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ORIGINAL RESEARCH

Temporal overlap in use of shared latrines by brown hyena and spotted hyena

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Keywords

latrine use; scent marking; interspecific competition; temporal partitioning; camera trap; spotted hyena; brown hyena; carnivores.

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Abstract

Scent marking at latrines is used by a variety of mammals for communicating an individual's reproductive status, social rank, or territory. Both brown hyenas (*Parahyaena brunnea*) and spotted hyenas (*Crocuta crocuta*) make use of latrines. Previous research showed that the presence of the more dominant spotted hyena negatively affects the presence of brown hyena. As both species rarely occur in the same area, little is known about the temporal patterns of using shared latrine sites. Central Tuli, Botswana, is home to one of the highest densities of both spotted and brown hyena in southern Africa. We conducted a camera trap study and monthly scat counts for monitoring the visitation and defecation rates of brown and spotted hyenas at shared latrines to examine the temporal patterns of latrine use. Our results showed seasonal differences in latrine use, with lower visitation and defecation rates for both species during the wet season. We found high temporal overlap in latrine use for the two species. However, the time interval between consecutive spotted – brown hyena visits was larger than for consecutive brown hyena–spotted hyena and consecutive conspecific visits during the dry season, suggesting that brown hyena seem to show fine-scale temporal avoidance of spotted hyenas at shared latrine sites. The presence of spotted hyenas, or other large carnivores, could possibly inhibit intraspecific communication for brown hyena at shared latrine sites.

Introduction

Scent marking is part of the olfactory communication that is widespread among mammal species (Bradbury & Vehrencamp, 1998; Gorman & Trowbridge, 1989). Scent marks can be used for sharing information on an individual's reproductive status, social rank, or territory (Dröscher & Kappeler, 2014; Gorman & Trowbridge, 1989; Jordan et al., 2007; King et al., 2017). Sites where scent marks, such as faeces, urine, or glandular secretions, are repeatedly deposited by conspecifics (Gorman & Trowbridge, 1989) or sympatric species (Apps et al., 2019) are known as latrines. Latrines are used by several mammals, such as European badgers *Meles meles* (Roper et al., 1993), small spotted genets *Genetta genetta* (Espírito-Santo et al., 2007), lemur species such as the eastern lesser bamboo lemur *Hapalemur griseus* (Irwin et al., 2004) and different hyena species *Hyaenidae* (Mills, 1989). The temporal variability and the spatial distribution of latrine use can be related to the function of the latrines. Temporal variability of latrine use is caused by short-term or seasonal changes, for example, by breeding behaviour, changes in food availability, or abiotic environmental conditions (Rosell, 2001). The spatial distribution of latrines can give information on different scent-marking strategies, such as core marking or border marking, which depend on territory size (Gorman & Mills, 1984).

While research on the role of olfactory communication has mainly focused on intraspecific communication, it is thought that latrines also play a role in interspecific communication (Apps et al., 2019; King et al., 2017). Olfactory communication between members of different species can influence ecological processes such as intraguild competition (Apps et al., 2019), because faecal odours remain in the environment for a long period of time and indicate the presence of potential predators or competitors at some point in time (Hughes et al., 2012). Intraguild competition can result in spatial or temporal partitioning of space use. Dominant predators select favourable spatial or temporal niches, while subordinate species must balance the trade-off between resource acquisition and the costs of increased competition (De Satgé et al., 2017; Dröge et al., 2017; Heithaus, 2001; Périquet et al., 2015). For the subordinate species to avoid dominant predators in time or space, the subordinate species needs to be able to detect the presence of dominant species. Besides making use of olfactory cues for detecting predators or competitors (Apfelbach et al., 2005; Jones et al., 2016), animals can also make use of visual cues and auditory cues (Hughes et al., 2012), which indicate a more immediate risk.

A broader understanding of the spatial and temporal use of shared latrines improves the understanding of latrine functions and their possible role in interspecific interactions. The aim of this study was to investigate the temporal patterns of shared latrine use for brown hyenas (*Parahyaena brunnea*) and spotted hyenas (*Crocuta crocuta*). Like all species in the *Hyaenidae* family, spotted hyena and brown hyenause latrines when defecating (Gorman & Mills, 1984), and both species may use the latrine sites for intraspecific communication. With scavenging being an important part of the dietary intake of the brown hyenas (Mills & Maude, 2005), they are thought to compete with spotted hyenas as both species exploit shared resources (Mills, 1984). The more dominant spotted hyena can pose a competitive threat to the brown hyena through kleptoparasitism or predation (Mills, 1990). The presence of spotted hyena can, therefore, negatively impact the presence of brown hyena (Mills, 1984; Mills & Funston, 2003; Williams et al., 2020). The brown hyena, however, can also benefit from scavenging opportunities when larger carnivores such as spotted hyenas are present (Mills, 1990; Stein et al., 2013; Williams et al., 2018). Because brown and spotted hyenas are rarely found in the same area, research on hyena latrine use has mainly been focused on latrine use of the two species separately (Gorman & Mills, 1984; Hulsman et al., 2010; Kruuk, 1972; Vitale et al., 2020). While literature on multispecies latrine use is scarce, there are some examples of carnivore species sharing marking sites (Allen et al., 2017; Apps et al., 2019; Edwards et al., 2022; King et al., 2017; Verschueren et al., 2021). In areas where both hyena species co-occur, the less dominant brown hyena might avoid using latrine sites at the same time as the spotted hyena, resulting in temporal partitioning.

