

Interpack communication in African wild dogs at long-term shared marking sites

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Scent marks deposited as semiochemical signals are a primary mode of communication for a broad range of mammal species. Such scent signals are often deposited at specific, frequently visited marking sites called latrines. Despite descriptions of widespread latrine use by numerous mammal species, detailed understanding of site visit rates and latrine function is lacking. Here we report for the first time a quantitative assessment of scent-marking behaviours that represent interpack olfactory communication by African wild dogs, *Lycaon pictus*, at latrines visited by multiple resident neighbouring packs, hereafter called a 'shared marking site' (SMS). We show that multiple packs visited specific SMSs frequently and regularly throughout the year, with a notable decrease in visits during the 3-month denning season coinciding with a contraction in range size. In addition to resident neighbouring packs, dispersing individuals visited and scent-marked at SMSs, suggesting that latrines function at least in part as sites communicating information about residence and possibly reproductive status. Further detailed investigation of the relevance of latrine use to territorial behaviour, ranging, habitat use and dispersal in this species is required, particularly as it may have direct applied conservation implications for this wide-ranging but territorial endangered species.

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Olfactory information gleaned from chemical signals is a primary mode of mammalian communication (Macdonald, 1980; Rails, 1971; Thiessen & Rice, 1976). It is generally understood that urine and faeces commonly represent scent marks, but specific glandular secretions have been described as scent marks for some species (Macdonald, 1985). Scent marking is often concentrated at a specific site, called a latrine, where urine, faeces and other deposits, including those from glandular secretions, might build up over time from repeated use by the same individual or, in the case of social carnivores in particular, from multiple individuals of the same species (Macdonald, 1985). Understanding the spatial and temporal patterns of scent marking at latrine sites is important for inter-pack intraspecific competition and space use in species.

Latrine use is widespread in the Carnivora and has been documented in at least 34 species across seven families. Both spotted

hyaena, *Crocuta crocuta*, and brown hyaena, *Hyaena brunnea*, leave their scats in large middens (Gorman & Mills, 1984; Henschel & Skinner, 1991; M. G. L. Mills & Gorman, 1987), and male cheetah, *Acinonyx jubatus*, repeatedly defecate and urinate at shared marking trees (Cornhill & Kerley, 2020; Kusler et al., 2019; Marnewick et al., 2006). In the Canidae specifically, latrine use has been documented in kit foxes, *Vulpes macrotis* (Ralls & Smith, 2004), coyotes, *Canis latrans* (Bowen & Cowan, 1980), Ethiopian wolves, *Canis simensis* (Sillero-Zubiri & Macdonald, 1998), grey wolves, *Canis lupus* (Barja et al. 2004), golden jackals, *Canis aureus* (Macdonald, 1979), raccoon dogs, *Nyctereutes procyonoides* (Ikeda, 1984), dholes, *Cuon alpinus* (Johnsingh, 1982; Thinley et al., 2011), maned wolves, *Chrysocyon brachyurus* (Dietz, 1984) and swift foxes, *Vulpes velox* (Darden & Dabelsteen, 2008). Despite widespread use, the functions of latrines are still not fully understood for many species (Buesching & Jordan, 2019).

A recent review (Buesching & Jordan 2019) suggested five broad, and not mutually exclusive, functions for mammal latrines: (1) communication regarding territory and/or resource defence; (2)

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communication centres and/or advertising information about reproductive status; (3) landmarks aiding in orientation; (4) parasite avoidance; and (5) predator–prey interactions. Where a territory is defined as an area defended (individually or by a social group) against others of the same sex or species (Burt, 1943), latrines are often thought to signal 'ownership' of that territory to limit intruders' access to food, sleeping/breeding sites or mates. Residents commonly use scent marks to signal a threat to intruders or an intention to defend resources (Kaufmann, 1983) throughout the year, but territories may be seasonally established and defended, as in water voles, *Arvicola terrestris*, where marking peaks during the breeding season (G. L. Woodroffe et al., 1990), and in meerkats, *Suricata suricatta*, where marking peaks during periods of territorial intrusions (Jordan et al., 2007). While the majority of studies suggest or assume a territorial function to marking, emphatically distinguishing between the above hypotheses is problematic.

Traditionally it was thought that latrines formed a 'scent fence' that keeps intruders out (e.g. Hediger, 1949), yet there are mounting examples of territorial intrusions by nonresidents in many species (e.g. dwarf mongoose, *Helogale parvula*, Rood, 1983; African lion, *Panthera leo*, McComb et al., 1994), discrediting this hypothesis. Despite this, there remain numerous examples of latrines being more commonly located close to territory borders (e.g. Ethiopian wolves, Sillero-Zubiri & Macdonald, 1998; spotted hyaena in some environments, Mills & Gorman, 1987; Henschel & Skinner, 1991; brown hyaena, Gorman & Mills, 1984) than core areas. Such border-marking strategies suggest a role of latrines in territorial communication (Johnson, 1973), or at least the intention to communicate with neighbours and other conspecifics that might approach from outside their territory boundaries, but other marking strategies can also achieve the same end. In solitary or wide-ranging species, maintaining fresh scent marks along a large territorial border can be energetically costly (Macdonald, 1980) making it more economical to distribute scent marks strategically throughout a territory. Effective scent marking of, either around or throughout, a territory can be seen as an honest signal of ownership, as only a long-term resident in good condition may be able to distribute and frequently replenish scent marks effectively. Regardless of the strategy employed, Gosling (1982) argued that 'scent-matching' is the likely mechanism underpinning territoriality by scent marking. By comparing scents encountered in the environment with the scent of a potential owner, intruders could identify territory owners and avoid or de-escalate potentially risky confrontations (e.g. Gosling, 1982; Gosling & McKay, 1990).

Beyond territoriality, latrine function may also be linked to information transfer such as the advertisement of reproductive status. As metabolic waste products, faeces and urine also serve to excrete endocrine metabolites, which may advertise an animal's reproductive state (e.g. Schwarzenberger et al., 1996). All carnivores have anal glands (McColl, 1967), and in some species the substance secreted contains information relating to sex (e.g. steppe polecat, *Mustela eversmannii*, and Siberian weasel, *Mustela sibirica*, Zhang et al., 2003; brown bears *Ursus arctos*, Rosell et al., 2011), group membership (e.g. spotted hyaena, Burgener et al., 2008; Theis et al., 2013) and individuality (e.g. giant panda, *Ailuropoda melanoleuca*, Zhang et al., 2008). As such, latrines may function as a communication hotspot allowing efficient transfer of a range of information with conspecifics.

African wild dogs, *Lycaon pictus*, are a wide-ranging but territorial pack-living species, with annual ranges between 367 and 999 km² in northern Botswana, within which they travel daily distances of 6.6–10.6 km (Pomilia et al., 2015). African wild dogs typically maintain their territories year-round, yet ranges can contract to ca. 27% of the annual range during the 3-month denning

season (Creel & Creel, 2002; Frame et al., 1979; Pomilia et al., 2015). Packs overlap with their neighbours, the extent of which varies between study populations (see Creel & Creel, 2002; Mills & Gorman, 1997; Reich, 1981) and within them. In our study population alone, overlap has been documented from less than 12% (Parker, 2010) to 56% overlap (Jackson et al., 2017). Some of this variation may potentially be explained by interpack relatedness, with related neighbours overlapping more than unrelated neighbours (Jackson et al., 2017).

