Spatial and temporal overlaps between leopards (*Panthera pardus*) and their competitors in the African large predator guild

K. Rafiq[1,2] (iD), M. W. Hayward[3,4] (iD), A. M. Wilson[5], C. Meloro[1] (iD), N. R. Jordan[2,6,7], S. A. Wich[1], J. W. McNutt[2] & K. A. Golabek[2]

[1]School of Natural Sciences and Psychology, Liverpool John Moores University, Liverpool, UK
[2]Botswana Predator Conservation Trust, Maun, Botswana
[3]School of Environmental and Life Sciences, University of Newcastle, Newcastle, NSW, Australia
[4]Centre for African Conservation Ecology, Nelson Mandela University, Port Elizabeth, South Africa
[5]Structure and Motion Lab, Royal Veterinary College, University of London, Hatfield, UK
[6]Centre for Ecosystem Science, University of New South Wales, Sydney, NSW, Australia
[7]Taronga Conservation Society, Dubbo, NSW, Australia

Abstract

Understanding the mechanisms facilitating coexistence within species assemblages is a key consideration for conservation as intact assemblages are necessary for maintaining full ecosystem function. The African large predator guild represents one of the few remaining functionally intact large predator assemblages on Earth, and as such, represents a unique study system to understand competitive interactions. Yet, relatively little is known of the coexistence mechanisms between some of its intermediately sized members, particularly leopards (*Panthera pardus*). Here, we use overlapping spatio-temporal activity and GPS data on lions (*Panthera leo*), leopards, African wild dogs (*Lycaon pictus*) and cheetahs (*Acinonyx jubatus*) to examine spatial interactions and temporal partitioning between leopards and other guild members in northern Botswana. We found that at the population level, male leopard space use and activity patterns were largely unaffected by intraguild competitors. Leopards showed minimal movement coherence with competitors (avoidance or attraction) when moving through areas of home ranges shared with intraguild species. Moreover, we found evidence to support the hypothesis that guild species' activity patterns are primarily driven by light availability rather than predator avoidance. Our results suggest predator avoidance has a limited impact on broad-scale leopard spatio-temporal niches, with aspects of the leopards' ecology and life history likely facilitating its ability to thrive in close proximity to competitors. Considered alongside other studies, our results suggest that landscape-level approaches to conservation may be suitable for aiding leopard conservation.

Introduction

Competition is an important structuring force within species assemblages and can impact species distributions (Berger & Gese, 2007), densities (Creel & Creel, 1996), population dynamics (Chesson & Kuang, 2008) and behaviours (e.g. space and time use; Mori, Ferretti, & Fattorini, 2019). These processes can be impacted through exploitation competition, where species respond to limited resource availability caused by competitor resource use (Sarà *et al.*, 2005). They can also be impacted through interference competition, where resource access is limited directly, during physical confrontations between species, and/or indirectly through the risk or fear of encountering competitors and the costs that may be incurred (Du Preez *et al.*, 2015; Palomares and Caro, 1999; Willems & Hill, 2009). Across many landscapes, predation risk has a heterogeneous spatio-temporal distribution (Willems & Hill, 2009; Creel, Winnie, & Christianson, 2013; Oriol-Cotterill *et al.*, 2015). Heterogeneity is thought to be a critical component for coexistence between species (Chesson, 2000), and a species' perception of this landscape of risk influences their movements and activity patterns (e.g. Du Preez *et al.*, 2015; Oriol-Cotterill *et al.*, 2015). Indeed, within some ecosystems, spatial and temporal partitioning are thought to be key components in facilitating coexistence between competitors (Durant, 1998; Hayward & Slotow, 2009).

Understanding the mechanisms facilitating coexistence between sympatric large carnivores is relevant to ecosystem

functioning because such species often provide key ecosystem and economic services that have disproportionally large effects relative to that species' density (Estes *et al.*, 2011; Ripple *et al.*, 2014). For example, large carnivores can help regulate ecosystem function through mesopredator suppression (Ripple *et al.*, 2014) and can provide public health benefits to coexisting human populations (Braczkowski *et al.*, 2018). These effects, however, are context-dependent, with species assemblages being one of the key contextual factors influencing carnivore impact and with intact communities of predators thought to support higher biodiversity (Haswell, Kusak, & Hayward, 2017). Maintaining intact predator assemblages is thus important in maintaining full ecosystem function (Haswell *et al.*, 2017), and understanding the mechanisms facilitating coexistence within such assemblages is critical to conservation (Winterbach *et al.*, 2013).

The African large predator guild is one of the few remaining functionally intact large predator assemblages on Earth and, as such, represents a unique study system to understand coexistence (Dalerum *et al.*, 2009). This large predator guild exhibits intense interspecific competition between its six largest species – lion (*Panthera leo*), spotted hyaena (*Crocuta crocuta*), leopard (*Panthera pardus*), African wild dog (*Lycaon pictus*), cheetah (*Acinonyx jubatus*) and brown hyaena (*Hyaena brunnea*) (e.g. see Swanson *et al.*, 2014; Périquet, Fritz, & Revilla, 2015). In general, this guild exhibits a size-mediated asymmetrical dominance hierarchy, with the circumstances of encounters (e.g. competitive group size) impacting their outcomes (Cooper, 1991; Lehmann *et al.*, 2016). Intraguild studies involving leopards have often focussed on competition between leopards and lions (e.g. Du Preez *et al.*, 2015; Miller *et al.*, 2018), despite the fact that leopards co-occur and compete with other guild members across their African range. As such, relatively little is known of spatio-temporal interactions involving leopards and other members of the guild (but see Vanak *et al.*, 2013; Rafiq *et al.*, 2019).

We used high-resolution GPS data collected from GPS collars deployed on sympatric lions, leopards, wild dogs and cheetahs in northern Botswana to investigate spatial interactions and temporal partitioning between male leopards and other large predator guild members. Spotted hyaena and brown hyaena were not included within this study because of a lack of GPS data. First, we investigated the potential for interactions between leopards and their competitors by measuring the extent to which dyads (pairs) of GPS collared leopards and competitors used shared areas of their respective home ranges. We then investigated dynamic interactions within leopard-competitor dyads, that is, if there was avoidance or attraction between dyad members when moving through shared areas. We hypothesized that if the risk associated with meeting a competitor has an impact on leopard space use at the scale of our analyses, there would be negative movement coherence, that is avoidance, within leopard–lion and leopard–wild dog dyads but that there would be no movement coherence with cheetahs. We predicted this because of (1) the high-mortality risks associated with lion encounters (Bailey, 2005; Balme *et al.*, 2013);and (2) the higher levels of asymmetry in competitive body mass between leopards and lions, and leopards and

wild dog packs (cumulative mass),than between leopards and cheetahs (Kingdon, 2013).

