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Scent marking strategies of a solitary carnivore: boundary and road scent marking in the leopard

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Abstract

Scent marking, where individuals deposit signals on objects in the environment, is a common form of chemical signalling in mammals and is thought to play a critical role in maintaining social organisation within wide-ranging, spatially-dispersed populations. Senders, however, can incur scent marking costs through mark production, time investment in patrolling and depositing/maintaining mark sites, and increased risk of detection by predators and prey. To mitigate these costs, senders can adapt spatial patterns of scent marking to increase the probabilities of their scent marking being encountered by intended receivers. Relatively little, however, is known of the spatial scent marking placements of many wide-ranging carnivore species, with most studies focussing on scent mark form and function. Here, we use detailed observational data collected from over seven years of following individual leopards and high-resolution GPS radio collar data to investigate the spatial placements of scent marks within a leopard population in northern Botswana. We found that male leopards within our study area exhibited a boundary scent marking strategy by showing higher investments in the maintenance of marking sites in peripheral areas of their home range. We also found that leopards scent marked over four times as frequently and investigated over three times as frequently when travelling on roads than when travelling along natural routes, suggesting that roads may function as key locations for olfactory information. Compared to leopards from less productive ecosystems, such as the Kalahari, our results (1) suggest that leopards can be highly flexible in their marking strategies, with strategies impacted by the surrounding environment, and (2) provide evidence that human-modifications of the environment now play an important role in facilitating social cohesion within this solitary carnivore.

Keywords: communication, leopards, olfaction, *Panthera pardus*, road ecology, scent marking, territory maintenance

Introduction

Scent marking, where individuals deposit signals on objects in the environment, is a common form of chemical signalling in mammals and is thought to have functional roles in territoriality and mate acquisition (Gosling and Roberts, 2001; Macdonald and Loveridge, 2010). Whilst the roles of scent marks appear relatively consistent across species, scent marking behaviours vary between and within populations, and across landscapes (Allen et al., 2016a). Senders incur scent marking costs through mark production, time investment in patrolling and depositing/maintaining mark sites, and increased risk of detection by predators and prey (Gosling and Roberts, 2001; Hayward and Hayward, 2010; Hughes et al., 2012). To mitigate these costs, senders must make decisions on the optimal placements of scent marks. For example, they can select for areas or objects that increase the probabilities of signals being encountered by intended receivers, as is seen in Eurasian lynx (*Lynx lynx*), which increase scent marking frequencies along routes frequently travelled by conspecifics (Allen, Hočevar, de Groot, & Krofel, 2017; Krofel, Hočevar, & Allen, 2017).

Even though it can be difficult to ascribe actual function to scent marks without considering the responses of receivers, the spatial placements of marks can provide insights into the optimal scent marking strategies for communication (Gosling and Roberts, 2001). The spatial marking strategies employed by senders are likely dependent on the interplay between a number of factors, including resource distributions (Zhou et al., 2015), home range sizes (Gorman & Mills, 1984), and movement patterns of conspecifics (Krofel et al., 2017). As such, the placements of scent marks can vary considerably across closely related species and also within different populations of the same species. Gorman and Mills (1984), for example, found that the spatial marking strategies of hyaena species varied between ecosystems. Within highly productive landscapes, home ranges were small and scent marks were concentrated along borders: in less productive landscapes, home ranges were larger and hinterland scent marking strategies, i.e. where signals are concentrated within central home range areas, were favoured and more economical than border strategies (Gorman & Mills, 1984).

Human modifications to the environment may also impact scent mark placements by altering the space use of intended receivers (Wilmers et al., 2013). Roads, in particular, may promote scent marking efficiency by increasing scent mark encounter rates if they are preferentially used by intended receivers. In some species, for example, roads channel individual movements because of their positive effects on prey encounter probabilities (Fahrig & Rytwinski, 2009) and landscape permeability (Abrahms et al., 2016). However, although roads are thought to promote scent marking efficiency for some species (Krofel et al., 2017), results have been mixed, and other species have shown similar marking rates when travelling on roads and natural routes (Zub et al., 2003). This suggests that marking on roads carries costs. Disturbance from road traffic may, for example, decrease the persistence of scent marks and thus reduce the overall benefits of road marking. Additionally, it seems likely that dominant competitors will preferentially use roads, while inferior competitors will avoid them (Hayward et al., 2015; Mahon, Banks, & Dickman, 1998), thereby challenging the ubiquity of individual species responses. Thus, there likely exists a trade-off in the use of roads for scent marking, and its resolution is likely to be species and context dependent (Zimmermann, Nelson, Wabakken, Sand, & Liberg, 2014).

Scent marking is widespread amongst felids and plays a critical role in maintaining social organisation within their wide-ranging, spatially-dispersed populations (Sunquist &

Sunquist, 2002). However, relatively little is known of the spatial scent marking placements of many wide-ranging felid species, with most studies focussing on scent mark form and function (Allen et al., 2017), and relatively little is known of the impact of roads on the scent marking behaviours of felids (but see Krofel et al., 2017).

