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Spatio-temporal factors impacting encounter occurrences between leopards and other large African predators

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Running title: Encounters between large African predators

Abstract

Encounters between individuals can have implications for a range of processes, including disease transmission, information transfer, and competition. For large carnivores, difficulties in directly observing individuals and historical hardware limitations of GPS collars mean that relatively little is known of the spatio-temporal factors contributing to encounters. The African large predator guild represents one of the few remaining functionally intact guilds of large carnivores on the globe and so represents a unique study system for understanding competitor interactions. We explored the drivers of male leopard (*Panthera pardus*) encounters with lions (*Panthera leo*), African wild dogs (*Lycaon pictus*) and cheetahs (*Acinonyx jubatus*) in the context of habitat characteristics and temporal activity overlaps. Using high resolution (five minute GPS fixes) data from 48 large African carnivores from 2012 to 2018, we quantified encounter occurrences between male leopards and other guild species and related these to habitat type (open vs closed), activity overlaps, and moonlight levels. Leopards met wild dogs 4.56 ± 1.15 (standard error), lions 3.11 ± 0.56, and cheetahs 2.27 ± 0.73 times per month. All species instigated encounters, but leopard instigated encounters with dominant competitors appeared to reflect imperfect information on risk, primarily occurring within habitats with limited visibility. Moreover, encounters peaked during periods of high temporal overlap, suggesting that, although previous research indicates temporal activity patterns may not be driven by predator avoidance, temporal overlap has implications for competitor dynamics. Our results show how habitat characteristics and niche overlaps contribute to encounters between competitors and provide an example of how niche shifts within competitor assemblages can impact competition between species.

Keywords: African carnivores, coexistence, competition, interaction dynamics, intraguild encounters, *Panthera pardus*, temporal overlap

Introduction

Encounters between individuals of free-ranging species can inform a range of ecological processes, including disease transmission (Craft *et al.*, 2011), information transfer (Berger, Swenson, & Persson, 2001), and competition (Jordan *et al*., 2017). Large carnivore species and the interactions between them can also help to regulate and structure ecosystems (Ripple *et al.*, 2014). Carnivore impacts are context dependent (e.g. depending upon co-occurrence with other carnivores) and exist within a network of interactions that together structure and regulate communities (see Haswell, Kusak & Hayward, 2017). Encounters amongst members of large carnivore assemblages can thus have cascading effects throughout lower trophic levels because encounters can impact species population dynamics, distributions, densities, and behaviours (e.g. Groom, Lannas, & Jackson, 2017). Yet, relatively little is known of direct encounters between species and of the impact that population-level niche partitioning may have on encounter rates and behaviours at a local scale. This is important to understand because species often show a degree of plasticity that allows them to shift their positions along niche-axes in response to changing environmental factors, such as climate, resource distribution, and human activity (Kitchen, Gese & Schauster, 2000; Gaynor *et al.*, 2018; Rabaiotti & Woodroffe, 2019). Such changes in activity, space-use and behaviour could conceivably impact encounter rates and competition dynamics.

Whilst previous studies have investigated spatio-temporal partitioning in the context of intraguild competition (e.g. Edwards, Gange & Wiesel, 2015; Rich *et al.*, 2017), few have quantified and explored the factors predisposing encounters. Encounters between large carnivores have traditionally been difficult to study because these species typically occur at low-densities, are wide-ranging, and move over landscapes that are logistically difficult for researchers to navigate (Gittleman, 2001). To overcome these challenges, GPS collars have historically been used to study large carnivore ecology (Wilmers *et al.*, 2015). These too, however, have been ill-suited in their ability to quantify interactions because hardware limitations, e.g. battery capacity and size, inhibited their ability to collect GPS data at high logging rates, meaning that encounters could go undetected between data points (Du Preez *et al.*, 2015). Thus, much of what we do know of direct large carnivore interactions is typically based on opportunistic sightings from ground-vehicles (e.g. Bailey, 2005; Schaller, 1976) and from intensive-monitoring of select areas of interest, such as kill sites, *via* camera traps (e.g. Selva, Jedrzejewska, Jedrzejewski, & Warak, 2003). Whilst useful, such data are often qualitative, captured over short spatio-temporal scales, and can be biased towards landscapes suited to opportunistic sightings, such as the short grasslands of the Serengeti (Schaller, 1976). Recent advances in GPS collar operational times and sampling rates (< five minute GPS fix intervals) offer an opportunity to address these limitations and provide exhaustive GPS monitoring that captures interactions that previously would have been missed (Jordan *et al.*, 2017). However, their application to large carnivore interactions has thus far been limited (but see Broekhuis *et al.*, 2019; Elbroch & Quigley, 2017; Jordan *et al.*, 2017).

