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Article

Research Article

Similarities between lions and sympatric carnivores in diel activity, size and morphology

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Abstract

Temporal separation in diel activity between species can be caused either by different realized niches or by competition avoidance. Morphologically similar species tend to have similar ecological niches. Therefore, morphological similarities among sympatric species may be related to both overlap in diel activity and possibilities for competition. In carnivores, competition is often strong and asymmetric. Africa contains one of the most species rich carnivore assemblages in the world, where the African lion (*Panthera leo*) is dominant wherever it is present. Using camera trap data on South African carnivores, we evaluated how overlap with lions in diel activity related to similarities to lions in body mass, skull and long bone morphology. We found a positive association between overlap in diel activity with lions and similarities in log body mass, but we only observed this association using dry season activity data. We found no associations between overlap in diel activity with lions and similarities in either long bone or skull morphology, nor did we find associations between differences in overlap in diel activity within species between one reserve with and one without lions and morphological similarity with lions. Our results suggest that niche utilization rather than avoidance of lions dictated carnivore diel activity, although we acknowledge that lion avoidance could have been manifested in spatial rather than temporal separation. Our study supports recent suggestions of context dependencies in the effects of apex predator presences.

Introduction

Sympatric animal species often space their periods of activity differently along the predictable diel cycle. Although most research on such variation has focused on the physiological mechanisms that generate circadian clocks (Takahashi et al., 2001), variation in diel activity has also been suggested as a significant mechanism for ecological community structuring (Kronfeld-Schor and Dayan, 2003). For instance, temporal separation in activity may promote co-existence of otherwise incompatible species (e.g., Sergio and Hiraldo, 2008; Mahendiran, 2016; Andersen et al., 2020). Although such processes may not necessarily be present (Jaksic, 1982)], they can shape biogeographical patterns of species distributions (Pei et al., 2018) as well as predator-prey and food web dynamics (Otto et al., 2008).

Species interactions can be strong evolutionary forces influencing many aspects of animal behaviour (Schoener, 1974). If species with overlapping resource requirements coexist, different forms of competition may occur (Hardin, 1960). The two most common competitive processes are exploitative competition, which occurs when individuals indirectly compete for common resources, and interference competition, which occurs when a competitor directly alters the resource utilization of other species (Keddy, 2001). Both of these may impact diel patterns of animal activity, but through different mechanisms. Exploitative competition can do so by inducing niche shifts, which may lead to separations in diel activity due to contrasting resource requirements (MacArthur and Levins, 1967). Interference competition, on the other hand, is often asymmetric and therefore frequently lead to shifts in diel activity by subordinate species as a means to avoid direct interactions with dominant ones (Carothers and Jaksic, 1984).

Interference competition has been suggested to be particularly pronounced for members of the mammalian order Carnivora (hereafter referred to as carnivores), which often engage in intra-guild predation, i.e. the direct killing of sympatric species to reduce competition for resources (Polis et al., 1989; Palomares and Caro, 1999; Donadio and Buskirk, 2006). The combined pressures from competitive interactions and risk of intra-guild predation often lead to spatial or temporal avoidance of dominant species (Creel et al., 2001; Durant, 2000; Hayward and Slotow, 2009). Therefore, dominant carnivore species can have a considerable impact on sympatric communities, potentially regulating their behaviour, distribution and abundance Carvalho and Gomes (2004); Ramesh et al. (2012); Swanson et al. (2016); Ramesh et al. (2017). However, the generality of such avoidance mechanisms has recently been challenged (Cozzi et al., 2012; Rasmussen and Macdonald, 2012; Mugerwa et al., 2017; Bashant et al., 2020; Rafiq et al., 2020).

The African continent contains one of the most species rich assemblages of large carnivores on Earth (Dalerum, 2013), in which the African lion (*Panthera leo*) is the dominant species wherever it is present (Woodroffe and Ginsberg, 2005). However, the African lion population is declining due to habitat loss and human conflicts (Kissui and Packer, 2004; Becker et al., 2013; Riggio et al., 2013). Since the 1940s, many reserves in South Africa have been reintroducing lions to protect the species as well as to use their charisma as tourist attractions (Breitenmoser et al., 2001; Dalerum and Miranda, 2016). These reintroductions could affect the competitive dynamics of the resident car-

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nivore communities, potentially increasing intra-guild predation and competitive exclusion. Other large carnivores such as leopards (*Panthera pardus*), wild dogs (*Lycaon pictus*) and cheetahs (*Acinonyx jubatus*) are considered to be subordinate to lions and often suffer kleptoparasitism from the dominant species or are directly killed (Caro and Laurenson, 1994; Creel et al., 2001). Smaller species, on the other hand, may be influenced by lions indirectly through mesopredator release (Prugh and Sivy, 2020).

