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Seasonal spatio-temporal coexistence of leopard (Panthera pardus) and brown hyena (Parahyaena brunnea) in the hyper-arid landscape of southern Namibia

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Abstract: Competition and facilitation shape carnivore community structure, exerting top-down effects on subordinate species and prey and influencing spatio-temporal distributions. These dynamics have been widely studied in southern Africa's high-productivity, mesic environments, but remain poorly understood

in arid ecosystems, where low predator densities, distinct prey assemblages, and limited resources constrain species occurrence and reshape expected interspecific relationships. In hyper-arid inland Namibia, leopards and brown hyenas co-occur, occupying the apex predator niche left vacant by lions and spotted hyenas. Here, we investigated the pattern of spatio-temporal coexistence between these two competitors, assessing the roles of habitat, prey, and human activity in shaping habitat use and activity patterns. Using two years of camera trapping (71 stations, 533 km² private reserve), we estimated temporal activity patterns and overlap via kernel density functions, and applied multi-species single-season occupancy models to characterize spatio-temporal niches conditional on competitor presence across dry and wet seasons. Temporal overlap remained moderate (dry season: $\Delta = 0.68$, 95% CI = 0.57–0.79; wet season: $\Delta = 0.68$, 95% CI = 0.53–0.82), with different activity rhythms ($p < 0.01$). Co-occurrence shifted seasonally: leopards and brown hyenas were spatially independent in the dry season but exerted a positive influence on each other's occupancy in the wet season. Prey abundance, distance from water, and topography were the strongest drivers of marginal occupancy. Our findings showed that leopards and brown hyenas may compete for limited resources in hyper-arid environments, coexisting through consistent temporal partitioning, seasonal spatial independence under resource scarcity, and facilitation-driven co-occurrence during productive periods.

Key words: Spatio-temporal co-occurrence, Large carnivores, Niche partitioning, Desert, Camera trapping

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Introduction

Understanding the underlying ecological mechanisms maintaining stable carnivore assemblages is a key element to integrate in conservation and management planning, especially as these communities are shifting in space and composition due to anthropogenic pressures (Linnell and Strand 2000; Ritchie and Johnson 2009; Estes et al. 2011). As human populations expand into wilderness areas, increasing the occurrence of conflict encounters with wildlife (Nyhus 2016), removal and alteration of populations of apex predators are expected to occur more frequently (Ripple et al. 2016). Large mammalian apex predators exert top-down direct and indirect controls over prey and subordinate carnivore species, influencing their population dynamics, behavior, and trophic role (Estes et al. 2011). The consequent cascading effects following apex carnivore disappearance, either naturally or as consequence of human intervention, are thus difficult to predict (Linnell and Strand 2000; Estes et al. 2011; Ripple et al. 2016). Following long-term studies documenting trophic cascades after wolves (*Canis lupus*) reintroduction in North America (Ripple and Beschta 2012), other studies have investigated these patterns elsewhere. In Mozambique's Gorongosa National Park, the perceived presence/absence of apex predators (i.e., wild dogs *Lycaon pictus* and African leopard *Panthera pardus* ssp. *pardus*, hereafter 'leopard') was shown to modify feeding patterns and habitat use of prey species, affecting herbivore pressure on plant composition across habitats (Atkins et al. 2019). One well-documented consequence of apex predators' loss is *mesopredator release* whereby subordinate carnivores increase and occupy the apex predator niche, with negative implications for smaller prey species (Ritchie and Johnson 2009; Prugh et al. 2009). Consequently, generalist and adaptable predators, and subordinate species, are released from top-down pressure, leading to new coexistence and competition dynamics that restructure ecosystem functioning (Dyck et al. 2022).

Intraguild interactions between carnivore species range from facilitation to competition (Caro and Stoner 2003). Facilitation can occur during scavenging on an abandoned kill: it is a positive interaction where at least one partner benefits from the presence of the other without causing a negative effect (Bertness and

Callaway 1994). In carnivore communities, such carrion-mediated facilitation can generate positive spatial associations between predator and scavenger species, particularly when prey availability and kill rates are high (Selva and Fortuna 2007; Cortés-Avizanda et al. 2009). Competition can be direct or indirect (Vance 1984). Direct (i.e., interference) competition occurs when one species actively displaces a subordinate species from access to resources and can lead to intraguild predation events (Linnell and Strand 2000; Raimondi et al. 2023). Conversely, indirect (i.e., exploitative) competition occurs when a species consumes a limited resource, reducing availability for other co-occurring species (Vance 1984; Wiens 1993). These mechanisms shape diverse carnivore assemblages across multiple ecosystems (see Linnell and Strand 2000), with most intraguild interactions described as competitive (Linnell and Strand 2000; Caro and Stoner 2003). Nevertheless, species have evolved different strategies that allow competitors to coexist in the same area (Vance 1984; Vanak et al. 2013).

Resource partitioning (e.g., dietary niche partitioning) can effectively reduce competition between co-occurring species and has long been identified as the most important driver of community structure (Périquet et al. 2015; Dröge et al. 2017; Raimondi et al. 2023; Mills 2015). However, this strategy might be considered as a consequence of intraguild competition rather than a strategy to avoid it (Vanak et al. 2013). Another key aspect is habitat heterogeneity as a function of space and time, whereby species adjust their spatial and temporal niche to the presence and abundance of sympatric competitors and prey (Carothers and Jaksić 1984; Broekhuis et al. 2013; Périquet et al. 2015; Karanth et al. 2017; Vanak et al. 2013). Karanth et al. (2017), for example, found that three competitor species (i.e., tiger *Panthera tigris*, leopard, and dhole *Cuon alpinus*) alternated their spatio-temporal behavior and fine-scale avoidance strategies according to resource availability. Similarly, in lion (*Panthera leo*) and spotted hyena (*Crocuta crocuta*) dominated landscapes, subordinate species (i.e., cheetah *Acinonyx jubatus*, wild dog, and leopard) adopt large-scale avoidance or *predictive responses* (e.g., selecting areas with lower resource availability) or fine-scale *reactive responses* (i.e., short-term behavioral modification) depending on species, habitat, and risk-perception, allowing them to retain access to resource-rich areas (Broekhuis et al. 2013; Vanak et al. 2013; Dröge et al. 2017).