African wild dogs scent-mark using urine (Frame & Frame, 1976), and previous research into their scent-marking behaviour has mainly focused on intrapack communication (see Jordan et al., 2014, 2016), with some authors suggesting they use a 'cloud' strategy, where scent marks are distributed throughout their territory as opposed to preferentially along the borders (Parker, 2010). Recently, researchers reported that four packs used a discrete scent-marking site intensively over a period of 13 months (Apps et al., 2022). Beyond this discovery, little work has been done on interpack communication in African wild dogs, and previous studies aiming to understand the factors that underpin their ranging behaviour have overlooked this important aspect of their biology (e.g. Marneweck et al., 2019; Pomilia et al., 2015), despite its importance in understanding territoriality, and its potential applied role in managing ranging and movements around anthropogenic threats, such as through the BioBoundary project by Botswana Predator Conservation (BPC; see Jackson et al., 2012).

To investigate interpack communication in African wild dogs, we examined broad patterns of visits and scent-marking behaviour from data recorded at discrete locations in interpack boundary zones suspected (from direct observation during focal follows) and subsequently confirmed (by remote camera traps) to be marking sites shared by multiple packs of African wild dogs over multiple years. If interpack communication through scent marking is involved with territorial advertisement in African wild dogs, we would expect packs to visit these sites throughout the year (Creel & Creel, 2002). However, given that during the denning period a much smaller proportion of the annual range is used, we would also expect a reduction in visit rate to marking sites during this period. Additionally, if marking sites function solely for territorial advertisement, we would expect only resident territory-holding packs to scent-mark, as dispersing dogs do not have a territory to defend. Finally, after accounting for selection of these areas more generally, we would expect marking sites to be preferentially placed in locations that are easily discoverable by neighbouring packs and dispersing coalitions, for example along roads, which wild dogs use to commute (Abrahms et al., 2016), or in habitats that African wild dogs preferentially use, for example grasslands which wild dogs favour for hunting (Alting et al., 2021).

METHODS

Study Site and Population

Data for this study were collected over 2 years (January 2019 to December 2020) on free-ranging African wild dogs in the eastern edge of the Moremi Game Reserve at the southern terminus of the Okavango Delta in northern Botswana. The area spans approximately 2600 km² (roughly centred on 19°31'S, 23°37'E), and comprises floodplains, woodlands and mixed tree savannah. Annual rainfall in the area ranges from 300 to 800 mm, falling in the rainy season (November–March), out of phase with the annual flood waters from the Angolan highlands, which typically arrive in June. The area supports numerous mammal species, including 21 species of carnivore (Rich et al., 2016), is livestock free and is crossed by a

network of vehicle tracks used primarily by photographic safari vehicles (see McNutt, 1996 for more details).

This subpopulation of African wild dogs has been studied since 1989 as part of BPCs' long-term population monitoring, and 107 of the 121 individuals in this study are of known age and origin. Immigrant adult individuals were assumed to be unrelated to residents and were aged according to tooth wear and pelage. Each individual was identified via its unique tricolour coat pattern, unique tail stripes and ear notches. These distinguishing features were all drawn or photographed a few weeks after emergence from a den or immigration into the population. In this study, a pack was defined as a group containing at least one adult male and one adult female, while nonresident individuals or nonresident, single-sex groups were classed as a disperser or dispersing coalition, respectively. A temporary pack was a mixed-sex group ($N > 2$) of African wild dogs that did not remain together for longer than 30 days before fragmenting back into dispersing coalitions. The dominant pair within a pack can be identified by their tandem overmarking behaviour (Jordan et al., 2013), along with other behavioural attributes such as mating during the breeding period in April/May and mate guarding by the male during this same period. Outside the breeding season, the dominant pair tend to rest together during the day, they are usually the focus of social activity during rallies prior to pack movement, and they feed first on any kills, with the exception of young pups and the individual(s) that made the kill (Jordan et al., 2022).

Finding Marking Site Locations

One to three individuals within each pack ($N = 7$) were fitted with radiocollars using either AWT VHF collars (Africa Wildlife Tracking cc, Pretoria, South Africa; 250 g) or Vectronic VERTEX Lite satellite collars (Vectronic Aerospace GmbH, Berlin, Germany; 330 g) following procedures described by Osofsky et al. (1996). African wild dogs were located either using radiotracking from the ground, or GPS coordinates sent via satellite from the collar. Satellite fixes were usually sent at ca. 0900 LMT when dogs were likely to be resting, to allow time for researchers to reach and locate groups on the ground for direct observations. Behavioural observations were recorded on an Android device using a custom form on the Kobo Collect app (<https://www.kobotoolbox.org/>). Direct observations of African wild dogs were conducted from a vehicle at distances of 10–40 m while they were resting and 20–200 m while they were moving, depending on vegetation, terrain and visibility. Scent-marking behaviour was recorded directly onto the Android device on each observed occurrence, with scent marking referring to urinations (raised leg and squat posture), defecations and rub and rolling (see Jordan et al., 2013 for detailed description). Sniffing, or investigation, occurred when the muzzle was directed at the ground for longer than 3 s.

If a dominant pair was observed scent marking in a boundary zone between pack ranges and any other members of the pack were seen to be sniffing or marking there, the location of this site was recorded as a potential shared marking site (hereafter SMS). A boundary zone was loosely defined as an area where multiple packs were known to range, as determined by GPS collar location data or direct observations. Boundary zones were targeted for this study because direct communication between packs can only take place where packs overlap. Potential SMSs were equipped with a camera trap (either a Reconyx Ultrafire or a Browning Strikeforce ProXD) set to record 20–30 s videos after each trigger event. Camera traps were mounted on metal poles 1–1.5 m above the ground and angled so that the field of view covered as much of the area as possible. Cameras were housed in custom-built protective metal boxes to protect from damage by elephants and other animals. If

African wild dogs did not visit the site within 3 months, the camera trap was moved to an alternative potential location. If African wild dogs did visit and mark at the location within 3 months, an extra one to three camera traps were deployed to maximize coverage of the SMS. Revisits of African wild dogs to monitored locations was crucial in confirming their status as an SMS as the 'cryptic' latrines are invisible for most of the year (some presence of scat may be seen at the end of the dry season).

Some SMSs were located at spotted hyaena latrines, several of which had been previously identified (Vitale et al., 2020), and which are easily recognized by the accumulation of large white scats. This link with spotted hyaena latrines led to a secondary method of identifying potential SMSs: overlaying historical movement data from GPS collars with a hyaena latrine database for the study area. GPS fixes within 30 m of an historical hyaena latrine were considered. Hyaena latrines with more than three visits by African wild dogs were subsequently investigated as potential SMS locations using the camera-trapping methods described above. As above, potential SMSs were confirmed when they had multiple visits from multiple groups of African wild dogs. SMSs were located along the periphery of the focal Apoka pack's range and were predominantly visited by this pack and their neighbours.

Monitoring and data processing

Data were collected over 24 months (mean study days per SMS \pm SD = 531.6 ± 139.1 , range 730–257 days) from 35 camera traps at 22 SMSs which were checked every 7–10 days, when SD cards and batteries were checked and changed as necessary. Cameras that were occasionally knocked over by elephants and other wildlife were restored to their previous position on discovery. Video data were backed up, archived on a hard drive and processed, with any visits from African wild dogs extracted for further investigation. Videos containing other animals were classified (species, date and time noted) and archived. For videos of African wild dogs, the date, time, SMS location, camera number and group ID were all recorded in a spreadsheet, along with whether any of the visiting dogs in a group were seen to sniff or scent-mark, which were separately recorded as binary responses (1 = yes, 0 = no). On six occasions, no individual African wild dogs in a group could be identified from camera trap videos; these visits were disregarded from all subsequent analyses.