Leopards (*Panthera pardus*) are solitary large felids, present in a range of habitats across Africa and Asia (Jacobson et al., 2016), including areas with high levels of human-development (Odden, Athreya, Rattan, & Linnell, 2014). They show intrasexual territoriality, with range overlap varying between populations, and scent marking behaviours that are thought to play a key role in helping them to maintain territories and find reproductive partners (Bailey, 2005; Mizutani & Jewell, 1998). Scent marks are placed throughout territories by both sexes and the observed scent marking behaviours are consistent with those seen in other felids (Allen, Wittmer, Setiawan, Jaffe, & Marshall, 2016; Bailey, 2005). Little is known, however, of how leopard scent marking placements change across ranges and the adaptive significance of such placements, and much of what we do know is based on the identification of scent sites *post-hoc* during spoor tracking surveys (Bothma, 2004; Jenny, 1996; but see Bailey, 2005). Thus, the results are typically biased to easily detectable scent mark types across substrates that leopards can be tracked along, and they are incapable of incorporating information on relative placements within home ranges into the analyses.

Here, we use detailed observational data, collected over seven years of following individual leopards, i.e. focal follows, and high-resolution GPS radio collar data to investigate the scent marking behaviours of leopards in northern Botswana. We used data from GPS radio collars to delineate male leopard home ranges and data collected from focal follows to investigate scent marking frequencies across different substrates and areas of the home range. We also took advantage of the high-resolution data provided by the radio collars to investigate scent mark revisitation times, which we considered to be a proxy of the time elapsed before scent marks at sites were replenished. Data from two leopard radio collars with spatio-temporal overlap were used in a case-study into the scent marking behaviours of neighbouring competitors within overlapping areas of their home ranges. We assumed that, as with many other felids, leopard scent marks have a functional role in territoriality (Macdonald and Loveridge, 2010), and so we generated a series of hypotheses to consider the spatio-temporal scent marking strategies used by leopards. We hypothesised that scent marking behaviours would occur most frequently and sites would be revisited more quickly within the boundary areas of home ranges rather than the central areas, i.e. that leopards would display a boundary scent marking strategy, since these are the areas where scent marks are most likely to be encountered by intruders (Gosling and Roberts, 2001). We also predicted that roads would impact scent marking behaviours. Specifically, we hypothesised that leopards would scent mark at higher frequencies on roads and would replenish these signals more often because of the potential of roads to channel conspecific movements (e.g. Krofel et al, 2017).

Methods

Study site

This study was carried out in northern Botswana in the south-eastern region of the Okavango Delta over an area of ~520 km^2. The study landscape was a heterogeneous mix of habitat types, dominated by regions of mopane and acacia-dominated mixed woodlands (Broekhuis, Cozzi, Valeix, McNutt, & Macdonald, 2013). The study area included Moremi Game Reserve and adjacent wildlife management areas that were primarily used for photographic tourism. There were between one and three safari lodges operating within the area throughout the study period, each typically running game drives twice daily, and one permanent research camp, operated by the Botswana Predator Conservation Trust (BPCT). As a result, there was a well maintained network of roads that dissected our study site (Figure 1), which remained relatively consistent throughout the study period, and many resident large carnivores were habituated to vehicles.

Behavioural observations

Scent marking data were collected by researchers from the BPCT during focal follows from October 2011 until December 2017. Data were collected on 12 leopards (eight males and four females) that were sufficiently habituated to directly observe without eliciting any obvious changes in behaviour. Leopards were individually distinguishable by their unique rosette pelage patterns (Grey, Kent, & Hill, 2013) and were located through a combination of spoor tracking and radio telemetry. Behavioural observations were carried out from within research vehicles at distances of 10–50 m and 20–100 m from leopards when individuals were resting and moving, respectively. Upon locating leopards, sessions were initiated regardless of whether leopards were inactive or active, and in this way, samples were not biased to the collection of active behaviours, such as scent marking. Data were recorded using a critical incident sampling protocol (Altmann, 1974) and collected on Palm TX units using Pendragon Forms (from 2011 until 2015) and on Android smartphones using the KoboToolbox application (from 2015 - 2017). When leopards scent marked or investigated substrates, the mark type (Table 1), substrate marked, and leopard identity were all recorded alongside GPS coordinates.

From 2015–2017, each marking site within the focal session was also assigned a unique ID so that combinations of behaviours at the same site could be identified, and the track type (road or natural) that the leopard was travelling along was recorded. Scent marks placed on the same substrate and within 0.5 m of other marks were defined as occurring at existing scent marking sites, i.e. counter marking. Roads were defined as routes whose regular use by ground vehicles resulted in semi-permanent vehicle signatures on the landscape. Spatio-temporal GPS coordinates were also collected during transitions between leopard behavioural states that were of interest to the wider BPCT project, for example, during transitions between inactive and active behaviours.

Radio collars

Across our study period, we fitted seven male leopards with GPS radio collars developed by the Royal Veterinary College, University of London (A. M. Wilson et al., 2013). Leopards were immobilised by a Botswana-registered veterinarian using a drug cocktail including two or more of ketamine (50 - 200 mg), metodomidine (2 - 5 mg), xylazine (225 - 250 mg) and Zoletil (6 - 250 mg). Whilst individuals were immobilised, radio collars were fitted and vital signs monitored for signs of stress. Reversal drugs, atipamezole (3 - 24 mg) or yohimbine (3 mg), were administered after immobilisation work was complete, and researchers within a vehicle remained with recovering individuals until their movement coordination returned to pre-immobilisation levels. Radio collars were fitted with GPS-inertial measurement units that allowed collars to switch between different sampling frequencies depending on the leopard's activity. GPS sampling frequencies switched between three states: five fixes per second during periods of high acceleration, one fix per five minutes during other periods of locomotion, and one fix per hour during periods of inactivity (A. M. Wilson et al., 2013). Radio collar GPS fixes were accurate to within 10 m (Wilson et al., 2013; supplementary information). Radio collars were fitted with mechanical (SIRTRACK) or bio-degradable material drop-off units, and all leopards were monitored until radio collars dropped-off. Radio collars weighed ~340 g and so represented < 2% of carnivore body masses. Radio collared individuals were visited at least every two to three weeks (with longer delays between visits due to logistical challenges, e.g. vehicle failures, field conditions) to check animal welfare, download radio collar data *via* radio link, and to collect scent marking data. No ill-effects of radio collars were observed on animal welfare. We were able to collect scent marking data during focal follows for four of the seven radio collared leopards.