Within the vast landscapes of sub-Saharan Africa, the mammalian community structure shows representatives from all trophic levels, from large herbivores (e.g., African Savanna elephant *Loxodonta*

africana) and top-predators (e.g., lion), to micro-mammals (e.g., elephant shrew *Elephantulus* sp.) (Estes 2012). It hosts one of the richest land carnivore assemblages in the world, with the apex predator niche represented by lions and spotted hyena, followed by subordinate species such as leopard, wild dog, cheetah, and brown hyena (*Parahyaena brunnea*), and a large diversity of mesocarnivores (e.g., jackals *Lupulella* sp., serval *Leptailurus serval*, caracal *Caracal caracal*, and African wildcat *Felis lybica*). In high-productivity, mesic environments the interspecific interactions within the large carnivore guild have been widely investigated (e.g., Durant 1998; Broekhuis et al. 2013; Barker et al. 2022; Vissia et al. 2022), whereas hyper-arid and desert systems have been, to our knowledge, largely overlooked, despite covering large portions of southern Africa and hosting some of its most endangered species (Durant et al. 2012). In these environments, competition and facilitation dynamics are shaped by low predator densities, different prey species assemblages, and reduced resource availability, modifying the expected species-species relationships (Mills 2015). In long-term studies in the arid southern Kalahari Desert (Mills 2015; Bothma 1998), large predators selectively prey upon uncommon or small-sized species outside their usual prey base: lions regularly hunted porcupines, while leopards frequently consumed smaller carnivores. The authors therefore suggested dietary niche partitioning as a key strategy to allow coexistence. Additionally, the dominant role of lions and spotted hyenas was mediated by the competitive advantage of smaller adaptable species, able to exploit a wider range of resources and survive extreme climate conditions. Subordinate species further benefited from dominant competitors through kleptoparasitism and scavenging on abandoned kills (Mills 2015).

Here, we argue that extending the investigation to hyper-arid environments can help better understand the ecological dynamics of overlooked and endangered ecosystems (Durant et al. 2012). This becomes important when considering how climate change is causing the expansion of drylands, with unpredictable consequences on species assemblages and interaction patterns (Durant et al. 2012; Estes et al. 2011). For this study, we focused on the mountainous desert landscapes of inland southern Namibia, hosting a viable example of a simplified carnivore guild in an environment characterized by limiting resources, high seasonality, and low population densities. We investigated the spatio-temporal dynamics between the two largest carnivore species in the Fish River Canyon. Following the eradication of lions and spotted hyenas across southern Namibia, the large carnivore guild now comprises leopard and brown hyena (Brown 2006; Ramello et al. 2025), with cheetahs occurring at very low densities.

The overarching aim of this study is therefore to investigate the fine-scale interspecific interaction dynamics between leopard and brown hyena, to better understand the limiting drivers that shape coexistence and spatio-temporal dynamics between subordinate carnivore species occupying similar ecological niches in the absence of top-down control. Through a two-years camera trapping protocol, we analyzed the occupancy, co-occurrence, and activity patterns of leopards and brown hyenas in relation to prey abundance, environmental factors, and human disturbance. We tested predictions on the effects of these variables on the seasonal occupancy of each species independently of each other, and on their effects on co-occurrence patterns (Supplementary Table S1). We interpreted spatial and temporal co-occurrence patterns as proxy for potential competition and facilitation interactions (Karanth et al. 2017); specifically, niche segregation (i.e., negative conditional occupancy and difference in activity rhythms) as indicative of competition mitigation strategies, whilst niche overlap (i.e., positive conditional occupancy and similar activity patterns) as suggestive of facilitation patterns (Davis et al. 2021; Cong et al. 2024; Vanak et al. 2013; Chaudhary et al. 2020). We expected to observe seasonal differences in competition/facilitation patterns according to the *fat-times lean-times* competition hypothesis (Wiens 1993; Linnell and Strand 2000). During the rainy summer months (Wet Season, WS), we predicted increased niche overlap between leopard and brown hyena, potentially driven by relaxed resource limitation and by indirect facilitation as increased leopard hunting success generates carrion, attracting brown hyenas to shared areas (Selva and Fortuna 2007; Cortés-Avizanda et al. 2009; Stein et al. 2013). Conversely, during the Dry Season (DS) as limited availability or clumping of resources are known drivers of increased competition (Davis et al. 2021; Wilson and Wolkovich 2011), we expected competitive pressures to increase, leading leopard and brown hyena to segregate more strongly in space and time, reducing the costs associated with interspecific competition (Vanak et al. 2013; Périquet et al. 2021). We further expected access to resources such as prey species, scavenging opportunities, and water to be a limiting factor in desert systems (Hayward and Slotow 2009; Edwards et al. 2016), with greater effects during the Dry Season (DS).