In this study, we investigated intraguild encounters involving four members of Africa's large predator guild: lion (*Panthera leo*), leopard (*Panthera pardus*), cheetah (*Acinonyx jubatus*), and African wild dog (*Lycaon pictus*), listed by descending individual body mass (see Kingdon, 2013). These species are members of one of the last intact guilds of large carnivores on the planet and, as such, represent a unique baseline study system to investigate interspecific encounters within a functionally intact group (Dalerum *et al.*, 2009). Specifically, we used custom-developed GPS collars to investigate encounters between male leopards and other large predator guild members within northern Botswana. Leopards are a solitary large felid that coexist and compete across much of their sub-Saharan range with other guild species (Jacobson *et al.*, 2016). Within some areas, for example, interspecific competitors are one of the main causes of leopard cub mortality (Balme *et al*., 2013), and the loss of kills to spotted hyaenas can depress leopard reproductive success (Balme *et al*., 2017). The numerical advantage and cumulative mass of wild dog packs also mean that wild dog encounters can present risks to leopards (Creel & Creel, 2002). Yet leopards remain, arguably, one of the lesser studied guild species in terms of direct encounters with other guild members. Further, although there is intense interspecific competition within the guild and the population-level outcomes of encounters have been well studied (e.g. Groom *et al*., 2017; Miller, Pitman, Mann, Fuller, & Balme, 2018), relatively little is known of the factors predisposing direct encounters.

We hypothesised that encounters between leopards and other guild members are the result of incomplete information rather than an omniscient knowledge of competitor risk. In particular, we investigated the role habitat structure may play in encounter occurrence because although it can facilitate coexistence between competitors (Janssen *et al.*, 2007), it can also impact the ability to acquire information on the location of other individuals (Boncoraglio & Saino, 2007) and relatively little is known of its impact on decision making. Under this imperfect information hypothesis, we predicted that encounters instigated by the movements of smaller competitors, dependent on the species involved, would occur primarily within closed than within open habitat types. This prediction was made because visual information, the best indicator of an animal's exact location, on competitors is likely to be harder to acquire within closed habitats and so the chances of stumbling into competitors may be greater.

We then investigated the temporal circumstances under which encounters occurred. We hypothesised that encounters across the diel cycle would occur most often during periods of high activity overlap between pairs of competitors (hereafter referred to as dyads) because guild members: (i) often compete for similar resources and thus are likely to be attracted to similar areas during periods of movement (Caro & Stoner, 2003) and (ii) may preferentially use the same landscape features (e.g. roads) as travel routes (Abrahms *et al.*, 2016). We also predicted that leopard-wild dog and leopard-cheetah nocturnal encounters would peak during periods of high illumination because wild dog and cheetah nocturnal activity levels are positively associated with light availability (Cozzi *et al.*, 2012). We predicted that, conversely, leopard-lion encounters would not, since lion activity is unaffected by nocturnal light levels (Cozzi *et al.*, 2012).