We then extended the temporal analyses of Cozzi *et al.,* (2012), which focused on lion, wild dog and cheetah activity patterns, to also include leopards. In the process, we tested two hypotheses concerning temporal partitioning between leopards and other guild species: (1) that leopard activity patterns are primarily driven by competitor avoidance and (2) that leopard activity patterns are more so driven by light availability (Cozzi *et al.*, 2012). Under the predator avoidance hypothesis, we predicted that leopards would have lower activity levels when lions and wild dogs are most active because of the risks associated with encounters (Cozzi *et al.*, 2012).We predicted that under the light availability hypothesis, leopard activity would increase in the twilight hours because light levels are low enough to aid hunting but still high enough to detect prey.

Materials and methods

Study area

The study covered an area of approximately 2600 km^2 and was located in northern Botswana on the south-eastern fringes of the Okavango Delta (Fig. 1). The study area included Moremi Game Reserve and two wildlife management areas (NG33/34) that were primarily used for photographic tourism. The landscape was a mosaic of habitat types but was dominated by mopane (*Colophospermum mopane*) and *Acacia* species woodlands (Broekhuis *et al.*, 2013). Annual precipitation was approximately 450 mm. Seasons were defined using historical rain data collected in a standard rain gauge by the Botswana Predator Conservation Trust at the core of the study area (−19°52'S, 23°63'E). For each year, the wet season was defined as taking place when the first measurable rainfall was recorded in the second half of the year and concluded on the date of the last recorded rainfall in the first half of the following year (i.e. running from approximately November until March). The dry season spanned the remainder of the year. Large carnivore densities within our study area were estimated as 1.90 (95% confidence intervals: 1.30–2.94) lions; 1.70 (0.78–4.53) male leopards; 2.40 (1.38–5.33) wild dogs; and 0.6 (no confidence intervals provided by study) cheetahs per 100 km^2 (Broekhuis, 2012; Rich *et al.*, 2019).

Data collection

From November 2011 to January 2018, we fitted 21 African wild dogs (from 11 packs), 14 lions (from 4 prides and 3 male coalitions), 8 male leopards and 5 cheetahs with GPS collars developed by the Royal Veterinary College (Wilson *et al.*, 2013). Male leopards (for brevity, herein leopards) and both sexes of lions, wild dogs and cheetahs were GPS collared. Details on collar deployment times and durations, time overlaps between collared individuals and social groups of collared individuals can be found in Fig. S1. GPScollars had inertial-measurement-unit activity derived GPS sampling rates, typically ranging from five fixes per minute, during periods of movement, to hourly fixes, during periods of rest (Wilson
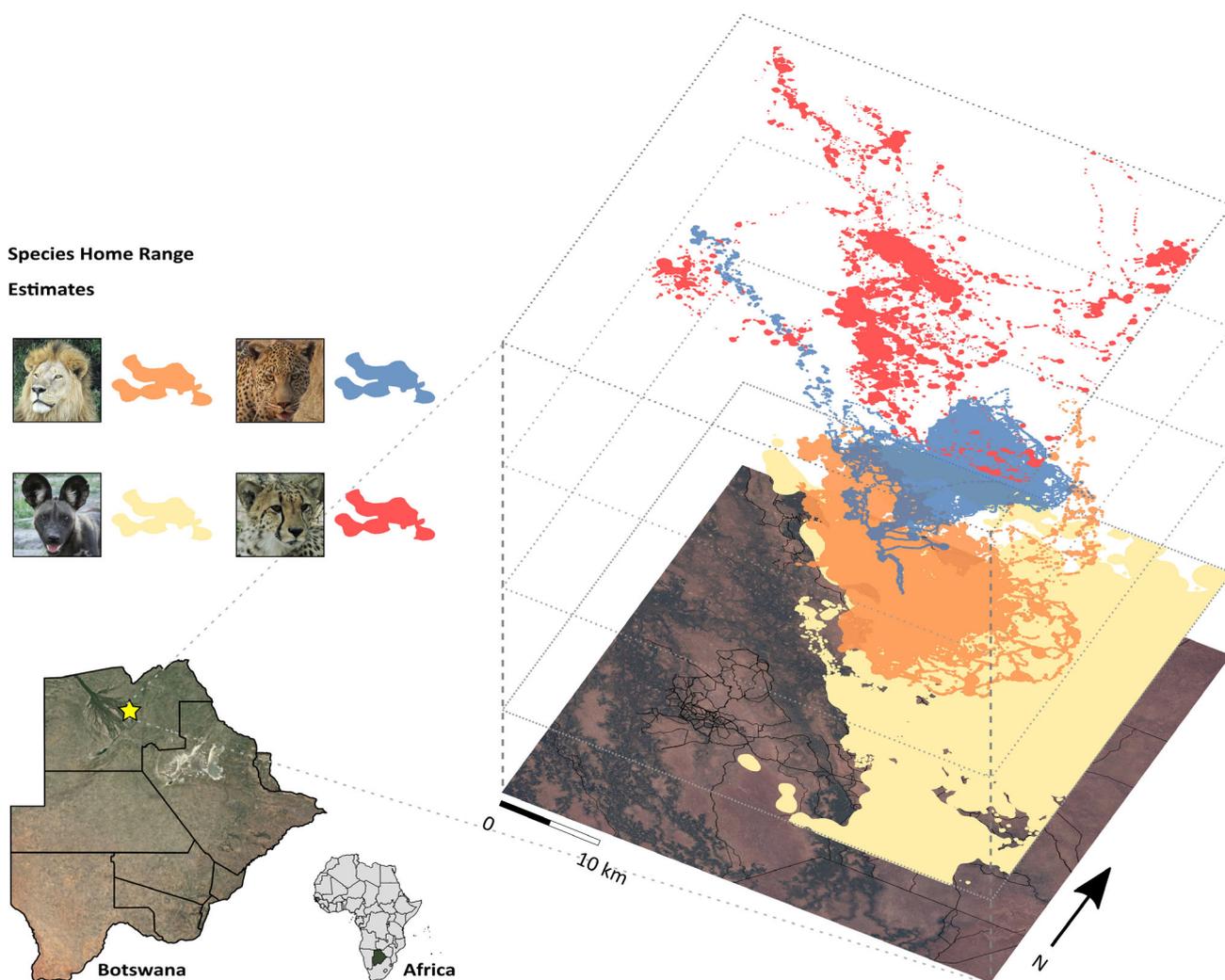
Figure 1 Map of the core study area showing its location within Botswana, Botswana's location within Africa (darkened), and the home ranges of the GPS collared large carnivore species. Home ranges were derived from 95% kernel utilization distributions for each collared individual (or pack of wild dogs) using Brownian Bridge Movement Models. The core study area map was created using Bing satellite imagery obtained within the QGIS OpenLayers Plugin (Kalberer and Walker 2018). [Colour figure can be viewed at zslpublications.onlinelibrary.wiley.com]