Materials and methods

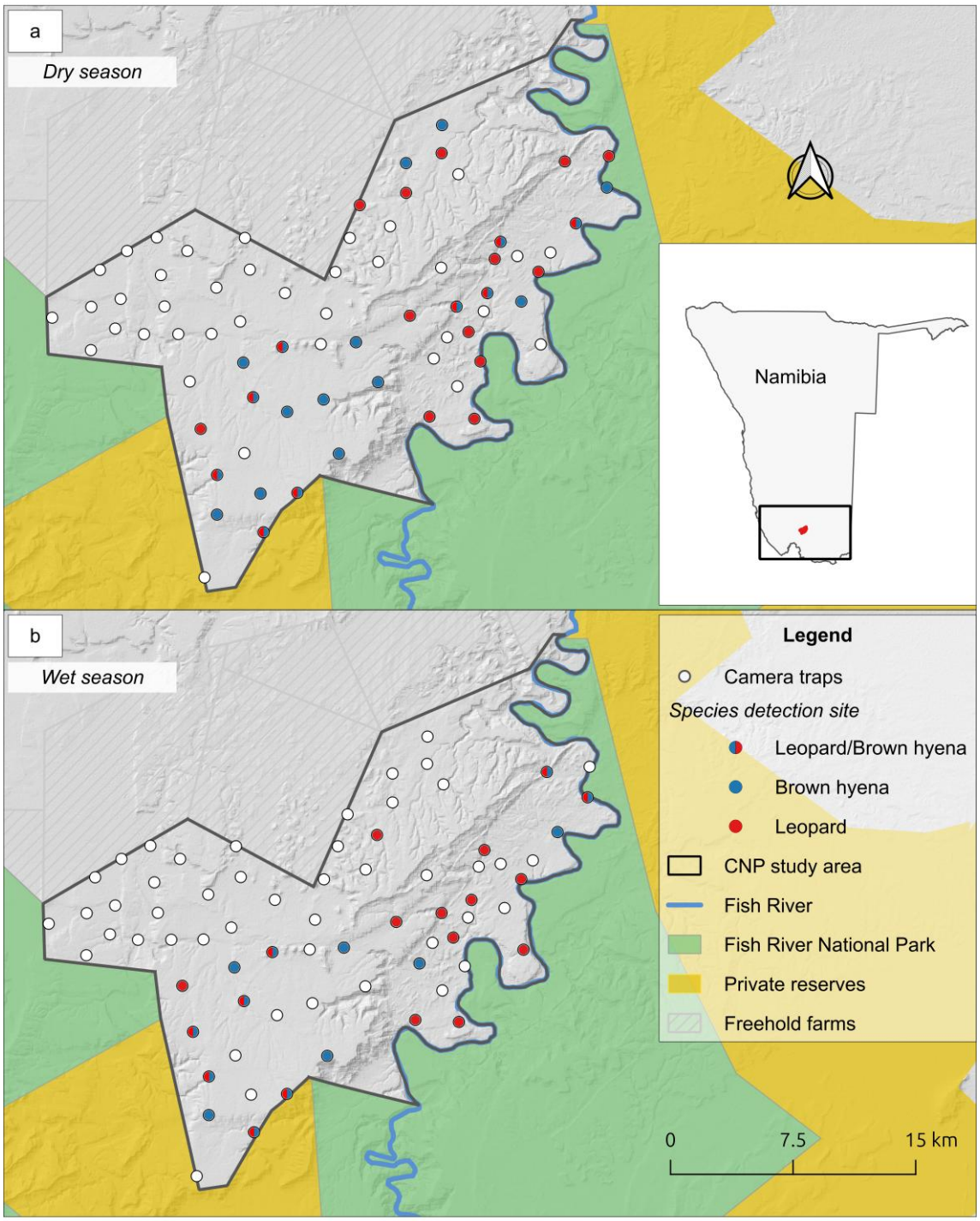
Study area

The study was conducted at Canyon Nature Park (CNP; centered at S 27.44466° E 17.54950° WGS84 datum), a private nature reserve located in southern Namibia along the western bank of the Fish River (Fig.

1). The property spans ca. 519 km^2, covering the north-western section of the Fish River Canyon and the surrounding upper plateau. CNP is part of the Greater Fish River Canyon Landscape consortium (GFRCL), which creates a network of interconnected conservation areas, both private and national. Through the GFRCL, an extensive ecological corridor is formed, connecting inland southern Namibia to the Sperrgebiet National Park along the coast and, through the Orange River, to South Africa's Richtersveld National Park.

CNP is characterized by a hyper-arid climate, with a DS spanning from May to October and a warm WS from November to April (Atlas of Namibia 2022). Temperatures range from a minimum average of 6–8 °C to a maximum average of 34–36 °C. Rainfall occurs mainly during the WS, but irregular precipitation can occur year-round, with an average annual rainfall < 100 mm (Atlas of Namibia 2022). The region is characterized by sparse desert-adapted vegetation typical of the Nama Karoo biome, with common formations of *Euphorbia gregaria* and *Rhigozum trichotomum* (Burke 2013). Perennial plant cover is scarce and tree species, such as *Acacia erioloba* and *Acacia karroo*, are mainly concentrated along dry riverbeds and kloofs (Burke 2013; Brown 2006).

The landscape of CNP can be divided into an upper plateau and a lower main canyon, with elevations ranging from 423 m a.s.l. to 1047 m a.s.l. The property was founded in 1995 with the acquisition of several small-livestock farms. Since its establishment, CNP has enforced conservation measures aimed at restoring natural habitats and facilitating natural recolonization of wildlife. Historically, the area has seen the eradication of large mammal species such as lions, savanna elephants, and spotted hyenas as a consequence of hunting and land-use practices (Brown 2006). Other species, such as leopard, brown hyena, caracal, and cheetah, have drastically declined. Recently, the establishment of protected areas and conservation policies has initiated a slow recovery of free-roaming wildlife throughout the GFRCL (Brown 2006). Today, a diverse array of mammal species can be commonly found in the area, including gemsbok (*Oryx gazella*), springbok (*Antidorcas marsupialis*), Hartmann's mountain zebra (*Equus zebra* ssp. *hartmannae*), kudu (*Tragelaphus strepsiceros*), giraffe (*Giraffa camelopardalis*), Cape grey mongoose (*Herpestes pulverulentus*), rock hyrax (*Procavia capensis*), Cape hare (*Lepus capensis*), small-spotted genet (*Genetta genetta*), and black-backed jackal (*L. mesomelas*).