Methods

Study area

This study took place in the Ngamiland region of northern Botswana and covered an area of approximately 2,600 km^2, within which the main habitat types were woodlands dominated by *Acacia* sp. and mopane (*Colophospermum mopane*) (Mendelsohn *et al.*, 2010; Cozzi *et al.*, 2013). The study area included community-operated wildlife management areas that were primarily used for wildlife tourism throughout the study period and areas of Moremi Game Reserve (Fig. 1).

GPS collars

From 2012-2018, we used GPS collars fitted with GPS-linked inertial measurement units (GPS-IMU) that were developed by the Royal Veterinary College, University of London (Wilson *et al.*, 2013). To conserve battery life and maximise collar deployment, collars switched between different sampling regimes based on GPS collar loaded configurations and GPS-IMU activity-derived behaviour classifications (see Wilson *et al*., 2013). These sampling regimes typically ranged from five minute GPS fixes during periods of locomotion to hourly fixes during periods of inactivity. In addition, when high fix-rate configurations were loaded onto collars, during periods of high acceleration, five fixes per second were recorded (Wilson *et al*., 2013). When high fix-rate configurations were not loaded onto collars, the five minute fix-rate was the highest resolution of data collected. Data were stored on GPS collars and available to download *via* radio link to a hand held base station. Further details on collar development and specifications can be found in the supplementary material of Wilson *et al*., 2013.

To fit collars, immobilisations were carried out by a Botswana-registered veterinarian after animals were located through spoor tracking, opportunistic sightings, and/or the use of baited capture sites. Immobilisation cocktails were typically delivered *via* an air-pressure powered dart gun (Telinject USA; Dan-Inject, USA; or Pneu-Dart, USA) with drug combinations and quantities varying with species and individual mass and determined by the veterinarian (see Hubel *et al*., 2016; Wilson *et al*., 2018, 2013). Collar weights for lions (~970g), leopards (~550g), wild dogs, and cheetahs (~340g) represented < 2% of estimated collared animal body masses. Collars were typically fitted with bio-degradable or electronic (Sirtrack Ltd, New Zealand) drop-off units. Collars with no drop-off unit were manually removed from animals following the completion of the study or upon collar expiry. Carnivore vital signs were monitored throughout immobilisations, and we prioritised collar attachment over body measurement and biological sample collection. Most immobilisations were concluded within 60 minutes after darting and reversal drugs were administered intramuscularly. Animals were then monitored from a ground-vehicle until animal movements and coordination returned to pre-immobilisation levels, based on researcher knowledge of the study species. In total, we immobilised and GPS collared 8 leopards, 14 lions (from 4 prides and 3 male coalitions), 21 African wild dogs (from 11 packs), and 5 cheetahs. For lions, wild dogs, and cheetahs, we GPS collared individuals of both sexes, and for leopards, only males were collared to minimise the collar to animal weight ratio. Mean collar deployments were 356.67 (± 277.80, standard deviation) days for lions, 190.90 (± 51.70) days for leopards, 176.89 (± 131.47) days for wild dogs, and 200.44 (± 111.76) days for cheetahs. Further details on collar deployments, including specific timings and durations, can be found in the supplemental material. Animals were visited at least every two to three weeks to download GPS collar data and check welfare. We noticed no ill-effects of GPS collar deployments.

All work was reviewed and approved by Liverpool John Moores University's ethical committee (reference number: CM_KR/2016-7) and Botswana's Department of Wildlife and National Parks (permit number: EWT 8 / 36 / 4 xxxv (31)).