Our study was conducted in Central Tuli in Botswana, an area with one of the highest densities of both spotted hyenas and brown hyenas in southern Africa (Vissia et al., 2021). We tested the hypothesis that brown hyena and spotted hyena show temporal partitioning at shared latrine sites. Because brown hyenas would likely try to avoid direct encounters with spotted hyenas, low overlap in temporal activity between brown and spotted hyenas at latrine sites would be expected. Furthermore, we expected that the time interval between a latrine visit of a spotted hyena followed by a brown hyena was longer than the time interval between consecutive conspecific visits or the time interval between a brown hyena visit followed by a spotted hyena visit. Lastly, we expected a decrease in latrine use during the wet season.

Methodology

Study area

This study was conducted in Central Tuli, a protected area of approximately 600 km^2 in South-East Botswana (Fig. 1). Central Tuli is characterised by Mopane bushveld (domination by *Colophospermum mopane*) with shrubs and trees, riverine woodland, and the abundant presence of rocky outcrops (Vissia et al., 2021). Rain mainly falls during the wet season, which spans from November to April, with an average annual rainfall of approximately 350–400 mm (Maruatona & Moses, 2022). The established carnivore species in the area are spotted hyena, brown hyena, leopard (*Panthera pardus*), black-backed jackal (*Lupulella mesomelas*), bat-eared fox (*Otocyon megalotis*), African wildcat (*Felis sylvestris lybica*), African civet (*Civettictis civetta*), honey badger (*Mellivora capensis*), and

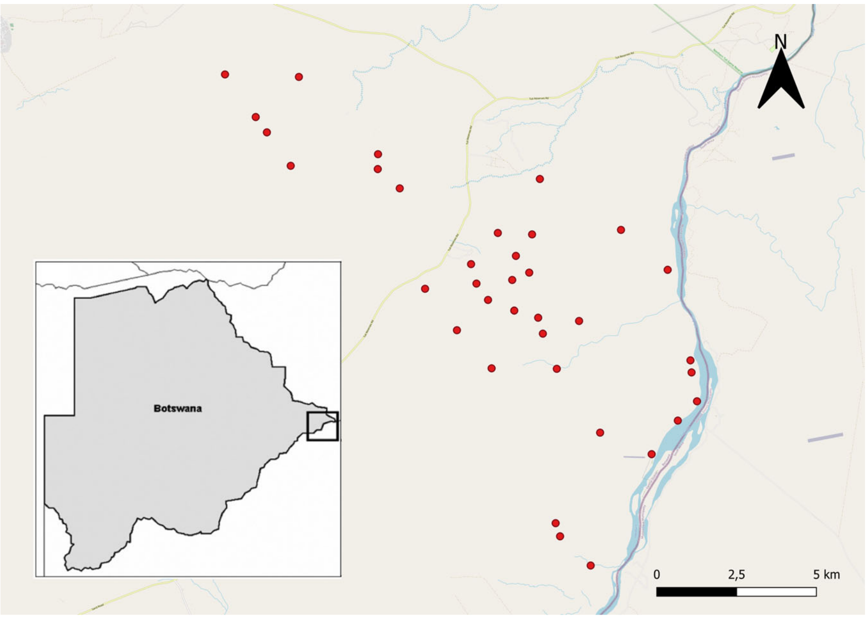

Figure 1 Map of Central Tuli, Botswana. The camera trap stations are indicated by the red dots.

small-spotted genet (*Genetta genetta*). Transient individuals of lion (*Panthera leo*), wild dog (*Lycaon pictus*) and caracal (*Caracal caracal*) also pass through the study area occasionally.

Data collection

Camera traps and direct latrine characteristics (i.e., number of scats) were used to record the latrine use of spotted and brown hyenas. As hyena latrines are mainly placed along roads or at easily detectable sites and landmarks (Gorman & Trowbridge, 1989; Kruuk, 1972; Vitale et al., 2020), we opportunistically identified latrines along roads by driving through the area. Latrines were defined as a site that contained at least three hyena scats. Hyena scats are easily recognised by their distinctively white colour due to their high calcium content (Kruuk, 1972). We mapped the locations of the latrines with a handheld GPS. Bushnell Trophy E3 (n = 16), Bushnell Core-trail (n = 13), or Spartan Lumen (n = 7) cameras were placed at the latrines at knee height to collect photographs of visiting animals. The cameras were operational 24 h a day, and at each trigger event, three pictures were taken with a 0 s interval. A total of 37 latrine sites were monitored between April 2021 and March 2022. As the first rains arrived in Tuli at the end of November 2021, we considered the months December–April to be the wet season and May–November as the dry season.

Camera trap data were collected monthly, and the cameras were checked for damage and battery status. A “visit” was defined as a single hyena or a group of hyenas recorded by the camera. We assumed that all animals captured by the limited range of view of the camera visited the latrine site with the purpose of sharing or collecting information. Pictures taken within 15 min of each other of the same species at the same site were excluded from the analysis as they could not be regarded as independent visits, unless it was possible to identify the hyenas as different individuals (following Vissia et al., 2021, based on Kolowski & Forrester, 2017). The unique spot patterns or front leg stripe patterns for spotted and brown hyenas respectively, were used for individual identification. When an identifiable hyena was recorded within 15 min of a hyena that was unidentifiable or vice versa, only the first visit was included in the analysis. Because spotted hyenas live in clans that often travel together, recordings of multiple individuals travelling in a group were considered as one independent visit.

