopards visited marking sites with varying frequencies: typically once a week, occasionally on two consecutive days, or even more frequently. However, there were exceptions; two specific sites experienced visits at intervals ranging from every one to five days and every one to six days, respectively (Fig. 3). In terms of age and sex related activity, adults visited sites and performed olfactory behaviours more frequently than subadults observed in our sample, which tended to simply walk past. Overall, males had shorter visiting cycles than females at sites observed in our sample (1–2 times/week for males vs. 1 time/1–2 weeks for females). Regardless of the behaviours, both males and females had a modal stay duration of 3 s at marking sites (meanFemale = 17.33 s, N = 57; meanMale = 13.04 s, N = 68) (Fig. 4). There was more variation in the visit durations of subadult individuals than territorial adults, but the average visit duration was generally higher in subadults than in adults (Fig. 2). The most frequently recorded olfactory activities in our sample of observations were spraying, rubbing, and investigating bushes (Table 3). There was no significant difference in the frequency of these behaviours between the control and treatment sites (Fisher exact two-tailed test, p = 0.2, N = 41). The average olfactory activity duration was 7.37 s for females (Mean investigating = 13.25 s, SD = 10.66, N = 10; Mean rubbing = 7.55 s, SD = 8.41, N = 20; Mean spraying = 2.77 s, SD = 2.27, N = 18; Mean others = 14.33 s, SD = 39.51, N = 3) and 15.26 s for males (Mean investigating = 11.22 s, SD = 8.00, N = 9; Mean rubbing = 5.33 s, SD = 3.59, N = 6; Mean spraying = 3.25 s, SD = 1.64, N = 4; Mean others = 51.25 s, SD = 17.46, N = 4) (Fig. 5). Durations are reported as means, with standard deviations given for the individual olfactory activities; the full distributions are shown in the boxplots (Fig. 4, Fig. 5). Inferential comparisons among treatments rest on the generalised linear mixed-effects models (Table 4).

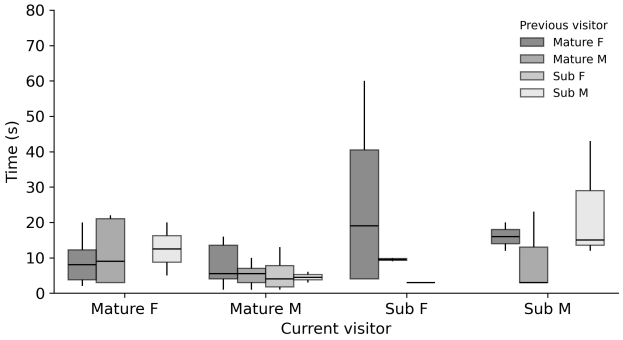


Fig. 2. Time spent at marking sites by leopards based on the sex (F stands for females, M for males) and status (mature adults or subadults) of the current and previous visitors. Data are pooled across groups and outliers do not appear on the graph. Only pair sample sizes > 1 are represented. Designations: $N_{MatureF\text{-}F} = 20$, $N_{MatureF\text{-}M} = 13$, $N_{MatureF\text{-}SubM} = 2$, $N_{MatureM\text{-}F} = 14$, $N_{MatureM\text{-}M} = 22$, $N_{MatureM\text{-}SubF} = 4$, $N_{MatureM\text{-}SubM} = 2$, $N_{SubF\text{-}MatureF} = 4$, $N_{SubF\text{-}MatureM} = 2$, $N_{SubM\text{-}MatureF} = 2$, $N_{SubM\text{-}MatureM} = 3$, $N_{SubM\text{-}M} = 3$.

Table 3. Leopard behaviour by treatment condition and sex in the western sector of the SSGR, 03.05.2021–02.07.2021

Behaviour	Control F	Control M	Hyena F	Hyena M	Lion F	Lion M	Total
Walk	21	31	6	12	1	9	80
Olfactory activity	20	6	3	5	6	5	45
Total	41	37	9	17	7	14	125

Note: Values are counts of independent, sexed detection events (n = 125); four events involving unsexed individuals are excluded. «Walk» denotes a leopard passing the site without any olfactory activity; «Olfactory activity» denotes any investigating, spraying, rubbing, scraping, rolling, urinating or defaecating. «Control» denotes detections made when no scat was present (including treatment sites before scat was added). «Hyena» and «Lion» detections made when the respective scat was present.

