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Spatiotemporal sharing and partitioning of scent-marking sites by cheetahs and leopards in north-central Namibia

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Abstract

Scent-marking sites may facilitate interspecific information gathering and could help to minimise the risk of encounter with interspecific competitors. Recent evidence from South Africa shows that cheetahs avoid dominant predators at scent-marking sites, which may delay or inhibit intraspecific communication in cheetahs. However, little is known on whether this pattern of avoidance occurs elsewhere in the cheetah's range. We analysed a 9-year camera trap data set from north-central Namibia to explore interspecific use of marking sites by cheetahs and leopards. We documented frequent sharing of marking sites, which was likely facilitated through temporal segregation and by availability of alternative sites that were species-specific. We did not identify a stronger avoidance response of cheetahs to leopards than to conspecifics, suggesting that delayed communication by cheetahs resulting from predator avoidance may be limited in our study area. Seasonality affected patterns of marking site visitation, which may be attributed to behavioural changes in relation to reproduction or resource availability, or to differential detectability of olfactory cues among seasons. We recommend further research to better understand carnivore scent-marking, including behavioural responses to olfactory cues and environmental conditions, as well as intra- and interpopulation differences.

KEYWORDS
Acinonyx jubatus, carnivore, competition, heterospecific, interspecific, olfactory, *Panthera pardus*, seasonality

Résumé

Les sites de marquage olfactif peuvent faciliter la collecte d'informations interspécifiques et pourraient contribuer à minimiser le risque de rencontre avec des concurrents interspécifiques. Des preuves récentes provenant d'Afrique du Sud montrent que les guépards évitent les prédateurs dominants sur les sites de marquage olfactif, ce qui peut retarder ou inhiber la communication intraspécifique chez ces derniers. Cependant, nous ne savons pas vraiment si cette tendance d'évitement se produit ailleurs au sein de l'aire de répartition du guépard. Nous avons analysé un ensemble de données de pièges photographiques recueillies sur une période de 9 ans dans la région

centre-nord de la Namibie pour étudier l'utilisation interspécifique des sites de marquage par les guépards et les léopards. Nous avons documenté le partage fréquent des sites de marquage, qui a probablement été facilité par la ségrégation temporelle et la disponibilité de sites alternatifs spécifiques à l'espèce. Chez les guépards, nous n'avons pas observé de réaction d'évitement plus forte à l'égard des léopards qu'à l'égard de leurs congénères, ce qui suggère que le retard de communication des guépards résultant de l'évitement des prédateurs peut être limité dans notre zone d'étude. La saisonnalité a affecté les tendances de marquage lors des visites des sites, ce qui peut être attribué à des changements de comportement liés à la reproduction, à la disponibilité des ressources, ou aux différences en matière de détectabilité des signaux olfactifs entre les saisons. Nous recommandons la réalisation de recherches plus approfondies afin de mieux comprendre le marquage olfactif des carnivores, notamment les réactions comportementales aux signaux olfactifs et aux conditions environnementales, ainsi que les différences intra et interpopulation.

1 | INTRODUCTION

Olfactory communication through scent-marking occurs commonly in the life history of mammals (Johnson, 1973; Ralls, 1971). The most important functions of marking target conspecifics include advertising dominance when establishing territories, and displaying reproductive status during mating seasons (Bothma & Coertze, 2004; Eaton, 1970; Sunquist & Sunquist, 2002). Scent-marking sites are also used to gain information on sympatric competitors, predators and prey (Apfelbach et al., 2005; Apps et al., 2019; Bytheway et al., 2013; Li et al., 2013; Parsons et al., 2018). Some species may even visit marking sites for scent acquisition, possibly to deter other predators (Allen et al., 2017).