et al., 2013).Collars also continuously recorded and binned into 30 s windows triaxial accelerometer data, with each window having two activity measurements recorded for the three axes. These measurements were (1) the largest peak-to-peak acceleration over the 30 s window and (2) the mean of the mean acceleration values calculated over 15 x two second blocks within the 30 s window (Hubel *et al.*, 2018).

We initially located un-collared target carnivores through a combination of spoor-tracking, opportunistic sightings and baits. Once located, target carnivores were immobilized by a Botswana-registered veterinarian. Immobilization drug cocktails typically contained two or more of ketamine, medetomidine, xylazine and Zoletil, depending on the species being immobilized and estimated target weights (see Wilson *et al.*, 2013, 2018; Hubel *et al.*, 2016). During immobilizations, we prioritized collar attachment and collected body measurements and biological samples, if time permitted. During this time, we monitored the individual's vital signs, typically completed all work on immobilized individuals within 60 min, and provided drug reversals immediately after completion. Collar weights were less than 2% of carnivore body masses and weighed ~ 970 g for lions, ~550 g for leopards and ~ 340 g for cheetahs and wild dogs. We either removed collars following battery expiry or fitted collars with a degradable cotton strip or mechanical drop off unit (Sirtrack, New Zealand).All work was approved by Botswana's Department of Wildlife and National Parks under research permit numbers 'EWT 8/ 36/ 4 xxxv (31)' and 'EWT 8/ 36/ 4 xxxviii' and by Liverpool John Moores University's ethical committee, under permit 'CM_KR/ 2016-7'.

GPS collar data were available to download *via* UHF radio link, and we visited animals every two to three weeks by

ground vehicle to communicate with collars and check on their welfare. Mean (±standard deviation) data collection days per collar deployment were 356.67 (±277.80) days for lions; 200.44 (±111.76) days for cheetahs; 190.90 (±51.70) days for leopards; and 176.89 (±131.47) days for wild dogs.

We carried out all post-download data processing and statistical analyses in the R language and environment for statistical computing (R Core Team, 2018).

Preparing spatial data

To prepare data for spatial analyses, we removed GPS fixes with horizontal accuracy >10 m. To avoid pseudoreplication, for home-range estimation, when multiple lions or wild dogs within the same social group were GPS collared over the same time period, we used only the data from the collared animals that had the greatest number of overlapping collar days with GPS collared leopards. There were three time periods for which we had GPS collar data from leopards: April until October 2012, September 2015 until April 2016 and November 2016 until December 2017.This translated to approximately 11, 16 and 37leopard months of data for each period, respectively. For example, if three leopards were GPS collared over the same two month period, this represented six leopard months of data.

Home-range analyses

We separated lion, cheetah and wild dog data into the three periods that corresponded with leopard GPS collar deployments. Seasonal kernel utilization distributions were then created for each individual using Brownian Bridge Movement Models in the R package *adehabitatHR* (Calenge, 2006), with the location error parameter defined as 10 m, based on GPS error specifications by Wilson *et al.* (2013). Home ranges and core areas were defined using 95% and 50% utilization distributions. We then assessed the joint space use within leopard-competitor dyads across home ranges and core areas with the utilization distribution overlap index (UDOI), a 3D measure of overlap in space use (Fieberg & Kochanny, 2005), using the *wildlifeDI* package (Long, 2014). UDOI values typically range from 0 to 1, indicating no utilization distribution overlap and complete overlap of utilization distributions that are uniformly distributed, respectively. However, values of >1 are possible and indicate high levels of overlap between utilization distributions that are non-uniformly distributed (Fieberg & Kochanny, 2005).

We used linear mixed-effects models with UDOI as the response variable and guild species and/or season included as the predictor variables to investigate whether UDOI differed between leopards and each of the guild species. A variable ('dyad') composed of leopard ID and competitor ID (for cheetah) or social group ID (for wild dog and lion encounters) was included as a random effect to account for repeated sampling of leopard-competitor dyads, that is across seasons and years.

We applied an information theoretic approach to select the most parsimonious model from all possible model combinations, that is with and without species and season included as predictors. Akaike's information criterion corrected for small sample sizes (AIC_C) was used to rank models, with lower values indicating higher levels of support (Burnham & Anderson, 2002). Models within six AIC_C units of the highest ranked were retained within a candidate set of models in order to ensure a 95% chance of the most parsimonious model being retained (Richards, Whittingham, & Stephens, 2011). When multiple models were present within the candidate set, we used multimodel averaging to improve inference through the comparison of individual model parameter estimates (Burnham & Anderson, 2002). Model parameters whose confidence intervals did not encompass zero were interpreted as having a significant impact on the response (Grueber *et al.*, 2011).

Dynamic interactions

We used Benhamou's IAB metric to test for attraction and avoidance within leopard-competitor dyads when both dyad members were in shared areas of their home range. This analyses were implemented with the *wildlifeDI* package (Benhamou *et al.*, 2014; Long, 2014). IAB was chosen to quantify dynamic interactions because it is less prone to Type 1 or 2 statistical errors than other dynamic interaction metrics and its calculation of *P*-values within the framework of the test allowed intuitive interpretation of the results (Miller, 2015). To account for variable fix rates between dyad members' collars (e.g. if one member was stationary), we resampled downloaded GPS data to regular inter-fix intervals of five minutes and used linear interpolation to assign spatio-temporal coordinates. The threshold for defining simultaneous fixes within the IAB framework was set at ½ of the sampling intensity (i.e. 2.5 min) and the critical distance set to 200 m (Long, 2014). The critical distance was based on previous measurements suggesting 200 m as the maximum distance that lions would be seen by leopards within intermediately vegetated habitats within our study area (Rafiq, 2016).Analyses were repeated with critical distance thresholds set to 100 m and 1000 m, and results followed the same pattern (see Tables S1-S3).