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200 **Fig. 1** Map representing camera traps placement, detection sites for leopard and brown hyena (a: dry season;

201 b: wet season) across the sampling area, and location of the study site of Canyon Nature Park (CNP) within

the context of surrounding protected areas and freehold farms. The inset map shows its geographic location in Namibia

Data collection and extraction

Data collection was conducted over two consecutive years, from May 2023 to April 2025. Camera trap (CT) stations covered a total sampling area of 533 km^2 (estimated via 100% minimum convex polygon) with 71 camera sites (Fig. 1), each identified by an alphanumeric code (e.g., FR01). All stations were equipped with a single CT device. Different camera trap models (Wosport, Bushnell, Ranger, Digitgarden, Bolyguard, and Wolfang) were used throughout the sampling period and rotated across stations to avoid sampling biases and cover all the available environments (Rovero and Zimmermann 2016). From May 2023 to April 2024, 52 CT sites were active, while from May 2024, 19 additional CTs were deployed following the acquisition of a neighboring farm, increasing the extent of the study area. For temporal analysis we included data collected from the 71 CTs. For occupancy analysis we considered data from 48 CTs, active throughout both sampling years.

CT placement was selected *a priori* by superimposing a standardized 2 × 2 km grid, built in QGIS (v. 3.28; Dawson et al. 2022) designed to capture a diverse array of target species (i.e., medium to large carnivores), achieving a mean distance between CTs of 2075.67 m ± 60.61 SE. Considering field access limitations, CTs were placed in the most suitable location close to grid-cell' centroids. Game paths, artificial waterholes, natural springs, forced passages, and carnivore marking spots were preferentially selected as camera sites to increase capture probability of target species (Rovero and Zimmermann 2016).

Devices were checked every ca. 25 days, during which batteries and SD cards were replaced. CTs were set to operate 24h a day, capturing a sequence of three photos followed by a 5-minute inactivity period during which the motion sensor was non-receptive (Rovero and Zimmermann 2016). Devices were set 30–50 cm above ground, 2–4 meters from the frame area and secured on rocks and trees.

Data filtering and species identification were conducted manually, then processed using the *camtrapR* package (Niedballa et al. 2023) to obtain a complete dataset of independent detections. All detections separated by less than 15 minutes for the same species and CT station were collapsed into a single event to reduce temporal pseudo-replication (Rovero and Zimmermann 2016; Ramello et al. 2025). The dataset was

subsequently divided by season (i.e., DS = May–October; WS = November–April), with data belonging to the same season pooled for the two successive years (Rovero et al. 2013; Wevers et al. 2021).

Temporal activity patterns and overlaps

The analyses were performed following the workflow described in Sogliani et al. (2026). We analyzed the two seasonal subsets: WS and DS. Civil time was converted to true solar time through the *sunTime* function within the *overlap* R package to account for the local variation in sunrise and sunset and better reflect natural light conditions (Nouvellet et al. 2012).

To test whether species exhibited a non-random temporal distribution, the Hermans-Rasson uniformity test (HR test, *T*) was applied via the *HR_test* function of the *CircMLE* R package (Landler et al. 2019). Temporal activity patterns were then estimated non-parametrically by kernel density functions using the *activity* and *overlap* R packages (Rowcliffe 2022; Meredith and Ridout 2024). The coefficient of temporal overlap (Δ), ranging from 0 to 1, was computed as the area under the two density curves (Ridout and Linkie 2009). The Δ_1 estimator was applied when at least one of the two species had fewer than 50 independent records, and the Δ_4 estimator otherwise (Ridout and Linkie 2009; Meredith and Ridout 2024). To assess the reliability of overlap estimates, 95% Confidence Intervals (CIs) were obtained by bootstrap resampling with 10,000 replicates. Overlap coefficients were classified according to Sogliani et al. (2026) as follows: very low ($\Delta \leq 0.35$), low ($0.36 \leq \Delta \leq 0.50$), moderate ($0.51 \leq \Delta \leq 0.75$), high ($0.76 \leq \Delta \leq 0.90$), and very high ($\Delta > 0.90$). Given that overlap estimators are descriptive, we further evaluated whether the activity patterns of each pairwise comparison differed significantly using the Mardia-Watson-Wheeler test (MWW test, *W*) for homogeneity of circular distributions, as implemented in the *circular* R package (Mori et al. 2025). The test was conducted three times to account for ties, and results remained unchanged across replicates. Additionally, a bootstrap-based (1,000 iterations) comparison of kernel densities was performed using the *compareCkern* function of the *activity* R package (Rowcliffe 2022), to estimate the probability that two circular distributions come from the same activity pattern.

To calculate peak and minimum activity times, we computed circular kernel density estimates and extracted local maxima and minima along the 24-h cycle using the *circular* R package. To assess the modality of diel activity distributions, we applied Hartigan's Dip Test and Silverman's Test (500 bootstrap iterations) via

the *diptest* and *multimode* R packages, respectively (Maechler 2024; Ameijeiras-Alonso et al. 2021). The Dip Test evaluates departures from unimodality, whereas Silverman's Test tests the null hypothesis of a unimodal distribution (Silverman 1981; Hartigan and Hartigan 1985).

Daily variables describing sunrise (top edge of the sun appearing at the horizon), sunset (sun completely below the horizon), nightStart, and nightEnd were calculated for each unique CT date using the *getSunlightTimes* function in the *suncalc* R package (Thieurmel and Elmarhraoui 2022). Each detection event was classified as daytime, twilight, or nighttime according to these astronomical boundaries (Gerber et al. 2024). Diel phenotypes were assigned for each species using the *Diel.Niche* R package (Gerber et al. 2024) under the 'general' hypothesis set, which distinguishes standard diel categories and separates bimodal and trimodal patterns based on activity proportions across light periods. The 'selection' hypothesis set was used to determine the selected diel periods depending on time availability in each period of the day (Gerber et al. 2024).

Covariates selection and extraction for the occupancy analysis

A total of 11 covariates, extracted through the QGIS software (v. 3.28; Dawson et al. 2022) by using the geoprocessing tools of SAGA NextGen processing provider, were selected for this work (see Supplementary Table S1). As suitable environmental covariates, we selected: elevation, Topographic Position Index (TPI), Topographic Ruggedness Index (TRI), Normalized Difference Vegetation Index (NDVI) as mean seasonal value of vegetation productivity, and the Euclidean distance to the nearest water sources. Biological and anthropogenic covariates were computed in the form of a Relative Abundance Index (RAI). The RAI was calculated for each camera site as the number of independent capture events of variable *i* divided by the total sampling effort, multiplied by 100 (Rovero and Zimmermann 2016). As suitable biological covariates, we included potential prey species (i.e., actively hunted or scavenged): springbok, Cape hare, rock hyrax, and large ungulate species > 100 kg (i.e., mountain zebra, gemsbok, and kudu) grouped as proxy for scavenging opportunity; while as anthropogenic covariates we accounted for the different disturbance induced by humans on foot and by motorized vehicles. The sampling effort was computed as the number of camera days each CT was actively recording data during the sampling period.

