Varying degrees of spatio-temporal partitioning between large carnivores in a fenced reserve, South Africa

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Running page head: Carnivore spatio-temporal partitioning

Abstract

Context. The spatio-temporal partitioning of large carnivores influences interspecific competition and co-existence within small, enclosed reserves. Lions (*Panthera leo*), spotted hyaenas (*Crocuta crocuta*), and leopards (*Panthera pardus*) are the three largest African carnivores and have the greatest potential for intra-guild competition, particularly where space is limited.

Aim. To investigate the spatio-temporal partitioning between lions, hyaenas, and leopards in a small (*ca* 68 000 ha), enclosed nature reserve in South Africa; Madikwe Game Reserve (MGR), South Africa.

Methods. We deployed 110 camera traps across MGR from 26/08/2019 to 6/05/2020. Von Mises kernel density plots were used to investigate daily temporal partitioning between the three species. A multiple-species, single-season occupancy model was used to investigate daily spatial occupancy patterns.

Key results. We found both temporal and spatial exclusion between lions and spotted hyaenas on MGR. However, no evidence was found of spatio-temporal partitioning between lions and leopards, and spotted hyaenas and leopards.

Conclusions. Exploitative and interference competition on MGR might be high enough to warrant spatio-temporal partitioning between lions and spotted hyaenas to avoid the negative effects of intra-guild competition. Contrastingly, patterns observed between leopards and the lions and spotted hyaenas preclude the possibility of top-down control by superior carnivores.

Implications. These findings call for an adaptive management approach, where both carnivore and prey species composition are constantly monitored. Management strategies such as these will allow for the conservation of valuable resources (i.e. prey species) to ensure persistence of large carnivore populations across African ecosystems.

Keywords: activity patterns, Africa, camera trap, carnivores, intra-guild competition, niche partitioning, niche separation, occupancy

Introduction

Large carnivores (>20 kg) are integral to ecosystems through their potential of top-down control of ecological communities (Ripple *et al*. 2014). The coexistence of large carnivores is influenced through processes such as interspecific competition for shared resources, such as food and habitat (Vanak *et al.* 2013). Given the crucial role that large carnivores play in maintaining ecosystem functioning, their globally declining numbers (owing to habitat loss, human–wildlife conflict, and poaching) are alarming (Miller *et al*. 2001; Goldberg *et al*. 2015). Accurate population biology, abundance and guild-structure assessments of large carnivores within their remaining natural ranges are key to assisting in appropriate conservation plans (Pettorelli *et al*. 2010). Understanding the dynamics of intraspecific and interspecific interactions, an important component of intra-guild competition, is crucial to sustaining each

species' numbers (Hayward *et al*. 2007*a*; Yiu *et al.* 2017). Research on carnivore space use and how it is influenced by the presence of other carnivore species (Steyn and Funston 2009) furthers our understanding of intra-guild competition (Caro and Stoner 2003; Donadio and Buskirk 2006), potential spatial avoidance or partitioning, and, ultimately, population persistence (Steyn and Funston 2009; Périquet *et al*. 2014).

Africa is unique because it hosts the only largely intact large carnivore guild worldwide (Hayward and Slotow 2009). Spotted hyaenas (*Crocuta crocuta*), leopards (*Panthera pardus*) and lions (*Panthera leo*) are the dominant large carnivores in Africa, and, subsequently, the most prone to intra-guild competition (Hayward and Slotow 2009; Vanak *et al.* 2013; Pereira *et al*. 2014; Périquet *et al.* 2015). Spotted hyaenas are flexible in their behaviour, habitat tolerance and preferred prey species (Holekamp and Dloniak 2010). The wide dietary breadth of spotted hyaenas can lead to a high degree of prey overlap with other carnivores, most notably lions (~60% overlap; Hayward 2006; Hayward and Kerley 2008; Périquet *et al.* 2014; Comley *et al.* 2020*a*). Leopards are the most widespread large carnivore found throughout Africa (du Preez *et al*. 2014; Swanepoel *et al*. 2015; Jacobson *et al*. 2016). Owing to their smaller body size and solitary hunting strategy (Estes 2012), leopards are subject to a high degree of exploitative competition from lions and spotted hyaenas (Caro and Stoner 2003). Lions' large body size and social hunting behaviour make them the most dominant African carnivore (Packer *et al*. 1990; Mosser and Packer 2009). Lion population numbers are increasing in South Africa (Bauer *et al*. 2015), which calls for appropriate management strategies as these increased numbers affect intraspecific dynamics and other carnivore species through increased competition (Hayward and Hayward 2006; Hunter *et al*. 2007; Miller *et al*. 2013).