Since wild dog pack members regularly move together, to avoid pseudoreplication, if multiple pack members were GPS collared over the same time period, we used only the data from the GPS collar with the greatest temporal overlap with the GPS collared leopard. In contrast, the fission–fusion structure of lion prides (Packer, Scheel, & Pusey, 1990) meant that we regularly observed pride members to move in the absence of others. As such, all leopard–lion dyads were included within the IAB analyses, regardless of whether multiple lions within a pride were GPS collared over the same time period.

Activity patterns

We used the mean of the mean acceleration values of the X-axis (fore-aft direction) as a proxy for activity levels (Hubel *et al.*, 2018). As such, activity was based on absolute activity levels rather than *a priori* thresholding into active and inactive categories (*a la* Cozzi *et al.*, 2012; Hubel *et al.*, 2018).To

avoid pseudoreplication, for wild dog packs, we only used data from a single GPS collar within the pack over a given period, but we again used all lion data due to their fission–fusion social structure (as outlined previously). To investigate the impact of light levels on carnivore activity patterns, we subdivided each day into five periods reflecting the main activity periods within the literature, morning, afternoon, evening twilight, night and morning twilight (*sensu* Cozzi *et al.*, 2012) (Table 1) and looked at peaks in activity across periods. Periods were defined using sunlight phases obtained from the R package *suncalc* (Agafonkin & Thieurmel, 2018). To avoid pseudoreplication, we calculated the mean activity values for each period so that there was only one period value per individual per day (Cozzi *et al.*, 2012).For each species, to test whether activity differed across diel periods and identify periods when species were most active, we used a series of linear mixed-effects models. Period was included as the dependent variable and the periods mean temperature as a covariate. In cases where activity was statistically significantly different between periods, the estimated marginal means post hoc test, with Tukey's adjustment, was used to compare differences between pairs of periods (Lenth, 2019). Daily mean temperatures for each period were obtained from hourly measurements taken by the Maun Airport meteorological station (location: 23.426, −19.976) (Wolski, 2018).

We specified a series of linear mixed-effects models to test for the impact of nocturnal light levels on carnivore activity. For this, we used only the data that were collected during the dry season since, unlike the wet season, there is limited cloud cover to obscure nocturnal light levels (Cozzi *et al.*, 2012). We specified separate models for each species, with nocturnal activity set as the response variables. Activity levels were transformed using the square root or logarithmic transformations, where necessary, to satisfy assumptions of residual normality. The proportion of the moon illuminated and lunar phase were obtained from the *suncalc* package for each day. Within models, the proportion of the moon illuminated was used as a proxy for nocturnal light levels and was included as the explanatory variable; nocturnal activity from the previous day and temperature was included as covariates; and individual identity was included as a random effect (Cozzi *et al.*, 2012).We applied a similar information theoretic approach for model selection as outlined previously to select the most parsimonious model from a series of candidate models derived from all possible permutations of the

global, but we used the standard Akaike's information criterion (AIC) to rank models.

To easily visualize differences in predator activity with moon illumination, we also grouped and calculated mean activity values across three periods of moon phase: new moon, when <95% of the lunar disc is visible; half-moon, when 47.5 to 52.5% of the lunar disc is visible; and full moon, where >95% of the lunar disc is visible.

Throughout the results, we report all mean values with the standard error. Given the statistical challenges in quantifying variance in mixed models (e.g. see Rights & Sterba, 2019), standardized effect sizes were not calculated. Instead, where appropriate, we provide data allowing for interpretation of unstandardized effect sizes (i.e. differences in group means) (*a la* Pek & Flora, 2018).

Results

Home-range overlap

Across the three time period categories, all eight leopards had utilization distributions overlapping with one or more lion, cheetah and/or wild dog pack utilization distribution. One leopard had GPS data available across all three time periods. In this case, data between the periods were considered independent because data from the same seasons were collected in different years. We found no evidence that the amount of overlap in leopard-competitor home-range and core area utilization distributions differed across the competitor species (Table 2). Effect size statistics, in the form of unstandardized mean differences, can be interpreted from Table S4.

Dynamic interactions

Most leopard-competitor dyads had limited to no overlap in utilization distributions (Table S2). Consequently, following the approach of Benhamou *et al.* (2014), we filtered dyads with overlaps less than a critical threshold. Specifically, we removed dyads for which the UDOI was less than 0.1. This threshold was chosen to minimize the impact of including dyads where direct interaction would likely not occur (Benhamou *et al.*, 2014), whilst still allowing for an adequate number of dyads to be included within the analyses. After filtering, we were left with 10 unique leopard–lion, 16 leopard–wild dog and 5 leopard–cheetah dyads for our analyses.

Table 1 Definitions of the time periods used in our analyses

Period	Definition
Morning	Beginning at sunrise, when the edge of the sun appears on the horizon, and ending at solar noon, when the sun is in its highest position.
Afternoon	Beginning at solar noon and ending at the onset of evening civil twilight.
Evening twilight	Beginning when evening civil twilight starts and ending when it is dark enough for astronomical observations.
Night	Beginning at the end of evening twilight and ending at the onset of morning nautical twilight.
Morning twilight	Beginning at the onset of morning nautical twilight and ending at sunrise.

For our study, we defined the same periods used by Cozzi *et al.* (2012) and used times specified within the R package *suncalc* (Agafonkin & Thieurmel, 2018).

Table 2 Summary of candidate models (Δ AIC$_C$ < 6) and averaged model parameters from linear mixed-effects models investigating differences in UDOI (utilization distribution overlap index) between leopards and lions, wild dogs, and cheetahs

Model	K	R²	AICc	Δ AICc	Wi
Home range (UD95)					
Species	5	0.295	391.272	0.000	0.583
Season + species	6	0.307	392.018	0.745	0.402
Core area (UD50)					
Species	5	0.070	473.357	0.000	0.570
Null	3	0.002	475.587	2.229	0.187
Season + species	6	0.070	475.660	2.303	0.180
Season	4	0.002	477.781	4.424	0.062

Parameters	Estimate	SE	Adj. SE	Confidence Intervals Lower	Upper
Home range (UD95)					
Intercept	−3.545	0.899	0.911	−5.330	−1.759
Species (wild dog)	0.856	0.540	0.547	−0.215	1.928
Species (lion)	−0.631	0.539	0.546	−1.701	0.439
Season (wet)	−0.198	0.344	0.347	−1.257	0.287
Core area (UD50)					
Intercept	−7.315	0.820	0.831	−8.944	−5.686
Species (wild dog)	0.668	0.860	0.870	−0.874	2.654
Species (lion)	−0.584	0.819	0.828	−2.490	0.934
Season (wet)	−0.022	0.315	0.319	−1.354	1.169

AIC$_C$ = Akaike's information criterion corrected for small sample sizes; Δ AIC$_c$ = difference between this models AIC$_C$ with the lowest AIC$_C$ value out of all models; K = degrees of freedom; Wi = Akaike weight.