All field work was approved by the Department of Wildlife and National Parks (DWNP), Botswana, (permit no: EWT 8 / 36 / 4 xxxv (31)). Darting and radio collaring activities were approved by DWNP and darting reports submitted to the department after every leopard capture.

Home range, boundary, and overlap area classifications

Kernel utilisation distributions (KUDs) for radio collared leopards were estimated using a bivariate distribution and plug-in bandwidth selection ($H_{\text{plug-in}}$) in the R environment for statistics (R Core Team, 2018) using the packages *ks* (Duong, 2017) and *adehabitatHR* (Calenge, 2006). The 95% isopleths were extracted from KUDs and used to represent individual leopard home ranges. Boundary areas were then visualised by filling holes within 95% polygons and shrinking outer home range boundaries by 1,000 m using the *rgeos* package (Bivand & Rundel, 2017). The 1,000 m definition was based on preliminary analysis showing that, on average, leopard home ranges overlapped with neighbours by 1,040 m (± 283.46, standard error). Scent marks within 1,000 m of outer boundaries were thus defined as occurring within boundary areas and those over 1,000 m from boundaries were defined as within central areas. For one pair of neighbouring leopards (CHK & GSE_12), we also had scent marking and GPS data from each individual over the same sampling period. We defined the overlapping area of their 95% isopleths as the ‘overlap area’ and refer to it as such throughout the remainder of this paper.

Road marking classification

A geospatial vector file of the main roads within the study area, georeferenced manually by driving roads, was provided by the BPCT. Visual inspection of the map showed that it contained most roads within the area; however, some roads were intermittently present throughout the study period and so were under-represented within the map. Leopard focal session tracks were reconstructed from spatio-temporal coordinates and leopards were defined as travelling on roads when two or more consecutive timestamps were within 15 m of the nearest road. The 15 m threshold was used to account for GPS positional errors and was validated by matching the classification from this threshold against recorded track types of our 2015–2017 data subset. The threshold classification method had 92% accuracy with classifications derived from focal sessions, with visual inspection suggesting that the majority of discrepancies were due to under-representation of roads within the geospatial vector file. Thus, we assumed our 15 m threshold robust enough to assign track types to all pre-2015 data.

Revisitation times to scent marks

We calculated scent mark revisitation times for radio collared leopards by linearly interpolating leopard GPS fixes at one second intervals, creating a 15 m buffer, i.e. 15 m radius, around scent marking site coordinates, and identifying how long after scent deposition or after their previous visit, leopards took to return to the site. This 15 m buffer was chosen to account for GPS sampling errors. Where there were multiple scent marks deposited at the same GPS coordinates within the same session, we used only one scent mark to avoid pseudoreplication. We could not account for non-linear leopard movements between raw fixes. Thus, although there were scent marking sites where we had no revisits, we cannot conclusively say that individuals did not return to them during our sampling period. To account for this, we removed those sites that were not revisited from our dataset and calculated the mean revisitation times to the remaining scent marks. The visitation times of CHK and GSE_12 to one another's scent marks within the overlap area were also calculated using the methods above.

Statistical analyses

We calculated distances that leopards travelled during focal sessions from reconstructed tracks, which we then used to represent scent marking and investigating behaviours as frequencies (per km). We excluded from our analyses sessions with tracks shorter than 100 m to avoid inflated frequencies resulting from short follow distances. For example, if a leopard marked four times over a 20 m distance, this would have given an inflated marking frequency of 200 scent marks/km. For each session, we segmented reconstructed tracks into periods of travel on roads and natural routes, and for those individuals with GPS data. We further segmented these tracks into periods of travel within boundary and central areas of home ranges. Scent mark counts and distances travelled for different segments of the same road/natural routes and boundary/central areas combinations within each focal session were then summed to give overall values for each unique combination for that session.

Due to the data being non-normal and resilient to any change in the distribution after any kind of transformation, we employed the Mann-Whitney U test to compare frequencies between marking and investigating behaviours and to compare behaviour frequencies between sexes.

To investigate behaviour frequencies within different home range areas and on different track types, we used a series of linear mixed-effects models using the *nlme* R package (Pinheiro, Bates, DebRoy, & Sakar, 2016). Separate models were fitted for overall scent marking and investigating behaviours and for each of the top two scent marking behaviours. We used counts as responses and an offset of log (track length) was included within models to account for variation in the distances leopards were observed between focal sessions. Leopard identity was included within models as a random effect to control for repeated sampling of the same individuals. To account for unequal variances across leopards and increasing variance with track length, we specified and included variance structures for leopard identity and session distance in the models as weights (Zuur 2009). Linear mixed-effects models were also used to model revisitation times and also included leopard identity as a random effect. Models looking at scent marking and investigating behaviours across different track types used the full scent marking dataset, i.e. included both male and female leopards, and included track type as an explanatory variable. Leopard sex was not included as a fixed effect because sex was encoded for within our leopard identity random effect. A data subset that included only the leopards which we had GPS data for, i.e. only male leopards, was then used to investigate behaviour frequencies across boundary and central areas and scent mark revisitation times. These models included track type, location within the home range, and an interaction between track type and location as fixed effects. Models investigating behaviour frequencies and revisitation times within the CHK-GSE_12 dyad used a subset of the GPS and scent marking datasets for CHK and GSE_12 that were collected over the same time period. Location (with three levels: boundary, central, and overlap area) was included as an explanatory variable within these models but track type was not included because of limited sample sizes.