Carnivore guilds in Africa are among the most diverse in the world, with limited extinctions and relatively few threatened species compared with other continental carnivore guilds (Dalerum et al., 2009). Of the 39 carnivore species in South Africa, at least 24 are involved in some type of interspecific scent-marking (Apps et al., 2019). The cheetah (*Acinonyx jubatus*) is a subordinate species within the African large carnivore guild and is constrained to minimise interactions with dominant predators through fine-scale avoidance behaviours (Broekhuis et al., 2013; Durant, 1998, 2000; Swanson et al., 2016; Vanak et al., 2013). Intraguild hostility from larger predators may explain their wide-ranging behaviour, so that cheetahs are unable to frequently patrol territory borders (Marker et al., ,2008, 2018). Hence, scent-marking is centred in core areas of cheetah territories, where they often revisit notable sites, such as large trees and termite mounds (Eaton, 1970; Kusler et al., 2019; Melzheimer et al., 2020).

Cheetah communication may be inhibited or delayed by other predators (Cornhill & Kerley, 2020a). In KwaZulu-Natal, South Africa, cheetahs took longer to return to marking sites when lions (*Panthera leo*) and leopards (*P. pardus*) were the previous species to visit the site (Cornhill & Kerley, 2020a). Intraspecific communication remained the primary role, yet the presence of other predators influenced the cheetah's behaviour (Cornhill & Kerley, 2020a). While this form of interference competition has been explored at the individual level for cheetahs, its population-level implications still need to be quantified (Cornhill & Kerley, 2020a). Furthermore, whether such patterns exist beyond the scale of one study remains to be assessed under varying environmental conditions and in different carnivore guilds.

We analysed a 9-year camera trap dataset to understand how cheetahs and leopards share and/or partition marking sites. Camera trap surveys were conducted in a free-ranging study system in north-central Namibia with no other top predators, except brown hyaenas (*Hyaena brunnea*). Cheetahs may use multiple marking sites to cope with interference at shared sites (i.e. marking sites visited by cheetahs and leopards during the same survey), so we expected a proportion of marking sites to be partitioned (i.e., cheetah-specific and leopard-specific sites) (Cornhill & Kerley, 2020a; Eaton, 1970). Additionally, cheetahs may visit marking sites at different times of the day to avoid dominant predators (Hayward & Slotow, 2009). We also analysed differences in marking behaviours that may indicate differential use of sites as different olfactory cues could possibly reduce interspecific detectability (Burger et al., 2006). Lastly, cheetahs and leopards show territorial aggression and/or avoidance towards each other and/or conspecifics (Bailey, 2005; Wachter et al., 2018). Thus, we investigated whether interspecific avoidance exceeded conspecific avoidance to understand the strength and direction of interference competition at shared marking sites (Harmsen et al., 2009). We also investigated whether seasonal differences affected this interaction as changes in resource availability and/or detectability of olfactory cues may influence the potential for cheetah-leopard interactions.

2 | METHODS

2.1 | Study area

The study covered 371 km^2 (100% Minimum Convex Polygon of camera trap locations) of freehold (i.e. privately owned) farmland in north-central Namibia (20°28'56"S, 17°2'24"E; Figure 1). The area is semi-arid with an annual rainfall of 400–500 mm concentrated during the wet season (November to April) (Mendelsohn et al., 2002). The wet season is relatively hot (mean daily temperature: 22.7°C) and humid (mean relative humidity: 70–80%) (Mendelsohn et al., 2002). The dry season (May to October) is colder, with exception of October (mean daily temperature: 17.9°C) and dry (mean relative humidity: 10–20%), with little to no rainfall (Mendelsohn et al., 2002). The study area is a partially fenced, free-movement area characterised by thornbush and tree and woodland savannah vegetation, where bush encroachment is prevalent (Barnard, 1998). Land use practices include wildlife conservation, eco-tourism, hunting and livestock production (Marker-Kraus et al., 1996). Cheetahs and leopards are top predators in the system as lions, spotted hyaenas (*Crocuta crocuta*) and African wild dogs (*Lycaon pictus*) were

extirpated in the 1980 s (Stein, 2010). The other large carnivore in the area is the brown hyaena, which is mainly a scavenger (Mills & Mills, 1978) and which marks at community latrines and grass stalks (Mills et al., 1980). Mesocarnivores include aardwolf (*Proteles cristatus*), bat-eared fox (*Otocyon megalotis*), black-backed jackal (*Canis mesomelas*), caracal (*Caracal caracal*), honey badger (*Mellivora capensis*) and serval (*Leptailurus serval*). Carnivore prey species present include common duiker (*Sylvicapra grimmia*), eland (*Taurotragus oryx*), gemsbok (*Oryx gazella*), kudu (*Tragelaphus strepsiceros*), plains zebra (*Equus quagga*), red hartebeest (*Alcelaphus buselaphus*), springbok (*Antidorcas marsupialis*), steenbok (*Raphicerus campestris*), warthog (*Phacochoerus africanus*), scrub hare (*Lepus saxatilis*) and springhare (*Pedetes capensis*).