Statistical Analysis

Statistical tests were carried out in R version 4.1.1 (R Development Core team, 2021). To investigate temporal use of SMSs in the context of territoriality, only pack visits were considered for this first analysis, as packs had territories to maintain, whereas dispersers did not. A series of generalized linear mixed models (GLMMs) were run using the glmmTMB package in R (Brooks et al., 2017) with a binomial error distribution, using the number of visits per month (a count) as the dependent variable. Data were tested for overdispersion, zero inflation was accounted for, and an offset for the number of days monitored was applied to account for uneven monitoring periods between sites. We included 'group' identity (a categorical name), SMS 'location' (a categorical name) and 'year' as random terms. To further investigate temporal patterns in SMS use, data were split into two seasons, 'denning' or 'nondenning', corresponding to the 3-month annual denning season (June–August inclusive) when pups are born and provisioned at a fixed den site (McNutt et al., 2019). GLMMs were applied to these data, using the specifications above. We used Akaike's information criterion (AIC) to select the most plausible model from a set of credible options testing various error distributions; model averaging was not used as only one explanatory variable was tested.

Table 1

Generalized linear mixed-effect model with binomial distribution exploring the effect of month of the year on number of visits to shared marking sites (SMS) by African wild dogs

| Fixed term | Estimate | SE | z | CI (2.5, 97.5%) | P |
|-------------|----------|-------|---------|------------------|------------------|
| (Intercept) | -3.945 | 0.258 | -15.296 | (-4.450, -3.439) | <2e-16 |
| Feb | 0.244 | 0.254 | 0.961 | (-0.254, 0.743) | 0.336 |
| Mar | -0.018 | 0.266 | -0.066 | (-0.540, 0.505) | 0.947 |
| Apr | 0.290 | 0.269 | 1.079 | (-0.237, 0.817) | 0.281 |
| May | 0.356 | 0.273 | 1.304 | (-0.179, 0.890) | 0.192 |
| Jun | -0.588 | 0.375 | -1.571 | (-1.322, 0.145) | 0.116 |
| Jul | 0.016 | 0.311 | 0.051 | (-0.593, 0.625) | 0.959 |
| Aug | -0.161 | 0.293 | -0.550 | (-0.736, 0.413) | 0.582 |
| Sep | 0.374 | 0.255 | 1.465 | (-0.126, 0.874) | 0.143 |
| Oct | -0.013 | 0.272 | -0.047 | (-0.547, 0.521) | 0.963 |
| Nov | -0.154 | 0.276 | -0.559 | (-0.695, 0.386) | 0.576 |
| Dec | 0.202 | 0.242 | 0.833 | (-0.273, 0.676) | 0.405 |

Data comprised 482 visits by packs to 22 SMS. Zero inflation was accounted for, and an offset was included to control for days when camera traps were not functioning. We included 'group' identity (a categorical name), SMS 'location' (a categorical name) and 'year' as random terms to account for repeated measures. CI: confidence interval. Significant P value is shown in bold.

Akaike weights were calculated to show relative importance of these models (Akaike, 1974, p. 215).

To investigate whether visits by territory owners were more likely to include marking behaviour than visits by dispersing coalitions, we ran a series of GLMMs with a binomial error distribution (1 = scent marking occurred, 0 = no scent marking occurred). Temporary packs and unknown dogs were disregarded from this analysis. We included group status 'Status' (Pack or Disperser), the time since the previous visit 'timeLastVisit', the

status of the previous visitor 'statusPrevVisitor' (Pack or Disperser) and whether the previous visitor was the same or different to the current visitor 'prevVisitor', and all two-way interactions, as explanatory variables. We included 'group' ID, SMS 'location' and 'year' as random terms. We used AIC to select the most plausible model from a set of credible options including all combinations of the likely terms and their two-way interactions. Group size was disregarded from the analysis as it was highly correlated with status of visitor (correlation coefficient = 0.69). As the Akaike weight of the best model was <0.09 (Grueber et al., 2011), model averaging was conducted using the MuMin package in R (Bartoń, 2020), again using an AIC deviance of <2 units (Burnham & Anderson, 2004).

To investigate the environmental factors that may underpin SMS location, we ran a resource selection function (RSF) using the 22 SMS locations compared to 220 random points generated from focal follow data sessions with the core study pack and their neighbours using the amt package in R (Manly et al., 2002; Signer et al., 2019). The RSF compares 'used' (SMS) versus 'available' (random points) locations to determine relative probability of use of environmental features, thereby revealing selection for SMS locations. To generate random points that accurately represented available locations for potential SMS locations and controlled for any bias in detection likelihood by observers, random points were selected from the GPS data of 355 h of observational follows of packs from vehicles covering 282 km. GPS locations where changes in collective behavioural states occurred (i.e. changes from resting, walking, hunting, eating, etc) were recorded during follows, and these locations were interpolated by generating intervening waypoints each minute between them. In this way, the