Encounter identification

Raw datasets were resampled to create regular trajectories of fixes at one minute intervals through a combination of linear interpolation and down sampling of high-resolution GPS data. For example, this meant that during periods of low-acceleration movement (e.g. walking), the known locations of individuals, occurring at five minute intervals, were linearly interpolated with inferred locations, occurring at one minute intervals. Interpolation was carried out within the R environment for statistical computing (R Core Team, 2018). GPS collars were not programmed to record fixes at precise times, and so interpolation compensated for differences in GPS timestamps. To filter erroneous GPS locations from our dataset, prior to interpolation, we removed GPS fixes with > 10 m horizontal accuracy and removed fixes that required individuals to have travelled at speeds exceeding 15 m/s between locations > five minutes apart. Although large African predators can reach maximum speeds that exceed these values, these speeds typically occur over short distances and are unlikely to have been sustained over five minute step lengths (Hubel, Golabek, Rafiq, McNutt, & Wilson, 2018; Wilson *et al.*, 2013).

Leopard-competitor (i.e. lion, wild dog, or cheetah) dyads that showed temporal overlap in collar deployments were then cross-referenced to find encounters using the R package *wildlifeDI* (Long, 2014). Putative encounters were defined as occurring when simultaneous fixes from dyad members were within 200 m of one another. The range at which species may detect one another is likely dependent on a range of factors, including habitat density, vigilance levels, and the species involved (e.g. Gorini *et al.*, 2012). We chose the 200 m threshold distance to define encounters because a pilot study suggested this as a conservative measure of the distance leopards may visually detect competitors within woodland habitats (Rafiq, 2016) and the value followed previous guidelines for defining interactions in solitary carnivores (Elbroch & Quigley, 2017). Further, for lion and wild dog encounters, since collared individuals can travel in prides and packs and the group's location was based on a single individual's location, it is possible that other individuals within the group were closer to leopards than GPS data suggested. Following Long (2014), the temporal threshold for defining fixes as simultaneous was set at ½ of the iterated sampling intensity, i.e. fixes within 30 seconds of one another were defined as simultaneous. The encounter location and encounter time were defined as the mid-point between the encountering individuals' GPS locations, when species were at their closest, and the time that this occurred. The encounter area was defined by a 100 m radius around the encounter location. New encounters could not occur until dyad members had vacated the encounter area and had been separated by > 200 m for at least 24 hours since their last encounter (Elbroch & Quigley, 2017).

Encounter rates

We used a subset of our data, from 2012 to 2016, to calculate encounter rates because this is when we had the most leopard-competitor GPS collars deployed at the same times that overlapped spatially (Figure S1). We calculated an adjusted measure of encounter rates for each leopard using the following equation:

$$ERi = \frac{E}{T_C} \text{ x } \frac{D_{HR}\, x\, T_C}{S_A}$$

Where ER_i is the encounter rate for leopard *i*; E is the total number of leopard-species encounters; T_C is the number of months the leopard was GPS collared; D_{HR} is the estimated number of individuals of the competitor species within the leopard's home range, using density estimates for the study area from Rich *et al.*, (2019) for lion and wild dog, and Broekhuis (2012) for cheetah; and S_A is the total number of months that leopard *i* overlapped with GPS collared individuals of the species. For example, if leopard *i* overlapped with two individuals of the species for three and five months each, the S_A was eight. Leopard home ranges were defined as 95% utilisation distributions created using Brownian Bridge Movement Models (Horne *et al*., 2007), with the location error parameter defined as 10 m, based on GPS error in Wilson *et al.,* (2013). By considering competitor density, this equation provided an estimate of leopard-competitor encounters that accounted for the fact that not all individuals of the competitor species were GPS collared. Since wild dogs travel in packs (Creel & Creel, 2002), leopard-wild dog encounter rates were calculated for packs.

Classification of habitat types

Encounters were manually classified into open and closed habitat types based on canopy cover at each encounter location using Google satellite imagery from the OpenLayers plugin (Kalberer & Walker, 2018) within QGIS (QGIS Development Team, 2018). Specifically, a 100 metre circular buffer was applied to the encounter location and encounters were classified into open habitats, with little to no canopy cover, and closed habitats, with at least 50 % of the area covered by canopies separated by less than 5 m.