There was movement coherence (i.e. actual movement interaction >0 and attraction or avoidance P < 0.05) in one leopard–lion dyad (avoidance); and two leopard–wild dog dyads (attraction and avoidance); but no leopard–cheetah dyads. All dyads that showed either attraction or avoidance had low IAB index values with observed and expected values of less than 0.006 and 0.002, respectively (Table S2). We repeated the analyses with dyads with UDOI <0.1 and found similar results as above. As such, we assumed that there was no bias in keeping only dyads with UDOI >0.1 and retained only these dyads within our main analyses.

Activity patterns

Species' activity differed across diel periods and by temperature (Table S5). All species had activity levels that peaked during evening twilight or night. Leopard, wild dog and cheetah activity peaked during evening twilight. Wild dog also showed a bimodal activity pattern with a peak in activity also occurring during morning twilight (Fig. 2; Table S6). Lion activity peaked at night but was only marginally lower during evening twilight (Fig. 2). Cheetah was the only species to show high levels of activity during the morning diel period. Moonlight illumination had no impact on lion or leopard nocturnal

activity levels but did have a positive association with wild dog and cheetah activity (Tables 3–4). Mean lion and leopard nocturnal activity levels were similar across moon phases, but wild dogs and cheetahs were on average 2.37 and 1.67 times more active, respectively, during full than new moon phases (Fig. 3).

Discussion

We found limited evidence for spatial or temporal avoidance between male leopards and other large predator guild species within our study system. Our results support the hypothesis that, at a population level, male leopards are minimally impacted by guild members in terms of broad-scale space use and activity (Balme et al., 2017b; Miller *et al.*, 2018).

Leopards showed low levels of spatial overlap in their core use areas with areas intensively used by other guild species but did not completely avoid them. Given that the levels of leopard home-range and core area overlap did not significantly differ between guildspecies, despite different levels of risk posed by each, we find it unlikely that competitor avoidance was the primary force driving low levels of spatial overlap. Instead, these patterns may reflect species' resource distributions and the selection of different habitat features by each species, likely related to differences in their ecology and life histories. Within similar landscapes to that of our study, leopards, for example, select for intermediately vegetated habitat types associated with high (most likely preferred) prey densities and prey catchability, independent of lion presence (Miller *et al.*, 2018). In contrast, lions select for open habitats with higher densities of large, preferred prey species (Miller *et al.*, 2018). Without the inclusion of vegetation maps, we can make limited inferences on the drivers of leopard home-range selection from our study's data. Accurate maps were unavailable at the time of this study, and creating high-resolution, accurate maps is ongoing but non-trivial (Oeser *et al.*, 2019). Nevertheless, measures of utilization distribution overlap provide a useful indication of the potential for dynamic interactions (Benhamou *et al.*, 2014). In this respect, our analyses suggest that the potential for interference competition, based on home-range overlap, within leopard-competitor dyads is similar across the species dyads.

Interestingly, however, male leopards within our study area ignored intraguild competitors (and *vice versa*) when moving. We found limited evidence of movement coherence amongst leopard-competitor dyads, suggesting that when leopards and other large predators are moving through shared areas of their home ranges, they move independently of one another: dynamic avoidance or attraction is rare. Although some leopard-competitor dyads showed movement coherence, the low observed movement interaction values suggest that, whilst statistically significant, there was no biologically meaningful avoidance or attraction. Rather, there was independent movement between the species most of the time with occasional periods of attraction or avoidance. This may reflect movement in search of unique preferred prey resources (Hayward & Kerley, 2008).
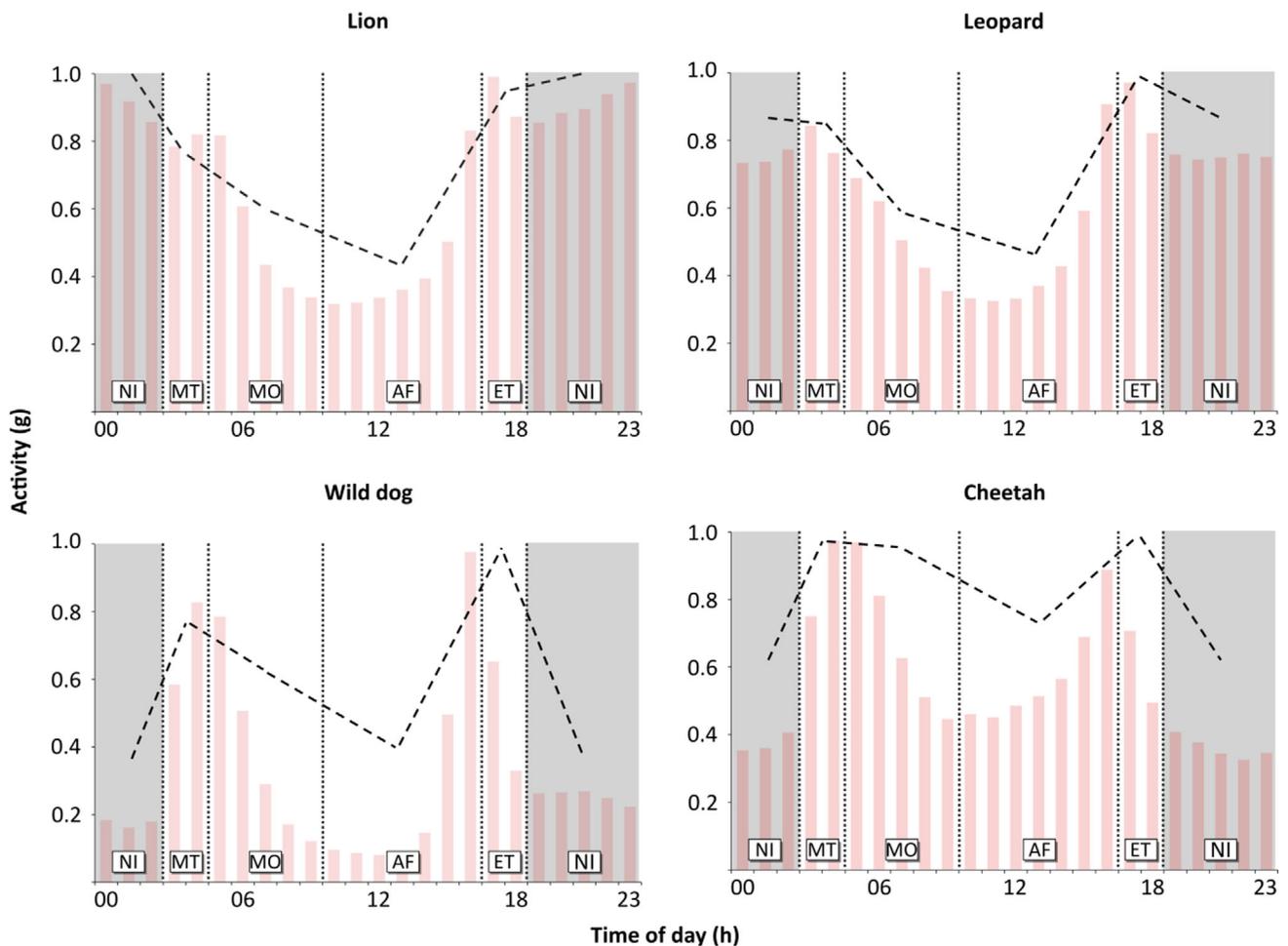
Figure 2 Mean species activity levels for morning twilight (MT), morning (MO), afternoon (AF), evening twilight (ET) and night (NI) diel periods (dashed line). Standard errors are between 0.004 and 0.044 and so cannot be visualized on graphs. The background bar plots show mean species activity levels blocked into hourly periods. To account for species-level differences in activity values, activity values for each species are standardized against the species' highest activity level across the five periods (dashed) or across the 24 h blocks (bar plot). [Colour figure can be viewed at zslpublications.onlinelibrary.wiley.com]