2.2 | Camera trapping

Between November 2005 and February 2014, we conducted nine camera trapping surveys, which lasted between three to five months (Table 1). Camera traps were set at trees and termite mounds, initially to monitor cheetah activity (Fabiano et al., 2020). Sites were
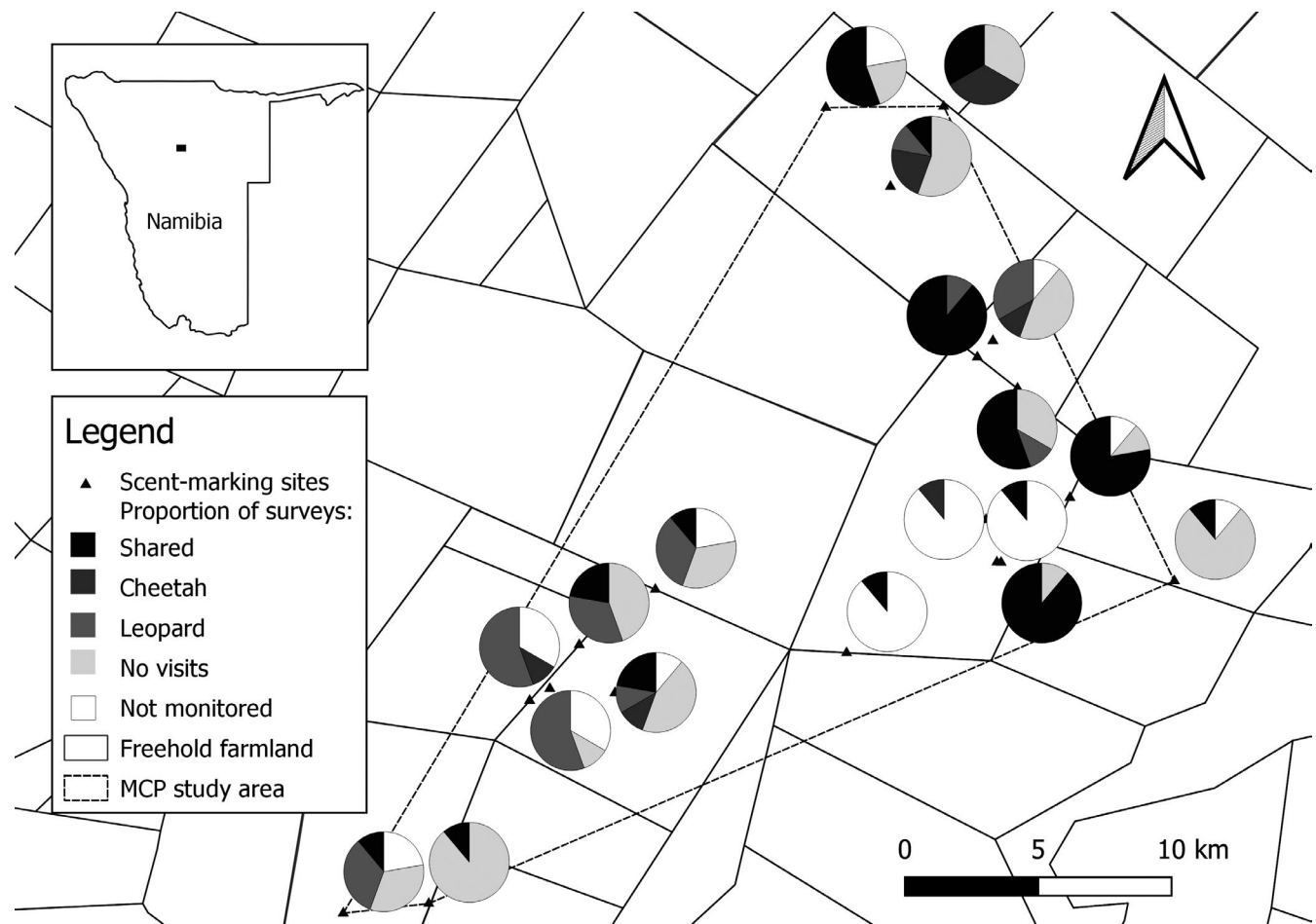
FIGURE 1 Map of scent-marking sites shared and partitioned by cheetahs and leopards between 2005 and 2014 on freehold farmland in north-central Namibia. Pie charts indicate the proportion of surveys (*n* = 9) that the site was visited by both species ('Shared'), only cheetahs, only leopards, not visited and not monitored