One way to help conserve species, including large carnivores, is through translocations and reintroductions to nature reserves (Breitenmoser et al. 2001). Through the active reintroduction of large carnivores into nature reserves, enclosed reserves have promoted large carnivore conservation in South Africa (Hayward et al. 2007b; Hunter et al. 2007; Hayward and Somers 2009). However, in South Africa, these nature reserves are often small and fenced (with predator-proof fencing; Hayward et al. 2007a) and require intensive management interventions (Smith 2006; Hayward and Somers 2009; Rostro-García et al. 2015). Consequently, successful reintroductions necessitate constant monitoring of large carnivore populations within these reserves to understand the dynamics within populations and inter-species processes (Hayward et al. 2007b; Trinkel et al. 2008).

The spatio-temporal utilisation and partitioning of large carnivores in these small, enclosed reserves is still poorly understood (Vanak et al. 2013; Yiu et al. 2017; Comley et al. 2020b). Various studies have focused on the interactions between lions and spotted hyaenas (e.g. Trinkel and Kastberger 2005; Watts and Holekamp 2008; M'soka et al. 2016; Sogbohossou et al. 2018) and lions and leopards (e.g. du Preez 2014; Stein et al. 2015; Balme et al. 2017a). Little research has been published on the effects of leopard activity on spotted hyaena activity (or vice versa), even though these two species have reported temporal activity overlaps of between 80% (Hayward and Slotow 2009) and 90% (Comley et al. 2020b). It seems that the activity overlap depends on both leopard and spotted hyaena abundance (Bothma and le Riche 1984; Balme et al. 2007).

Increased competition between large carnivore species through artificially high population densities (or rapid population growth) and the associated high degrees of territory overlap because of restricted space (Palomares and Caro 1999; Hayward and Kerley 2008) are points

of concern and require monitoring and research (Ewen *et al*. 2012). This is particularly true in South Africa, where a large diversity of carnivore species is found throughout various fenced nature reserves throughout the country (Wentzel *et al*. 2021). With most large carnivore population numbers increasing in fenced nature reserves in South Africa (Miller and Funston 2014; Bauer *et al*. 2015; Welch and Parker 2016), these populations require effective management. Obtaining data on intra-guild competition and the effect large carnivores can have on each other is crucial to develop these effective management strategies. Therefore, our study aimed to determine whether spatial and temporal partitioning among lions, spotted hyaenas and leopards exists in the Madikwe Game Reserve (hereafter Madikwe) in South Africa. Madikwe was chosen because it has all three species, which are closely monitored by North West Parks and Tourism Board (NWPTB) reserve personnel through direct observation and camera traps. The study looked at: (1) determining temporal activity overlap between pairwise combinations of the three species; (2) investigating lion, spotted hyaena and leopard spatial use in a spatially explicit system on Madikwe; and (3) comparing lion, spotted hyaena and leopard conditional space-use in a spatially explicit system on Madikwe.

Materials and methods

Study site

Madikwe (including two private concessions that are open to Madikwe and which were also surveyed) is a ~75 000 ha provincial reserve situated in South Africa, bordering Botswana on the northern fence line of the park (24°45′02.2″S, 26°16′38.0″E; Fig. 1*a*). This tourism-based reserve has a wide variety of vegetation types, including mixed bushveld, Kalahari bushveld, arid sweet bushveld, and turf thornveld (Mucina and Rutherford 2006). The reserve is fenced with 150 km of electrified predator-proof fencing, enclosing approximately 86 mammal species. The two main topographical features that influence the park are the Dwarsberg

Mountains running along the southern border of the reserve and the Rant van Tweedepoort escarpment towards the north (Cox 2020). The rainy season on Madikwe extends from October to April, with temperatures averaging 30°C and an average rainfall of 701 mm (Cox 2020). The dry season is from May to September, with an average daily temperature of 23°C and an average rainfall of 82 mm (Cox 2020). There are approximately 81 (±3.96 s.d.) spotted hyaenas and 24 (±1.17 s.d.) leopards, estimated from the subadult to adult populations, on Madikwe (Honiball 2021). The lion population for Madikwe is known, and there were 33 adult and subadult individuals (four prides in total) at the time of this study (NWPTB, unpubl. data 2020).