Table 4. Best model outputs displaying model reference (Ref), Akaike Information Criterion (AIC), degrees of freedom (DF), model deviance (Dev), random effect's standard deviation (SD), coefficient estimates of fixed effects (control, spotted hyena scats, lion scats groups) and their respective lower and upper bounds (LCI, UCI) for 95% confidence interval and t-value and p-value

Ref	AIC	DF	Dev.	SD random effect	Fixed effect coef.	LCI	UCI	t-value	p-value
1a	901	119	889	Previous visitor = 0.39	Control = 2.53	2.14	2.92	12.68	–
				Current visitor = 0.25	Spotted hyena = 2.89	1.31	3.04	-1.47	0.14
				–	Lion = 3.18	2.29	4.06	2.54	0.01
2a	443.7	66	431.7	Previous visitor = $2.8e^{-5}$	Control = 2.00	1.50	2.50	7.79	–
				Current visitor = 0.41	Spotted hyena = 1.38	0.16	2.60	0.93	0.09
				–	Lion = 2.67	1.65	3.69	0.01	0.01
3a	1543.7	47	1533.7	Previous visitor = 0.10	Control = 13.70	13.33	14.08	2×10^{-16}	–
				–	Spotted hyena = 13.70	12.83	14.58	0.99	0.99
				–	Lion = 13.94	13.03	14.85	0.39	0.39

Note: Model 1a describes the time spent at marking sites by leopards based on both current and previous visitors' identities. Model 2a describes the duration of leopard olfactory activity as a function of the identities of both current and previous visitors. Model 3a describes the visit interval of leopards at a marking site given the identity of the previous visitor.

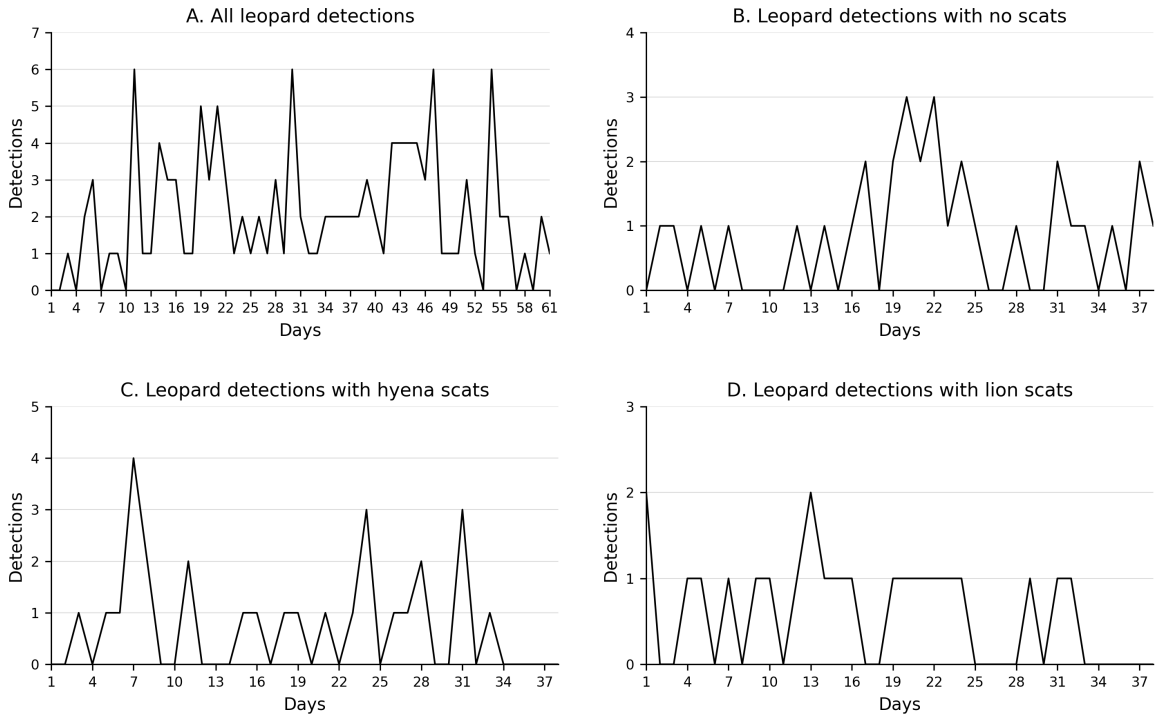


Fig. 3. The number of detections of leopards across sites during the 61-day survey period (A) and the 38-day treatment period across control (B), spotted hyena (C) and lion (D) sites, respectively, added no scats, spotted hyena scats, or lion scats.