TABLE 1 Sampling effort for nine camera trap surveys conducted in north-central Namibia between 2005 and 2014, including the survey period, the number of shared sites, partitioned sites, unvisited sites and monitored sites, and the ratio of independent cheetah visits to independent leopard visits

Survey dates	Shared sites	Cheetah sites	Leopard sites	Unvisited sites	Monitored sites	Trap nights	Ratio cheetah: leopard
Nov 2005 - Feb 2006	2	2	0	11	15	180	4.7:1
Jul 2007 - Oct 2007	7	0	0	12	19	630	8.3:1
Jul 2008 - Nov 2008	4	1	0	10	15	480	3.9:1
Jul 2009 - Oct 2009	5	0	1	10	16	450	5.0:1
Jul 2010 - Oct 2010	7	1	5	2	15	1518	1.2:1
Nov 2010 – Apr 2011	6	2	5	2	15	1991	2.6:1
May 2011 - Oct 2011	8	1	3	3	15	1840	1.8:1
Nov 2011 - Feb 2012	3	2	8	2	15	990	1.5:1
Oct 2013 - Feb 2014	5	0	1	9	15	600	5.4:1
Mean	5	1	3	7	16	964	3.8:1
SD	2	1	3	4	1	622	2.2

identified by field crews that conducted systematic searches of features deemed conducive to cheetah marking.

We used analogue infrared Cuddeback® DeerCam™ DC200 (DeerCam, Park Falls, WI) cameras from 2005 to 2009 and digital infrared Bushnell® Trophy Cam™ (Kansas) cameras from 2010 to 2014. To increase detection probability, we placed two cameras per station, facing each other at a slight angle, mounted ~75 cm above the ground and 5 m apart (Negrões et al., 2012). Cameras were programmed to take pictures with a 30 s delay between triggers. Each trigger produced a burst of photographs consisting of three images taken within 1 s. We visited camera sites every 2–7 days to check for functionality, change film/memory card and/or batteries. Cheetah and leopard photographs from developed films were logged into a spreadsheet, while photographs from digital cameras were stored using an automated software for camera trapping data management following Harris et al., (2010). Data from paired camera trap stations were merged to create a contiguous dataset.

2.3 | Data analysis

Photographs were classified into independent visits, using as criterion a minimum of 30 min between consecutive photographs (O'Brien et al., 2003). We calculated 'interval between visits' as the time between two subsequent visits at the same site when the camera trap remained active. We grouped time intervals into four categories, depending on the preceding and following species: cheetah-cheetah, leopard-leopard, cheetah-leopard and leopard-cheetah. Time intervals for the first two categories may include subsequent visits by the same individual as we did not classify records to the individual level. This may limit our interpretation of conspecific avoidance responses, but this was inherent to the analysis (Harmsen et al., 2009). Per survey, we identified

the number of shared sites, partitioned sites (cheetah-specific, leopard-specific) and unvisited sites (i.e., no visits by both species). We presented these numbers as proportion of total monitored sites per survey.

To determine the intensity of cheetah and leopard use of scent-marking sites, we estimated single-species activity patterns using the R package *camtrapR* (Niedballa et al., 2016). We calculated the coefficient of overlap (0: no overlap – 1: total overlap) between cheetahs and leopards using the R package *overlap* (Ridout & Linkie, 2009) and compared the activity patterns using the Watson-Wheeler test in the R package *circular* (Agostinelli & Lund, 2017). This was done for both the wet and the dry season.