Besides latrine visits, the deposition of scats was used as a measure for latrine use. Every month, the number of scats per hyena species at each latrine site was counted. Defecation of brown and spotted hyenas was distinguished by their size and shape based on expert knowledge by experienced trackers. The scats of the two species can be distinguished by their size and shape. The scats of spotted hyenas are usually larger than those of brown hyenas (±150 g and 50 g respectively). Furthermore, the individual pellets of a spotted hyena scat are more rounded and have a smooth surface, while the surface of the pellets of brown hyena often has wavy lines on the surface (Stuart & Stuart, 1994). During the first camera deployment and each time after the monthly count, we relocated the scats a few meters into the bushes with a shovel. By doing this, the scats with their accompanying scents were still present near the latrine while at the same time we could prevent the recounting of scats. The scent of other scent markings (such as urine/pastings) remained unaffected as well, as we did not remove any sand or vegetation from the latrine sites.

Statistical analyses

All analyses were performed using R (version 4.2.2; R Core Team, 2022). Generalized linear mixed modelling (GLMM) was used to assess (1) whether the defecation rate of a species was associated with the visitation rate of the same species, (2) whether the visitation rate of brown hyena was associated with the visitation rate of spotted hyena and vice versa, and (3) whether season affected visitation and defecation rates. We used latrine site as a random factor. Rates were calculated based on monitoring periods of approximately 1 month (i.e., days between subsequent check-ups, mean ± SD = 29.6 ± 5.19). The visitation rate (average number of visits/day) per species per camera trap station was calculated as the total number of independent visits of the corresponding species in a monitoring period divided by the number of 24-h trap days in that monitoring period. The same was done for the defecation rates (average number of scats/day) per species per latrine site. For the GLMMs, a negative binomial distribution with a logarithmic link function was used because of overdispersed count data. If a camera was found not to be recording the site for the whole monitoring period (i.e., between consecutive camera check-ups) due to disturbance by wildlife or an exhausted battery, the data of that camera for this specific monitoring period was not included in this analysis.

To investigate temporal differences in latrine use, the daily temporal activity patterns for each species and their overlap were estimated by kernel density estimation (following Ramesh et al., 2017; Sogbohossou et al., 2018). The temporal overlap was calculated with the use of the ‘Overlap’ package (Meredith & Ridout, 2014; Ridout & Linkie, 2009). The coefficient of overlap (Δ) ranges from 0 to 1, indicating no overlap, and complete overlap respectively. We used the estimator Δ_4 because of large sample sizes (>50), following recommendations of Meredith and Ridout (2016). For calculating the 95% confidence intervals for the coefficient of overlap, we used 10 000 bootstrapping samples. The difference in activity patterns was tested for statistical significance using the nonparametric Mardia-Watson-Wheeler test in the R package ‘Circular’ (Agostinelli & Lund, 2017). Identical time records on different days (captures obtained in the same hour and minute) were altered by adding 1 s to the raw data to meet the requirements of the test (following Villafañe-Trujillo et al., 2021).

To test whether the time interval between visits was affected by the species that visited the latrine previously, we calculated the time interval between visits at shared latrines during the wet (n = 34) and the dry season (n = 33). When latrine sites were not visited by one of the two species during the wet and/or dry season, the sites were excluded from the analysis. With the R package 'lmerTest' (Kuznetsova et al., 2017), a linear mixed-effect model was created with time interval as the response variable, the visitor species (BH/SH), previous visitor species (BH/SH) and their interaction effect as predictor variables and camera trap station as a random factor (following Verschueren et al., 2021). The response variable was raised to the power of 1/6 to meet the model assumption of normality. Afterwards, a pairwise comparison with Tukey adjustment was carried out to check for differences in visit combinations. This analysis was done separately for both the dry and the wet seasons.

Lastly, to investigate the fine-scale temporal patterns at shared latrine sites, we determined the temporal spacing between consecutive interspecific visits and consecutive intraspecific visits (following the methods of Cusack et al., 2017). For the temporal spacing between consecutive interspecific visits, we determined the time between the detection of species A (reference detection) and the closest detection of species B (proximal detection) in the 12 h after the reference detection for each site at which the two species co-occurred. We considered proximal detections occurring within 12 h after reference detections to match the length of a full night. We carried out this analysis once with brown hyena as the reference species and once with spotted hyena as the reference species. As described in Cusack et al. (2017), for each hour, a detection probability was obtained by dividing the number of detections of species B (proximal detections) within a 1-h bin by the total number of detections of species B. Expected distributions for each hour bin were generated by randomizing the timing of proximal detections 1000 times to test whether the observed detection probabilities were different from the random temporal spacing between detections of two species at shared camera traps. For each iteration, the randomisation procedure selected a new date at random from the survey period of the corresponding camera trap and selected a new time by sampling the activity pattern probability density function for species B. Lastly, the number of hours separating the randomized proximal detections and the unchanged reference ones was derived. The expected values of detection probability for each hour bin were compared to the observed value using a standard permutation test, with a significance level of $\alpha = 0.05$. The same method was used for consecutive intraspecific visits, but only the closest detection of the following visit of an individual of the same species was used. This analysis was carried out for the wet and dry seasons separately.