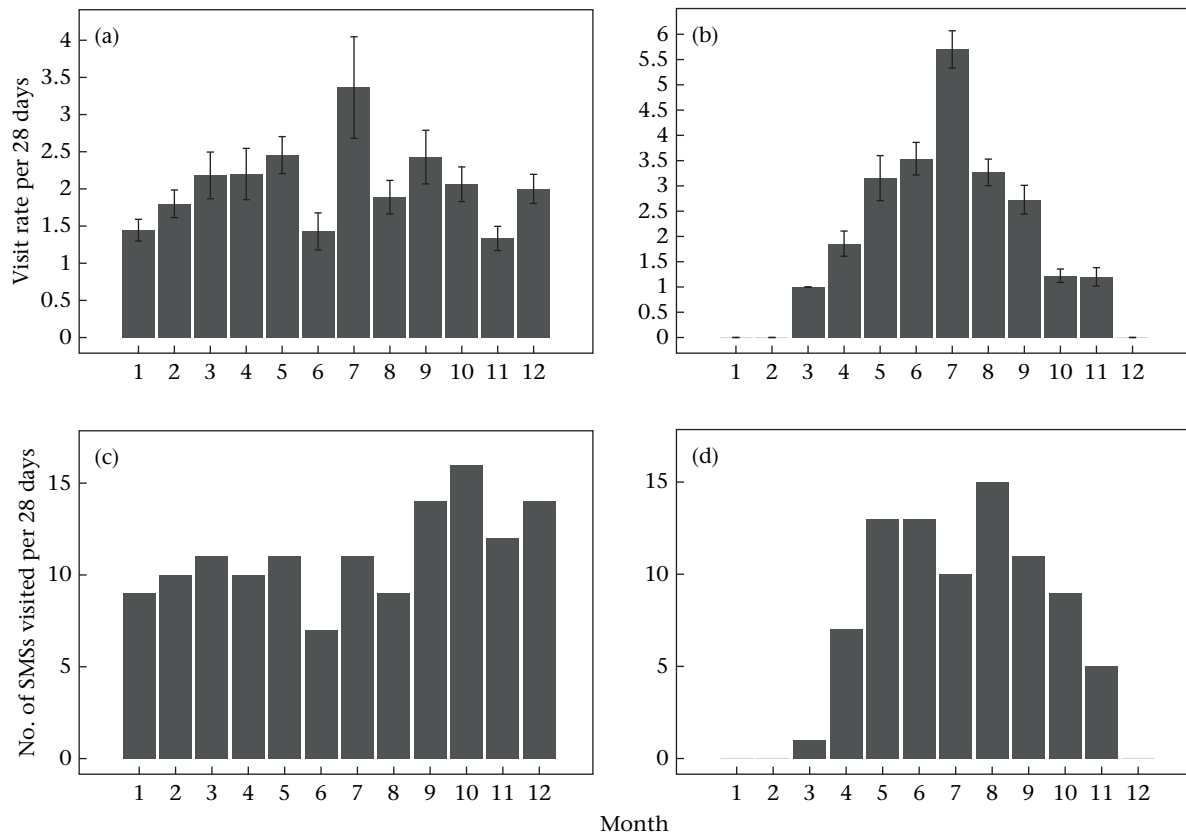


Figure 1. Mean number of visits to shared marking sites (SMSs) each month by (a) the Apoka focal pack and (b) dispersers compared to the number of discrete shared marking sites (SMSs) visited by (c) the Apoka pack and (d) dispersers, each month. Error bars represent SEs. Data comprise 286 visits to 22 sites by the Apoka pack and 284 visits to 20 of these same sites by dispersers. Rates are standardized to 28 days to account for different month length throughout the year. Data from the Apoka pack only are presented here for visualization, as other packs have SMSs monitored over only a limited part of their ranges.

Table 2

Generalized linear mixed-effect model with binomial distribution exploring the effects of season on number of visits by African wild dogs to shared marking sites

| Fixed term | Estimate | SE | z | CI (2.5, 97.5%) | Pr (> z) |
|------------------|----------|-------|---------|------------------|------------------|
| (Intercept) | -4.168 | 0.235 | -17.764 | (-4.628, -3.708) | <2e-16 |
| SeasonNONDENNING | 0.363 | 0.160 | 2.264 | (0.049, 0.677) | 0.024 |

Data comprised 482 visits by packs to 22 SMS. Zero inflation was accounted for, and an offset was applied to control for days when camera traps were not functioning. We included 'group' identity (a categorical name), SMS 'location' (a categorical name) and 'year' as random terms to account for repeated measures. CI: confidence interval. Significant *P* values are shown in bold.

amount of time spent in different habitats, and on or off road, was sampled. Random points were selected from these waypoints (actual and interpolated). Environmental covariates tested between used and available points included distance to roads, distance to pans, distance to water (permanent), elevation (Reuter et al., 2007) and distance to different habitat types (grassland, floodplain, mixed species and mopane woodland; Bennitt et al., 2014). All environmental data were transformed from a presence/absence raster layer to a proximity to nearest feature layer and resampled to a 20 m resolution where necessary. Road data were accumulated from GPS tracks of BPC researchers using roads in the study area, and pan locations were aggregated from recorded BPC researcher locations of pans, buffered by 100 m, and rasterized to a 20 m resolution proximity layer. Coefficients were tested for correlation to ensure that no model included covariates with $|r| > 0.6$ (Hinkle et al., 2003), and then were standardized. We used a stepwise model selection process to determine which covariates significantly predicted selection for an SMS location and compared AIC scores to select the final model. To assess model performance, we performed a bootstrapping procedure whereby we selected randomly from our data set with replacement and reran our final model 1000 times. We then visually investigated the beta values for our model covariates as well as their *P* values to evaluate how often our terms were significant in predicting relative SMS site selection, as well as the trends in their relative selection strength.

Ethical Note

Ethics approval for this study was provided by UNSW Animal Ethics Committee (Approval number: 20/166B; application title: Large carnivore ecology and conservation research (Botswana);

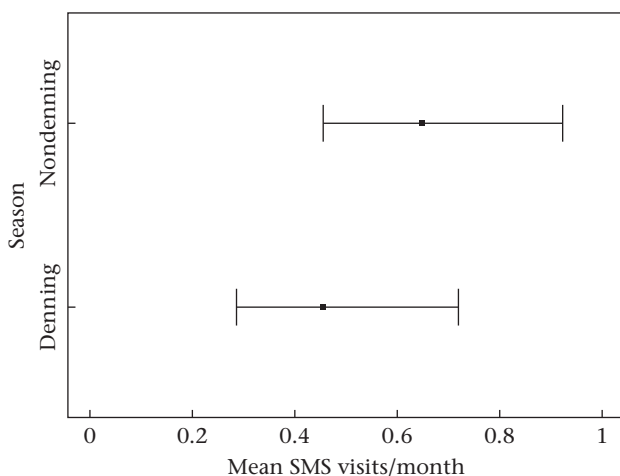


Figure 2. Estimates of mean monthly visits to shared marking sites (SMSs) by packs of African wild dogs in non-denning and denning seasons. Estimates are back-transformed means. The whiskers delineate the 95% confidence intervals derived from a generalized linear mixed model accounting for zero inflation using data from 482 visits by packs to 22 sites.

Chief Investigator: Dr Neil Jordan). This study used an already established study population of African wild dogs monitored and maintained by BPC; no specific animals were collared for this study. Any collared animals had previously been collared by a Botswana registered wildlife veterinarian following procedures described by Osofsky et al. (1996). African wild dogs weigh on average 22 kg, so collars weighed approximately 1.1–1.5% of an adult's body weight. This population of African wild dogs has been collared in this way since 1989; there have never been any noticeable impediments to any collared individuals' locomotion or general welfare.

Camera traps were used to monitor scent mark site locations using methods described above and were set to record night-time videos using infrared to minimize disturbance to any animals. No disturbance was recorded among African wild dogs, with camera traps being chiefly ignored (any investigation was by curious young individuals).

Regarding behavioural observations, all individuals are habituated to vehicles and every care was given to minimize the disturbance to any individuals that were present during a data session by maintaining a respectful distance.

RESULTS

A total of 22 SMSs were identified and monitored for this study, 55% ($N = 12$) of which were at spotted hyaena latrines. Over 24 months, African wild dogs visited these SMSs 782 times. A total of 38 identifiable groups visited the sites; 34% of the groups that visited were packs ($N = 13$ packs), 21% of the groups that visited were temporary packs ($N = 8$) and 45% of the groups that visited were dispersing coalitions ($N = 17$). Each site was visited by 7 ± 3.6 groups of African wild dogs (range 2–16 groups visiting a site). Owing to their unstable nature, temporary packs were also disregarded from subsequent analyses in this paper. Accordingly, 63% of the remaining 766 visits to SMSs were by packs, while the remaining 37% of visits were by dispersers. Scent marking occurred on 73% of all included visits to SMSs ($N = 556$), 78% of visits by packs and 63% of visits by dispersers. Sniffing occurred on 91% of all visits ($N = 698$) and 91% of both pack and disperser visits.

There was no effect of month on the 482 visits to SMSs by resident packs of African wild dogs, indicating that dogs visit SMSs throughout the year (Table 1, Fig. 1). Visits to individual sites were infrequent and sporadic yet visits to all sites collectively ensured a continued visit rate throughout the year. However, African wild dogs visited SMSs significantly less during the denning season (Table 2, Fig. 2). Of the 482 visits by packs, 59% ($N = 286$) of the visits were by the focal pack Apoka, with the remaining 41% ($N = 196$) of visits by other packs.