Camera-trap set-up

On Madikwe, clustered camera traps were deployed from the 26 August 2019 until the 6 May 2020 (Fig. 1*b*) and serviced monthly. A clustered approach was used to deal with potentially low detections and maximise the area covered (Rich *et al.* 2019). To determine the cluster locations, a grid overlay consisting of 8 km by 8 km square blocks was generated in QGIS (Version 3.10; QGIS Development Team 2009) and overlayed over Madikwe (Fig. 1*b*). This grid size was used to encompass the smallest potential home range (i.e. female leopard home range of 34.8 km^2; Devens *et al.* 2018) of the study species to ensure the probability of detection was greater than zero (Karanth 1995; Odden *et al*. 2014). In addition, a 4 km by 4 km central block was established within these blocks to avoid overlapping cluster sites (Fig. 1*b*).

The camera traps (Cuddeback IR Model C1309) were placed within the central block. Sites were chosen on the basis of indications of the three large carnivore species (tracks/scat) or on the basis of the presence of suitable trees for baiting. Therefore, some camera traps were placed outside of the central blocks if no suitable sites were found within the central block. Each cluster contained five unbaited camera trap sites and five baited camera trap sites. Each site

consisted of two camera traps to photograph both left and right flanks of animals passing by and to improve the chance of survey detection (O'Connor *et al*. 2017). The mean spacing of camera traps was 469.06 m (±347.60 s.d.). Cluster sites were deployed for 21 days, after which they were moved to the next location. The cluster sites on the western side of the park were set up first, after which they were moved anti-clockwise to ensure that areas that would become inaccessible during the rainy season were covered first.

All camera traps were fixed to metal stakes by using wires and had a steel casing to protect them from adverse weather conditions and animal interference. Camera traps were placed 40–50 cm off the ground and were offset by 2 m to avoid flashing directly at each other. The grass was slashed, and any obtrusive vegetation was cut back around each camera trap to avoid camera traps triggering owing to vegetation movement. Each camera trap was placed facing a game trail or within a drainage line but never close to den sites or waterholes. Ideally, each camera trap was placed facing in a northerly or southerly direction to avoid the sun glare; however, this was not always possible because of the obstruction by vegetation or the direction of a game trail. Each camera trap was set to take four photos every 0.5 s when triggered by passing wildlife, with a delay of 30 s between separate trigger events. At night, the camera trap was set to take a single photograph with a delay of 30 s between separate trigger events because of the limitations of the camera trap settings.

Using impala meat provided by Madikwe from their annual predator management quota, 10 kg portions of bait were set up at half of the camera traps in each cluster to lure predators (Tumenta *et al*. 2010; Satterfield *et al*. 2017; Joubert *et al*. 2020). Trees with single, straight trunks were chosen for bait placement. A single piece of meat was tied with thick anchor wire ≥3.5 m from the ground. The wire was secured so that only the meat would fall when the bait was pulled,

and the wire would remain in place (i.e. no risk of injury to the animal). Baits consumed were not replaced, in which case the scent left behind acted as the lure (Joubert *et al*. 2020). Following the deployment methods outlined above, camera traps at bait sites were set up 2 m away from the baited tree. The following data were recorded from each camera trap site: unique camera ID, date placed, global positioning system (GPS) location, the habitat it was in, and elevation (m).

This study was conducted with ethical approval from the Nelson Mandela University Animal Ethics Committee (A19-SCI-NRM-001) and with North West Parks and Tourism Board's permission.

Data analyses

All camera trap photographs were processed in CameraBase (version 1.7; Tobler 2012). In CameraBase, photographs were sorted down to species level and sex wherever possible. Only photographs of leopards, spotted hyaenas and lions were imported. Data from the two camera traps at each cluster site were condensed (i.e. photographs of each camera trap station were combined), but different camera trap stations in the cluster were treated as separate points. The total number of independent photographic capture events per camera station was determined for each species. Using this information, a map was created in QGIS (version 3.10; QGIS Development Team 2009) for each species to determine where the animals were captured most frequently and which parts of the reserve each species preferred.

Temporal analysis

The database created by CameraBase was exported to Microsoft Excel (version 16.42), and the species and time of photographic capture data were extracted. Separate capture events were

determined as any captures more than 30 min apart (Rovero and Zimmermann 2016). Therefore, any captures that were within 30 min of each other were removed from the data. Captures containing more than one animal were treated as separate capture events (i.e. a capture with two individuals resulted in two capture events). Unbaited and baited camera traps were identified by assigning a zone value of '1' to unbaited camera traps and a zone value of '2' to baited camera traps. Times were converted into numerical values by changing the cell-formatting from 'Time' to 'General'. Because combining captures from both baited and unbaited traps for analysis could have confounded the results (i.e. the influence of bait on temporal patterns), the temporal analysis was run separately for unbaited and baited camera traps. Data were imported into RStudio (version 1.1.463; R Core Team 2018) interface in R (version 4.0.2). The numerical values for time were converted into radians (Ridout and Linkie 2009) in the 'overlap' package (version 0.3.3; Meredith and Ridout 2020) to be used for further analysis.