Results

A total of 37 latrines were monitored with camera traps between April 2021 and March 2022, resulting in 8560 camera trap days (3951 and 4609 days in the dry and wet season, respectively). A total of 34 latrines were visited by both brown and spotted hyenas during the wet season and 33 during the dry season. A total of 5152 independent visits were captured across all camera trap stations during the monitoring period, of which 2290 and 2862 were for brown and spotted hyenas, respectively. A total of 656 brown hyena visits and 957 spotted hyena visits were captured during the wet season, and during the dry season, 1634 brown hyena visits and 1905 spotted hyena visits were captured. For 1172 and 1758 occasions (at least one of) the visiting individual(s) could be identified in the photos for brown hyena and spotted hyena, respectively. Scent-marking behaviour (i.e., urinating, defecating, or pasting, whether or not with sniffing) was captured on camera on 242 and 105 occasions for brown and spotted hyenas, respectively. The behaviour of sniffing was captured on camera for 355 and 390 occasions for brown and spotted hyenas, respectively. Rolling was recorded on camera for one occasion for brown hyena and for five occasions for spotted hyena. A total of 32 different brown hyenas and 56 different spotted hyenas were identified.

Visitation and defecation rates

Figure 2 shows the difference in the defecation rates and visitation rates between the different seasons for both species. The visitation and defecation rates were significantly lower in the wet season than in the dry season for both brown and spotted hyenas, (Fig. 2, Table 1). The defecation rates of each species were positively correlated with the visitation rates. The visitation rates of brown and spotted hyenas were both positively correlated with the visitation rate of the other species (Table 1).

Temporal overlap in shared latrine use

Latrines were visited throughout the night by both hyena species (Fig. 3). Brown hyena detections were highest during dawn and dusk, especially in the evenings from 18:00–20:00 h. The activity patterns of the brown and spotted hyena were significantly different from each other during the wet ($W = 52.10$, d.f. = 2 and $P < 0.001$) and dry seasons ($W = 91.74$, d.f. = 2 and $P < 0.001$), probably due to the large sample sizes. Nonetheless, there was high temporal overlap between the two species, indicated by the overlap coefficient estimate of $\Delta_4 = 0.78$ (CI: 0.73–0.83) in the wet season and $\Delta_4 = 0.81$ (CI: 0.78–0.83) in the dry season. The temporal patterns are similar for dry and wet seasons.

Time interval between visits at shared latrines

The time interval for visits at shared latrines in the dry season was influenced by the visiting species ($F_{1,3432} = 19.35$, $P < 0.001$), but not by the species that visited the latrine previously ($F_{1,3432} = 3.39$, $P = 0.066$). The interaction effect of visiting species and previous visiting species was also significant ($F_{1,3409} = 29.33$, $P < 0.001$) during the dry season. For the wet season, only the interaction effect of visiting species and previous visiting species was found to be significant ($F_{1,1525} = 22.51$, $P < 0.001$).

The mean time interval between subsequent visits was highest when a spotted hyena visit was followed by a brown hyena visit in both seasons (Fig. 4). A pairwise comparison for the dry season showed that the mean time interval for consecutive

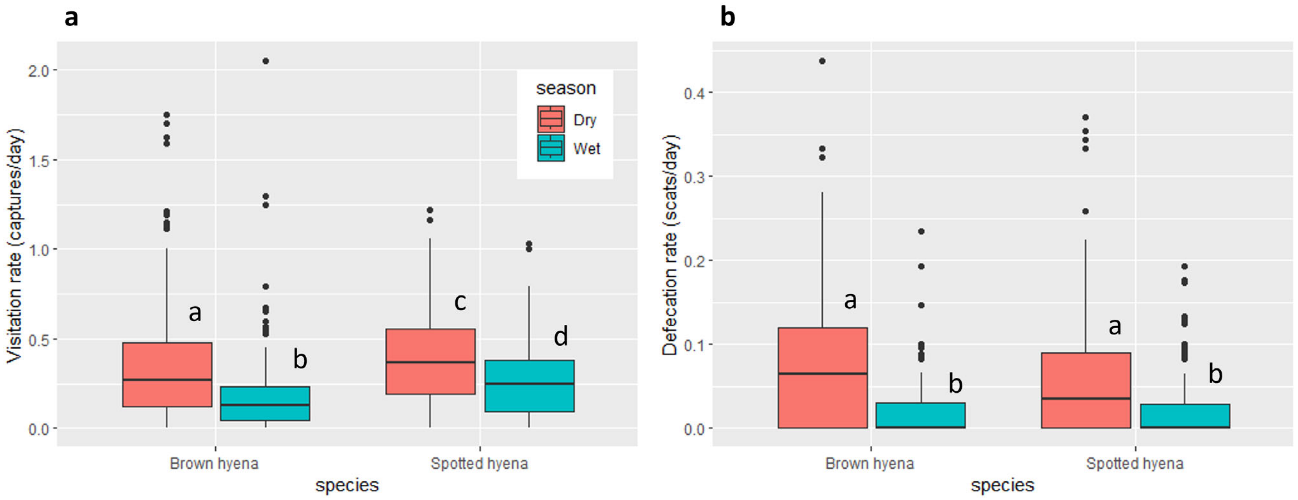

Figure 2 Distribution (median, 25 and 75% quartiles as well as maximum and minimum) of visitation rates (a) and defecation rates (b) of brown and spotted hyenas for the camera trap stations in Central Tuli in different seasons. The outliers are indicated by black dots. The letters indicate the significant differences between the means of the different combinations according to the Generalized linear models followed by a Tukey test. Note that the scales of the y-axes are different.