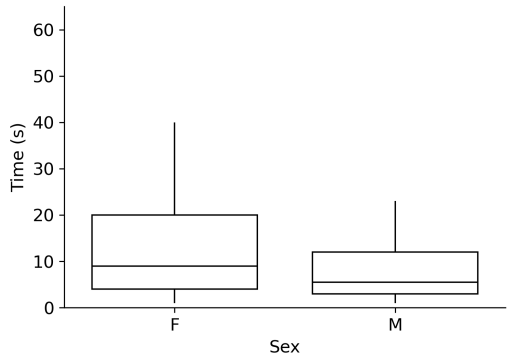


Fig. 4. Time spent by female (F; N = 57) and male (M; N = 68) leopards visiting 43 marking sites between 03.05.2021–02.07.2021 in the SSGR. Data are pooled across groups, and outliers do not appear on the graph.

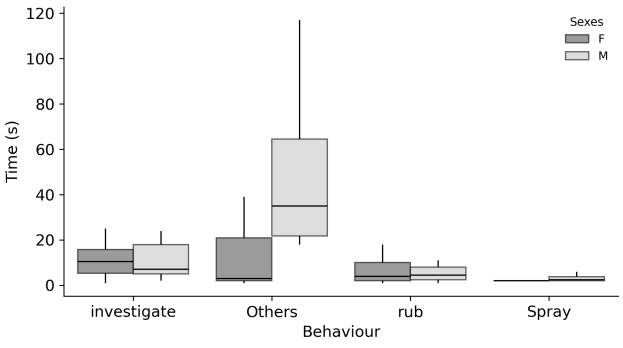


Fig. 5. Time spent by leopards in the SSGR investigating (N_{Female} = 10, N_{Male} = 9), spraying (N_{Female} = 18, N_{Male} = 4), rubbing (N_{Female} = 20, N_{Male} = 6), and rolling, scraping, defaecating and urinating grouped under the **«others» category** (N_{Female} = 3, N_{Male} = 4). Data are pooled across groups, and outliers do not appear on the graph.

Influence of competitor scats on leopard behaviour

Lion and spotted hyena scats were added to seven sites, respectively, and 13 sites served as a control. Overall, control (no-scat) conditions accounted for 80 leopard detections (seven females detected 41 times, seven males detected 36 times, one cub and two unidentified leopard photos), detections with spotted hyena scats present numbered 27 (five females detected nine times, five males detected 16 times and two unidentified leopard photos), and detections with lion scats present numbered 22 (three females detected seven times, five males detected 13 times and two unidentified leopard photos) (Fig. 3). The difference in the proportions of males and females was not significant between the control and treatment groups (Fisher exact two-tailed $p > 0.05$). Camera traps also recorded spotted hyenas moving past the monitored scent-marking sites (11 detections at control sites, 12 detections at lion-scat sites and 16 detections at spotted hyena-scat sites), alone or in groups, without showing interest in the targeted objects or translocated scats. Lions were detected on five occasions (one at a control site, four at lion-scat sites and none at spotted hyena-scat sites) walking past the marking sites (either alone or in a group, both males and females, and a cub). These animals did not show interest in the marking sites or scats except for one male that investigated the targeted bush, scraped over the translocated lion scat, and sprayed the bush.