Von Mises kernel density plots were created for each separate species for the unbaited and baited data. Overlap plots and estimates were obtained for pairwise combinations of each species: leopards and spotted hyaenas, leopards and lions, and spotted hyaenas and lions. The estimator of overlap (denoted Dhat in the 'overlap' package, see Meredith and Ridout 2020), used to approximate densities, was set at 'Dhat 1' for sample sizes smaller than 50 (leopards and lions in the unbaited survey, lions in the baited survey) or 'Dhat 4' for sample sizes larger than 50 (spotted hyaenas across all surveys, leopards in the baited survey; Meredith and Ridout 2020). Confidence intervals were obtained using bootstrap estimates, with 10 000 permutations run. The 'basic0' confidence interval was used from the available output to adjust for bootstrap bias (Meredith and Ridout 2020).

Spatial analysis

A detection output file for each species was exported from CameraBase to Microsoft Excel. The detection output file consisted of detection and non-detection counts, '1' and '0' respectively, with one line representing one camera trap site. When there was no camera trap present at the site during the survey period (possibly owing to the rotation of camera trap stations), 'NA' values were indicated. One detection output file was created for each species. In total, 110 different lines represented the 55 unbaited camera traps and the 55 baited camera traps. Occasions were condensed into 5-day periods. A 5-day period was used to ensure that there were enough sampling occasions per camera trap, since each camera trap station was active for only 21 days. Model fit was evaluated using the 'parboot' function in 'unmarked' to ensure that the condensing interval of each species was appropriate. A separate covariate file was created in Excel, containing site-specific covariates for each camera trap site, including camera trap ID, GPS coordinates (latitude and longitude), elevation (m), vegetation types (grassland, *Dichrostachys* shrubland, grassland/shrubland, mountainous slope shrubland, riverside vegetation, dolomite koppie vegetation), and presence of bait ('yes' or 'no'). The detection files and the covariate file were imported into the RStudio interface. Covariates were tested for multicollinearity using a global model in the package 'olsrr' measuring variance inflation factors (VIF) and tolerance values (Hebbali 2020; version 0.5.3). No covariates indicated multicollinearity (VIF < 4.0 and tolerance value > 0.2) and were all used for subsequent analyses (Hair *et al*. 2010; Wang *et al*. 2018). We tested for model convergence by plotting the global model residuals using the 'qqnorm' function in RStudio. A multi-species, single-season occupancy analysis (Fiske and Chandler 2011; Rota *et al*. 2016) was run using the packages 'unmarked' (Fiske and Chandler 2011; version 1.0.1), 'ggplot2' (Wickham *et al*. 2020; version 3.3.2), and 'AICcmodavg' (Mazerolle 2020; version 2.3-1). Specifically, the 'occuMulti' function was used from the 'unmarked' package, which is based on the

methodology of Rota *et al.* (2016). This model accommodates for interactions among multiple species without the assumption of asymmetric interactions (i.e. a dominant and a subordinate species) and is the first to allow for the inclusion of covariates in co-occupancy modelling (Rota *et al.* 2016; Lahkar *et al*. 2021). Multi-species occupancy models provide an efficient approach to study community ecology, and it allows for reliable inferences about observed patterns (MacKenzie *et al*. 2017; Devarajan *et al*. 2020).

Because of the clustered location of the camera traps, our sites could not be considered as independent and, therefore, we used occupancy and occupancy probability only to inform on space use (Rovero and Zimmermann 2016). We retain the use of 'occupancy probability' in a traditional analytical sense, as described by MacKenzie *et al.* (2017). We acknowledge the importance and power that spatial autocorrelation can have in occupancy probability (Dormann *et al*. 2007; Gaspard *et al*. 2019) and that the 'occupancy probabilities' denoted going forward are, in essence, a calculation of space use probability.

The three separate detection files were collated within 'unmarked' to compare the space use between species and determine conditional occupancy values for the three species. Eight different occupancy models were created with varying influences on detection probability and occupancy probability (Table 1). Elevation and habitat type were used as covariates influencing the occupancy probability, and the presence or absence of bait was used as a covariate influencing the detection probability. The eight models were compared using the Akaike's information criterion (AIC; Burnham and Anderson 2004). The model with the lowest AIC value was considered the most parsimonious and was used to calculate detection and estimated occupancy probabilities. We reported the top five models with the lowest AIC values (see Appendix Table A1 for the full list of models with AIC values). Detection probabilities were

calculated for each species separately. The conditional occupancy probability (i.e. occupancy probability of a species conditional on the detection or non-detection of another species) was calculated for each possible pairwise combination (Rota *et al*. 2016). Because of the low sample size, no three-level interactions were considered.