An information theoretic approach was used to rank all combinations of models derived from the global model using Akaike's information criterion corrected for small sample sizes (AIC_C) (Burnham & Anderson, 2002). Models within six AIC_C units of the highest ranked were retained within a candidate model subset (Richards, Whittingham, & Stephens, 2011). A model averaging approach was then applied to identify model parameters with a significant impact on the response, i.e. model averaged parameters which were shown to have confidence intervals excluding zero (Grueber, Nakagawa, Laws, & Jamieson, 2011). Candidate models from which model parameters were estimated are included as supplementary tables (Tables A1– A4). Throughout the results, we report model predicted means with standard errors.

Results

Overview

We collected data over 786 hours of leopard observations that took place over 491 focal sessions, on eight male and four female leopards, during which leopards were followed for over 143.22 km. We recorded 894 occurrences of scent marking behaviours and 663 occurrences of investigating behaviours by five male and two female leopards. The majority of focal follow hours occurred in the early evenings (42%, *N* = 330) and early mornings (26%, *N* = 204) during peak leopard activity and when light conditions aided data collection (Hubel et al., 2018), followed by data collected during the day (24%, *N* = 189) and night (8%, *N* = 63).

Scraping and spraying were the most common scent marking types – accounting for 83% (*N* = 746) of all scent marks observed (Table 2). Leopards were documented scent marking or investigating nine main substrate types, with grasses, shrubs, and trees accounting for approximately 90% of all marking sites (Figure 2). Most scrape (*N* = 301) scent marks were on grass (81%) and most sprays were on shrubs (52%, *N* = 195) and trees (34%, *N* = 127).

Leopards visibly investigated 65% (*N* = 244) of scent marking sites from our 2015–2017 subset before scent marks were deposited, but 82% of all substrates that were investigated (*N* = 299) went on to be scent marked (*N* = 244). Approximately 57% (*N* = 213) of deposit sites had only one scent marking behaviour carried out at them. Scraping and squat urinating commonly occurred at the same marking sites, with most scrapes, from our 2015-2017 subset, (84%, *N* = 131) involving leopards squat urine counter marking on the site after scraping.

Overall, we documented that leopards scent marked (7.82 ± 0.73 marks/km) more frequently than they investigated substrates (5.93 ± 0.64 investigations/km) (Mann-Whitney U test: $N_{1,2} = 148$, U = 12 582, $P < 0.05$). Since other felid studies have primarily focussed on scrape and spray marks, we also calculated marking frequencies for these behaviours and found that frequencies did not significantly differ between the two scent mark types (Mann-Whitney U test: $N_{1,2} = 148$, U = 11 060, $P = 0.881$) (Table 2). Scent marking frequencies between the sexes were similar for overall scent marking (Mann-Whitney U test: $N_{♂} = 128$, $N_{♀} = 20$, U = 1574, $P = 0.098$), scraping (Mann-Whitney U test: $N_{♂} = 128$, $N_{♀} = 20$, U = 1588, $P = 0.075$), and spraying (Mann-Whitney U test: $N_{♂} = 128$, $N_{♀} = 20$, U = 1321, $P = 0.816$) behaviours. There was also no significant difference in investigating frequencies between the sexes (Mann-Whitney U test: $N_{♂} = 128$, $N_{♀} = 20$, U = 1478, $P = 0.262$).

<u>Scent marking on roads</u>

Leopards scent marked and investigated over three times as frequently when travelling on roads than natural routes (Table 3; Figure 3). Scrape marks followed the same pattern, with higher marking frequencies on roads than natural routes, but sprays were deposited at similar frequencies across both track types (Table 3; Figure 3).

Scent marking across home ranges

Male leopards scent marked in both boundary and central areas of their home ranges and did so at similar frequencies (Table 4; Figures 4-5). Although there was no overall effect of location within the home range on investigation frequencies, there was an interaction between location and track type (Table 4). Specifically, although investigating behaviour frequencies when travelling on roads appeared similar in boundary and central areas, leopards investigated more frequently within boundary than central areas along natural routes (Figure 6). This appears, however, to be a reflection of the relatively small standard errors associated with travel along natural routes relative to those associated with travel along roads. No interaction effect between location and track type was detected on scent marking frequencies.

When analysing the CHK-GSE_12 dyad, we found that a leopard's location within its home range, i.e. within the central, boundary, or overlap area, had no impact on scent marking frequencies (Table 5). There was, however, an impact of location on investigating, with leopards investigating at higher frequencies in boundary than overlap or central areas of their home range (Table 5; Figure 7).