Overall, the GLMEM accounting for visitor identity provided a better fit for data than the GLM and other GLMEMs (Table 1, Table 4). For the three selected models, relatively little variation exists between individuals (random effects < 1), and the models displayed narrow confidence intervals around estimates (Table 4). Model 3a first showed that leopards visited more often when lion scats were added (coef. = 13.94) and less often when spotted hyena scats or no scats were added (both coef. = 13.70) (Table 4). However, the relationship was insignificant ($p > 0.05$, df = 47) (Table 4), and the post hoc Tukey test confirmed the insignificant difference in visit frequency for control–spotted hyena ($z = 0.01$, $p = 1.00$), control–lion ($z = -0.85$, $p = 0.67$), and lion–spotted hyena ($z = -0.78$, $p = 0.71$) pairs. Second, model 1a revealed a significant relationship between leopard stay duration at marking sites and the addition of lion scats ($p = 0.011$, df = 119). Leopards stayed longer at marking sites with lion scats (coef. = 3.18 s) than at control sites (coef. = 2.53 s, $z = -2.54$, $p = 0.030$) and sites with spotted hyena scats (coef. = 2.89 s, $z = -3.31$, $p = 0.0027$) (Table 4). Visit duration was not significantly different between the control and spotted hyena groups ($z = 1.47$, $p = 0.31$). Leopards performed olfactory activities for a longer time at sites with lion scats (coef. = 2.67 s) than at control sites (coef. = 2.00 s, $z = -2.50$, $p = 0.03$) or spotted hyena sites (coef. = 1.38 s, $z = -3.15$, $p = 0.005$) (Table 4). There were no effects of spotted hyena scats on olfactory duration compared to control sites ($z = 1.68$, $p = 0.21$) (Table 4).

Discussion

In this paper, we have added to the understanding of the effects of intra- and interspecific olfactory interactions on leopards. This is among the first studies to monitor scent-marking sites of leopards in a mixed woodland savanna system in Africa (compared to the existing detailed observations in the Kalahari desert (Bothma & le Riche, 1984, 1995; Bothma & Coertze, 2004)); those Kalahari studies were conducted in a more arid habitat and a different season, which may contribute to some of the differences we observed). Overall, our predictions were only partially supported: leopards used marking sites for both mating and territorial advertisement, as expected, but females marked more than males, contrary to our prediction, and neither lion nor spotted hyena scats deterred leopards as we had predicted.

Most monitored marking sites that detected leopards were visited and marked by at least two individuals on multiple occasions. This supports the intraspecific communication role hypothesis of scent marking in leopards and stresses the collective use of specific marking sites by leopards. This has previously been found by Eisenberg (1970) in Wilpattu National Park, Sri Lanka and by Bailey (1993) in Kruger National Park, South Africa.

The use of marking sites in leopard mating interactions was evident by the high proportions of consecutive male–female or female–male visits to marking sites. Male leopards appeared to mainly use marking sites to assert their dominant status and for reproductive purposes, as initially predicted. This behavioural strategy correlates with the use of marking sites by other felids such as male cheetahs (Cornhill & Kerley, 2020b), male *Puma concolor* Linnaeus, 1771 in the USA (Allen et al., 2015), and male *Panthera tigris* Linnaeus, 1758 in Nepal (Smith et al., 1989). As for females, it was difficult to evaluate the oestrus status, and only four cases were confirmed: females rasped and/or scent marked more intensively than non-oestrous females, grabbing branches with their forelegs, and assiduously rubbing their

face, neck, and back against the bush as described by Sadleir (1966), and/or were sighted soon after mating with males in the area (A. Gervais, unpublished field observations). Females known to be denning were also detected scent marking or walking past the sites, whereas Bothma & Coertze (2004) mostly reported male leopard scent marking in the Kalahari and rarely observed pregnant females and non-oestrus females at scent-marking sites.

The high visitation rate and scent-marking activity of female leopards of any reproductive status in the SSGR suggest a greater importance of marking sites for territory advertising purposes in females than expected. Competition for territories is expected to be greater in areas of high leopard density, which may explain why individuals of the same sex shared some marking sites and, hence, had no obvious reproductive function. However, le Roex et al. (2022) found both sexes showed relaxed territoriality in a high density area, with considerable intrasexual overlap occurring among both sexes, suggesting they avoid risk.