Table 1. List of all eight occupancy models run for the spatial analysis of lion, leopard and spotted hyaena space use in the Madikwe Game Reserve.

Model number	Occupancy probability covariate	Detection probability covariate
Model 1	~1; constant	~1; constant
Model 2	~elevation	~1; constant
Model 3	~habitat	~1; constant
Model 4	~elevation + habitat	~1; constant
Model 5	~elevation	~baited
Model 6	~habitat	~baited
Model 7	~elevation + habitat	~baited
Model 8	~1; constant	~baited

Results

Descriptive results

In total, 79 of the 110 camera traps detected at least one of the three large carnivores. The unbaited camera traps produced 227 photographic detections across 1984 camera trap nights compared with 2384 photographic detections across 1863 camera trap nights for the baited camera traps. In total, 30 lion photographic capture events were recorded across both surveys (unbaited; $n = 13$ and baited; $n = 17$), with an average rate of 2.14 photographic capture events per camera trap where the species were detected ($n = 14$). In total, 339 spotted hyaena photographic capture events were recorded, with an average rate of 5.14 photographic capture events per camera trap ($n = 66$). Of those, 62 photographic capture events were recorded during the unbaited survey, compared with 297 photographic capture events recorded during the

baited survey. Lastly, 71 leopard photographic capture events were recorded (unbaited, $n = 18$; and baited, $n = 44$), amounting to an average rate of 2.37 photographic capture events per camera trap ($n = 30$). Lion detections were low overall, with most detections coming from baited camera traps in the northern part of Madikwe (Fig. 2a). Leopards occupied most of the reserve, with slightly higher detections around the northwest and central parts of Madikwe (Fig. 2b). Spotted hyaena detections were high throughout the entire reserve (Fig. 2c).

Temporal analysis

Lion activity was mainly crepuscular on Madikwe (Fig. 3a, d). There was an additional activity peak during the baited survey around the midday hours (Fig. 3d). Leopards (Fig. 3b, e) and spotted hyaenas (Fig. 3c, f) exhibited bimodal peaks in activity at dawn and dusk across baited and unbaited detections. A moderate degree of overlap (0.46) was observed between leopards and lions, with an increase in overlap to 0.60 in the baited survey (Fig. 4a, d, Table 2). The highest daily temporal overlap (0.79) was found between leopards and spotted hyaenas, which increased even further to 0.86 with the addition of bait to the camera trap (Fig. 4b, e, Table 2). The lowest overlap coefficient (0.38) was observed between spotted hyaenas and lions, increasing to 0.57 for the baited survey (Fig. 4c, f, Table 2).

Spatial analysis

No site-specific covariates had a statistically significant influence on the probability of occupancy ($P > 0.05$). However, the presence of bait had a significant effect on the probability of detection. The model with the lowest Δi (ΔAIC) value incorporated a constant (~1) occupancy probability for all species with a detection probability that varied according to whether a camera was baited or not (Table 3). Detection probabilities were higher for the baited survey than for the unbaited survey. The probability of detection was highest for spotted

hyaenas (0.39 ± 0.10 s.d.; Table 4) and lowest for lions (0.11 ± 0.08 s.d.; Table 4) in the baited survey. Leopards and lions had equal detection probability in the unbaited survey (Table 4). Lions had the lowest space use throughout the park but more frequently utilised areas where spotted hyaenas were not present, with the probability of occupancy dropping from 0.39 (±0.23 s.d.) to 0.28 (± 0.16 s.d.) in the presence of spotted hyaenas (Table 5). Similarly, spotted hyaena space use increased in areas without lions (Table 5). Spotted hyaena space use was also higher in areas with leopards, increasing from 0.62 (± 0.16 s.d.) to 0.87 (± 0.11 s.d.; Table 5). Leopards had the highest space use in areas with spotted hyaena presence, with a 0.33 increase in the occupancy estimate in areas with spotted hyaena presence (Table 5). The detection/non-detection of lions did not appear to influence leopard space use on Madikwe.

Table 2. Ranked Akaike information criterion (AIC), difference between the top-ranked model and the ith model (Δi), with AIC weight (Wi) of the top five models investigating the occupancy of lions, leopards and spotted hyaenas in the Madikwe Game Reserve, with covariates influencing the probability of occupancy (Ψ) and the probability of detection (p).