Across 2019 and 2020, Apoka visited all 22 sites, with each site visited 13 ± 10.86 (SD) times (range 1–43 visits per site). Apoka visited 11.40 ± 2.64 (SD) sites each month (range 7–16 sites/month). The lowest number of visits (7) occurred in June and the highest (16) in October.

All other packs visited 21 sites, with each site visited 9.3 ± 5.3 (SD) times (range 0–19 visits per site). Other packs visited

Table 3
Generalized linear mixed-effect model exploring how the likelihood of marking (1 = mark, 0 = no mark) in African wild dogs at shared marking sites may be affected by various factors

| Model | Fixed terms | | | | | | | | | | | df | logLik | AICc | Delta | Weight | Deviance | Dispersion |
|-------|-------------|-----|-----|-----|-------|-----|-----|-----|-----|-----|-----|----|----------|---------|-------|--------|----------|------------|
| | (Intercept) | (a) | (b) | (c) | (d) | (e) | (f) | (g) | (h) | (i) | (j) | | | | | | | |
| 1 | 0.762 | + | + | + | | | | | | | | 6 | -404.795 | 821.704 | 0.000 | 0.047 | 809.6 | 1.013 |
| 2 | 0.725 | + | + | + | | | | | | | + | 7 | -403.830 | 821.812 | 0.107 | 0.045 | 807.7 | 1.012 |
| 3 | 0.830 | + | + | | | | | | | | | 6 | -404.958 | 822.030 | 0.326 | 0.040 | 809.9 | 1.014 |
| 4 | 0.617 | + | + | | | | + | | | | | 5 | -406.026 | 822.134 | 0.429 | 0.038 | 812.1 | 1.015 |
| 5 | 0.859 | + | + | + | | | + | | | | + | 8 | -403.089 | 822.374 | 0.670 | 0.034 | 806.2 | 1.012 |
| 6 | 0.859 | + | + | + | | | + | | | | + | 8 | -403.089 | 822.374 | 0.670 | 0.034 | 806.2 | 1.012 |
| 7 | 0.859 | + | + | + | | | | | | | + | 8 | -403.089 | 822.374 | 0.670 | 0.034 | 806.2 | 1.012 |
| 8 | 0.687 | + | + | + | -0.18 | | | | + | + | | 9 | -402.438 | 823.122 | 1.418 | 0.023 | 804.9 | 1.012 |
| 9 | 0.594 | + | + | | -0.18 | | | | | + | | 7 | -404.538 | 823.228 | 1.524 | 0.022 | 809.1 | 1.014 |
| 10 | 0.729 | + | + | + | -0.17 | | | | | + | | 8 | -403.518 | 823.232 | 1.528 | 0.022 | 807.0 | 1.013 |
| 11 | 0.829 | + | + | + | | | + | | | | | 7 | -404.622 | 823.397 | 1.693 | 0.020 | 809.2 | 1.013 |
| 12 | 0.829 | + | + | + | | | + | | | | | 7 | -404.622 | 823.397 | 1.693 | 0.020 | 809.2 | 1.013 |
| 13 | 0.829 | + | + | + | | | | | | + | | 7 | -404.622 | 823.397 | 1.693 | 0.020 | 809.2 | 1.013 |
| 14 | 0.607 | + | + | + | -0.47 | | | | + | | + | 10 | -401.550 | 823.400 | 1.696 | 0.020 | 804.9 | 1.012 |
| 15 | 1.042 | + | | | | | | | | | | 4 | -407.809 | 823.672 | 1.968 | 0.018 | 815.6 | 1.014 |

Factors are (a) identity of previous visitor (PrevVisitor), (b) the status of the current visitor (Status), (c) the status of the previous visitor (StatusPrevVisitor), (d) the time since a previous visit (Time PrevVisit), and all two-way interactions; (e) prevVisitor*Status; (f) prevVisitor*statusPrevVisitor; (g) prevVisitor*timeLastVisit; (h) Status*statusPrevVisitor; (i) Status*timeLastVisit; (j) statusPrevVisitor*timeLastVisit. Data comprise 766 visits by packs and dispersers to 22 SMS. AICc compares models with equivalent data, and models with AICc<2 (15/113 models run) were included in model-averaging estimates (Table 4). Location and Group were included as random terms to account for repeated measures.

8.92 ± 4.68 (SD) sites each month (for visited sites range 2–16 sites/month). The lowest number of visits (2) occurred in June and July and the highest (16) in February and December. These trends must be considered with caution as SMSs were monitored over a limited part of their ranges only.

Twenty sites were visited by dispersers, with each site visited 14.20 ± 12.78 (SD) times over the study period (range 0–49 visits per site). Of these, dispersers were detected at 9.89 ± 4.59 (SD) sites each month (for visited sites range 1–16 sites/month). Dispersers were not detected at all at SMSs between December and February inclusive.

We found that the type of group (pack or disperser) did not predict which individuals were more likely to mark at SMSs (Tables 3, 4), although there was a nonsignificant trend towards increased marking by packs. There was a nonsignificant trend of an increased likelihood of African wild dogs' scent marking at an SMS if they were the previous visitor, although the confidence intervals encompass zero.

The RSF analysis revealed that proximity to roads, grassland and water were significant environmental covariates when African wild dogs selected SMS locations (Table 5, Fig. 3). SMSs were more likely to occur closer to roads, while both grassland and locations close to water features were avoided. Of the 22 SMSs, 17 were situated on a road, where scent marks were regularly found on or within 1 m of a road. All other environmental covariates were not significant in

SMS selection. The distribution of bootstrapped beta values and *P* values (Fig. 4.) demonstrates that there was consistent negative selection for proximity to roads in predicting relative selection for African wild dog SMSs, and that this term was predominantly statistically significant. While the positive selection for proximity to water was close to zero, the distribution of *P* values shows that this selection was consistently statistically significant as well. Selection for proximity to grasslands was noisier: while there was generally strong positive selection for proximity to grassland, the distribution of *P* values for this covariate overlapped widely with 0.05, which implies that we should evaluate this term with caution. Note that negative beta values for proximity terms imply that the animal prefers values closer to 0 (e.g. selection), and therefore positive beta values for proximity terms imply avoidance.

DISCUSSION

Here we provide the first quantitative assessment of African wild dogs' latrine use, a behaviour exhibited by many other carnivores, and we show that these sites are visited by multiple groups, including established territorial packs and dispersing coalitions. Sites were visited throughout the year, including during the annual denning season when African wild dogs' ranges can contract to 27% of their nondenning range (Pomilia et al., 2015), although visits were significantly lower during this time. Spatially, and after taking

Table 4
Model-averaged results of a generalized linear mixed-effect model with binomial distribution of the factors that may impact the likelihood of a pack of African wild dogs marking (1) or not (0) at a shared marking site

| Fixed term | Estimate | SE | z | CI (2.5, 97.5%) | Pr (> z) |
|--|----------|-------|-------|-----------------|--------------|
| (Intercept) | 0.898 | 0.454 | 1.974 | 0.006, 1.790 | 0.048 |
| prevVisitorDIFFERENT | -0.710 | 0.382 | 1.857 | -1.460, 0.039 | 0.063 |
| statusPrevVisitorPack | -0.069 | 0.384 | 0.181 | -0.822, 0.683 | 0.856 |
| StatusPack*statusPrevVisitorPack | 0.172 | 0.375 | 0.459 | -0.563, 0.907 | 0.646 |
| prevVisitorDIFFERENT*StatusPack | -0.339 | 0.554 | 0.610 | -1.426, 0.749 | 0.542 |
| prevVisitorDIFFERENT*statusPrevVisitorPack | 0.058 | 0.244 | 0.239 | -0.419, 0.536 | 0.811 |
| timeLastVisit | -0.041 | 0.130 | 0.318 | -0.296, 0.213 | 0.751 |
| prevVisitorDIFFERENT*timeLastVisit | 0.059 | 0.147 | 0.399 | -0.229, 0.347 | 0.690 |
| statusPrevVisitorPack*timeLastVisit | 0.014 | 0.082 | 0.174 | -0.146, 0.174 | 0.862 |

Model-averaged outputs are from all models presented in Table 3 with delta AICc<2. Data comprise 766 visits by packs and dispersers to 22 shared marking sites. CI: confidence interval. Significant *P* value is in bold.