Since carnivore morphology closely reflects niche requirements (Polly et al., 2017), morphological characteristics could be related to diel activity both through niche separation and avoidance mechanisms (Davies et al., 2007). In particular, we would expect opposite relationships between overlap in diel activity and the morphological similarity of sympatric species if diel activity is driven by niche requirements versus by avoidance of interference competition. If niche requirements, which for carnivores primarily relate to prey availability (Carbone and Gittleman, 2002), dictate activity patterns, we would expect a positive association between overlap in diel activity and morphological similarities. Under the assumptions that interference competition leads to temporal partitioning of activity (Carothers and Jaksic, 1984) and that interference competition is positively related to similarity in niche requirements (manifested in morphological traits, i.e. morphologically similar species share similar ecological niches), we would contrastingly expect a negative relationship between overlap in diel activity and morphological similarities if diel activity is influenced by avoidance of interference competition (Fig. 1).

In this study we use data from camera traps to quantify these relationships between lions and sympatric carnivore species in a small South African reserve. We hypothesize that strong competition from lions in morphologically and ecologically similar species will lead to shifts in diel activity patterns to avoid the potentially fatal consequences of not avoiding such competition (Palomares and Caro, 1999; Creel et al., 2001; Davies et al., 2007). We expect that such diel activity shifts in species that are morphologically similar to lions will generate negative relationships between diel activity overlap with lions and morphological similarity, and also a negative relationship between diel activity overlap within species between one reserve with and one without lions and morphological similarities to lions.

We relate overlap in diel activity to similarity to lions in body size as well to size independent variation in long bone and skull morphology. While body size is likely the most important morphological characteristic defining the scope for competitive interactions among carnivores (Sinclair et al., 2003), shape variation in morphological variables may be equally, or even more, important for ecological characteristics (Grossnickle, 2020). Both long bone and skull characteristics are closely related to different niche requirements (Van Valkenburgh, 1987; Taylor, 1989; Lewis, 1997; Van Valkenburgh, 2007; Samuels et al., 2013). Long bones, e.g., bones in limbs that are longer than they are wide, are found in extremities and contain some of the more defin-

ing components of carnivore skeletal structure (Ewer, 1973). The proportions and relative sizes of long bones are indicative of habitat preferences (Lewis, 1997; Meloro, 2011; Meloro et al., 2013), movement patterns (Iwaniuk et al., 2000) and hunting tactics (Andersson, 2004; Meachen-Samuels and Van Valkenburgh, 2009). The morphology of skull and dental characteristics, on the other hand, is primarily related to foraging patterns and dietary preferences, including possible scavenging (Radinsky, 1981; Davies et al., 2007; Meloro and O'Higgins, 2011; Figueirido et al., 2011). By relating overlap in diel activity to these contrasting morphological characteristics we are therefore able to interpret our results in terms of different dimensions of potential niche separation.

Methods

Study Areas

The study area includes two reserves in the Waterberg Biosphere Reserve (UNESCO heritage site) which is located in the Limpopo province, South Africa (Fig. 2a). The two reserves, Welgevonden Game Reserve (Welgevonden – 24°18′42″ S, 27°50′2″ E) and Lapalala Wilderness (Lapalala – 23°30′54″ S, 28°9′36″ E), are both privately owned and are environmentally similar. However, while lions were introduced into Welgevonden in 1998 (Kilian, 2003), at the time of study they had not been present in Lapalala since they were regionally extirpated probably in the early 20th century (Dalerum and Belton, 2015).

Rainfall is seasonal (Codron et al., 2005). From April to September the area experiences a dry season with limited rainfalls and colder weather with a minimum and maximum temperature of 20 °C in July (mid-dry). The wet season occurs from October to March, is highly humid with abundant precipitation and has fluctuating temperatures ranging from 14 °C to 30 °C. Overall mean annual precipitation is approximately 500 mm (Périquet et al., 2017). The minimum mean precipitation values are in June, July and August, ranging from 0 to 50 mm, whereas precipitation peaks in December, January and February with a mean maximum of 390 mm (Mzezewa et al., 2010). Vegetation mainly consists of Waterberg Mountain Bushveld and the topographically consists of elevated plateaus, undulating rocky hills and deep valleys (Isaacs et al., 2013).

Welgevonden was formed in 2001, although it became a conservation area in 1993. The reserve consists of 38200 ha of previous cattle farms (Kilian, 2003). Welgevonden is owned by over 50 different landowners, is open to the public and contains 15 commercial game lodges and several private ones that host guests (Dalerum and Belton, 2015). In the reserve, game viewing is allowed, but only in designated vehicles with consistent colour schemes and using certified guides. Hunting is not permitted. Lapalala was formed in 1981 and covers 36000 ha of previously commercial farmlands. In contrast to Welgevonden, it was closed to the public during this study, but a Wilderness School with educational programmes was present and occasional guided hunts were allowed (Dalerum and Belton, 2015).