Table 1 Generalized Linear Mixed Models of brown (BH) and spotted hyena (SH) with visitation rates and defecation rates as dependent variables (in the columns) and latrine site as a random effect

	SH visitation rate	BH visitation rate	SH defecation rate	BH defecation rate
SH visitation rate		0.247** (0.13, 0.37)	0.206* (0.01, 0.41)	
BH visitation rate	0.162** (0.07, 0.26)			0.225** (0.09, 0.37)
Season (wet)	−0. 239** (−0.40, −0.07)	−0.563** (−0.77, −0.36)	−0.920** (−1.29, −0.55)	−1.385** (−1.69, −1.08)
Intercept	−1.119** (−1.32, −0.92)	1.316** (−1.59, −1.05)	−3.249** (−3.61, −2.89)	−2.715** (−2.97, −2.46)

Season is included as a factor, and the wet season has negative coefficients, meaning the dependent variables are lower for the wet season than for the dry season. The table includes coefficient estimates, confidence intervals (in brackets) and corresponding *P*-values ($^{*}P < 0.05$, $^{**}P < 0.01$). Sample size is 291.

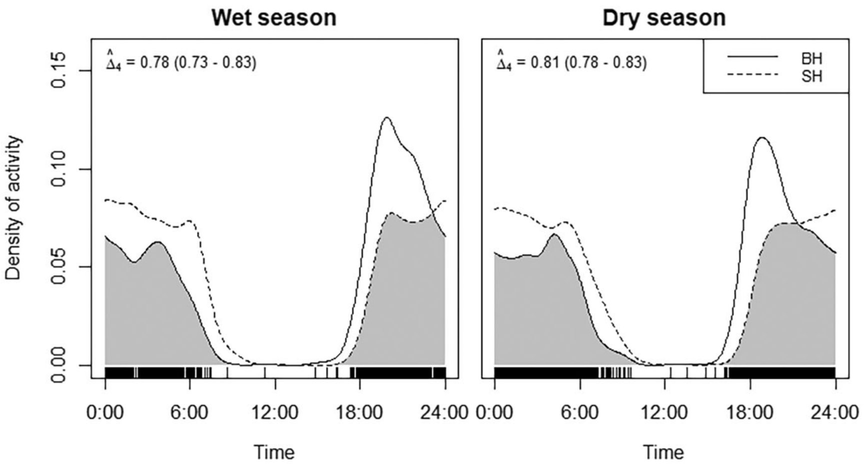

Figure 3 The kernel density estimates of the activity patterns of brown hyena (solid line) and spotted hyena (dashed line) in Central Tuli, Botswana, for the wet and dry seasons. The overlap coefficient (Δ_4) is indicated by the grey area under the minimum of the two density estimates in the plot. The tick marks on the x-axis represent all activity samples for brown hyena (wet: $n = 776$, dry: $n = 1723$) and spotted hyena (wet: $n = 1045$, dry: $n = 2117$).

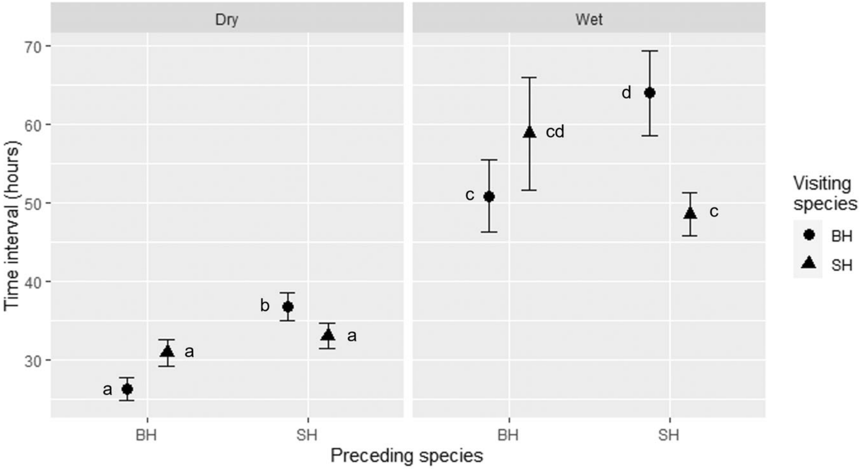

Figure 4 Mean time interval between visits for brown hyena (BH) and spotted hyena (SH) at shared latrines in response to the preceding species. Error bars show standard errors. The letters indicate the significant differences between the different species combinations according to a pairwise comparison using the Tukey correction. Note that the y-axis does not start at zero and that the analysis was carried out separately for wet and dry seasons.

spotted hyena-brown hyena visits ($n = 682$) differed significantly ($P < 0.001$) from the mean time interval of consecutive brown hyena-spotted hyena visits ($n = 686$) and consecutive conspecific visits ($n = 888$ for brown hyena, $n = 1180$ for spotted hyena). For the wet season, the mean time interval for consecutive spotted hyena-brown hyena visits ($n = 260$) differed significantly ($P < 0.001$) from the mean time interval of consecutive conspecific visits ($n = 378$ for brown hyena, $n = 627$ for spotted hyena) but not from consecutive brown hyena-spotted hyena visits ($n = 264$). Generally, the mean time intervals between both consecutive interspecies and conspecific visits during the wet season were longer than for the dry season.

Fine-scale temporal patterns at shared latrines

The temporal spacing for consecutive conspecific visits at the same latrine was determined (Fig. 5). Brown hyenas were more likely to be detected within 1–4 h of each other at the same latrine site during the dry season (Fig. 5). During the wet season, they were most likely to be detected within 2 h of each other. Spotted hyenas were more likely to be detected within 2 h of each other at the same latrine site during the dry season. During the wet season they were most likely to be detected within 1 h of each other.