Our results are consistent with the literature on spatial partitioning responses between leopards and lions (e.g. Du Preez *et al.*, 2015; Map utla *et al.*, 2015; Miller *et al.*, 2018). For example, Du Preez *et al.* (2015) found that avoidance by leopards of lions was dependent upon habitat cover, and, consequently, the species were often found in close proximity. Similar trends were presented by Maputla et al. (2015) and Balme *et al.* (2019) who both found limited evidence of leopard space use being strongly influenced by top-down effects. This is in contrast to other species, such as wild dogs, which have been shown to more prominently adapt their space use in response to top-down pressures (e.g. Darnell *et al.*, 2014). Whilst dietary niche separation may be one mechanism through which competition is avoided (Du Preez *et al.*, 2017), co-occupation of shared habitat patches may also be facilitated by aspects of the leopard's life history that, in comparison to other guild species, make them particularly well suited to coexistence within these areas, with avoidance of competitor encounters then occurring at a finer spatial scale (e.g. Rafiq *et al.*, 2019). For example, leopards are a cryptic and solitary species and so may be able to maintain a relatively low risk of detection by dominant competitors whilst moving through shared areas (Bailey, 2005). This is in contrast to wild dogs, whose distance from other pack members when mobile and whose mode of movement (i.e. fanned out and coursing) (Hubel *et al.*, 2016) may make them predisposed to increased detection and ambush by larger predators.

Instead of leopard space use being strongly influenced by top-down forces, leopards may instead adjust aspects of their behaviour when within high risk locations, such as seeking refuge in trees when detected by competitors (Stein, Bourquin, & McNutt, 2015; Balme *et al.*, 2017). In other words, responses to competitors are likely to be scale and context-dependent (see Vanak *et al.*, 2013).Whilst such behaviours can impose fitness costs upon individuals (e.g. loss of kills or hunting opportunities), these costs for male leopards within our

Table 3 Summary of linear mixed-effects candidate models (Δ AIC < 6) looking at the effect of moonlight illumination on large predator guild species nocturnal activity levels

Models	K	R^2	AICc	Δ AICc	Wi
Lion					
Previous day's activity + moon illumination + temperature	6	0.310	16970.960	-	0.608
Previous day's activity + temperature	5	0.310	16971.830	0.877	0.392
Leopard					
Previous day's activity	4	0.299	4066.616	-	0.501
Previous day's activity + moon illumination	5	0.299	4068.160	1.544	0.231
Previous day's activity + temperature	5	0.299	4068.633	2.016	0.183
Previous day's activity + moon illumination + temperature	6	0.299	4070.161	3.545	0.085
Wild dog					
Previous day's activity + moon illumination + temperature	6	0.242	13727.270	-	1.000
Cheetah					
Previous day's activity + moon illumination + temperature	6	0.280	2553.024	-	0.817
Previous day's activity + moon illumination	5	0.276	2556.071	3.048	0.178

Within the models columns, models are grouped by species (bold).

AIC_C = Akaike's information criterion corrected for small sample sizes; Δ AIC_c = difference between this models AIC_C with the lowest AIC_C value out of all models; K = degrees of freedom; Wi = Akaike weight.

Table 4 Model averaged parameters from linear mixed-effects candidate models (Δ AIC < 6) (specified in Table 3) looking at the effect of moonlight illumination on large predator guild species activity levels

				Confidence Intervals	
Parameters	Estimate	SE	Adj. SE	Lower	Upper
Lion					
(Intercept)	7.038	0.363	0.364	6.325	7.751
Previous day's activity*	0.017	0.001	0.001	0.015	0.019
Moon illumination	−0.090	0.099	0.099	−0.319	0.023
Temperature*	−0.040	0.007	0.007	−0.053	−0.027
Leopard					
(Intercept)	7.873	0.448	0.449	6.993	8.753
Previous day's activity*	0.012	0.002	0.002	0.008	0.016
Moon illumination	−0.039	0.115	0.115	−0.472	0.225
Temperature	0.000	0.009	0.009	−0.034	0.037
Wild dog					
(Intercept)	4.820	0.482	-	3.879	5.763
Moon illumination*	3.602	0.238	-	3.133	4.067
Previous day's activity*	0.009	0.001	-	0.007	0.010
Temperature*	0.086	0.017	-	0.051	0.121
Cheetah					
(Intercept)	2.457	0.276	0.276	1.916	2.998
Previous day's activity**	0.007	0.001	0.001	0.004	0.009
Moon illumination*	0.292	0.082	0.083	0.130	0.453
Temperature*	0.011	0.008	0.008	0.002	0.025

Within the parameters column, parameters are grouped by species (bold).