Model	nPars	AIC	Δi	Wi
Ψ(~1) + p(~baited)	12	1028.07	0.00	0.71
Ψ(~habitat) + p(~baited)	27	1030.07	2.00	0.26
Ψ(~elevation) + p(~baited)	15	1036.53	8.46	0.01
Ψ(~1) + p(~1)	9	1040.55	12.48	0.00
Ψ(~elevation + habitat) + p(~baited)	30	1043.17	15.10	0.00

nPars is the number of parameters in each model.

Discussion

Small, fenced, protected areas are common in South Africa, which may mitigate human–carnivore conflict and negative human influences (Hayward and Kerley 2009). However, they can perpetuate intraspecific competition within the large carnivore guild (Palomares and Caro 1999; Hayward *et al.* 2007*b*). Our study suggested little temporal overlap between spotted

hyaenas and lions on Madikwe (0.38; unbaited survey). Conversely, there was temporal overlap between spotted hyaenas and leopards (0.79; unbaited survey), and leopards and lions (0.46; unbaited survey). We observed an increase in temporal overlap for all pairwise species interactions at baited camera traps across the study site, indicating increased competition at sites where food was easily accessible. For all three species, temporal activity patterns appear partially resource-driven owing to the increase of temporal overlap between species in the presence of bait. Food acquisition might be favoured over the avoidance of competition among sympatric large carnivores (Cozzi *et al.* 2012; Maputla *et al.* 2015; Mugerwa *et al.* 2017). Spotted hyaenas and lions appeared to avoid each other spatially, whereas spotted hyaenas and leopards, and lions and leopards utilised similar areas. Hayward (2006) and Périquet *et al.* (2014) found that the high dietary overlap between lions and spotted hyaenas can lead to spatial partitioning between them to avoid interference competition. On Madikwe, lions and spotted hyaenas have the highest dietary overlap among the three large carnivores (80%), followed by leopards and spotted hyaenas (64%) and leopards and lions (54%; Honiball *et al.* 2021). A lower dietary overlap between leopards and the other two large carnivores (Hayward and Kerley 2008; Balme *et al.* 2017*b*; Havmøller *et al.* 2020; Honiball *et al.* 2021), and the consequently reduced chance of interference competition, could negate the need for spatial exclusion between leopards and spotted hyaenas, and leopards and lions.

Our results indicated that there was no temporal exclusion between leopards and lions. During the baited study, the coefficient of overlap increased to 0.60 (from 0.46; unbaited survey), indicating moderate temporal inclusion. Others also found a lack of temporal exclusion between leopards and lions (see Graf *et al.* 2009; Hayward and Slotow 2009; Balme *et al.* 2017*b*; Miller *et al.* 2018; Rafiq *et al.* 2020). Leopards and lions did not appear to affect each other spatially, similar to other studies (see Maputla *et al.* 2015; Miller *et al.* 2018; Balme *et*

al. 2019; Rafiq *et al*. 2020). The dietary overlap between lions and leopards (ranging from 35.1% to 58.6%; Hayward 2006; Hayward and Kerley 2008; Balme *et al.* 2017*b*) is less than that of lions and spotted hyaenas, potentially reducing the need for these carnivores to avoid each other in space. Lack of spatial avoidance could also be due to the cryptic colouration of leopards, allowing them to remain undetected for longer (Miller *et al*. 2018) or due to a low incurred cost of inhabiting similar areas (Balme *et al*. 2017*b*). Additionally, through behavioural changes such as prey caching, leopards can avoid interference competition by hoisting kills into trees (Stein *et al*. 2015; Balme *et al*. 2017*a*).

Leopards and spotted hyaenas on Madikwe did not avoid each other temporally, with a moderately high (0.79; unbaited survey) to very high (0.86; baited survey) degree of temporal overlap. Although few studies have investigated temporal partitioning between leopards and spotted hyaenas, there is some evidence to support our findings of no temporal partitioning between the two species (see Hayward and Slotow 2009; Comley *et al*. 2020*b*). A lack of spatial partitioning was also found between leopards and spotted hyaenas, with conditional occupancy increasing for leopards in the presence of spotted hyaenas, and spotted hyaenas in the presence of leopards. In particular, spotted hyaenas appeared to be present in areas utilised by leopards. Because spotted hyaenas are kleptoparasites, they could gain an advantage by occupying areas with leopards, increasing their opportunities to steal kills before leopards get a chance to hoist it (Höner *et al*. 2002). The preference of similar areas between leopards and spotted hyaenas on Madikwe, coupled with limited space, the high population density of spotted hyaenas, and the heterogeneous distribution of spotted hyaena space use could impede avoidance behaviours of leopards. Alternatively, patterns seen at the spatial and temporal level (spatial and temporal overlap instead of avoidance) could be driven by resource availability and behavioural plasticity (Maputla *et al*. 2015; Périquet *et al*. 2015; Rafiq *et al*. 2020). For

example, by seeking cover and caching prey in trees (Balme *et al.* 2017*a*), leopards might not need to change their spatial and temporal patterns to avoid spotted hyaenas actively.