Table 5
Logistic regression results of the resource selection function of shared marking site selection by African wild dogs

| Explanatory variable | Model | | | | |
|--------------------------------|--------------------------------|---------------------------------|---------------------------------|---------------------------------|---------------------------------|
| | (1) | (2) | (3) | (4) | (5) |
| Proximity to roads | -96.907*** (-155.980, -37.833) | -102.107*** (-163.544, -40.671) | -106.437*** (-167.382, -45.492) | -114.935*** (-180.356, -49.515) | -114.900*** (-180.071, -49.729) |
| Proximity to pans | | 17.325 (-7.069, 41.718) | 29.881 (-1.085, 60.846) | 30.695 (-2.501, 63.892) | 31.383 (-2.143, 64.910) |
| Digital elevation | | | | | -1.063 (-8.625, 6.500) |
| Digital elevation ² | | | | | 0.077 (-6.865, 7.020) |
| Proximity to water | 0.593*** (0.227, 0.959) | 0.550** (0.174, 0.926) | 0.764** (0.261, 1.268) | 0.926*** (0.344, 1.509) | 0.948** (0.340, 1.556) |
| Proximity to grassland | 344.822*** (129.927, 599.673) | 357.934*** (141.937, 573.896) | 385.612*** (156.155, 615.070) | 382.564*** (148.790, 616.338) | 396.745** (135.770, 657.720) |
| Proximity to mixed species | | | | 5.239 (-55.877, 66.355) | 3.468 (-58.818, 65.753) |
| Proximity to mopane | | | | -36.699 (-90.542, 17.145) | -35.990 (-90.228, 18.249) |
| Proximity to floodplain | | | -5.894 (-14.846, 3.057) | -9.107 (-19.464, 1.250) | -9.659 (-20.750, 1.432) |
| Constant | -1.906*** (-2.455, -1.358) | -2.129*** (-2.781, -1.477) | -1.774*** (-2.619, -0.928) | -1.185 (-2.393, 0.023) | -1.159 (-2.381, 0.063) |
| Observations | 242 | 242 | 242 | 242 | 242 |
| Log likelihood | -62.068 | -61.418 | -60.815 | -59.857 | -59.830 |
| AIC | 132.136 | 132.835 | 133.629 | 135.714 | 139.660 |

Table showing model estimates (beta values) and their 95% confidence intervals (in parentheses) for the models run (1–5). The resource selection function was performed using 22 shared marking site locations 'used' compared to 220 randomly generated points from focal follow data 'available'. Explanatory variables include proximity to roads, proximity to pans, digital elevation, proximity to water, and proximity to four main habitat types in our study area: grassland, floodplains, mixed species and mopane. Each model is ranked based on AICc values; the model with the lowest AICc value was selected.
* $P < 0.1$; ** $P < 0.05$; *** $P < 0.01$.

preferences for these features during general movements into account, SMSs were preferentially placed close to roads (unsealed vehicle tracks) and away from grasslands and water. These results are based largely on one core pack of African wild dogs visiting a small sample of SMSs; any inferences are therefore limited.

The large annual ranges of African wild dogs make interpack communication both challenging and energetically costly. Direct encounters between neighbouring packs occur only occasionally (approximately once every 6 months, Jordan et al., 2017), and unlike other canids (e.g. dingoes and wolves; Déaux & Clarke, 2013; Harrington et al., 1978) long-distance calls are not exhibited in this species (Webster et al., 2010), so communication with neighbours must occur by other means. It has long been speculated that chemical signalling via scent marking is the mechanism by which packs communicate, with mounting evidence in support (see Chisholm et al., 2019; Jackson et al., 2012; Jordan et al., 2013). Scent marking at specific sites like latrines is an effective way for individuals or groups to communicate with conspecifics from neighbouring territories, and the use of latrines for this purpose is documented in many mammals (Brown & Macdonald, 1985). Given their ecology, latrine use is to be expected in African wild dogs, and has been noted (Apps et al., 2022), but before now neither their behavioural use nor spatial characteristics have been quantified, despite intensive focus on their scent communication (Jordan et al., 2013, 2014; Parker, 2010; Tshimologo, 2014). Here we provide the first study focusing on African wild dogs' use of multiple latrines (SMSs), by multiple packs, over multiple years, and we suggest that communication between groups occurs via scent marking.

The function of latrine use is poorly understood, but two of the more supported theories suggest they function as a mechanism for territorial advertisement or as an information centre (Buesching & Jordan, in press). While these two functions are distinct, they are not mutually exclusive, and investigating temporal and spatial patterns may give insights into specific latrine functions (Buesching & Jordan, 2019). Resident packs of African wild dogs visited latrines throughout the year, supporting the theory that latrine function may be linked to territorial advertisement. If territorial advertisement were not a function of visits to SMSs, upkeep of visits and maintenance of territorial signals throughout the year would not be a priority, especially when resources are being diverted from alternative purposes. Visit rate during the annual denning period is significantly reduced, yet still occurs, indicating that territory maintenance is important to African wild dogs even when the primary energetic goals of this period are geared towards successful raising of offspring (Creel & Creel, 2002), and ranging retreats drastically into approximately a quarter of the annual range (Pomilia et al., 2015). For the core pack, for which we have the most complete picture of SMS use throughout a year, the lowest number of sites visited in a month occurred in June, while the most sites visited in 1 month occurred in October. This dip during the denning season, and subsequent peak after denning is consistent with the findings of Pomilia et al. (2015); packs are constrained during the denning season, but once they are free from the den packs utilize the full extent of their annual range and re-establish their territorial boundaries and replenish scent marks at SMSs.