Encounter occurrences

To investigate encounter occurrences, we used our full 2012 to 2018 data set. For each encounter, we recorded the timings that dyad members arrived into the encounter area. If members arrived within 30 seconds of one another, they were assumed to have arrived simultaneously. Otherwise, we assumed that the second species arriving into the encounter area instigated the encounter, i.e. their movement was responsible for setting the encounter into motion, irrespective of whether encounters were intended. We then used a series of Fisher’s exact tests to investigate counts of leopard and competitor instigated encounters across competitor species and habitat types. We used the R package *suncalc* (Agafonkin & Thieurmel, 2018) to derive moonlight illumination levels and lunar phases for the day of each encounter, and we used a series of Kuiper’s one sample tests for uniformity of circular data (Jammalamadaka & Sengupta, 2011) to assess whether leopard and competitor instigated encounters were equally distributed across diel and lunar cycles. We also used graphical displays to make descriptive inferences of the impact of moonlight illumination on encounter onsets. When considering distributions of encounters across lunar cycles and moonlight illumination levels, we used a subset of our data that contained only encounters occurring during the night, which we defined as the period after the day’s end of evening civil twilight and before the start of the following day’s morning nautical twilight.

Results

Overview and encounter rates

In total, we recorded 115 leopard-competitor encounters. Specifically, male leopards encountered GPS collared lions 64 times, wild dogs 43 times and cheetahs 8 times (Fig. 1). For each competitor species, after adjusting for only a portion of their populations being GPS collared, this translated to 4.56 ± 1.15 leopard-wild dog pack, 3.11 ± 0.56 leopard-lion, and 2.27 ± 0.73 leopard-cheetah encounters per leopard per month (mean ± standard error).

Encounter occurrences

There were only two instances where species arrived into encounter areas at the same time, which may represent random encounters when dyad members were both moving. Overall, all species were as likely to instigate encounters by approaching leopards first, with or without intent, as leopards were to instigate encounters with them (Fisher's-exact test, p = 0.555) (Table 1).

Leopards were less likely to instigate lion encounters within open habitats than within closed habitats (Fisher's exact test, p = 0.037). In contrast, leopard-wild dog (Fisher's exact test, p = 0.060) and leopard-cheetah (Fisher's exact test, p = 1.00) encounters were instigated equally by both dyad member species within both habitat types. All five leopard-wild dog encounters within open habitats were, however, instigated by wild dogs, suggesting that rejection of the alternate hypothesis may be due to low samples sizes rather than lack of an effect (Table 1).

Table 1: Summary of leopard and competitor instigated encounters across open and closed habitats

Dyad	Open habitat		Closed habitat		Total
	Leopard instigated	Competitor instigated	Leopard instigated	Competitor instigated	
Leopard-lion	1	9	25	28	63
Leopard- wild dog	0	5	18	19	42
Leopard-cheetah	1	1	4	2	8
Total	2	15	47	49	113

Overall, leopard-lion encounters were non-uniformly distributed across the diel cycle, with encounters typically occurring during the night (68% of encounters; n = 63, Kuiper test statistic (k) = 3.056, $p < 0.01$). This was also the case when considering lion (70% of encounters; n = 37, k = 2.385, $p < 0.01$) and leopard (65% of encounters; n = 26, k = 2.321, $p < 0.01$) instigated encounters separately (Fig. 2). Across the lunar cycle, overall, leopard-lion encounters were uniformly distributed (n = 43, k = 0.864, $p > 0.15$), as were those encounters specifically instigated by lions (n = 26, k = 0.707, $p > 0.15$) and those instigated by leopards (n = 17, k = 1.306, $p > 0.15$). Encounters did, however, appear non-random in respect to nocturnal light levels and, independent of the instigating species, peaked during periods of high moonlight. Interestingly, lion instigated encounters also showed an additional peak during periods of low moonlight (Fig. 2).