On Madikwe, there was evidence of temporal exclusion between spotted hyaenas and lions (0.38; unbaited survey). However, temporal exclusion decreased slightly with the inclusion of a baited element (0.57), suggesting the benefit of a potential meal could outweigh the possible negative effects of interspecific competition. Although various studies have reported no temporal exclusion between lions and spotted hyaenas (see Hayward and Hayward 2006; Hayward and Slotow 2009; Comley *et al.* 2020*b*), temporal exclusion can vary on the basis of prey or predator densities, environmental factors and anthropogenic influences (Hayward and Slotow 2009; Schuette *et al.* 2013; Penido *et al.* 2017; Sogbohossou *et al.* 2018). However, being an enclosed reserve, direct anthropogenic effects (i.e. edge effects or human–carnivore conflict) are likely to be limited.

Additionally, spotted hyaenas and lions were more likely to utilise areas where the other species was not present; both spotted hyaena and lion conditional occupancy decreased in the presence of the other. The mutual decrease in occupancy suggests that spotted hyaenas and lions avoid each other spatially at the park-wide scale. These findings differ from those of other studies, which have largely indicated a high degree of spatial overlap between lions and spotted hyaenas in areas they both occupy (Périquet *et al*. 2014; Swanson *et al*. 2016). Dröge *et al*. (2017) found that spatial partitioning can also be influenced at smaller scales (e.g. at kill sites or during direct encounters) because of a high predator abundance in certain areas, which could explain the spatial avoidance observed on Madikwe between lions and spotted hyaenas. With the high density of spotted hyaenas on Madikwe and high dietary overlap between lions and

spotted hyaenas (80% on Madikwe; Honiball *et al.* 2021), spatial avoidance at the park-wide scale is likely to be necessary to mitigate intra-guild competition (Périquet *et al.* 2014).

Due to the small sample size for both lions and leopards, caution must be taken when making inferences from this research and it is important to note that spatial overlap between species Temporal overlap increased with the addition of a baited element at camera trap stations for each pairwise combination, and bait had a significant positive effect on detection probabilities for all three large carnivores. Baited studies have been shown to improve detection rates (du Preez *et al.* 2014; Satterfield *et al.* 2017; Joubert *et al.* 2020) and can aid in increasing capture rates to improve the accuracy of population estimates when targeting elusive species such as leopards (du Preez *et al.* 2014; Tarugara *et al.* 2019; Joubert *et al.* 2020). Furthermore, studies have shown that baits have little to no influence on ranging behaviours (Gerber *et al.* 2012; du Preez *et al.* 2014; Braczkowski *et al.* 2016) and temporal activity (Gerber *et al.* 2012; Braczkowski *et al.* 2016) and thus baited studies are still reliable for spatio-temporal analysis of large carnivores (Joubert *et al.* 2020). However, in our study, there was an additional peak in activity during midday for lions in the baited study. Although lions are mainly crepuscular and nocturnal (Hayward and Hayward 2006; Hayward and Slotow 2009), diurnal activity peaks still occur, primarily to capitalise on hunting opportunities (van Orsdol 1984; Power 2002). The peak in our data corresponded to a single event, during which a pride of lions (both males and females) was lying in front of one of the baited camera traps. Therefore, it is likely that the diurnal peaks observed during our baited study correspond to the opportunistic behaviour of lions in response to the bait.

Due to the small sample size for both lions and leopards, caution must be taken when making inferences from this research, and it is important to note that spatial overlap between species