Occupancy analysis

To account for marginal and conditional occupancy of leopard and brown hyena during the two seasons, we ran two multi-species single-season occupancy models (Rota et al. 2016) implemented in the *unmarked* R package (Chandler et al. 2023). Temporal and population closure assumptions were assumed unviolated for two consecutive years, as animals are reported to use habitats more or less uniformly within the same seasons (Rovero et al. 2013). Detection/non-detection binary matrices were created for each season and species, where 1 indicated a detection event and 0 a non-detection. We discretized DS matrices at 5-day intervals (i.e., sampling occasions) and at 10-day intervals for the WS to maximize model fit (Rovero and Zimmermann 2016).

Within each season, we performed multi-species single-season occupancy analysis and model selection independently for each category of site covariates (i.e., by sub-setting environmental, biological, and anthropogenic covariates). This enabled us to maximize the likelihood of obtaining a good estimation of parameters and, at the same time, avoid model overparameterization and overfitting (Hair et al. 2019). The only covariate included in both environmental and biological models was 'distance from water', to explore if the effect of prey species abundance could be an artifact of water accessibility. All covariates were standardized at z-score during model fitting through the *scale* base function in *R*. RAI covariates were log-transformed (*ln*) before standardization to reduce variance. To model detection probability, we included the sampling effort as an observation covariate. Multicollinearity among covariates was tested using the Variance Inflation Factor (VIF), through the *vifstep* function found in the *usdm* R package (Naimi et al. 2014). Considering the relatively low number of carnivore detections, we selected a conservative VIF threshold ≤ 5 (Hair et al. 2019).

To assess the goodness-of-fit of each model, the most complex models, i.e., those containing the additive effects among covariates for each subset, were tested using the parametric bootstrap *parboot* function, found in the *unmarked* R package (Chandler et al. 2023), with 1,000 replicates based on the chi-square statistic (Mackenzie and Bailey 2004). Additionally, we checked for overdispersion by estimating the $\hat{c}$ as the ratio between the observed chi-square statistic and the mean of the chi-square statistics obtained from the simulations (Mackenzie and Bailey 2004). Values close to 1 indicate adequate model structure, while $\hat{c} > 1$ indicate overdispersion.

Marginal occupancy was modeled by assuming independence (max order = 1) between leopard and brown hyena to identify those covariates influencing occupancy probability for each species. Model fitting followed a backward elimination process (Hair et al. 2019), where the most complex model was simplified at each stage, until only significant covariates remained. Additionally, we fitted an intercept-only model assuming independence, by setting occupancy and detection probability as constant. This was included in the model selection process as a benchmark, to evaluate if more complex models could better explain occupancy and detection probability compared to an over-simplified model. Subsequently, the candidate models were ranked using the second order Akaike Information Criterion (AICc) (Akaike 1974; Burnham and Anderson 2004). The top-ranking model (i.e., $\Delta AICc = 0$) and the models showing $\Delta AICc < 2$ and AIC weight > 0.1 were considered as candidates for the best model explaining marginal occupancy. The covariates appearing in the top-ranking model(s) showing a significant or quasi-significant effect on marginal occupancy for each species were selected to be included in conditional occupancy analysis.

In this step, to reduce model complexity, we built models with single covariates as predictors of conditional occupancy between leopard and brown hyena. All models were then ranked according to AICc values (Akaike 1974; Burnham and Anderson 2004). The top-ranking marginal occupancy independence-model was included as a benchmark in the model selection process to assess if there was stronger support for dependence or independence between species.

All statistical analyses and figures were produced using the software R (v. 4.3.2; R Core Team 2023), and statistical significance was set at $p < 0.05$.

Results

The camera trapping effort was 38,277 trap-days, of which 19,604 in the DS and 18,673 in the WS, for 71 camera sites. We recorded a total of 37,350 independent detection events, totaling 32 identified species, including humans. Species considered for this study, excluding vehicles, accounted for 19,394 independent captures, of which 10,901 (54%) during the DS and 8,493 (46%) during the WS (Supplementary Table S2). CT stations that recorded leopard and brown hyena detections divided by season are shown in Fig. 1.

Diel activity patterns and temporal segregation

Both species exhibited significant departures from a random distribution of activity throughout the 24-hour cycle in both seasons (HR test, all $p < 0.005$), indicating structured diel activity rhythms. Kernel density estimates and diel phase classification showed that leopard was consistently cathemeral across seasons (Fig. 2; Supplementary Table S3). During the DS, leopard activity was concentrated during nighttime (50.6%), followed by twilight (21.0%), with more limited daytime activity (28.4%), resulting in the selection of night–twilight periods. Activity was clearly bimodal, with peaks at 06:12 and 19:44. In the WS, leopard activity was more evenly distributed between daytime and nighttime (40.4% each), although twilight remained the selected period (19.3%). Activity peaks occurred at 06:43 and 22:33, indicating the persistence of a bimodal pattern, although less pronounced than in the DS (Fig. 2). In contrast, the brown hyena was consistently nocturnal in both seasons, with most detections occurring at night (82.4% in the DS and 75.7% in the WS), followed by twilight (15.7% and 13.5% in DS and WS, respectively), whereas daytime activity remained marginal (2.0% and 10.8% in DS and WS, respectively). During the DS, brown hyena showed a predominantly unimodal pattern with a single activity peak at 00:45, whereas in the WS activity was concentrated around two nocturnal peaks at 04:47 and 22:50 (Fig. 2).