Leopard-wild dog encounters, overall, peaked during early evening and morning hours (65% of encounters; n = 42, k = 2.124, $p < 0.01$) (Fig. 2). For leopard instigated wild dog encounters, there was no significant difference in the distribution of encounters across the diel cycle (n = 18, k = 1.586, $p > 0.10$); in contrast, wild dog instigated encounters peaked in the morning hours (63% of encounters; n = 24, k = 2.722, $p < 0.01$) (Fig. 2). Overall, leopard-wild dog encounters were uniformly distributed across lunar phases (n = 13, k = 1.222, $p > 0.15$) and so were those encounters specifically instigated by leopards (n = 7, k = 0.959, $p > 0.15$). Wild dog instigated encounters were non-uniformly distributed across lunar phase (n = 5; k = 1.904, $p < 0.025$), with four out of five encounters occurring between moon phases of 0.48 and 0.61, i.e. encompassing the waxing and waning periods closest to the full moon. In respect to nocturnal light levels, leopard-wild dog encounters peaked during periods of high moonlight, regardless of which species instigated the encounter. There was also a second smaller peak in encounters during periods of low moonlight when considering leopard and wild dog instigated encounters together (Fig. 2).

Leopard-cheetah encounters occurred most frequently at night (75% of encounters; n = 8, k = 1.973 $p < 0.025$). Encounters were uniformly distributed across lunar phases (n = 6, k = 1.243 $p > 0.15$), but did appear to peak during periods of intermediate nocturnal light availability (Fig. 2). Due to a limited leopard-cheetah night encounters sample size (n = 6), we did not investigate leopard and cheetah instigated encounters separately.

Discussion

Our study showed that overlap of activity patterns (see Rafiq, 2019) contributes to increased contacts between African predators. Across the diel cycle, encounters with guild members peaked during periods of shared temporal activity (Cozzi *et al.*, 2012), suggesting that activity overlaps increase competitor contact rates and that the costs of these overlaps are not fully offset by partitioning along other niche axes. Animal activity patterns often show behavioural plasticity to changing environments (e.g. Frey *et al.*, 2017; Gaynor *et al.*, 2018; Rabaiotti & Woodroffe, 2019), and our results suggest that within competitor assemblages, changes to species activity patterns that increase activity overlap could increase the strength of interference competition. For example, activity patterns are commonly thought to be driven by bottom-up forces (Kronfeld-Schor & Dayan, 2003), and so simplification of prey resources (Creel *et al.*, 2018) could conceivably lead to increased niche overlap across multiple axes (e.g. dietary, spatial, and temporal) within assemblages. Such shifts could lead to greater levels of top-down suppression of subordinate competitors, potentially inhibiting population growth and increasing a population's susceptibility to localised extinctions through stochastic events (Carbone, Toit, & Gordon, 1997).

Our results also suggest that encounters between African large predator guild members reflect imperfect information within heterogeneous environments, and to our knowledge our study is the first to look at encounters between large carnivores within this context. Male leopards within our study area instigated encounters with lions within closed habitats as often as lions did, but they rarely instigated encounters within open habitats. This suggests that: (i) habitats with reduced visibility limit the leopard's ability to accurately assess immediate competitor risk; and (ii) habitat structure plays a role in mediating encounter occurrences between competitors (Janssen *et al.*, 2007). It is possible that some encounters within our distance threshold were 'near-misses', where individuals remained unaware of one another's presence. However, by definition, and given that few leopard instigated encounters occurred within open habitats, this is most likely to have occurred within closed habitats and thus also supports the role of habitat structure in mediating encounters (Janssen *et al*., 2007). These findings align with previous work in which leopard avoidance behaviours to lions were greatest within open than within closed areas (e.g. Du Preez *et al.*, 2015), suggesting that the costs and benefits of encounters, and likely detectability, vary across habitats.

In open habitats, long-range detection of competitors may have allowed leopards to adapt movement directions to maintain spatial distances over the encounter threshold, whereas in closed habitats, detection may have been limited to short-distances.