does not necessarily lead to a high actual encounter rate at a fine scale (e.g. at kill sites; du Preez *et al.* 2015). Contrastingly, spatial avoidance between species does not preclude the possibility of fine-scale and opportunistic encounters, for example, at carcasses. Although our best-fit model did not include vegetation type as a covariate, habitat is still an important influence on spatio-temporal partitioning in large carnivores (Périquet *et al.* 2014; Maputla *et al.* 2015; Swanson *et al.* 2016; Rafiq *et al.* 2019). Leopards are highly adaptable and can use a wide range of terrains for hunting (Odden *et al.* 2014; du Preez *et al.* 2017). The plasticity of their hunting behaviour enables leopards to exploit niches that neither spotted hyaenas nor lions can. In addition, their tree-climbing abilities (with or without a kill; Balme *et al.* 2017*a*) also allow leopards to coexist with spotted hyaenas and lions in the same area, without the need for spatio-temporal partitioning. However, spotted hyaenas require more expansive, open areas to run down prey (Kruuk 1972; Périquet *et al.* 2014), whereas lions require vegetation cover to stalk their prey (Funston *et al.* 2001; Hopcraft *et al.* 2005). Even though habitat type did not significantly influence spatial partitioning on Madikwe, it was an important influence on occupancy in our second-best model, and thus it is still an important influence to consider when evaluating large carnivore space use. Lastly, prey distribution and density play a vital role in the spatio-temporal partitioning of large carnivores (Hayward *et al.* 2007*a*; Ramesh *et al.* 2012; Swanson *et al.* 2016). However, baits at camera traps can negatively affect the capture of prey species (Rocha *et al.* 2016; Mills *et al.* 2019). Therefore, our study cannot account for the influence of prey on the conditional space use of the three large carnivores on Madikwe. Even though the prey population could not be accounted for, and habitat type was not found to significantly influence spatial patterns of the three large carnivores on Madikwe, our results still provide insights into spatio-temporal partitioning among leopards, spotted hyaenas and lions.

Increasingly, fine-scale behavioural and habitat changes are being examined to explain patterns observed in carnivore space and time use (du Preez *et al*. 2015). Moving forward, these are components that should be included in spatio-temporal analysis of carnivore communities to further our understanding of coexistence facilitation. In small, fenced reserves, ensuring adequate habitat (tall trees and dense bush) can become a management priority when targeting the conservation of leopards. Especially in areas with high spotted hyaena densities, as is the case for Madikwe, there is always a risk of leopard population decline because of them being outcompeted (Comley *et al*. 2020*a*). Therefore, monitoring predator populations is crucial in any reserve (Packer *et al*. 2013; Winterbach *et al*. 2013; Elliot *et al*. 2020) and should be one of the focal management goals on Madikwe. Given the spatial and temporal exclusion between spotted hyaenas and lions on Madikwe at the park-wide scale, consistent carnivore monitoring will provide an 'early warning' system to alert managers who can intervene appropriately to prevent the loss of crucial large carnivore biodiversity.

In addition to predator monitoring, an ecosystem-based approach that involves monitoring resource heterogeneity and prey composition is necessary for management plans moving forward. The resource-driven patterns of spatio-temporal partitioning call for a close examination of prey populations on any reserve (Périquet *et al*. 2014, 2015; Maputla *et al*. 2015). If predators change their prey preference on the basis of intra-guild competitive effects, any change to prey composition could increase interference competition and even localised extinction (Périquet *et al*. 2014; Creel *et al.* 2018). The lack of evidence for top-down control in many large carnivore intra-guild interactions, as seen on Madikwe when examining patterns between leopards and lions, and leopards and spotted hyaenas, further promotes ecosystem landscape-level approaches to carnivore management (Sanderson and Trolle 2005; Rafiq *et al*. 2020). The landscape of fear might not be as important as hunting opportunities when shaping carnivore distribution patterns, calling for an adaptive management strategy that encompasses

all aspects influencing spatio-temporal partitioning (Wallach *et al*. 2015; Swanson *et al*. 2016; Balme *et al*. 2019). Intra-guild competition incorporates both benefits and costs and can change at any moment (Périquet *et al*. 2014). Therefore, continuous monitoring, in combination with adaptive management, is key in ensuring large carnivore persistence in small, fenced reserves.

Conclusion

Spatio-temporal patterns among lions, spotted hyaenas and leopards on Madikwe provide an insight into intra-guild competition among large carnivores. Owing to generally high dietary overlap between lions and spotted hyaenas and a high density of the latter species (approximately 10.8 spotted hyaenas per 100 km^2) on Madikwe, lions and spotted hyaenas appear to exclude each other in space and time. Contrastingly, lions and leopards do not appear to actively avoid each other, whereas spotted hyaenas and leopards utilise similar areas. The facilitation of this coexistence could be due to lack of top-down control, behavioural changes that lead to a decrease in direct competition, and fine-scale habitat-use patterns that influence the potential for spatio-temporal overlap (Cozzi *et al*. 2012; Rich *et al*. 2017). Uncovering patterns such as those in this study provide key insights into large carnivore spatio-temporal partitioning, directly influencing future management strategies. By improving our understanding of interactions within the large carnivore guild, robust adaptive management plans can be put in place to conserve species that are key to the functioning of African ecosystems.

Conflicts of interest

The authors declare no conflicts of interest

Acknowledgements

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