During the course of this study, the lion population in Welgevonden consisted of 8–14 adults distributed across 2 prides and a coalition of males. This density is representative for other private reserves throughout South Africa (Miller and Funston, 2014). Resident carnivores occurring in both reserves included leopards, brown hyenas (*Parahyeana brunnea*), black-backed jackals (*Canis mesomelas*), caracals (*Caracal caracal*), African civets (*Civettictis civetta*), African wildcats (*Felis lybica lybica*), slender mongooses (*Galerella sanguinea*), small-spotted genets (*Genetta genetta*), large-spotted genets (*Genetta maculata*) and honey badgers (*Mellivora capensis*). White-tailed mongooses (*Ichneumia albicauda*) and servals (*Leptailurus serval*) were only observed in Welgevonden. Individual cheetahs were occasionally present in both Welgevonden and Lapalala, small groups of spotted hyenas (*Crocuta crocuta*) were occasionally present in Welgevonden, and wild dogs were present only in Lapalala (Ramnanan et al., 2013). Neither cheetahs nor spotted hyaenas held stable populations within either reserve, and the observed animals were likely transient individuals, e.g., subadult males. Both reserves contained large communities of ungulates dominated by plains zebras (*Equus quagga*), blue wildebeests (*Con-
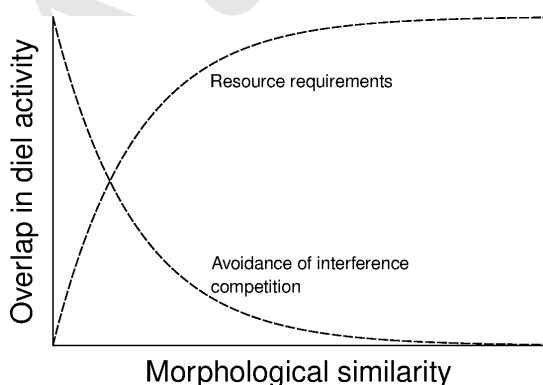
Figure 1 – Hypothetical relationships between overlap in diel activity and morphological similarities between species if resource requirements and avoidance of interference competition dictate diel activity patterns, assuming morphological similarity is positively associated with similarity in resource use.
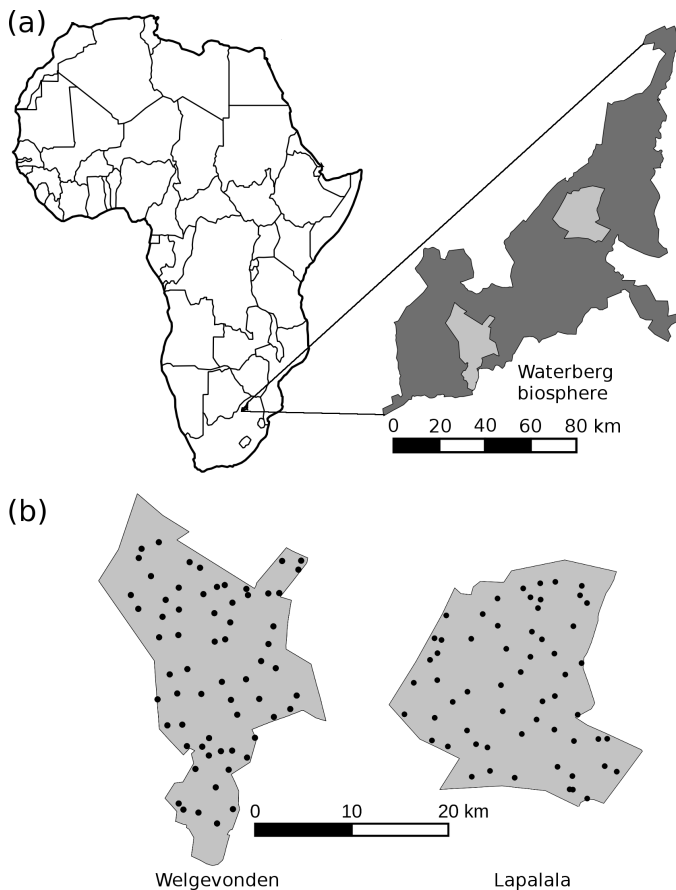
Figure 2 – Locations of the study areas within the Waterberg Biosphere Reserve (a) and outlines of each reserve including the locations of camera traps used for the study (b). During the study, Welgevonden hosted a population of 8 to 14 adult lions, whereas Lapalala has been lion free most likely since the turn of the past century.

nochaetes taurinus), impalas (*Aepyceros melampus*) and kudus (*Tragelaphus strepsiceros*). White (*Ceratotherium simum*) and black rhinos (*Diceros bicornis*) occurred in both reserves, but elephants (*Loxodonta africana*) occurred only in Welgevonden during the study. Although elephants can have substantial effects on vegetation structure, heavy management activities, such as bush clearing and controlled fires (Isaacs et al., 2013), lead to minimal differences in the vegetation structure between the reserves.

Quantification of diel activity patterns

We surveyed Welgevonden from 17 November 2008 to 26 December 2008 for the wet season and from 13 May 2009 to 12 August 2009 for the dry season, and Lapalala from 8 November 2008 until 18 December 2008 for the wet season and from 15 May 2009 to 24 July 2009 for the dry season.