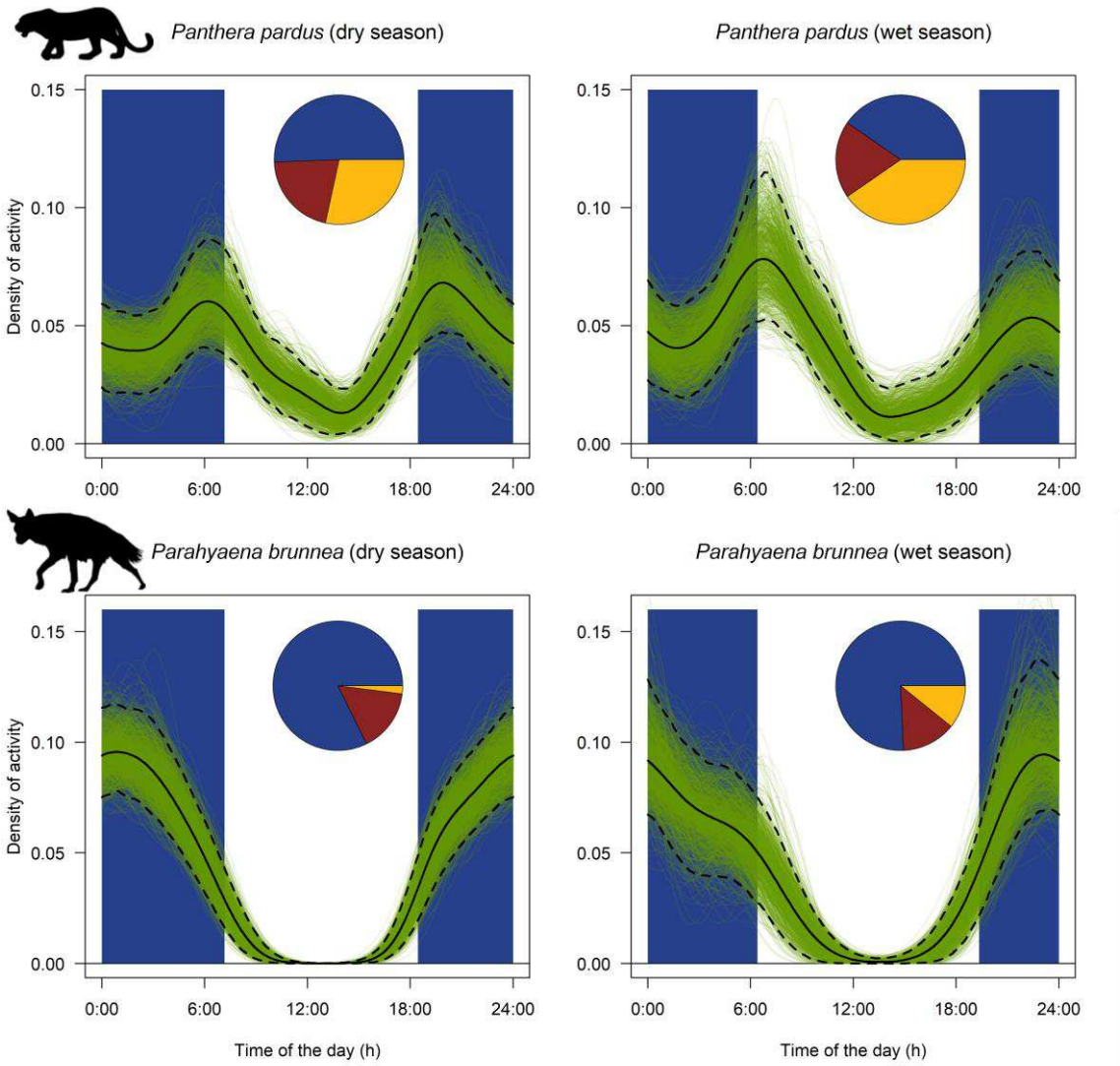


Fig. 2 Proportions of diel activity periods and kernel density estimates of daily activity patterns of leopard and brown hyena during the DS and the WS. Pie charts illustrate the relative frequency of detections during daytime (amber), twilight (red), and night-time (blue). Kernel density estimates depict 24-h activity rhythms. Sunrise occurred at approximately 06:24 and sunset at approximately 19:21 (solar time). Blue rectangles indicate dark hours; green lines represent bootstrapped activity estimates; dashed lines show 95% confidence intervals; solid lines indicate mean activity

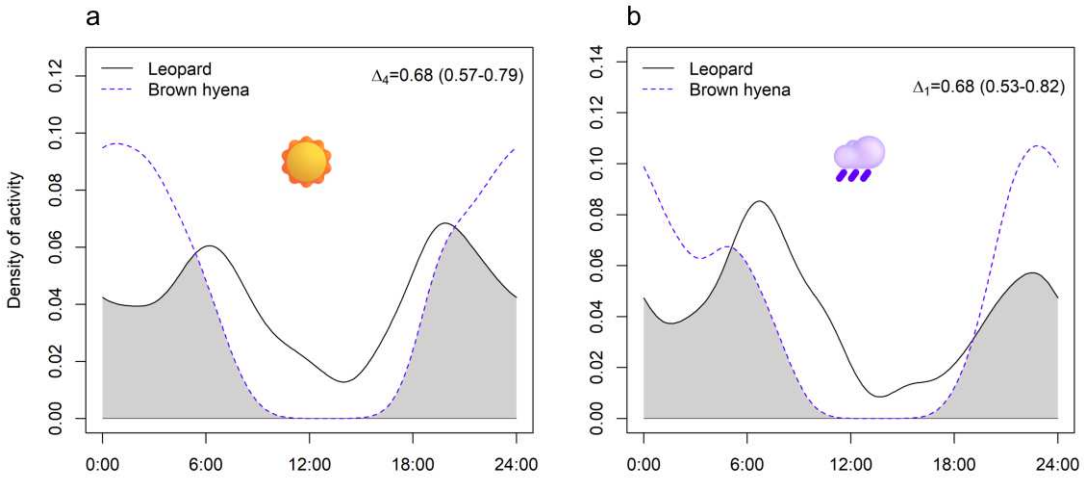
Modality tests supported these patterns. Leopards showed significant departures from unimodality in both seasons, with stronger evidence in the DS (Dip test: $p = 0.0015$; Silverman's test: $p = 0.04$) than in the WS (Dip test: $p = 0.01$; Silverman's test: $p = 0.14$). Brown hyena also showed significant departures from

unimodality according to the Dip test in both seasons (both $p < 0.001$), although Silverman's test provided weaker evidence of multimodality (DS: $p = 0.05$; WS: $p = 0.12$).