Revisitation times

On average, leopards revisited scent marks 29.55 ± 0.54 days (*N* = 215) after they were deposited. Although revisitation times to scent marks deposited on roads (*N* = 128; 28.64 ± 0.49 days) were statistically significantly shorter than on natural routes (*N*= 87; 30.90 ± 1.12 days) (Table 6), the scale of the change suggested little biological significance. There was an interaction between track type and home range location (boundary *vs.* central) on revisitation times to scent marks (Table 6; Figure 8). Specifically, revisitation times remained similar for scent marks deposited on natural routes in central and boundary areas of home ranges but decreased by 51% when travelling on roads in boundary than central areas (Figure 8).

When analysing the CHK-GSE_12 dataset, we found that leopard revisitation times to their own scent marks were lower in overlap areas (*N* = 31; 17.73 ± 2.53 days) than in central (*N* =120; 40.89 ± 3.86 days) and boundary home range areas (*N* = 55; 35.98 ± 4.46 days) (Table 6). It took on average 25.36 ± 3.51 days (*N* = 33) for leopards to encounter scent marks left in the overlap area by their neighbour.

Discussion

Leopards within our study area adapt their scent marking and investigating behaviours based on the location within their home range and on the medium upon which they are travelling. Although scent marking frequencies remain consistent across home ranges, male leopards exhibit a boundary scent marking strategy by revisiting boundary scent marking sites on roads more quickly than scent marks in central areas, presumably for scent site maintenance and investigation. Within our study area, higher investment in scent marking behaviours at boundaries, particularly within overlap areas, may have increased scent marking efficiency and helped to establish social dominance by increasing the chances of active signals being encountered by neighbouring competitors. Scent marking within central areas may then primarily aid mate acquisition. We speculate that our male leopards may thus scent mark at similar rates throughout home ranges to facilitate finding a mate but prioritise maintaining marks at boundary locations because of the potential to lose both territory and long-term mating opportunities. Thus, scent marking at boundaries may facilitate the defence of central home range resources and reduce exploitation competition, e.g. for reproductive opportunities, within central home range areas (Peres, 1989). These results caution against ascribing function to scent marks purely from spatial distributions (Gosling and Roberts, 2001). Future studies would benefit from considering the receivers of signals at different locations, e.g. by camera trapping scent sites (Allen et al., 2016b), and the olfactory information contained within scent marks, e.g. using scent presentation experiments (e.g. Allen et al., 2014; Jordan et al., 2010) or chemical profiles of scent marks (Vogt et al., 2016), in order to fully appreciate scent mark functions.

Male leopards scent marked at frequencies in overlap areas comparable to other areas of their home range but investigated their non-overlapping boundary areas at higher frequencies – although we acknowledge that our overlap areas for GSE and CHK in 2012 were likely an underestimate given that not all leopards within our study system were radio collared. Regardless, such spatial patterns of scent marking investment may occur if neighbours and strangers compete for different resources and so represent different levels of threat to the investigator (Müller & Manser, 2007). In other words, male leopards may investigate at higher frequencies in non-overlapping boundary areas to identify dispersing males looking to establish new territories. That revisitation times to scent marks in the overlap area were lower than elsewhere in the home range also suggests an importance of maintaining familiarity with stable neighbours through regularly maintained scent marks. Whether there are community communication sites within these overlap areas that are used to communicate with conspecifics (e.g. Allen et al., 2014) and maintain familiarity is unknown. Camera trap placements at scent marking sites within areas where leopard home ranges overlap could be used to investigate this further.

Consistent with our predictions, male leopards had higher scent marking and investigating frequencies when travelling on roads than when travelling along natural routes, suggesting that roads may function as key locations for olfactory information. This may occur because roads increase mark encounter frequencies, perhaps by channelling leopard movements and increasing landscape permeability, as they do for other species of large carnivores (e.g. Abrahms et al., 2016; Zimmermann et al., 2014). This has implications for the exploitation of these signals by unintended receivers as it increases mark encounter probabilities for all species that use roads as movement corridors (Hughes et al., 2012). Interspecific eavesdropping is particularly common amongst southern African carnivores, with some data suggesting higher occurrences of interspecific than intraspecific counter mark (Apps et al., 2019) and other data suggesting that hyaena latrines have functions as multi-species scent marking sites (Vitale, 2017). Leopards may thus incur costs from increased road marking if signals are encountered by unintended receivers that might alter their behaviours in ways that could be maladaptive to the sender. For example, predator odours can lead to increased vigilance of prey (Parsons et al., 2018; but see van der Meer et al., 2012). Further, although most human-traffic within the study area was diurnal and so occurred outside of peak leopard activity periods (Hubel, Golabek, Rafiq, McNutt, & Wilson, 2018), minimising direct disturbance to scent marking leopards, the costs (or benefits) of traffic on scent mark degradation are unknown. For example, it is unknown whether traffic can help distribute scent marks more widely, i.e. by capturing signals on tyres. Ultimately, the decision to scent mark on roads likely reflects a number of trade-offs in the costs, such as eavesdropping and mark disturbance, and benefits, such as increased conspecific encounter probabilities, of road marking.