Fine-scale temporal patterns for consecutive visits of different species at the same latrine are shown in Fig. 6. Spotted hyenas showed a tendency to be detected more often than expected within 1–2 h after detection of a brown hyena in the dry season and within 1 h in the wet season. While brown hyenas were detected more often than expected 6 h after the detection of spotted hyena at shared latrines in the dry season and after 2 h in the wet season.

Discussion

This study is the first to investigate the use of shared latrines by brown and spotted hyena. We studied the temporal patterns of shared latrine use in Central Tuli, Botswana. Overall, we found that the visitation rate and defecation rates of a species were positively associated with each other for both brown and spotted hyenas, where approximately 20% of the visits involved (recorded) defecation. Both the visitation rates and defecation rates were significantly lower during the wet season for both hyena species. Furthermore, we found that the visitation rates of both hyena species were positively associated with each other, indicating no spatial partitioning between the species at latrine sites. There was also high overlap in temporal activity for the two species. However, the mean time interval for consecutive spotted hyena-brown hyena visits at shared latrine sites was larger than the mean time interval for consecutive brown hyena-spotted hyena visits and consecutive conspecific visits during the dry season. Fine-scale temporal patterns showed that spotted hyenas visited shared latrines more often than expected within 1 h after a brown hyena visit, while the opposite was not true.

Our results showed that the defecation rates of both hyena species were lower during the wet season. Scat degradation within the time between checking the latrines could have caused a negative bias in our scat counts, especially during the wet season when coprophagous beetle activity is higher (Vitale et al., 2020). From our camera trap photos, we have observed that a brown hyena scat had degraded completely within 24 days after deposition during the wet season in March. However, visitation rates of both hyena species were also found to be lower during the wet season, suggesting that the role of latrines might be less important during the wet season. The same seasonal effect on visitation and defecation rates was

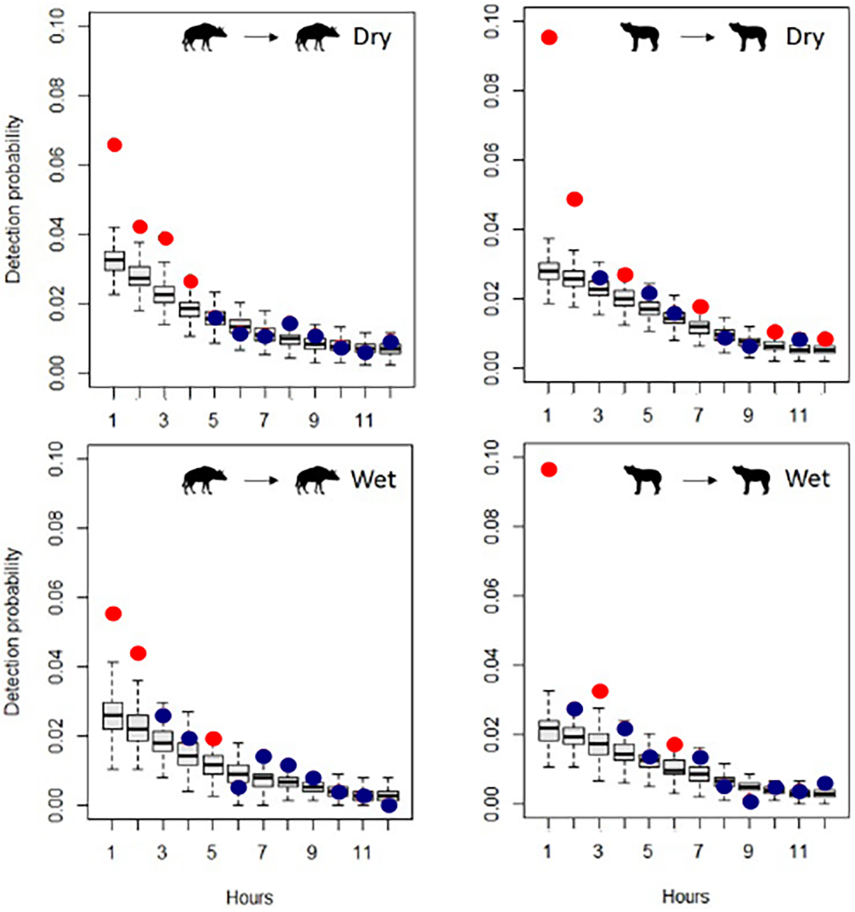

Figure 5 Left: Observed (dots) and expected (grey boxplot) detection probabilities of a brown hyena for the first time within 12 h after the detection of a brown hyena at the same latrine in the dry and wet seasons. Right: Observed (dots) and expected (grey boxplot) detection probabilities of a spotted hyena for the first time within 12 h after the detection of a spotted hyena at the same latrine in dry and wet seasons. Red dots indicate the hours with significant differences between the expected and observed detections (with α = 0.05), based on a standard permutation test. Note that hour 0 is not shown on the x-axis as this hour represents the reference detection.

found for spotted hyenas in the Okavango Delta (Vitale et al., 2020). In general, the function, and therefore seasonal use, of latrines can be related to a variety of things such as territory defence, food source defence, or mate acquisition (Buesching & Jordan, 2022). For example, Eurasian badgers tend to have more active latrines during the mating season (Roper et al., 1993). While for hog badgers it has been found that latrine activity is higher when food abundance is low (Zhou et al., 2015). Because spotted and brown hyenas do not have a clear breeding season (Lindeque & Skinner, 1982) and prey is generally more abundant in the wet season because of synchronised calving events (Owen-Smith & Ogutu, 2013), the reduced use of latrine sites might be caused by decreased territorial behaviour among different hyena clans (Vitale et al., 2020). However, it was not possible to test this hypothesis in our study because data on prey abundance were not available.