In Welgevonden, we placed 104 camera traps paired in 52 stations for the wet season and 116 camera traps in 58 camera stations for the dry season. In Lapalala, we placed 114 cameras paired in 57 stations in the wet season and 118 camera traps in 59 stations in the dry season (Fig. 2b). In each reserve, the camera stations were deployed in a grid with 6.25 km^2 cell size and the resultant density was between 17–20 camera traps per 100 km^2. We conducted the survey with a block-wise system where the total number of cells ranged from 45 to 65 for each reserve. We surveyed 13–15 cells simultaneously for 18 to 20 days, after which the cameras were moved to a new set of 13–15 cells until we covered the whole area (Swanepoel et al., 2015). We placed the camera trap stations on vehicle roads or on animal paths, facing the roadway or the path clearance, since both roads and paths are used frequently by carnivores in these reserves. The camera traps were secured inside boxes and set out 50 cm above the ground. They stayed active in the field for a total of 132 days in Welgevonden, 40 days in 2008 and 92

days in 2009, while in Lapalala the cameras were active for a total of 112 days, with 41 days in 2008 and 71 days in 2009.

In Welgevonden, we used digital infrared camera traps of the type Moultre I40 Digital Game Camera (Moultrie Feeders, Birmingham, AL, USA), while we used a combination of these and film cameras in Lapalala (DeerCam DC100, Non Typical Inc., Park Falls, WI, USA; StealthCam MC2-GV, Stealth Cam, Grand Prairie, TX, USA; Trailmaster TM 1550, Goodson Associates Inc., Lenexa, KS, USA). For digital cameras, the trigger mechanism was activated by movement sensors, while film cameras were activated by active infrared detector beams. We set trap delays at 1 min for digital and 8 min for film cameras. Due to a slow digital camera trigger speed, we baited each camera trap with a mix of rotten eggs and fermented fish to increase chance of capturing useful pictures (Swanepoel et al., 2015). While such baiting has been suggested to improve the likelihood of capturing useful images for species detection, it has not been shown to bias the relative detection of different species (Gerber et al., 2012). We loaded film camera traps with Fujifilm ISO 400 and we visited the sites every 4–5 days to replace baits and change films. For digital cameras, the pictures were stored on SD memory cards.

For each image obtained during the camera trap survey, we recorded mammalian species, number of individuals, date, time and location. For this study, we extracted observations of all carnivore species, including the information of trap station, time of observation, season of the camera trapping event and species observed. We discarded all captures of the same species taken at the same camera station within 30 minutes, as well as cheetahs and spotted hyenas in Welgevonden since they did not belong to the resident carnivore community of this area (Dalerum and Belton, 2015).

We estimated diel activity pattern of each species using a kernel density estimator based on the time stamp of camera trap observations, converted to radians (Ridout and Linkie, 2009). We used a non-parametric estimation of the common area under two density distributions Δ as an index of temporal overlap in activity (Schmid and Schmidt, 2006), which ranged from 0 (no overlap) to 1 (complete overlap). This estimator was calculated numerically by taking a large number of equally spaced values between 0 and 2π, T, and summing

$$\Delta = \frac{\sum\limits_{T}^{i=1} min\{f(t_i), g(t_i)\}}{T}$$

where in our case $T=128$, and $f(t_i)$ and $g(t_i)$ are the two estimated density distributions of activity. This formulation has been recommended for sample sizes below 50 observations (Ridout and Linkie, 2009). We calculated a temporal overlap index between each species and lions using activity data only from Welgevonden, and temporal overlap index within species between the two reserves. We calculated overlap indices for each season separately, due to strong seasonal influences in both predator prey relations (Périquet et al., 2017; Chizzola et al., 2018) and in the relationships among resident carnivores (Bashant et al., 2020). We only included species that had at least 5 observations within each season and, for the comparisons between the reserves, in each reserve. We decided to use 5 observations as a threshold value because the kernel density estimator needed at least 3 data points to estimate the probability activity curves (Meredith and Ridhout, 2018). We argue that 5 observations will generate at least approximate activity distributions.

Quantification of morphological similarity

We used the body mass records from Smith et al. (2003), averaged across males and females. To describe long bone morphology, we measured total length for both fore (humerus and radius) and hind limb elements (femur and tibia) with the addition of the third metapodials. For skull morphology, we included skull length, skull width, length of the palate, width and length of the zygomatic arch, width and length of the mandible, width and length of the fourth upper premolar, the distance from the ventral border of the angular process to the dorsal tip of the condyle process (MAM – Moment Arm of Masseter) and the dis-

tance from the dorsal border of the coronoid process to the dorsal tip of the condyle process (MAT – Moment Arm of the Temporalis) as described in Radinsky (1981). We transformed the linear morphological variables to log-shape ratios (Mosimann, 1970), calculated as the log_{10} of the ratio between each linear measurement and the geometric mean for all long bone and skull characteristics, respectively. These ratios describe size-independent variation in long bone and skull morphology, and therefore provide potentially informative supplemental information to size alone with regards to niche requirements and ecological characteristics (Klingenberg, 2016).