*Indicates model parameters with a significant impact on activity levels.

study area are perhaps not as severe as those imposed by the use of suboptimal landscapes, a strategy seen in some other guild species (Mills & Gorman, 1997; Durant, 1998).As our dataset focused exclusively on male leopards, we acknowledge that female leopards may have alternative strategies and responses.

African large predator guild members also showed high levels of temporal overlap, adding to the growing body of evidence that temporal partitioning plays a limited role in facilitating competitor coexistence (Cozzi *et al.*, 2012; Rich *et al.*, 2017). We found that male leopard activity levels (1) peaked during evening twilight; (2) showed extensive temporal overlap with those of lions; and (3) along with lion activity levels showed no association with moonlight availability. In contrast, the largely diurnal cheetahs and primarily crepuscular wild dogs showed positive associations with moonlight availability,
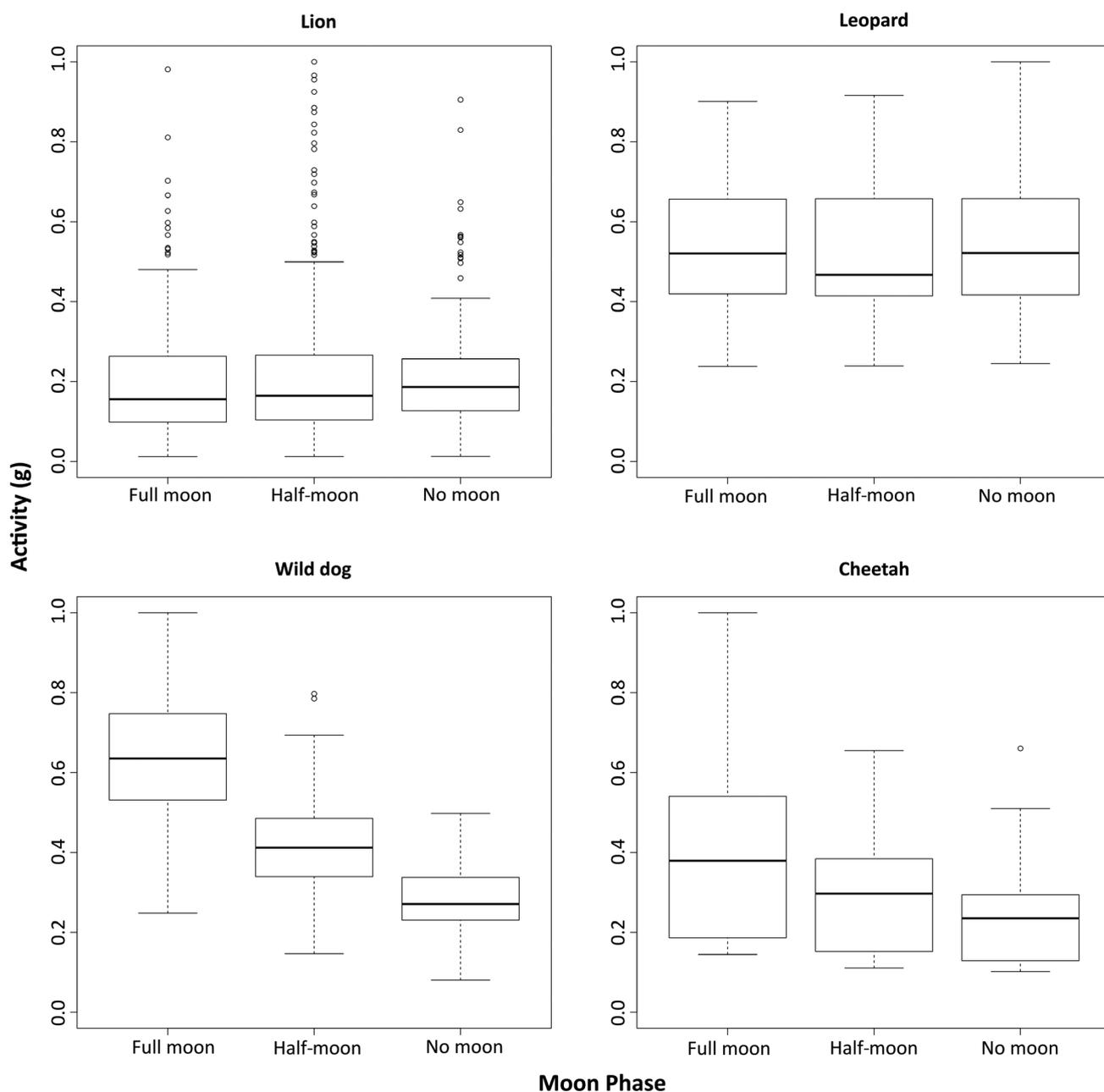
Figure 3 Box plot of predicted species nocturnal activity levels across Full moon, half-moon and new moon phases. To account for species-level differences in activity values, activity values for each species are standardized against the species' highest activity level across the three phases.

reflecting their ocular evolution (Ahnelt & Kolb, 2000). We acknowledge, however, that seasonal differences in other behaviours and/or distributions of other predators and prey species may affect the impact of moonlight on predator activity patterns across seasons.

Temporal partitioning across the diel cycle may be partially explained in the context of hunting (Cozzi *et al.*, 2012). For ambush predators, such as lions and leopards, low-light conditions increase hunting success (Funston, Mills, & Biggs, 2001;

Packer, Swanson, Ikanda, & Kushnir, 2011; Martins & Harris, 2013). Therefore, nocturnal activity levels may remain consistent across moon phases due to the need to meet minimum energetic requirements and the limited hunting opportunities available across other diel periods. In contrast, for cursorial hunters, such as cheetahs and wild dogs, increased light levels may provide advantages in maintaining visual contact with targets and reducing injury risks whilst chasing prey (Cozzi *et al.*, 2012). Foraging in nocturnal light may also provide the

additional advantage of allowing hunters to approach closer to prey without being seen (Rasmussen & Macdonald, 2012). Thus, wild dogs and cheetahs may preferentially engage in more nocturnal foraging behaviours during lunar phases when hunting success may increase. Further, unlike ambush predators, they may also otherwise be capable of meeting their energetic requirements during other diel periods, that is when the costs of nocturnal hunting outweigh the benefits (Creel & Creel, 2002; Cozzi *et al.*, 2012).