Our results did not demonstrate spatial partitioning between brown and spotted hyena, as the visitation rates of brown and spotted hyena were positively associated with each other. In addition, 34 and 33 out of the total 37 latrines that were monitored were shared by both species in the wet and dry seasons, respectively. The use of shared latrine sites could simply result from a similar preference of latrine site locations, independent of the other species. However, the use of shared marking sites is widespread among carnivores. Previous research showed that 24 out of the 39 carnivore species in Southern Africa are involved in some kind of interspecific scent marking. Sharing latrine sites could potentially serve a function of interspecies' olfactory communication (Apps et al., 2019).

Besides the spatial overlap, we also found high overlap in the temporal activity of the two hyena species. While brown hyenas avoid spotted hyenas in some areas (Mills, 1984; Mills & Funston, 2003; Williams et al., 2020), Vissia et al. (2021) found high temporal and spatial overlap of spotted and brown hyenas in Tuli, which is supported by our findings. Our results showed that during the wet season, no differences in mean time interval between consecutive spotted-brown hyena and

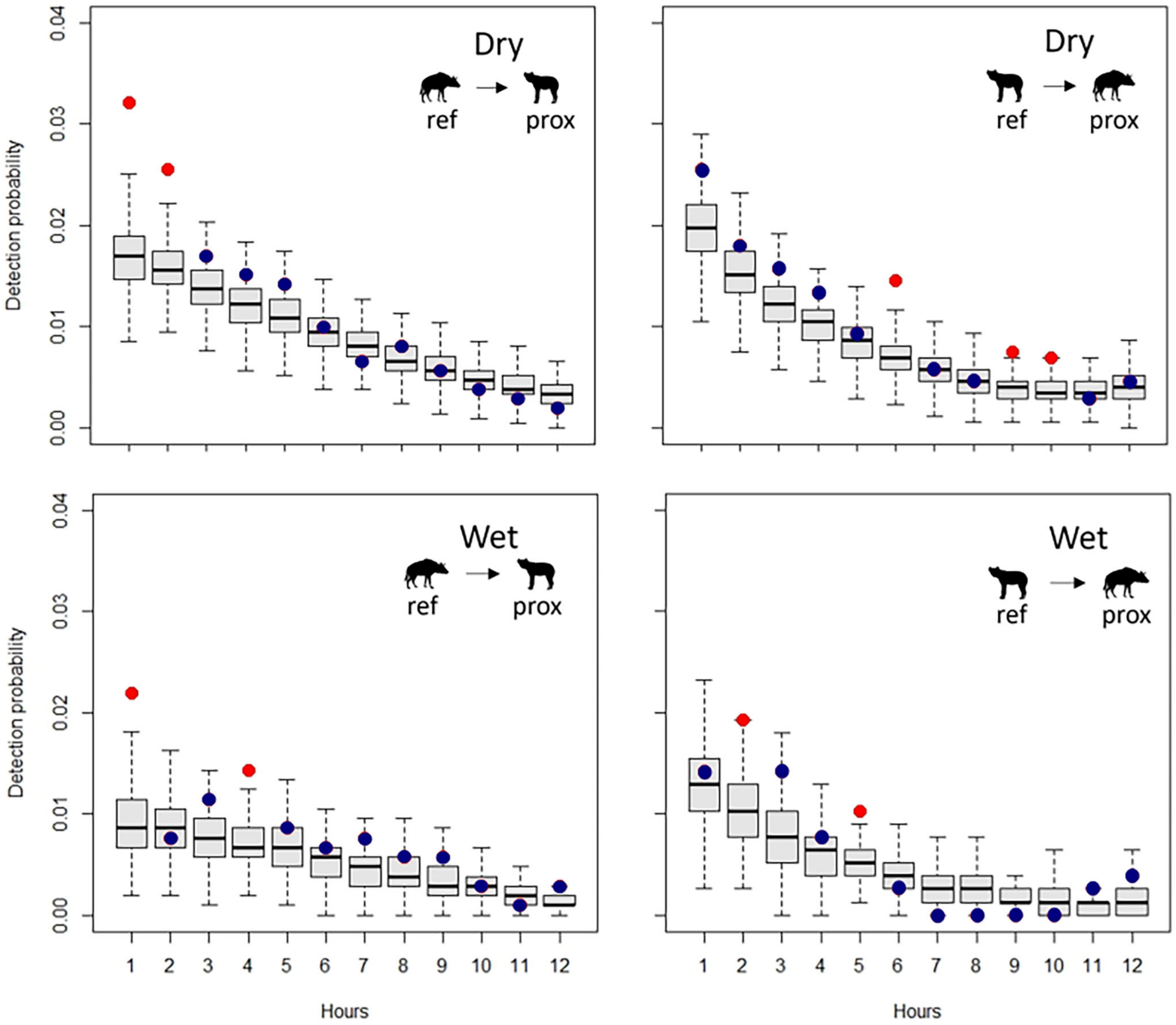

Figure 6 Left: Observed (dots) and expected (grey boxplot) detection probabilities of a brown hyena (proximal detection) for the first time within 12 h after the detection of a spotted hyena (reference detection) at the same latrine in wet and dry seasons. Right: Observed (dots) and expected (grey boxplot) detection probability of a spotted hyena (proximal detection) for the first time within 12 h after the detection of a brown hyena (reference detection) at the same latrine in wet and dry seasons. Red dots indicate the hours with significant differences between the expected and observed detections (with α = 0.05), based on a standard permutation test. Note that hour 0 is not shown on the x-axis as this hour represents the reference detection.