Females may occupy high-quality territories, whereas males distribute based on access to females (Bothma, 1998). Thus, in high leopard density habitats, we suggest that not advertising an active presence and territory ownership exposes females to territory invasion from neighbouring individuals or takeovers by new immigrants. In addition, in the western sector of SSGR, the male:female ratio was skewed towards males, a known feature of this high-density population, contributing to the greater pressure exerted on females in the area (Balme & Hunter, 2013). During the study, we recorded at least two infanticide events by males (see Results). Thus, the greater risks associated with not advertising their territory in the SSGR would explain why females frequently visited marking sites and scent marked proportionally more often than males, contrary to those in the Kalahari (Bothma, 1998). Males occupy larger territories. Advertising their dominant status and patrolling boundaries is energetically costly (Rafiq et al., 2020). We suggest that patrolling males pass through highly frequented leopard paths and marking sites but mainly react to females or intrusive male presence. This would explain why males did not engage in olfactory activities proportionally, although they visited sites more times than females. The higher frequencies of male–male (32%) and male–female/female–male (40%) olfactory interactions recorded and the greater number of sites shared by both sexes (38%) further provide some support for this. In essence, contrary to our second hypothesis, females used marking sites for territory advertising, and males had lower olfactory activity than expected.

Finally, a few subadults (18 of 122 detection events, ~15%) were detected walking by marking sites or only investigating bushes. We suggest that these individuals used scent-marking sites and chemical compounds left by conspecifics to gather information about the surrounding residents, their strengths, and territories. This is consistent with the small home range size and conspecific avoidance behaviour of subadult male leopards observed by Fattebert et al. (2013) in Phinda Private Game Reserve in South Africa. Overall, our observations correlate with a strong intraspecific dear enemy effect, whereby leopard individuals keep track of one another and advertise their presence to facilitate reciprocal avoidance or availability for mating.

We evaluated the relative importance of the olfactory landscape of fear and the dear enemy effect to assess the potential of interspecific scent marking in manipulating leopard movements. We simulated olfactory interactions with strong competitors using translocated lion and spotted hyena scats to scent-marking sites of leopards. We expected a delay in leopards returning to treatment sites, but neither the spotted hyena scats nor the lion scats affected the visit frequency of leopards. Therefore, the experiments did not verify the predicted deterrence effect of strong competitors (landscape of fear) on leopards. The behavioural response of leopards to lion scats differed from the repelled response of the cheetahs in Cornhill & Kerley (2020a), where cheetahs took longer to return to sites when a lion or a leopard was the previous species to visit that site.

Furthermore, lion scats caused leopards to stay significantly longer at marking sites and perform olfactory activity for a longer time. This again contradicted our predictions. In the cheetah study of Cornhill & Kerley (2020a), cheetah behaviour also changes at marking sites. Cheetahs increased the amount of time spent sniffing at scent-marking sites when lions or leopards, as opposed to cheetahs, were the previous visitors. This pattern also matches the behavioural responses of smaller carnivores such as *Mustela erminea* (Banks et al., 2016) and *Vulpes vulpes* (Garvey et al., 2017) exposed to predator and strong competitor scents. Leopards displayed typical behaviours of a dear enemy reacting to lion scats, spending more time gathering information and reciprocally signalling their own presence. These findings concur with the absence of spatial displacement of leopards by lions observed by du Preez (2014) and Miller et al. (2018). Overall, the data from our ex-

perimental outcomes did not validate our predictions at the interspecific level. Our data do not support the notion that sympatric, larger carnivores spatially displace leopards and instil fear in them.

Limitations and future directions

While we observed the animals' natural behaviour, we acknowledge potential biases, as highlighted by Webster & Rutz (2020). First, camera traps may not capture the full spectrum of scent-marking behaviours and interactions among species. Second, scent-marking sites may have been located because they are used more, creating a potential bias in the type of sites sampled. Third, faeces were collected when available, with no means of controlling the identity (sex, reproductive status, social rank, group membership) of the donor lions or spotted hyenas; inconsistencies in translocated foreign scent marks are a leading explanation for *Canis lupus* trespassing an olfactory biofence in the USA (Ausband et al., 2013). We also used scats for ease of collection, yet spotted hyenas rely strongly on anal pasting and lions on urine and sprays to mark territory (MacDonald, 1980), and Ferrero et al. (2011) found that 2-phenylethylamine in lion urine elicits avoidance in prey. More pronounced effects might therefore be obtained with artificial scent dispensers, or by translocating spotted hyena anal pastings and lion marking fluids rather than scats. Finally, the five-day camera checks entailed some human presence; although animals here are habituated to vehicles, a residual influence on visitation cannot be fully excluded.