Interestingly, Vanak *et al.*, (2013) found that leopards avoided areas recently occupied by lions during the dry season but not during the wet season. This may reflect the difficulties in assessing competitor risk during seasons with increased vegetation cover, e.g. when increased rainfall during wet seasons results in increased vegetation densities. Our leopard instigated lion encounters may thus have been a consequence of leopards approaching areas of interest (e.g. potential carcasses) without being aware of competitor presence or of opportunistic encounters arising from inadvertently occupying the same areas in close proximity to competitors. Our results suggest that, similar to prey detection, visual cues appear to be the primary sensory mechanism used in immediate risk assessment, whilst olfactory and auditory information appears to play a limited role, perhaps because such signals are not always available (Sunquist & Sunquist, 2002). Olfactory cues, for example, require suitable environmental conditions (e.g. wind direction) for detection, and the information they provide can depend on a range of factors, including olfactory signal location and time since deposition (Parsons *et al.*, 2018).

Leopard instigated encounters within closed habitats could also have occurred if leopards were aware of lion presence but still chose to approach. Such instances could have occurred because of the potential to acquire resources (e.g. prey), curiosity, or the ability to move quickly to a safe tree if attacked (Bailey, 2005). Whilst closed habitats can allow leopards to take refuge in trees, considering the increased ambush risks associated with these areas and mortality risks associated with encountering lions (Bailey, 2005; Hopcraft, Sinclair & Packer, 2005), we find the chance that they approach with intent unlikely. Instead, we suggest that such encounters within closed habitats likely reflect (i) the shared occupancy of these areas, perhaps occurring as a result of similar resource acquisition strategies (Balme *et al.*, 2017b), and (ii) the difficulties of detecting competitors within these areas.

Excluding cheetah encounters, for which we had a limited sample size to discuss inferences, encounters peaked for all dyads during periods of high moonlight illumination. Given that not all guild species' activity levels are influenced by moonlight availability (Cozzi *et al*., 2012), this may reflect the lower risks associated with approaching potentially contested resources during periods of high illumination, e.g. reduced lion ambush risks because of greater visibility (Funston, Mills & Biggs, 2001). Alternatively, encounter peaks across moonlight levels may have been driven by periodicity in the use of shared areas of home ranges, which in turn, may have been driven by periodicity in resource distributions (Riotte-Lambert, Benhamou & Chamaillé-Jammes, 2013). For example, impala (*Aepyceros melampus*), a favoured prey species of leopards (Hayward *et al*., 2006), can show periodicity in the use of some open habitats within their home range, with use declining during full moon periods (Riotte-Lambert *et al.*, 2013). If similar patterns of periodicity drive the space use of other prey species and/or cause prey to congregate into similar habitat patches, e.g. to reduce predation risk through mixed herd benefits (Schmitt, Stears & Shrader, 2016), then increased encounters during high moonlight illumination may reflect the attraction of competitors to habitat patches with high periodic resource availability.

Interestingly, leopard-lion and leopard-wild dog encounters also showed secondary peaks during periods of low light availability. This may simply reflect the impacts of low light levels on species detectability (Funston *et al.*, 2001). In other words, encounters may have increased during these periods because species were able to travel closer to other guild members, with or without intent, without being detected and species remained unaware of one another's presence. However, since leopard instigated lion encounters did not also show a peak during low moonlight periods, we speculate that leopards were still able to detect and avoid instigating lion encounters and that the other species' encounter peaks may have thus been species approaching guild members with purpose.