We recorded different marking behaviours using the scan sampling method on each consecutive trigger of photographs, which was approximately every 30 seconds (Lehner, 1992). Behaviours were classified following the ethogram constructed by Cornhill and Kerley (2020b). Scan sampling is a widely used method to quantify behavioural observations whereby all behaviours displayed by all individuals are recorded during pre-established sampling periods with fixed intervals (Altmann, 1974). There is a likelihood that some behaviours remain undetected, but the interval used is below the 5 minutes recommended to yield reliable information when applying this method (de Oliveira et al., 2018). Furthermore, given the extensive sampling period, this likelihood may be minimal. We assigned to each individual visit whether marking occurred, but we acknowledge imperfect detection. We used a chi-squared test to determine differences in the frequency of marking behaviours recorded for cheetahs and leopards.

At shared sites, we investigated how the time interval between visits differed between cheetahs and leopards in relation to the species that had previously visited the marking site. Female cheetahs may attract males after signalling oestrous events (Cornhill & Kerley, 2020b); thus, we excluded infrequent visits where females were recorded (n = 16) and those following female visits

(*n* = 14). For leopards, exploratory analyses using a subset of our records did not indicate intersexual attraction at marking sites (CCF, unpublished data). To investigate factors potentially influencing the time interval between visits, we used the R package *lmerTest* (Kuznetsova et al., 2017) to generate a linear mixed model with the time between visits as response variable. Explanatory variables included categorical covariates for the visitor species (cheetah/leopard), the previous visitor species (cheetah/leopard) and the season (wet/dry). We included the two-way interactions, and we designated scent-marking site and survey as random effects. The response variable was log-transformed to meet model assumptions of normality and heteroscedasticity. Goodness of fit model was estimated based on the marginal coefficient of determination (r^2 glmm(m)), which denotes the variance explained by fixed covariates, and the conditional coefficient of determination (r^2 glmm(c)), which shows the variance explained by both fixed and random effects (Nakagawa & Schielzeth, 2013). A significance level of 0.05 was used. All statistical analyses were performed in R version 3.4.3 (R Core Team, 2017).

3 | RESULTS

We detected 983 cheetah visits and 476 leopard visits at 19 scent-marking sites over 8679 trapping nights (Table 1). During this study, 79% of monitored sites were shared during at least one survey (Figure 1). The proportion of shared sites per survey was 34% of monitored sites, while the proportion of partitioned sites per survey was 6% (cheetah-specific) and 16% (leopard-specific), and the proportion of unvisited sites per survey was 44% (Figure 1, Table 1). Site selection changed over time. Additionally, the number of leopard-specific

sites tended to increase with time, while the number of unvisited sites tended to decrease (Table 1). Cheetahs visited marking sites more frequently than leopards, with a ratio of 3.8 (±2.2 *SD*):1. The mean number of independent visits per 100 trapping days was 13 (±8 *SD*) visits for cheetah and 4 (±2 *SD*) visits for leopards. The interval between cheetah visits was 2.6 (±7.1 *SD*) days and between leopard visits 3.3 (±5.4 *SD*) days.

Scent-marking sites were often visited at night, with activity peaks during dawn and dusk (Figure 2). Leopard activity mainly peaked during early mornings, while cheetah activity mainly peaked during the evening. Activity patterns were significantly different between cheetahs and leopards during both seasons (wet: W = 7.64, df = 2, *p* = 0.02; dry: W = 16.95, df = 2, *p* = 2.09E-4). Nonetheless, activity overlap was relatively high and was larger in the wet season (Dhat = 0.89) than in the dry season (Dhat = 0.82).

Scent-marking was observed during 19% of cheetah visits and 16% of leopard visits. The marking behaviour that was recorded most often for cheetahs was urinating (70%), followed by defecating (16%), tree scratching (12%) and rubbing (2%). For leopards, this was urinating (53%), followed by tree scratching (30%), rubbing (13%) and defecating (4%). The frequency of different marking behaviours at the sites was significantly different for cheetahs and leopards (χ^2 = 30.59, df = 3, *p* = 1.04E-6). Other behaviours recorded at marking sites included sniffing, vigilance, resting and moving.