brown–spotted hyena visits were found. This can be due to the decreased use of latrines during the wet season in general, as discussed above. However, during the dry season, the mean time interval between consecutive spotted-brown hyena visits is longer than for consecutive brown–spotted hyena and conspecific visits. The difference in time intervals between consecutive conspecific and interspecies visits could result from the behaviour of each species, independent of the other. Both brown and spotted hyenas are group-living species; individuals may travel together in loose subgroups or pairs (Mills, 1984). This increases the likelihood of detecting multiple individuals of the same species within a shorter time frame.

The results of the fine-scale temporal analysis suggested a similar pattern as mentioned above, where a spotted hyena is more likely to be detected at shared latrines within 1 h after a brown hyena detection but not vice versa. The difference in time intervals between consecutive interspecies visits can be explained in several ways. Firstly, patterns in inter-visit intervals of consecutive visits of brown hyena-spotted hyena and spotted-brown hyena could arise when there are large differences between the densities of both species. However, we do not expect this to be relevant in this case, because densities for brown (10.6 ± 1.9/100 km^2) and spotted hyena (14.9 ± 2.2/100 km^2) in our study area are quite similar (Vissia et al., 2021). Secondly, the observed patterns in the temporal analysis could be explained by the difference in the activity pattern of the two species. Brown hyenas have an activity peak in the evening between 18:00 and 20:00 h, whereas spotted hyenas become active later in the evening and remain active for longer in the morning.

The slight difference in temporal activity between the species can explain the observed pattern in our data but could in turn be the result of interspecific competition. The evening activity peak of brown hyena tends to be earlier in the Tuli area (around 18:00–20:00 h) than in Lapalala (around 20:00–21:00 h) (Hulsman et al., 2010). Both Lapalala and Tuli are located in the Limpopo area; however, spotted hyena was not present in the Lapalala study area. Therefore, our results suggest that brown hyenas might display fine-scale temporal avoidance of spotted hyenas. Fine-scale temporal avoidance patterns have been found for other competitive African predators as well (Searle et al., 2021). Further research using a higher density of camera traps or GPS tracking could give more insight into potential small-scale temporal or spatial avoidance between brown and spotted hyenas.

Avoidance behaviour of brown hyenas may reduce the risk of encountering a spotted hyena at a shared latrine site, but it could also inhibit intraspecific communication for brown hyenas at shared latrine sites. While scent communication is not the only way of intraspecific communication for hyenas, it is especially important for brown hyenas because they are less vocal than spotted hyenas (Mills, 1989). However, this study focused only on the use of latrines and scat deposition as a way for olfactory communication, while pasting is another important way of scent marking for spotted and especially brown hyenas (Mills, 1989). Hyena paste is a secretion produced by a special anal gland that is often deposited on vegetation (Gorman & Mills, 1984; Kruuk, 1972). It could be possible that brown hyenas invest more energy in pasting at other locations and are therefore less dependent on latrine sites for olfactory communication. Further study on the relative importance of pasting and use of latrine sites by brown hyenas could help to understand the biological implications of possible interference competition with regard to olfactory communication in areas where brown hyenas coexist with other large carnivores.

In conclusion, this study provides a better understanding of the temporal patterns of shared latrines by brown and spotted hyenas. This study also adds to the recent insights that the use of latrines and marking sites by multiple species is widespread. Our results show seasonal variation in latrine use for both brown and spotted hyenas, which is also found in other species. Furthermore, our results did not show spatial partitioning between brown and spotted hyenas at latrine sites, and both species have high overlap in temporal activity. However, brown hyenas seem to show fine-scale temporal avoidance of spotted hyenas at shared latrine sites. The presence of spotted hyenas, or other large carnivores, could possibly inhibit intraspecific communication for brown hyenas at shared latrine sites. Understanding this form of interference competition and its biological significance can be important for future conservation of the rare brown hyena species, which is ranked as Near Threatened by the IUCN Red List due to declining populations (Wiesel, 2015). Therefore, we recommend further research on small-scale movement and activity patterns with GPS tracking, and further investigation on the relative importance of pasting in scent communication of brown hyenas in relation to the use of latrines in areas with and without other large carnivores.

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Author contributions

Stella de Zeeuw: Conceptualisation (equal); data collection (supporting); data analysis (lead); methodology (equal); visualisation (equal); writing–original draft (lead). **Sander Vissia:** Conceptualisation (equal); data collection (lead); funding acquisition (lead); methodology (equal); resources (equal); visualisation (equal); supervision (equal); writing – original draft (supporting). **Frank van Langevelde:** Conceptualisation (equal); funding acquisition (supporting); methodology (equal); resources (equal); visualisation (equal); supervision (equal); writing–original draft (supporting). All authors contributed critically to the drafts and gave final approval for publication.

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Conflict of interest

All authors declare that they have no conflicts of interest.

Data availability statement

The data underlying this article will be shared on reasonable request with the corresponding author.

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