Leopards in less productive landscapes, where population densities are lower and home range sizes larger, such as those within the Kalahari (Bothma, 2004; 2012), may adopt different spatial scent marking strategies, as is seen in hyaenas across different ecosystems (Gorman and Mills, 1984). This idea is supported by the observation that our leopard scent marking frequencies were comparable to leopards within tropical rainforests (Jenny, 1996) but were approximately three times higher than leopards within the arid Kalahari (Bothma, 2004). Although each of these studies used different survey methods and focussed on different scent mark types (scrapes and sprays, respectively), comparisons with our results suggest that scent marking frequencies differ between landscapes for, at least, specific mark types. Leopard home ranges within the southern Kalahari were over five times larger than those within our study area (Bothma, 2004; Hubel et al., 2018). Thus, large territories may preclude efficient scent marking at home range boundaries so that Kalahari leopards adopt a hinterland marking strategy and perhaps reduce overall scent marking frequencies (Gorman & Mills, 1984) – this is additionally a likely optimal strategy given that leopards in arid areas occur at lower densities and so have a reduced likelihood of trespassing on conspecific territories (Kingdon, 2013). Additionally, the relative importance of scent marking behaviours in mediating encounters is likely to differ with habitat characteristics. As such, increased visibility within the Kalahari may mean that the role of vision in mediating encounters is more important than in closed habitats and so investment in scent marking behaviours is reduced. Given the lack of GPS data available for females, our results apply primarily to male leopards. Further, although we did not detect differences in scent marking frequencies between sexes, is it possible that female scent marking strategies may diverge from males, e.g. due to sexually dimorphic life-histories. For example, in other felids, females exhibit higher scent marking frequencies during oestrus to advertise sexual availability (Allen, Wittmer, & Wilmers, 2014; Logan & Sweanor, 2010), and it is possible that similar patterns may exist for leopards.

The seven main scent marking behaviours and three investigating behaviours we recorded are consistent with those documented in other solitary felids (Allen et al., 2016a; Smith et al., 1989; Vogt et al., 2014). We also recorded one occurrence of leopards scraping with their front feet. To our knowledge this has not been documented in the literature on leopards elsewhere and there may be population specific occurrences of this behaviour, as seen in pumas (*Puma concolor*) (Harmsen et al., 2010; Allen et al., 2014). Leopard scrapes were created throughout territories and were often accompanied by urine or faeces, suggesting that scrapes may act as visual cues and aid the discovery of accompanying scent marks (Allen et al., 2014). Further, although we may have missed instances where urine was deposited alongside scrapes, we find it unlikely that we missed urination at all single deposit scrape sites. Indeed, it is widely referenced within the literature that urine is not present at all scrapes (e.g. (Allen, Yovovich, et al., 2016; Harmsen et al., 2010; Smith et al., 1989). Thus, given that not all scrapes were accompanied by secondary scent marks, scrapes may also be used to deposit marks from inter-digital glands on the feet (D. Wilson & Mittermeier, 2009). This suggests that scrapes and urine scent marks may have different roles in communication. Multiple scent marks at sites were then typically a combination of signals likely coming from subcutaneous or inter-digital glands, such as scrapes and rubs, and those occurring from bodily excretions, such as sprays and urine (Harmsen et al., 2010). Such combinations of scent marking behaviours may facilitate scent matching and aid mate selection (for review see Candolin, 2003).

In summary, we have shown that male leopards are highly flexible in their scent marking behaviours and that human-modifications of the environment can play a key role in facilitating information transfer within this solitary species. Leopards were shown to exhibit a boundary scent marking strategy by showing higher investments in the maintenance of boundary located scent marks. Roads appear to play a particularly important role in information transfer, likely functioning as key locations for olfactory information that increase scent marking efficiency and thus help to maintain social cohesion. Our results also suggest a key role of familiarity in maintaining territoriality between neighbouring competitors and show that leopards exhibit higher frequencies of investigating behaviours in areas where they are conceivably most likely to encounter same-sex strangers. Thus we provide one of the few studies suggesting a *dear-enemy* effect in a solitary large carnivore, with most studies focussing on this effect within group-living species (Christensen & Radford, 2018). Our results also caution in using spatial data alone to infer scent marking strategies (Gosling and Roberts, 2001). As such, further research on the responses of receivers of scent marking signals and on the olfactory content of scent marks would provide further insights into the function of scent marking behaviours.

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Main tables

Table 1: Description of the ten scent communication behaviours recorded during focal sessions.

Category	Behaviour	Description
Scent marking	Scraping	Alternate raking of hind feet on substrate, may also include urinating over the substrate during or after the scraping.
Scent marking	Squat urinating	Squatting over substrate and urinating, in the absence of any scraping behaviour.
Scent marking	Spraying	Raising tail and spraying back urine onto substrate.
Scent marking	Rubbing	Rubbing face or body onto substrate. Can be done whilst leopard is standing or lying.
Scent marking	Defecating	Squatting over substrate and defecating.
Scent marking	Rolling	Lying and rolling several times on ground. Distinct from rubbing by back and forth rolling. May leave flattened vegetation.
Scent marking	Scratching	Using front claws to scratch substrate.
Investigating	Sniffing	Investigating by placing nose within 0.5 m of substrate and sniffing.
Investigating	Licking	Licking substrate (non-prey) or placing substrate within mouth and chewing for several seconds.
Investigating	Flehmening	Placing face within 0.5 m of substrate and inhaling scent whilst curling upper lip and exposing teeth. Facilitates mark investigation by vomeronasal organ.

Table 2: Summary of the occurrence and mean frequencies (per km) (± SE) of the scent communication behaviours documented during the study.