Temporal overlap between leopard and brown hyena was moderate and identical across seasons (Fig. 3a–b; Supplementary Table S4). Despite this similar degree of overlap, the MWW test detected significant differences in activity distributions between the two species in both the DS and the WS (Supplementary Table S4). Likewise, the *compareCkern* test indicated significant differences in kernel density distributions in both seasons (Supplementary Table S4), reflecting differences in the shape and timing of activity peaks despite the moderate temporal overlap.

Inter-season comparisons revealed high temporal stability in diel activity patterns for both predators, with both leopards and brown hyenas showing high overlaps between seasons (Supplementary Table S4). No significant seasonal differences in activity distributions were detected for either leopard or brown hyena, and *compareCkern* tests were likewise non-significant (Supplementary Table S4), confirming substantial seasonal consistency in activity rhythms.

Information on the diel activity patterns and temporal overlap with prey species and anthropogenic activities is provided in Supplementary Tables S3–S4.



375

376 **Fig. 3** Temporal partitioning in diel activity patterns of leopard and brown hyena across species and seasons.
377 Panels (a) and (b) show overlap between leopard and brown hyena during the DS and WS, respectively.
378 Overlap coefficients (Δ, C.I. 95%) are reported in each panel, and grey shading represents the area under
379 the activity density curve

380 *Multi-species single-season occupancy models*

381 The discretized occupancy matrix accounted for 37 5–day sampling occasions for the DS and 18 10–day
382 occasions for the WS. During the DS, leopards and brown hyenas were detected in 22 and 17 sites,
383 respectively, with 64 detection events each. For the WS, leopards were detected in 18 sites with 42 detection
384 events, while brown hyenas occurred in 12 sites with 22 detections.

385 No overdispersion was detected in any of the complex models (i.e., all displayed $\hat{c} \simeq 1$). Additionally, we
386 detected no multicollinearity issues for the selected covariates (i.e., all achieved VIF < 5). The *P. capensis*
387 and *A. marsupialis* RAI covariates were removed from the WS model fitting for marginal occupancy on
388 leopard and brown hyena respectively, due to lack of model fitting. RAI of vehicles was also excluded from
389 the conditional occupancy analysis for the WS for the same reason.

For the DS, the estimated mean marginal occupancy was 0.48 ± 0.09 SE (C.I. 95% 0.28 – 0.63) for leopard with a detection probability of 0.08 ± 0.01 SE (C.I. 95% 0.06 – 0.11) (Fig. 4). For brown hyena, mean marginal occupancy was 0.36 ± 0.11 SE (C.I. 95% 0.15 – 0.57), with a detection probability of 0.10 ± 0.02 (C.I. 95% 0.07 – 0.13). Marginal occupancy in the WS estimated for leopard was 0.44 ± 0.12 SE (C.I. 95% 0.22 – 0.64), with a detection probability of 0.11 ± 0.01 SE (C.I. 95% 0.07 – 0.17), while for brown hyena it was 0.29 ± 0.12 SE (C.I. 95% 0.12 – 0.55), with a detection probability of 0.09 ± 0.03 (C.I. 95% 0.05 – 0.16).

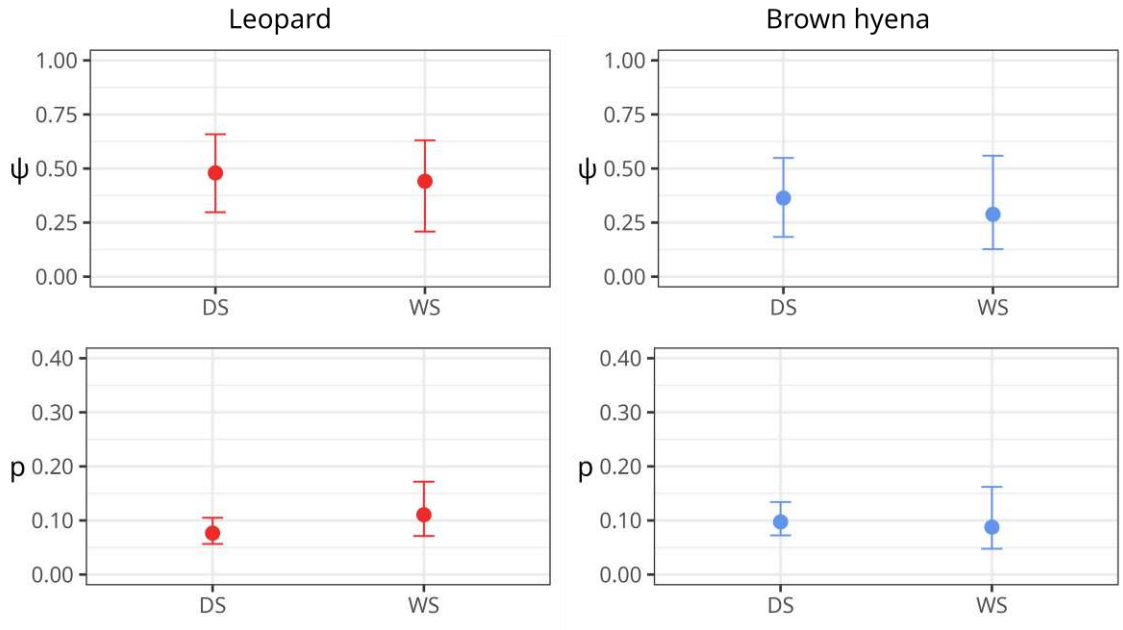


Fig. 4 Marginal occupancy (ψ) and detection (p) probability (±C.I. 95%) estimated for leopard (red) and brown hyena (blue) divided by seasons. Abbreviations: DS = dry season; WS = wet season

The effects of covariates retained in the best models for marginal occupancy on leopard and brown hyena are shown in Fig. 5 (for detailed information see Supplementary Tables S5–S7 and Figure S1–S3). In the conditional occupancy models testing for environmental covariates, we retained TRI for leopard as well as elevation and distance from water sources for brown hyena for both seasons. For the biological category, leopard's marginal occupancy was predicted by *P. capensis* and large ungulates in the DS, and by large ungulates during the WS; while brown hyena's marginal occupancy was predicted by large ungulates in both seasons. Anthropogenic models were built with vehicles and *H. sapiens* as predictors for leopard and brown hyena's marginal occupancy, respectively, during both DS and WS.