The scale of interspecific competition can vary across landscapes (Ripple *et al*., 2014), and we provide leopard-competitor encounter frequencies as a measure of the potential for interference competition. However, some caveats apply. Cheetah densities used to estimate encounter rates were based on whole counts from Broekhuis (2012), which may be unreliable since they do not account for detection probability (Hayward & Marlow, 2014). Yet they are the best measure of cheetah density within our study area, and so our cheetah encounter frequencies are presented tentatively. Further, within our study area, species densities vary across habitat types (Rich *et al*., 2019). As a result, it is likely that encounter rates also vary with habitat. Habitat-specific encounter rates were, however, not calculated because of the unavailability of accurate vegetation maps for our study area at the time of the study. The creation of high-resolution vegetation maps is ongoing, but non trivial (see Oeser *et al*., 2019). Paired with recent advances in analysing animal movement on continuous scales (Wang *et al*., 2019), we anticipate such maps will provide greater insights into the processes mediating encounters.

This was one of the few studies to directly investigate the drivers of direct encounters between large carnivores. Yet much remains to be done, and below we identify limitations to our approach and areas warranting further enquiry. Specifically, the complexity of our study system combined with the limited number of detected encounters prevented the inclusion of all potential factors impacting meeting occurrences. Resource distribution, for example, may also be a potential driver of encounters (e.g. Parsons *et al.*, 2019), yet subsampling of encounters by additional factors would have reduced effective sample sizes to unworkable levels. Unfortunately, due to the logistical challenges of working within such systems (Gittleman, 2001), with current technologies, these outcomes are near inevitable. Further, our analyses were restricted to data collected exclusively from male leopards. Female leopards were ~50% lighter than males in our study area (unpublished data), and the decision to collar only male leopards was made to minimise the ratio between the leopard collar weight and the weight of the animal. It is possible, however, that responses to competitors differ between the sexes, particularly during life-history phases when the reproductive costs of encounters are greater for females, e.g. during cub rearing (Balme *et al.*, 2013). As such, further work on the responses of females is warranted. Spotted hyaenas were also absent from our study, due to no individuals being GPS collared over the study period. However, spotted hyaenas can have significant impacts on leopard fitness through kleptoparasitism (Balme *et al.*, 2017a) and spatial capture-recapture studies suggest hyaenas actively track leopards (Balme *et al.*, 2019). Further work on the factors predisposing leopard-hyaena encounters is thus warranted. Finally, we were unable to validate the presence of prey carcasses at encounter locations due to logistical challenges in visiting encounter sites to identify kills. However, work is underway to remotely identify carcasses by using behavioural classifications from GPS collar accelerometer data.

In summary, we have shown that habitat characteristics and temporal overlap in activity patterns impact encounter occurrences between members of the African large predator guild. Our results suggest that encounters between competitors are influenced by factors which increase the difficulty in acquiring information on competitor risk and/or which increase niche axes overlaps. For example, changes in species' activity patterns that increase the level of temporal overlap between competitors may also increase encounter frequencies between them. This is particularly relevant given that we live in an era of rapid anthropogenic landscape modification, where human activities can alter the behaviour and ecology of species (Wilmers *et al.*, 2013; Dirzo *et al.*, 2014). Understanding the factors driving encounters can help predict the consequences of shifting niches and habitats for wildlife and can, ultimately, facilitate the planning of suitable landscapes for the coexistence of diverse competitor assemblages.

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Author contributions

KR, NJ, and KG conceived the study; KR collected the majority of the leopard data (with other data provided by the BPCT), carried out the analyses, and wrote the manuscript; all authors contributed critically to the drafts and gave final approval for publication.

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Fig. 1: Map of the core study area showing its location within Botswana and Africa and showing locations of leopard encounters with lions (triangle), wild dogs (pentagon), and cheetah (circle). Black lines on the satellite map represent roads. Community-owned wildlife management areas are grouped and shown as the dark shaded contiguous area covering most of the map. Moremi Game Reserve is shown as the light shaded area. The core study area map was created using Google satellite imagery obtained within the QGIS OpenLayers Plugin (Kalberer and Walker 2018).

Fig. 2: Leopard-competitor encounter peaks across diel cycles and moon illumination levels.