For both cheetahs and leopards, the time interval between visits was not affected by the previous species that visited the site (Figure 3, Table 2). Seasonality had a significant effect on time interval between visits, with longer intervals during the dry season compared with the wet season. This response was similar for both species and unaffected by the previous visitor species.
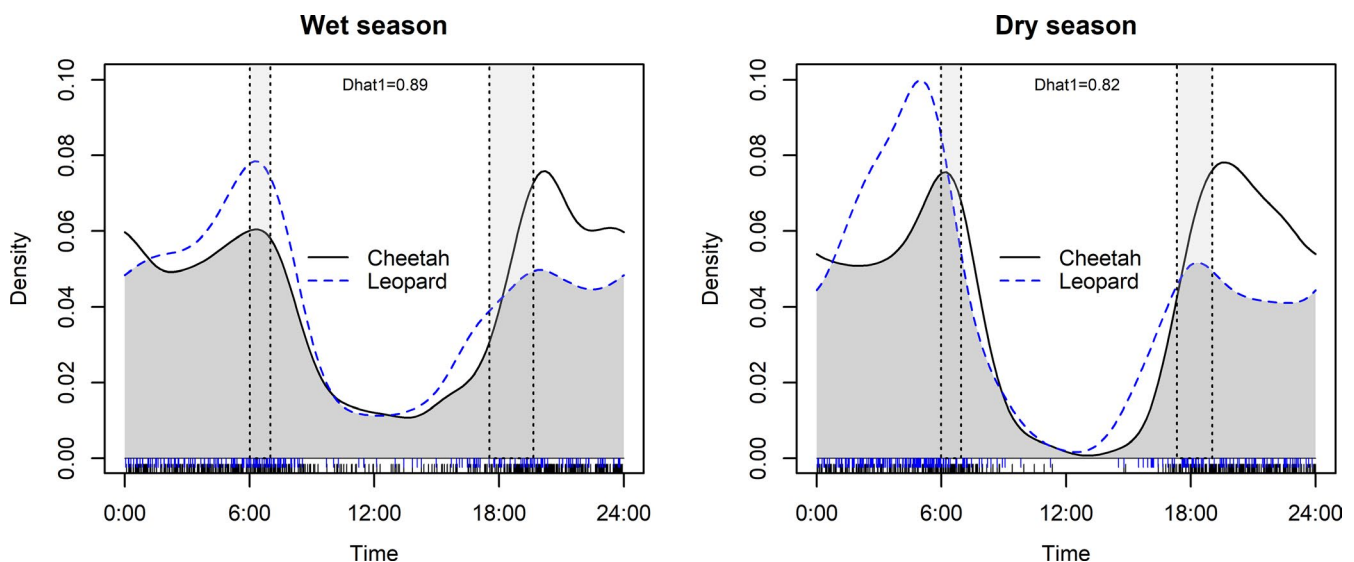
FIGURE 2 Seasonal activity patterns at scent-marking sites for cheetahs and leopards. The vertical dotted lines denote the earliest and latest sunrise and sunset times throughout the year. The dark grey area below the curves indicates the overlap in activity patterns between cheetah and leopard. Dhat1 is the coefficient of overlap
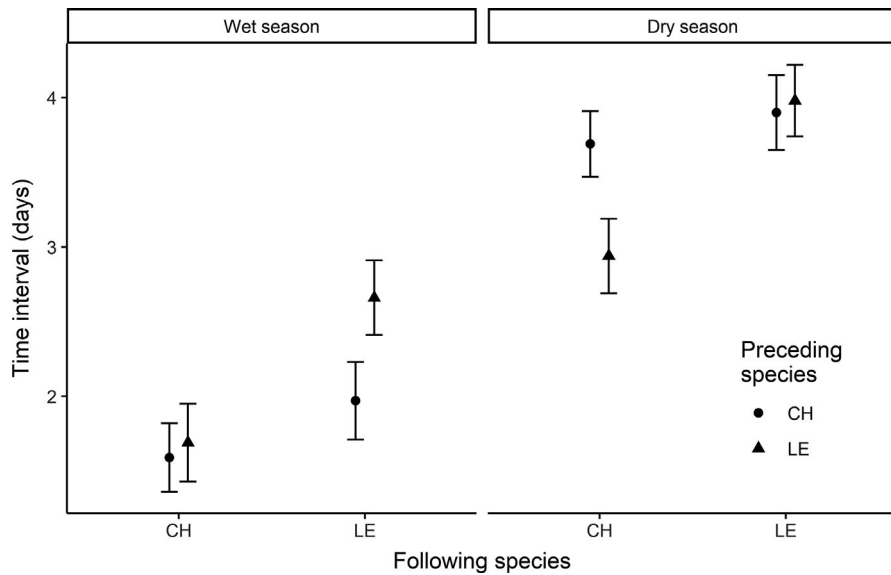
FIGURE 3 Time interval between visits for cheetah and leopard at scent-marking sites in response to the preceding and following species and season. Error bars show standard errors. CH, cheetah; LE, leopard