We made morphometric measurements on 2 to 17 adult individuals per species, mostly from eastern and southern Africa (Supplemental Information, Tab. S1–S3). We used both sexes when available and we did not use any individuals with morphological pathologies. The specimens belong to the Natural History Museum of London (UK) and the Royal Museum of Central Africa (Belgium). We measured the maximum long bone lengths using an osteometric board and/or a digital caliper with 0.01 mm of accuracy. Skull measurements were obtained from 2D photographs with the support of the `tpsDig2` software (Rohlf, 2015). The cranium was photographed in ventral view with the palate placed parallel to the photographic plan using a spirit level. Same applied to the lateral hemimandible. This ensured little distortion and good fidelity of three dimensional skull proportions with 2D (Muir et al., 2012; Cardini, 2014; Tamagnini et al., 2021). We used a lens with 100 mm focal length. We calibrated the measurement error on a sub-sample of 5 different species for which calliper measurements were collected. In all cases the error obtained after comparing calliper with 2D photos measurements was <5%.

Data analyses

We scaled and centred each morphological variable by dividing it with its standard deviation and subtracting the mean, so that each unit change was comparable for all metrics (Manly, 2004). We used log_{10} transformed data for body mass. We then calculated the differences in scaled log body mass between each species and lions, and separate Euclidean distances between each species and lions for scaled size-independent

long bone and skull metrics. For ease of interpretation, for each set of morphological characteristics (i.e., body mass, long bone morphology and skull morphology), we transformed the differences or Euclidean distances to similarity indices as:

$$s_i = 1 - \frac{d_i}{max(d)}$$

where s_i is the similarity to lions for the i-th species, d_i is the difference (for log body mass) or Euclidean distance (for long bone and skull morphology) to lions for the i-th species, and $max(d)$ is the maximum difference or Euclidean distance among the measured species. This index takes a value between 0 and 1, where 0 is the least similar species to lions and 1 is a species identical to lions.

We used linear models to relate pair-wise overlap in diel activity between each species and lions to corresponding similarities in body size and morphology, as well as to relate overlap in diel activity between the two reserves within each species to corresponding similarities to lions. For each dependent variable, i.e., activity overlap with lions and activity overlap between the two reserves, we ran separate models for activity data from the wet and dry seasons, respectively.

We performed the statistical analyses in R version 4.0.3 for Linux (http://www.r-project.org), using the contributed package `Overlap` for quantifying overlap in diel activity (Ridout and Linkie, 2009).

Results

Our study included a total of 1020 observations of carnivores in Welgevonden (790 in dry season and 230 in wet season) and 653 observations in Lapalala (504 in dry season and 149 in wet season). These observations included 13 resident carnivore species in Welgevonden and 11 species in Lapalala (Tab. 1), ranging in body mass from 0.6 to 50 kg, in diet from large mammals to arthropods, and had both terrestrial as well as partially arboreal locomotor patterns (Tab. 1). The majority of the carnivore species had nocturnal or crepuscular activity patterns. Only slender mongoose in both reserves and banded mongoose in Lapalala were mainly active during daylight (Supplemental Information, Fig. S6–S7).

Table 1 – Carnivore species detected during camera trap surveys in Welgevonden Game Reserve and Lapalala Wilderness, South Africa, as well as their average body mass (kg), broad diet category, general locomotor activity, and number of observations during each season. Observations were only counted as independent if made at least 30 min. apart. Only species with more than 5 independent observations for a specific season were included in the analyses. Body sizes are based on Smith et al. (2003), diet categories on Christiansen and Wroe (2007) and locomotor activity on Ortolani and Caro (1996).

Species name	Common name	Family	Body mass (kg)	Diet	Locomotor activity	Welgevonden Dry	Welgevonden Wet	Lapalala Dry	Lapalala Wet
Acinonyx jubatus[a]	Cheetah	Felidae	50.1	Large mammals	Terrestrial	5	0[2]	0[2]	0[2]
Atilax paludinosus	Marsh mongoose	Herpestidae	3.5	Omnivore	Semi aquatic	0[2]	0[2]	2[2]	0[2]
Canis mesomelas	Black-backed jackal	Canidae	8.5	Omnivore	Terrestrial	132	13	28	13
Caracal caracal	Caracal	Felidae	13.7	Small vertebrates	Terrestrial but climbs	30	11	18	3[2]
Civettictis civetta	African civet	Viverridae	12.0	Omnivore	Terrestrial	331	32	245	26
Felis lybica	African wildcat	Felidae	4.6	Small vertebrates	Terrestrial but climbs	4[6]	5	9	1[2]
Galerella sanguinea	Slender mongoos	Herpestidae	0.6	Omnivore	Terrestrial and Arboreal	18	1[2]	9	1[2]
Genetta genetta	Common genet	Viverridae	2.0	Omnivore	Terrestrial and Arboreal	8	6	0[2]	3[2]
Genetta maculata	Large-spotted genet	Viverridae	2.2	Omnivore	Terrestrial and Arboreal	15	3[2]	51	11
Hyaena brunnea	Brown hyaena	Hyaenidae	32.2	Medium sized mammals	Terrestrial	126	135	88	69
Ichneumia albicauda	Whilte-tailed mongoose	Herpestidae	3.5		Terrestrial but climbs	8	0[2]	0[2]	0[2]
Leptailurus serval	Serval	Felidae	12.0	Small vertebrates	Terrestrial but climbs	35	2[2]	0[2]	0[2]
Lycaon pictus	African wild dog	Canidae	22.1	Large mammals	Terrestrial	0[2]	0[2]	12[3]	1[3]
Mellivora capensis	Honey badger	Mustelidae	8.0	Omnivore	Terrestrial but climbs	35	8	16	1[2]
Mungos mungo	Striped mongoose	Herpestidae	1.9	Arthropods	Terrestrial but climbs	2[2]	0[2]	5[3]	8[3]
Otocyon megalotis	Bat-eared fox	Canidae	4.2	Arthropods	Terrestrial	0[2]	2[2]	0[2]	0[2]
Panthera leo	African lion	Felidae	161.5	Large mammals	Terrestrial	34	7	0[2]	0[2]
Panthera pardus	Leopard	Felidae	45.5	Large mammals	Terrestrial but climbs	48	14	23	14
Proteles cristata	Spotted hyaena	Hyaenidae	10.0	Arthropods	Terrestrial	0[2]	0[2]	0[2]	1[2]