Our results conflict with findings that leopard activity in some other areas is strongly influenced by lunar phase (see Martins & Harris, 2013; Van Cleave *et al.*, 2018). In pastoral livestock lands in central Kenya, leopard activity decreases with decreasing lunar light availability, with one hypothesis suggesting that this association can be explained by increased hunting success during low-light phases reducing the movement associated with hunting (Van Cleave *et al.*, 2018). The inherent assumption within this hypothesis is that leopard movement is largely driven by a need to meet energetic requirements. However, across species, activity patterns are modulated by a complex interplay of factors, including territoriality, age and climate(e.g. Brinkman *et al.*, 2005; Graf *et al.*, 2016). Leopard activity differences across study sites may reflect contextual differences across locations and suggests that temporal activity patterns likely arise from a complex interplay between different fitness requirements (e.g. hunting and territorial maintenance). Whilst the high-resolution nature of our dataset presents an opportunity to explore the drivers of activity in greater detail, it also presents non-trivial statistical challenges in analysing near-continuous, auto-correlated temporal data (Fieberg & Ditmer, 2012). Indeed, to date, most studies inferring activity patterns from animal-borne sensors have blocked the data within diel periods to avoid this issue (e.g. McLellan & McLellan, 2015; Van Cleave *et al.*, 2018). As such, the analyses presented within this paper are provided as a much needed extension of the Cozzi *et al.* (2012) study, and further detailed analyses of the drivers of leopard diel activity patterns are the focus of ongoing work.

Three key limitations of our study merit further discussion. First, a lack of data from female leopards limits our ability to make inferences on the competitive dynamics between them and other guild members. The decision to collar only males was made because female leopards were ~ 50% lighter than males in our study area (unpublished data). As such, we restricted the use of collars to male leopards in order to minimize the ratio between the collar and the animal's weight. It is conceivable, due to sex differences in body size, diet and offspring care (Bailey, 2005; Voigt *et al.*, 2018), that the sexes show different behavioural responses to avoid predators. Further research into this area is warranted. Secondly, challenges in capturing spotted and brown hyaenas led to their omission from our study. However, spotted hyaenas can impact the reproductive fitness of leopards through kleptoparasitism (see Balme et al., 2017a). Consequently, given the high density of spotted hyaena within our study area (Cozzi *et al.*, 2013) and their impact on leopards elsewhere (Balme et al., 2017a), it is possible that they exert a top-down effect on leopard spatiotemporal patterns that we were unable to measure in this study.

Finally, the small sample sizes inherent in *ex situ* large carnivore research, for example due to logistical challenges in collecting data, mean it is likely only possible to detect relatively large effect sizes. As such, we acknowledge the possibility that smaller effects of competitor species on leopard space use or activity may have gone undetected.

Our results suggest that top-down effects are not always a predominant regulatory force within intact ecosystems, as is commonly suggested (Terborgh, 2010). Within our study area, leopards successfully coexist as mesopredators amidst the highly competitive African large predator guild despite exhibiting no predator-avoiding spatial and/or temporal partitioning. In general, at the population level, and within landscapes relatively intact from anthropogenic disturbance, leopards seem unaffected by competitors (Balme et al., 2017b; Miller *et al.*, 2018). Thus, we found little evidence that interactions between leopards and other guild members can be understood within the mesopredator release framework, that is one of top-down suppression by dominant competitors (Allen *et al.*, 2017; Miller *et al.*, 2018).This provides a glimpse into the regulatory structure within a functionally intact predator guild whose baseline interactions are unlikely to have been impacted by megafauna extinctions (as have afflicted Australia, Europe and the Americas). As such, our results provide strong evidence that top-down regulation between dominant and subordinate competitors is not universal. Instead, the strength of top-down regulation is likely to be species- and population-specific and dependent on a number of environmental factors, such as resource availability, habitat structure and prey range (Swanson, Arnold, Kosmala, Forester, & Packer, 2016; Haswell *et al.*, 2017). Indeed, the strength of competition can vary drastically across stress gradients (Harvey, Gounand, Ward, & Altermatt, 2017), and consequently, the outcomes of intraguild competition for leopards may be different in heavily fragmented landscapes than our relatively intact location.

In summary, we have shown that the spatio-temporal behaviour of male leopards at our study location is minimally impacted by predator avoidance, and instead we speculate, may be primarily driven by resource acquisition. Our results suggest that leopards within undisturbed ecosystems, with relatively high productivity, can coexist alongside competitors with minimal impacts. As such, our study supports the idea that landscape-level approaches to conservation, wherein conservation strategies focus on healthy landscapes with the capacity to carry multiple species (Sanderson, Redford, Vedder, Coppolillo, & Ward, 2002), may be suitable for conserving leopard populations (Miller *et al.*, 2018). That said, in the absence of large scale spatial or temporal avoidance of competitors, it is likely that leopards adapt finer-scale behaviours, such as dragging prey into trees, to perceived competitor risk or during the occurrence of direct competitor encounters. However, beyond prey caching (Stein *et al.*, 2015; Balme et al., 2017a), little is known of these coexistence mechanisms. Whilst such interactions were beyond the scope of this study, investigations into fine-scale coexistence mechanisms will provide greater insights into the factors allowing leopards to coexist within such a highly competitive predator assemblage.

Acknowledgements

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Figure S1. GPS collar deployment durations. GANT chart showing the deployment dates of all leopard GPS collars and temporally overlapping lion, wild dog and cheetah GPS collars.

Table S1. Summary of home range overlap and dynamic interaction values for leopard-competitor dyads with an UDOI > 1, with a distance threshold of 100 m**.**

Table S2. Summary of home range overlap and dynamic interaction values for leopard-competitor dyads with an UDOI > 1, with a distance threshold of 200 m.

Table S3. Summary of home range overlap and dynamic interaction values for leopard-competitor dyads with an UDOI > 1, with a distance threshold of 1000 m.

Table S4. Model predicted mean ($\pm$ standard error) utilisation distribution overlap index values for home range and core area overlaps between leopards and three other large carnivore species: lion, wild dog, and cheetah.

Table S5. Output of linear mixed-effects models investigating, for each species, activity across each of the five diel periods. For each species, individual identity is included as a random effect and temperature is included as a covariate. Within the parameter column, parameters are grouped by which species they represent (bold).

Table S6. Summary of post-hoc test output comparing species activity between each of the five diel activity periods. Activity pairs being contrasted are grouped and order by species (bold within 'Pairs').