TABLE 2 Model estimates predicting the time interval between visits as a function of the visiting species (cheetah/leopard), the preceding species (cheetah/leopard) and the season (wet/dry) for cheetahs and leopards at scent-marking sites in north-central Namibia between 2005 and 2014. Species = following species; SpeciesP = preceding species; [Le] = leopard; [Dr] = dry. Model goodness of fit is estimated based on the marginal coefficient of determination (r^2 glmm(m)) and the conditional coefficient of determination (r^2 glmm(c); see Methods)

Fixed effects	log(β)	log(SE)	B	p
(Intercept)	0.46	0.23	1.59	0.05
Species[Le]	0.21	0.17	1.24	0.22
SpeciesP[Le]	0.06	0.17	1.06	0.73
Season[Dr]	0.84	0.20	2.32	5.11E−3***
Species[Le] × SpeciesP[Le]	0.24	0.22	1.28	0.27
Species[Le] × Season[Dr]	−0.15	0.20	0.86	0.44
SpeciesP[Le] × Season[Dr]	−0.28	0.20	0.75	0.16
Random effects	**Variance**	**SD**		
Site	0.26	0.51		
Survey	0.08	0.28		
Residuals	2.16	1.47		
Model goodness of fit	**Coefficient**			
r^2 glmm(m)	0.06			
r^2 glmm(c)	0.19			

*$p < 0.5$, **$p < 0.01$, ***$p < 0.001$.

4 | DISCUSSION

Our results demonstrate that shared scent-marking sites are common on north-central Namibian farmland. Moreover, the proportion of visits by leopards was considerably higher (30% of all visits) than the proportion of combined visits by leopards, lions, spotted hyaenas and African wild dogs in KwaZulu-Natal (6% of all visits) (Cornhill & Kerley, 2020a). This suggests that the biological significance of interspecific communication may greatly vary across local and regional contexts and ultimately species ranges, and might be influenced by carnivore population densities.

Our findings support the hypothesis of spatial partitioning of sites, which may reduce interference competition at shared sites. Additionally, monitored sites were frequently unvisited, yet site selection differed over time. This suggests alternative availability of marking sites within the landscape. Temporal stability of cheetah communication hubs is high (Melzheimer et al., 2020); thus, it is unlikely that changes in site selection are caused by territorial shifts following takeovers. One explanation may be that environmental change over time alters site characteristics preferred by both species. Alternatively, increasing leopard densities, as is likely the case on Namibian farmlands (Richmond-Coggan, 2019), may reduce availability of cheetah marking

sites. We identified an increase in the proportion of leopard-specific sites, which may interfere with cheetah marking behaviour.

Cheetahs visited marking sites more frequently compared with leopards, but leopards may be more flexible in marking as they exhibit a boundary scent-marking strategy (Bothma & Coertze, 2004; Rafiq et al., 2020). Cheetahs may also need to return quicker to marking sites as it is suggested that cheetah marking fluid loses its attraction to conspecifics after only 24 hours (Eaton, 1974). Frequent visits to making sites might inadvertently expose cheetahs to risk of predation by leopards, which may be a potential limiting factor for cheetahs.