[a] Excluded from the analyses because it did not have resident populations
[2] Excluded from the analyses because of insufficient number of observations
[3] Excluded from the analyses because of insufficient number of observations for the population with lions
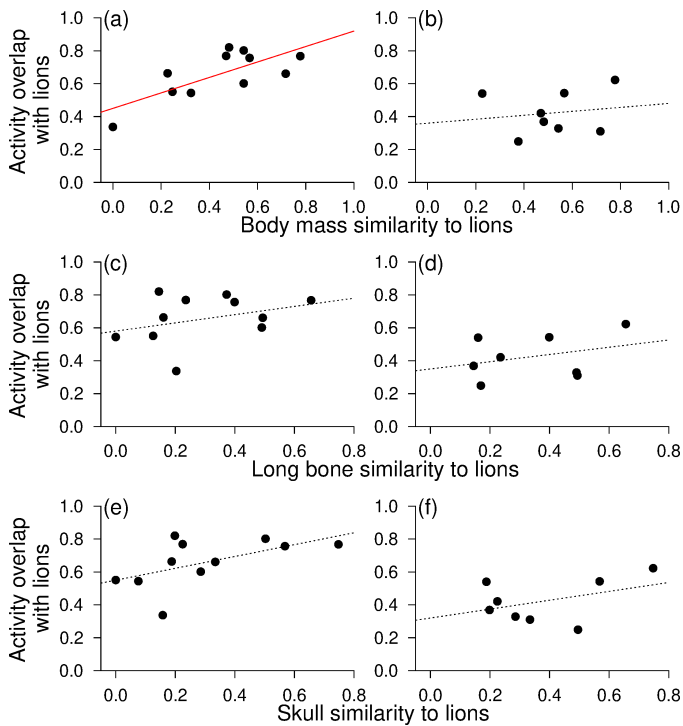
Figure 3 – Relationships between overlap with lions in diel activity and corresponding similarities to lions in log body mass (a-d) and size-independent skull morphology (e-f) for all sympatric carnivore species in Welgevonden. Data are presented for activity data for activity data from the dry (a, c, e), and the wet season (b, d, f) separately. Solid lines represent significant linear relationships, whereas dotted lines represent linear relationships that were not found to be statistically significant at a threshold of 0.05. Similarity is represented as an index ranging from 0 (the least similar species to lions among the measured species) to 1 (a species identical to lions).

Figure 4 – Relationships between overlap in diel activity between two reserves, one with and one without lions, within a community of sympatric carnivores and associated similarities between each species and lions in log body mass (a-b), size-independent long bone morphology (c-d) and size-independent skull morphology (e-f). Data are presented for activity data from the dry (a, c, e), and the wet season (b, d, f) season separately. Dotted lines represent linear relationships that were not found to be statistically significant at a threshold of 0.05. Similarity is represented as an index ranging from 0 (the least similar species to lions among the measured species) to 1 (a species identical to lions).

There was a significant positive relationship between overlap with lions in diel activity during the dry season and body mass similarities (β=0.47, SE_β=0.14, n=13, p=0.010, Fig. 3a), but no relationships between overlap in diel activity in the wet season and body mass similarities (β=0.12, SE_β=0.30, n=8, p=0.713, Fig. 3b). Overlap with lions in diel activity was not related to similarities in either size-independent long bone (dry season: β=0.25, SE_β=0.23, n=13, p=0.296, Fig. 3c; wet season: β=0.22, SE_β=0.27, n=8, p=0.432, Fig. 3d) or skull morphology (dry season: β=0.36, SE_β=0.18, n=13, p=0.072, Fig. 3e; wet season: β=0.27, SE_β=0.24, n=8, p=0.311, Fig. 3f). Coefficients of each species overlap with lions in diel activity are given in the Supplemental Information, Tab. S4.