Visits to an SMS alone does not indicate communication; scent marking (transmitting information) and subsequent sniffing (receiving information) are required for communication to occur. In common with previous studies of scent marking in this (Jordan et al., 2014) and other species (e.g. European badgers, *Meles meles*, Stewart et al., 2002; coyotes, Gese & Ruff, 1997; red foxes, *Vulpes vulpes*, Henry, 1977) we distinguished between these behaviours in this study, and found that sniffing occurred at almost all visits to SMSs by all groups of African wild dogs, while marking occurred at only close to three-quarters of visits. Visits to SMSs

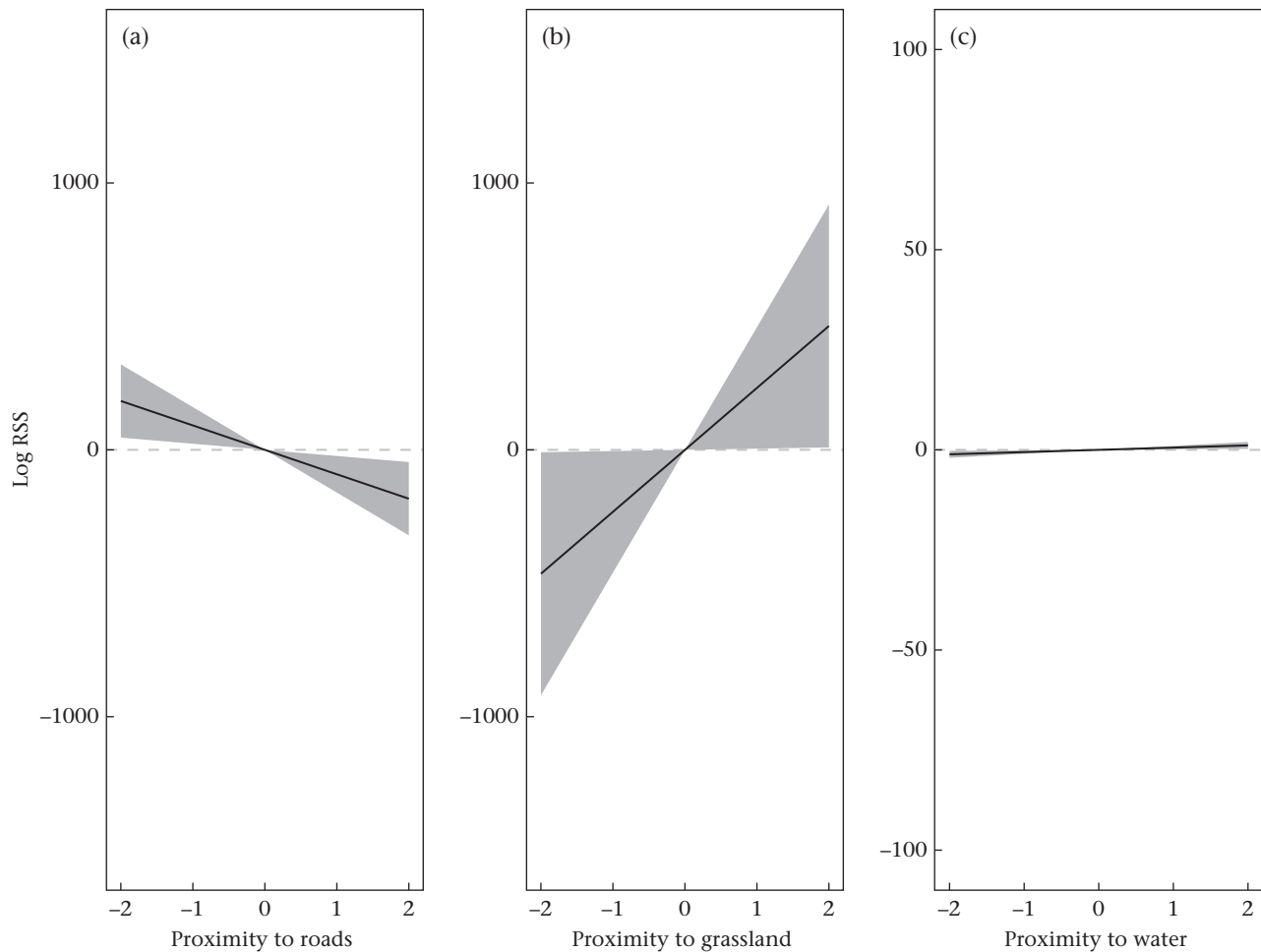


Figure 3. Log relative selection strength (RSS, natural logarithm; Avgar et al., 2017) for the environmental covariates of proximity to (a) roads, (b) grassland and (c) water, with 95% confidence interval in grey. RSSs were calculated by comparing selection scores of two different spatial locations that differed only in the covariate depicted on the x-axis.

were not restricted to resident (territory-holding) packs; dispersing coalitions of dogs also visited these marking sites. We found a weak tendency for groups of African wild dogs to be more likely to mark if they were the most recent previous visitor. This may indicate that some packs may be visiting SMSs only to receive information and may be more reluctant to transmit information if a neighbouring pack has previously marked. Alternatively, marking itself may stimulate remarking at an SMS, which may operate as positive feedback to help ensure adequate territorial marking, a behaviour seen in both grey wolves (Peters & Mech, 1975) and Ethiopian wolves (Sillero-Zubiri & Macdonald, 1998), although these conclusions should be considered with caution as the trend was nonsignificant.

Contrary to what one should expect if the function of SMS was purely territorial, during visits to SMSs both resident packs and dispersing coalitions investigated locations through sniffing, and they both deposited scent through marking. Despite packs marking on more visits than dispersers (78% of visits compared to 63% of visits, respectively), the likelihood of packs marking more than dispersers was nonsignificant. While communication by resident packs at SMSs indicates a role of territorial advertisement in latrine function, marking by dispersing coalitions would be unnecessary if this were the sole function of the marking sites. Our findings instead suggest that SMSs may be multifunctional; they may be a hotspot for information transfer and, potentially, allow reproductive advertisement alongside a likely core role in territorial

advertisement and maintenance. SMSs are unlikely to be used for navigation by dispersers; marking sites are found throughout African wild dog ranges and we have no evidence that dispersing individuals respect territory boundaries as other species do, such as Ethiopian wolves and red foxes, where floaters tend to inhabit gaps between territorial boundaries (Dekker et al., 2001; Sillero-Zubiri & Gottelli, 1995). Multifunctionality of latrines is not uncommon (Buesching & Jordan, in press), and is seen in European badgers (Stewart et al., 2002), honey badgers, *Mellivora capensis* (Begg et al., 2003), Ethiopian wolves (Sillero-Zubiri & Macdonald, 1998) and meerkats (Jordan et al., 2007).

Regardless of specific latrine function, it is clear that for inter-pack communication to occur, latrines need to be found by multiple groups. Our data showed that, even after controlling for bias in detection likelihood by observers, African wild dog SMSs were more likely to be situated closer to roads. As African wild dogs are more likely to select roads when travelling (Abrahms et al., 2016), this spatial placement pattern may aid in SMS discovery by conspecifics. This behaviour may also help explain site selection; it is intuitive that as dogs select roads when travelling, they would scent mark to demarcate their territories close to where they travel. Over half of the confirmed African wild dog SMSs were at known spotted hyaena latrines. While the high percentage of detected SMSs at hyaena latrines in our reported sample is likely to be related to that fact that one of our SMS detection methods was to monitor hyaena latrines specifically, the incidences of heterospecific use are still