Conclusions

In summary, leopards in this high-density population used scent-marking sites both for intraspecific communication and for gathering information, with females marking more actively than predicted, consistent with a role for marking in territorial advertisement as well as mating. Contrary to a landscape-of-fear prediction, lion and spotted hyena scats did not reduce leopard visitation; leopards instead investigated lion-scented sites for longer, a response more consistent with the dear-enemy effect. Translocated competitor scats are therefore unlikely to be effective as a stand-alone tool for deterring leopards in this ecosystem. Because animals are less likely to habituate to natural intraguild cues, however, further trials across different leopard densities and using alternative scent sources (for example lion urine or spotted hyena anal-gland secretions, artificial dispensers, or plant-based deterrents such as capsaicin) are warranted before the management potential of olfactory cues is ruled out.

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Supporting Information

Additional data for the paper by Gervais et al. (2026) may be found in the **Supporting Information**.

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МЕЖВИДОВОЕ МАРКИРОВАНИЕ ЗАПАХОМ: ЭКСПЕРИМЕНТАЛЬНОЕ ИССЛЕДОВАНИЕ ВЛИЯНИЯ ЭКСКРЕМЕНТОВ ЛЬВА И ПЯТНИСТОЙ ГИЕНЫ НА ПОВЕДЕНИЕ ЛЕОПАРДА В ЮЖНОЙ АФРИКЕ

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Одиночные хищные млекопитающие в значительной степени полагаются на маркировку запахом для коммуникации, причем запахами представителей как своего (конспецифичными) вида, так и других (гетероспецифичными) видов могут служить для них привлекающим или отпугивающим фактором. Цель данного исследования заключалась в изучении влияния внутри- и межвидовых обонятельных взаимодействий на *Panthera pardus* (далее – леопард), а также в проверке возможности использования гетероспецифичных запахов в качестве инструмента для отпугивания леопардов. Мониторинг активности леопардов по маркированию территории проводился в охотничьем резервате Саби-Сэнд (Южная Африка) с помощью фотоловушек, установленных на 43 маркировочных точках (в общей сложности 1450 ловушко-суток) в течение 61 дня в засушливый период 2021 года. Экспериментальная фаза длилась 38 дней и охватывала 27 точек. Было поставлено три задачи: (1) охарактеризовать внутривидовые коммуникативные функции маркировки запахом; (2) оценить влияние запахов доминирующих видов-конкурентов на поведение леопарда; и (3) определить потенциал этих запахов в качестве репеллента. Для симуляции присутствия *Panthera leo* (далее – лев) и *Crocuta crocuta* (далее – пятнистая гиена) на экспериментальные точки помещали свежесобранные экскременты этих видов. С помощью обобщенных линейных моделей со смешанными эффектами (GLMEM) мы сравнивали интервалы между визитами леопардов, продолжительность их пребывания и длительность поведенческих действий на экспериментальных и контрольных (без экскрементов) точках. На внутривидовом уровне в 40% случаев последовательных визитов на маркировочные точки фиксировались особи обоих полов. Вопреки нашему предположению о преобладании маркировочной активности у самцов, самки оставляли запаховые метки достоверно чаще, что указывает на выполнение метками леопардов функций как привлечения половых партнеров, так и демонстрации территориального статуса. Вопреки нашей гипотезе об избегании, частота посещений леопардами точек с экскрементами львов не изменилась, хотя продолжительность пребывания там значимо увеличилась, что свидетельствует о более сложном обонятельном ответе, чем простая реакция избегания. Наши результаты подтверждают гипотезу о том, что леопарды используют маркировочные точки для сбора информации о соседних особях того же вида и львах, а также для сигнализации о собственном присутствии. Мы не обнаружили убедительных доказательств того, что экскременты льва или пятнистой гиены могут отпугивать леопардов или использоваться в качестве инструмента управления популяциями диких животных. Полученные данные подчеркивают ключевую роль хемокоммуникации в территориальном поведении, а также демонстрируют как ее потенциал, так и ограничения для применения в природоохранной практике.

Ключевые слова: внутригильдийные взаимодействия, обобщенные линейные модели со смешанными эффектами, перемещенные экскременты, поведенческая экология, эффект «дорогого врага»