Overlap in diel activity between the reserves was not significantly related to similarities to lions in neither body mass (dry season: β=0.16, SE_β=0.15, n=8, p=0.323, Fig. 4a; wet season: β=0.00, SE_β=0.58, n=4, p=0.999, Fig. 4b) nor size-independent long bone (dry season β=0.07, SE_β=0.21, n=8, p=0.738, Fig. 4c; wet season β=0.02, SE_β=0.38, n=4, p=0.955, Fig. 4d) or skull morphology (dry season: β=-0.11, SE_β=0.17, n=8, p=0.539, Fig. 4e; wet season β=-0.24, SE_β=0.29, n=4, p=0.493, Fig. 4f). Averaged across all species overlap in diel activity between the reserves were higher in the dry (mean=0.76, sd=0.10) than in the wet (mean=0.69, sd=0.12) season (Supplemental Information, Tab. S5).

Discussion

We observed positive relationships between overlap in diel activity and body mass similarities to lions, but no relationships between overlap in diel activity and similarities in size-independent long bone and skull morphology. These results support the interpretation that diel activity of these carnivore species were primarily related to niche requirements, most likely prey availability. We appreciate that avoidance of lions by similar species could have occurred by means other than shifts in diel activity, for instance in spatial rather than temporal shifts in ac-
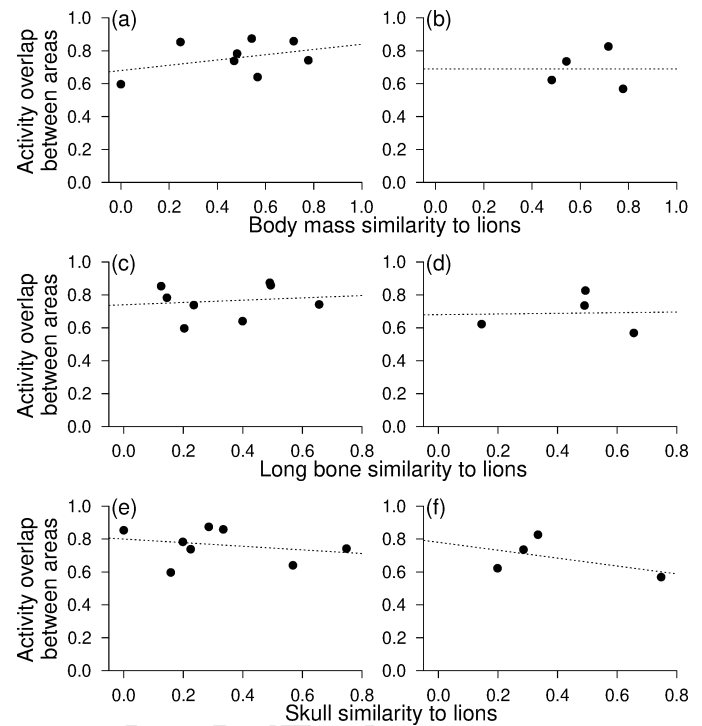
tivity. However, we note that the results came from a relatively small and fenced reserve, where we could have expected an accentuated effect of avoidance of a dominant competitor and limited possibility for spatial avoidance. Despite previous arguments of competition being an important structural force in carnivore communities (Palomares and Caro, 1999; Hayward and Slotow, 2009), a lack of competition effects has been observed previously (Wikenros et al., 2010). There are no doubts regarding regarding the ecological importance of apex predators (reviewed in Estes et al., 2011 and Ritchie et al., 2012). However, we argue that our results add to recent literature suggesting that the presence of apex predator species may not always have large effects on sympatric predator-prey communities (e.g., Middleton et al., 2013; Balme et al., 2017; Mugerwa et al., 2017), or such that such effects are highly context dependent across different spatial and tepmoral scales (Valeix et al., 2009; Périquet et al., 2017; Chizzola et al., 2018; Bashant et al., 2020; Wirsing et al., 2021).

The observed positive association between overlap in diel activity in lions and body mass similarities indicate that size related variation in resource and space use dictated patterns of diel activity rather than avoidance of interference competition and predation (Cassia Bianchi et al., 2016). The observed positive relationship between overlap with lions in diel activity and body mass similarities could, for instance, have been related to similar prey preferences and hunting behaviour among large species, combined with scavenging and kleptoparasitism, and a combination of similar hunting behaviour and predator avoidance for small ones. Positive associations between morphological similarities to lions and overlap in diel activity patterns have been observed previously for scavenging species such as jackals and hyaenas (Périquet et al., 2015; Swanson et al., 2016), although we suggest that for species which rarely scavenge, such as leopards, the observed overlap in diel activity was likely caused by similar hunting habits (Balme et al., 2017). We note that the largely crepuscular activity we observed among the carnivores correspond with the activity of both large and small prey on the reserves (authors observations), as well as activity of potential prey reported from similar environments (e.g., Bennie et al., 2014; Owen-

Smith and Goodall, 2014), which further lends support for niche driven diel activity in these carnivore communities.