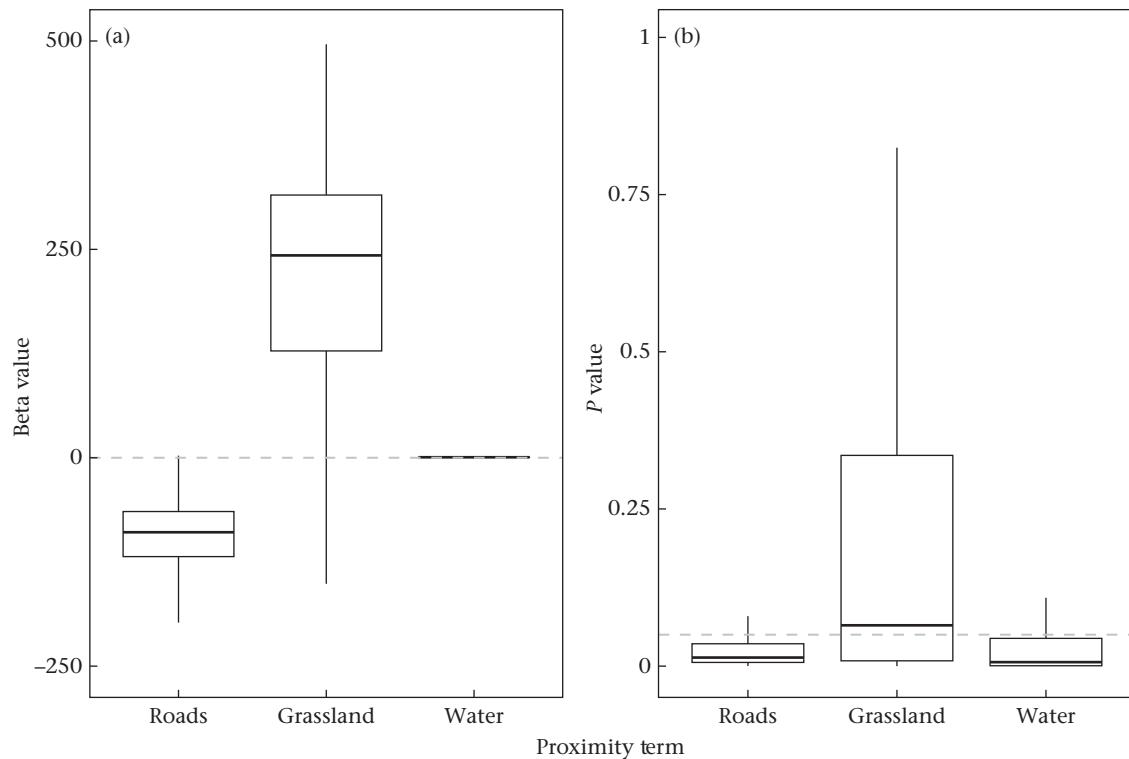


Figure 4. Box plot of the bootstrapped (a) beta values and (b) *P* values for environmental covariates of proximity to roads, grassland and water. The thick horizontal line indicates the median, the box edges depict the first and third quartiles, and the whiskers delineate the minimum and maximum of the bootstrapped values. Dashed horizontal lines depict a beta value of zero and a *P* value of 0.05, respectively.

considerable and warrant further investigation. For example, are the same sites selected independently by each species following similar criteria, or does one species begin using these sites in response to the other species' scents? Regardless of the mechanism of site selection, it is unusual that African wild dogs would select areas of potentially high-risk encounters with hyaenas, given the evidence of competition and spatial avoidance seen at multiple sites (e.g. Creel & Creel, 1996; Vanak et al., 2013). As it has been shown that spotted hyaena latrines in the landscape are also more likely to occur on roads (Vitale et al., 2020), the selection of road sites for marking is therefore unsurprising; many large carnivore species have been shown to use roads when travelling (Kautz et al., 2021; Whittington et al., 2005), and even adapt their marking strategies to favour scent marking along them, including three species at the study site (African wild dogs, this study; spotted hyaena, Vitale et al., 2020; leopards, *Panthera pardus*, Rafiq et al., 2020). Indeed, marking at roads, trails and junctions is a common strategy employed by carnivores in general (e.g. wolves, Barja et al., 2004).

SMS placement demonstrated strong selection away from grassland areas and weak selection away from water. Despite preferring to hunt in grassland areas (Alting et al., 2021; Fuller & Kat, 1990) African wild dogs may be choosing to avoid this habitat as a location for their communication as a means to avoid lions, which preferentially select grassland habitat in northern Botswana (Cozzi et al., 2013). Lions have been shown to have higher activity levels in prey-rich areas (Vanak et al., 2013), including in proximity to water (Grant et al., 2005). Avoidance of lions may be the underlying factor driving selection away from SMSs being positioned close to water and the associated floodplain habitat, which also supports higher lion densities than other habitat types (Cozzi et al., 2013). Lions account for 10% of known adult African wild dog mortality and 50% of pup mortality (R. Woodroffe &

Ginsberg, 1999). This high selection pressure (Groom et al., 2017) has been suggested to impact African wild dog populations more than other environmental variables, such as habitat, prey availability and other predator densities (Darnell et al., 2014; Mills & Gorman, 1997). Avoidance of lions has been attributed to other aspects of African wild dog ecology, such as their crepuscular activity (Hayward & Slotow, 2009; Saleni et al., 2007) and their wide-ranging behaviour (Creel & Creel, 2002). It would be unsurprising if avoidance of lions plays a role in the spatial distribution of SMSs, a discrete location to which African wild dogs repeatedly return to communicate with conspecifics. Alternatively, African wild dogs may avoid grassland areas due to limited visibility, while areas close to water may flood and wash chemical signals away.

Parker (2010) showed that African wild dogs employ a 'scent cloud' marking strategy as opposed to a 'scent fence' strategy, and scent-mark throughout their territory. Supporting this, Tshimologo (2014) showed that more marking occurred in the core of a range than in the intermediate and edge zones. Given this, it is likely that latrines may be found throughout the ranges of African wild dogs, not just along the border zones as we demonstrate here, evidence for which has been seen in our study area (M.J. Claase, personal observation). Similar marking strategies are seen in both brown and spotted hyaena in the Kalahari, where both species have large ranges and scent-mark at latrines throughout (Gorman & Mills, 1984; Mills et al., 1980; Mills & Gorman, 1987). This 'hinterland' or cloud scent-marking strategy is thought to be more energetically viable than the scent fence strategy in some circumstances, maintenance of which may be uneconomical when territories are large. In the Okavango Delta study area, territories are large (Pomilia et al., 2015), and a hinterland marking strategy may also be the most economical approach. Future research should focus on monitoring latrines both within the core and in the boundary zones of African wild dog territories for interpack visits, which would provide

important information on the optimal strategy for intercepting intruders in this wide-ranging species.

Understanding how communication between packs influences African wild dog territoriality can have direct conservation implications. One such conservation initiative is the BioBoundary project, which aims to deter carnivores from leaving protected areas by managing ranging behaviour through artificial scent marks (Jackson et al., 2012). Detailed RSF analysis could be used to inform placement of artificial scent marks along range peripheries, enabling specific areas to be targeted where African wild dogs are more likely to encounter scent. To further understand how SMS use may facilitate the development of a BioBoundary, a detailed study of individual patterns of SMS usage should be conducted.

Author Contributions

Megan J. Claase: Conceptualization, Methodology, Software, Formal analysis, Investigation, Data curation, Writing – original draft. **Michael I. Cherry:** Writing – review and editing, Supervision. **Peter J. Apps:** Writing – review and editing, Supervision, Project administration. **John W. McNutt:** Writing – review and editing, Project administration, Funding acquisition. **K. Whitney Hansen:** Software, Formal analysis, Writing – review and editing, Visualization. **Neil R. Jordan:** Software, Validation, Data curation, Writing – review and editing, Visualization, Supervision.

Data Availability

The data sets generated during and/or analysed during the current study are not publicly available as they contain potentially sensitive information on the long-term shared marking site locations of an endangered species. Data are available from the corresponding author on reasonable request.

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