We recorded crepuscular activity by both species, but with temporal partitioning at dawn and dusk. This reinforces knowledge that cheetahs adapt their activity patterns in response to risk (Bissett et al., 2015; Cozzi et al., 2012; Hayward & Slotow, 2009). However, activity overlap with leopards was high, so cheetahs likely also respond to the presence of this dominant predator at a finer scale (Broekhuis et al., 2013; Cornhill & Kerley, 2020a; Vanak et al., 2013).

We did not identify a stronger avoidance response of cheetahs to leopards (and *vice versa*) than to conspecifics. This suggests that delayed intraspecific communication by cheetahs resulting from predator avoidance may be limited in our study area. Importantly, our level of analysis differed from the analysis done by Cornhill and Kerley (2020b), whom compared time intervals between visits of the same individual for records with/without passage of a predator in-between. While this may allow more detailed analysis of individual responses, our findings remain relevant to understanding spatiotemporal interactions at the carnivore guild level.

Responding to the presence of dominant predators may require the detection of their scent marks. The lack of a stronger avoidance response may be attributed to the relatively low occurrence of recorded marking behaviours during individual visits. We acknowledge the bias of underestimating this proportion based on our camera trap procedure. Therefore, we recommend further consideration of behavioural responses to different olfactory cues using appropriate study designs, notably because experimentally placed predator scent affects cheetah behaviour (Cornhill & Kerley, 2020a).

The different types of marking behaviour by cheetahs and leopards may have evolved as a predator avoidance mechanism. Cheetahs scent-mark relatively more frequent through defecating, and their urine lacks important odorous sulphur compounds as well as a felid-specific urinary odour compound (tomcat compound or 3-mercapto-3-methylbutanol) associated with territorial marking (Apps et al., 2014; Burger et al., 2006). Therefore, olfactory cues of cheetahs may be non-detectable for their predators (Burger et al., 2006). Investigating the occurrence of countermarking between cheetahs and dominant predators would provide further insights on the direction of information flow at the guild level (Apps et al., 2019).

We found a seasonal response in time interval between visits. While for leopards this may be associated with seasonality in breeding and advertisement of reproductive status (Balme et al., 2013), cheetahs do not have a particular breeding season (Wachter et al., 2018). This response may also be associated with seasonal differences in environmental conditions that affect detectability of olfactory cues (Alberts, 1992; Reed et al., 2011; Wilder et al., 2005) and could possibly increase the risk of cheetahs encountering leopards at marking sites during the wet season. Alternatively, seasonal changes in prey and water availability may influence ranging behaviour and thus frequency of visits.

We did not account for intraspecific differences in leopards possibly affecting cheetah use of marking sites. Male and female leopards may present different levels of threat due to differences in their body size and in the time of the day when different sexes are most active (Havmøller et al., 2020). Cornhill and Kerley (2020a) identified variation in cheetah sensitivity to risk imposed by different predator species, but it remains to be assessed whether this is a species-specific or a body size response. Similarly, different spatial strategies in cheetahs (territorial vs. floater, see Melzheimer et al., (2018)) may result in different visitation patterns and/or avoidance responses, but GPS collar data are required to ascertain these strategies. Female cheetahs were captured infrequently by camera traps at marking sites, so our results reflect avoidance mechanisms of male cheetahs to leopards. We also acknowledge that our sampling may be biased towards detecting cheetahs, as the initial objective of the camera trap surveys was targeted to cheetahs.

In conclusion, we provide insights on scent-marking and spatiotemporal partitioning of marking sites by two competing carnivores on Namibian farmland. Cheetahs may avoid dominant predators by visiting marking sites at different times of the day, and by changing site selection to be the only carnivore that exclusively uses certain sites. These strategies may limit interference by leopards, but cheetahs likely also rely on more immediate cues. We recommend further research to better understand behavioural responses of predators to marking by other species in the carnivore guild, as well as the influences of environmental conditions, and intra- and interpopulation variability. Scent-marking sites play important roles in the functioning of carnivore communities (Apps et al., 2019); hence, we highlight the importance to protect and restore prominent natural features across semi-arid savannah ecosystems (Marker-Kraus et al., 1996; Walker et al., 2016).

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