Category	Behaviour	Occurrence	Behaviour frequency (per km) (mean ± SE)
Scent marking	Scraping	371	3.42 ± 0.41
Scent marking	Spraying	375	2.96 ± 0.30
Scent marking	Rubbing	71	0.58 ± 0.15
Scent marking	Squat urinating	20	0.31 ± 0.15
Scent marking	Defecating	16	0.26 ± 0.09
Scent marking	Rolling	36	0.25 ± 0.07
Scent marking	Scratching	5	0.04 ± 0.02
Investigating	Sniffing	622	5.64 ± 0.58
Investigating	Licking	23	0.19 ± 0.08
Investigating	Flehmening	18	0.10 ± 0.08

Table 3: Linear mixed-effects model (Δ $\text{AIC}_C < 6$) averaged parameters predicting scent communication behaviour frequencies across track types.

				Confidence Intervals	
Parameters	**Estimate**	**SE**	**Adj. SE**	**Lower**	**Upper**
All marking					
(Intercept)	1.075	0.141	-	0.796	1.355
Track type (road) *	0.703	0.219	-	0.271	1.137
All investigating					
(Intercept)	0.857	0.099	0.000	0.661	1.052
Track type (road) *	0.537	0.232	0.022	0.172	0.962
Scraping					
(Intercept)	0.533	0.092	-	0.095	0.828
Track type (road) *	0.669	0.169	-	0.337	1.000
Spraying					
(Intercept)	0.646	0.075	0.075	0.499	0.794
Track type (road)	0.054	0.119	0.120	-0.153	0.471

Within the parameters column, parameters are grouped by response variables for each model series (bold). All models included leopard identity as a random effect. Candidate models can be found in Table A1. * denotes parameters with a significant impact on the response.

Table 4: Linear mixed-effects model (Δ AIC$_C$ < 6) averaged parameters predicting scent communication behaviour frequencies across different home range locations and track types.

				Confidence Intervals	
Parameters	**Estimate**	**SE**	**Adj. SE**	**Lower**	**Upper**
All marking					
(Intercept)	1.384	0.238	0.240	0.913	1.855
Track type (road)	0.320	0.289	0.290	-0.250	0.890
Track location (boundary)	0.046	0.147	0.150	-0.245	0.337
Track type (road) x track location (boundary)	0.024	0.163	0.165	-0.298	0.347
All investigating					
(Intercept)	0.959	0.163	0.165	0.635	1.283
Track location (boundary)	0.022	0.200	0.202	-0.436	0.497
Track type (road)	0.233	0.290	0.292	-0.327	0.832
Track type (road) x track location (boundary) *	0.668	0.653	0.656	0.192	2.035
Scraping					
(Intercept)	0.774	0.180	0.182	0.417	1.130
Track type (road) *	0.427	0.229	0.230	0.076	0.856
Track location (boundary)	0.018	0.107	0.108	-0.310	0.424
Track type (road) x track location (boundary)	0.044	0.186	0.187	-0.381	1.246
Spraying					
(Intercept)	0.739	0.136	0.137	0.470	1.009
Track location (boundary)	0.053	0.121	0.121	-0.163	0.483
Track type (road)	0.006	0.096	0.097	-0.342	0.389
Track type (road) x track location (boundary)	0.007	0.078	0.079	-0.525	1.043

Within the parameters column, parameters are grouped by response variables for each model series (bold). All models included leopard identity as a random effect. Candidate models are presented in Table A2. * denotes parameters with a significant impact on the response.

Table 5: Linear mixed-effects model (Δ AIC$_C$ < 6) averaged parameters predicting CHK-GSE_12 scent communication behaviour frequencies across boundary, central, and overlap areas of home ranges.

				Confidence Intervals	
Parameters	**Estimate**	**SE**	**Adj. SE**	**Lower**	**Upper**
All marking					
Intercept	2.868	0.781	0.800	1.306	4.431
Location (central)	0.177	0.298	0.304	-0.578	0.613
Location (boundary)	0.356	0.398	0.406	-0.760	0.831
All investigating					
(Intercept)	0.906	0.303	0.306	0.307	1.505
Location (central)	0.215	0.310	0.313	-0.138	1.070
Location (boundary) *	0.328	0.424	0.427	0.032	1.395
All scraping					
(Intercept)	1.343	0.485	0.495	0.373	2.312
Location (central)	-0.033	0.181	0.184	-1.304	0.629
Location (boundary)	-0.052	0.257	0.261	-1.831	0.762
Spraying					
(Intercept)	1.042	0.324	0.329	0.397	1.687
Location (central)	0.060	0.276	0.281	-0.814	1.431
Location (boundary)	0.182	0.474	0.478	-0.408	2.276

Within the parameters column, parameters are grouped by response variables for each model series (bold). All models included leopard identity as a random effect. Candidate models are presented in Table A3. * denotes parameters with a significant impact on the response.

Table 6: Linear mixed-effects model (ΔAIC$_C$ < 6) averaged parameters predicting revisitation times across different home range locations and track types.

				Confidence Intervals	
Parameters	**Estimate**	**SE**	**Adj. SE**	**Lower**	**Upper**
All leopard					
(Intercept)	5.800	0.757	0.761	4.309	7.292
Location (boundary)	-0.104	0.645	0.648	-1.373	1.165
Track type (road) *	1.233	0.725	0.727	0.242	2.577
Track type (road) x Location (boundary) *	-1.769	1.144	1.147	-3.806	-0.624
CHK-GSE_2012					
(Intercept)	3.147	0.126	0.127	2.898	3.395
Location (overlap) *	-0.374	0.289	0.289	-0.909	-0.141
Location (boundary)	-0.110	0.171	0.172	-0.519	0.211

Within the parameters column, parameters are grouped by whether models were for all leopards or the CHK-GSE_12 subset (bold). All models included leopard identity as a random effect. Candidate models are presented in Table A4.