Because our results were largely driven by the diel activity patterns during the dry season, we suggest that overlap in diel patterns of activity among carnivores may be dynamic and context dependent. Although we appreciate that we had smaller sample sizes in the wet season, this finding agrees with previous observations on carnivore communities both in Africa (Vanak et al., 2013; Bashant et al., 2020) and Asia (Karanth et al., 2017). Such an interpretation would also resonate with previous findings of seasonal and context dependent indirect effects of lions on their main prey in these reserves (Périquet et al., 2017; Chizzola et al., 2018). A seasonal homogenisation of the spatial distribution of potential prey have previously been observed in the Waterberg (Isaacs et al., 2013), and ungulates in southern Africa have been observed to be active during a shorter time in the dry than in the wet season (Owen-Smith, 2008). We therefore suggest that the observed seasonal variation in the associations between overlap in diel activity and body mass at least partly could have been caused by seasonal variations in the availability and distribution of potential prey, but also by seasonal variation in vegetation cover and structure.

We found a significant association between overlap with lions in diel activity and body mass similarities, but not between overlap in diel activity and similarities in either size independent long bone (a proxy for locomotor characteristics, Van Valkenburgh, 1987) or skull (a proxy for dietary requirements, Werdelin, 1996) morphology. Our results therefore suggest that size related variation in resource use may have been more important determinants of diel activity than shape mediated variation in movement and diet. Despite carnivores being possible to group into morphologically based ecotypes (Werdelin, 1996), such an interpretation would agree with broad findings of the importance of carnivore body size for brain size, social behaviour and life history (Bekoff et al., 1984; Gittleman, 1986), as well as dietary requirements (Gittleman, 1985), in particularly prey size (Carbone et al., 1999). Our results therefore support previous studies highlighting the importance of animal body size variation for the regulation of ecosystem structure (reviewed in Holling, 1992), although variations in cranial and limb shape may also be important for carnivore niche partitioning among similarly sized species (Taylor, 1989; Van Valkenburgh, 1989). Mammalian carnivores have one of the most dramatic body size ranges among all mammals (Nowak, 1999), and our interpretation therefore reiterates previous suggestions that size related structuring of carnivore communities may have significant ecological importance (Johnson et al., 1996; Sinclair et al., 2003; Woodroffe and Ginsberg, 2005).

We acknowledge several, not necessarily mutually exclusive, caveats to our study. First, diel activity patterns are generally regulated by light through neurophysiological mechanisms (Cermakian and Sassone-Corsi, 2002). Since physiological mechanisms tend to be evolutionary conservative, the observed lack of effects of competition on activity patterns could have been caused by evolutionary constraints on diel activity rather than by a lack of competition taking place (Kronfeld-Schor and Dayan, 2003). Such evolutionary constraints may cause species to exhibit non-optimal behavioural phenotypes, particularly if trade-offs exist among behaviour which face opposing evolutionary pressures (Sih et al., 2004). Second, several studies have shown spatial avoidance as a response to competition (e.g., Tannerfeldt et al., 2002; Grassel et al., 2015; de Satgé et al., 2017), and we acknowledge that competition driven avoidance could have occurred in space rather than in time. Third, any temporal avoidance could have occurred at temporal scales not captured by our sample protocol. Such temporal context dependence has, for instance, been observed for anti-predatory behaviour of potential prey (Valeix et al., 2009), and similar context dependencies are likely to be present also for sympatric predator species (Karanth et al., 2017). Fourth, there could be a size dependent response to human activities that may have masked any effects of intra specific interactions. However, all animals were used to the game viewing activities in Welgevonden, and the activities in Lapalala were either highly localized (educational activities) or very rare (occasional hunts). We therefore regard it unlikely that human activities had strong effects on the diel

activity patterns observed. Finally, we cannot completely rule out that parts of our results were hampered by limited sample sizes, either in the low number of species for which we had a sufficient number of observations for, or by an insufficient number of observations within species for reliable estimates of temporal activity patterns. We also acknowledge that our study had an ecological sample size of one. However, we stress that studies based on direct field observations, such as this, needs to form an integral part of our inquiries into the reality we live in, even if it may hamper statistical sample sizes compared to data accumulated over time or space (Ríos-Saldaña et al., 2018).

To conclude, our study suggests that diel activity patterns within a sympatric carnivore community did not appear to have been influenced by an avoidance of lions, although we acknowledge that interference competition from lions could still have occurred but not been manifested in diel activity shifts. Instead, we suggest that our observations indicate that resources, such as prey availability, may have been important for determining the diel activity patterns of these carnivores. However, a seasonal variation in the association between overlap in diel activity and morphological similarities suggests that seasonal variation in resource abundance and distribution may have influenced such processes. While we highlight the importance of body size related variation in resource use for the observed diel patterns, we can not discard that, among similarly sized species, shape mediated variations in movement and broad dietary strategies may also play a role in structuring the activity patterns of sympatric carnivores.

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Supplemental information

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

Table S1 Specimens used for measuring morphometric data.

Table S2 Body mass as well as species averages for five long bone characteristics.

Table S3 Species averages for 11 skull characteristics.

Table S4 Pairwise coefficients of activity overlap between lions and co-occurring carnivore species in Welgevonden game reserve.

Table S5 Pairwise coefficients of activity overlap between two reserves.

Figure S6 Probability distributions describing diel activity patterns of carnivore species observed in Welgevonden Game Reserve.

Figure S7 Probability distributions describing diel activity patterns of carnivore species observed in Lapalala Wilderness.