Appendix tables

Table A1: Summary of candidate models (Δ $AIC_C < 6$) of linear mixed-effects modelling output predicting scent communication behaviour frequencies across track types.

Model	R^2	K	AICc	Δ AICc	Wi
All marking					
Track type	0.199	9	530.404	-	0.980
All investigating					
Track type	0.207	9	506.709	-	0.947
Null	0.161	8	512.463	5.754	0.053
Scraping					
Track type	0.187	9	567.454	-	0.997
Spraying					
Null	0.225	8	432.468	-	0.660
Track type	0.230	9	433.793	1.325	0.340

Within the model column, models are grouped by response variables for each model series (bold).

Table A2: Summary of candidate models (Δ AIC$_C$ < 6) of linear mixed-effects modelling output predicting scent communication behaviour frequencies across different home range locations and track types.

Model	R^2	K	AICc	Δ AICc	Wi
All marking					
Track type	0.208	7	393.460	-	0.452
Null	0.180	6	394.908	1.447	0.219
Location + track type	0.213	8	395.214	1.754	0.188
Location	0.180	7	397.166	3.705	0.071
Location + track type + location x track type	0.216	9	397.204	3.743	0.070
All investigating					
Location + track type + location x track type	0.278	9	372.464	-	0.584
Track type	0.229	7	374.613	2.148	0.199
Location + track type	0.238	8	375.733	3.268	0.114
Null	0.198	6	376.530	4.066	0.076
Location	0.200	7	378.616	6.152	0.027
Scraping					
Track type	0.132	7	339.114	-	0.588
Location + track type	0.133	8	341.235	2.121	0.204
Location + track type + location x track type	0.141	9	342.662	3.548	0.100
Null	0.078	6	343.059	3.945	0.082
Spraying					
Null	0.197	6	328.654	-	0.504
Location	0.203	7	330.224	1.570	0.230
Track type	0.198	7	330.902	2.249	0.164
Location + track type	0.204	8	332.441	3.787	0.076
Location + track type	0.206	9	334.477	5.823	0.027

Within the model column, models are grouped by response variables for each model series (bold).

Table A3: Summary of candidate models (Δ AIC$_C$ < 6) of linear mixed-effects modelling output predicting CHK-GSE_12 scent communication behaviour frequencies across central, boundary, and overlap areas of HR.

Model	R^2	K	AICc	Δ AICc	Wi
All marking					
Null model	0.540	4	363.071	-	0.910
Location	0.542	6	367.689	4.619	0.090
All investigating					
Null model	0.164	4	190.375	-	0.539
Location	0.226	6	190.691	0.316	0.461
Scraping					
Null model	0.527	4	284.114	-	0.902
Location	0.530	6	288.556	4.442	0.098
Spraying					
Null model	0.491	4	279.096	-	0.805
Location	0.507	6.00	281.930	2.834	0.195

Within the model column, models are grouped by response variables for each model series (bold).

Table A4: Summary of candidate models (Δ AIC$_C$ < 6) of linear mixed-effects modelling output predicting revisitation times across different home range locations and track types.

Model	R^2	K	AICc	Δ AICc	Wi
All leopard					
Location + track type + location x track type	0.051	6	1063.604	-	0.766
Location	0.015	4	1067.305	3.701	0.120
Location + track type	0.020	5	1068.316	4.712	0.073
CHK-GSE_2012					
Location	0.073	6	631.808	-	0.712
Null	0.044	4	633.618	1.810	0.288

Within the model column, models are grouped by whether models were for all leopards or the CHK-GSE_12 subset (bold).

Main figure legends

Figure 1: Map of the core study area (right) and its location within Botswana (left). Roads are shown within the core area as solid black lines. The core study area map was created using Google satellite imagery obtained within the QGIS *OpenLayers* Plugin (Kalberer & Walker, 2018).

Figure 2: Summary of the percentage of scent marking and investigating behaviours carried out on different substrate types.

Figure 3: Mean (± SE) leopard investigating and scent marking frequencies (per km) when travelling along roads and natural routes. * denotes behaviours where there is an impact of track type on behaviour frequency (i.e. the track type model parameter's confidence intervals exclude 0).

Figure 4: Mean (± SE) male leopard investigating and scent marking frequencies (per km) when travelling along boundary and central areas of home ranges. * denotes behaviours where there is an impact of home range area on behaviour frequency (i.e. the area model parameter's (or it's interaction's) confidence intervals exclude 0).

Figure 5: Distribution of male leopard follows (white circles) and scent communication behaviours (blue circles) across boundary (dark grey) and central (light grey) areas of leopard home ranges for individuals with GPS radio collars. Roads are depicted as black lines and leopard ID codes are provided in upper left corners of maps.

Figure 6: Mean (± SE) male leopard (a) investigating and (b) scent marking frequencies (per km) when travelling along road and natural routes in central and boundary home range areas.

Figure 7: Mean (±SE) scent marking and investigating frequencies (per km) for CHK and GSE_12 when travelling across boundary (non-overlap), central, and overlap areas of their home ranges. * denotes behaviours where there is an impact of home range location on behaviour frequencies (i.e. at least one of the location model parameter's confidence intervals exclude 0).

Figure 8: Mean number of days that it took leopards to return to scent marks in different areas of their home range and across different track types. Standard errors are ≥ 0.07 and ≤ 0.68 and so are not visible as error bars, but instead, they are presented alongside each plotted mean.