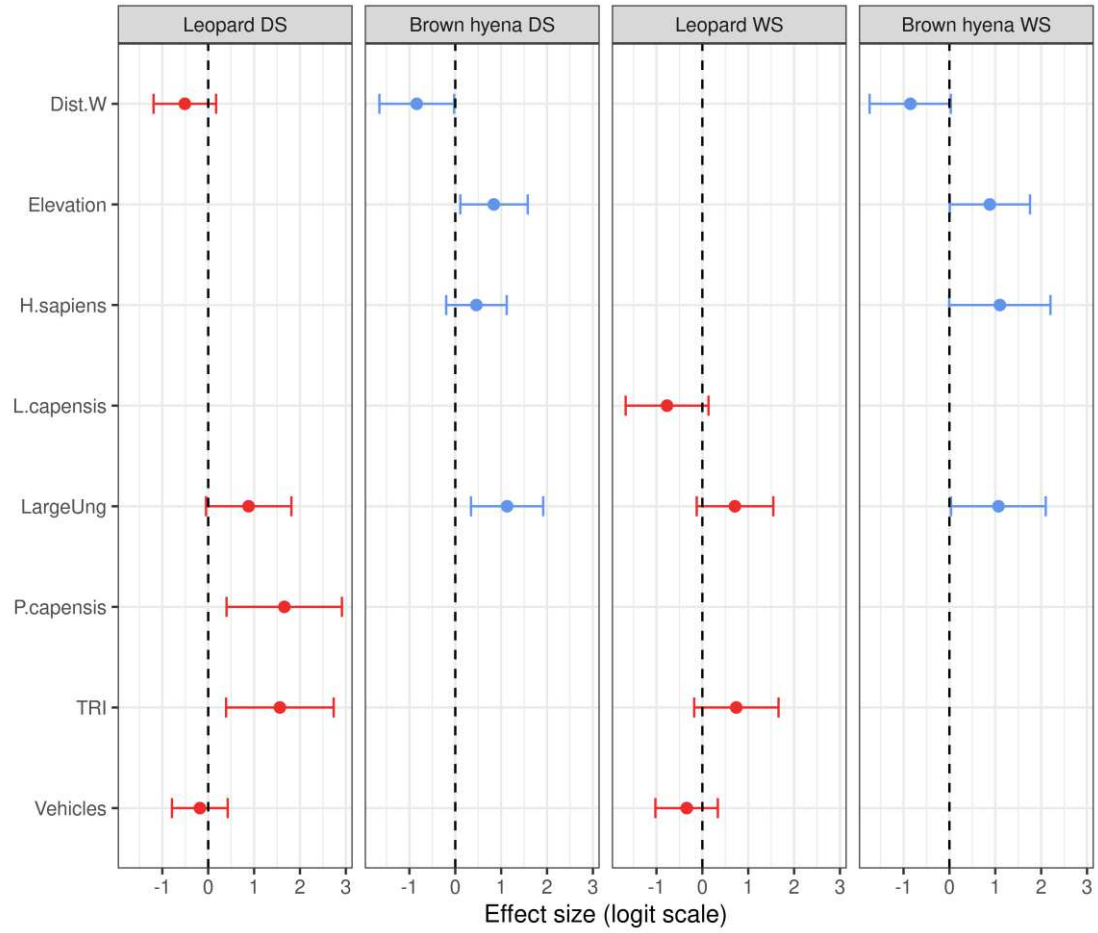


Fig. 5 Beta coefficients (logit-scale) and 95% Confidence Intervals displaying the covariates' effects on leopard and brown hyena's marginal occupancy probability (best models) during the two seasons. Abbreviations: DS = dry season; WS = wet season; Dist.W = distance from water; LargeUng = large ungulates; TRI = Topographic Ruggedness Index

For conditional occupancy testing for the effect of environmental covariates, in the DS the independence model parameterization ranked first among the candidate set (Table 1). During the WS, the most supported model was the intercept-only dependence model (Table 1). Independence was most supported during the DS, while models accounting for co-occurrence were most supported during the WS, with TRI and elevation playing a marginal role in defining species' co-occurrence.

During the DS, model selection for biological covariates showed the independence model as top-ranking model (Table 2). Similarly, the independence model also ranked first in the WS (Table 2). Biological covariates displayed no influence on co-occurrence patterns between leopard and brown hyena.

Model selection for anthropogenic covariates saw the independence model as the most supported model among the DS candidate set (Table 3). Conversely, for the WS the top-ranking model was the intercept-only dependence model (Table 3). Anthropogenic disturbance had no influence over co-occurrence patterns, with the two species displaying spatial independence in the DS.

During the DS co-occurrence was negligible, with weak support when accounting for the effect of environmental covariates. During the WS, the conditional occupancy models were always present in the competitor model sets for all covariate categories. Specifically, leopard's probability of site use increased conditional on brown hyena's presence (brown hyena present: psi = 0.69 ± 0.19 SE; absent: psi = 0.34 ± 0.12 SE) and, similarly, brown hyena's occupancy probability increased conditional on leopard's presence (leopard present: psi = 0.43 ± 0.14 SE; absent: psi = 0.17 ± 0.11 SE; Fig. 6).

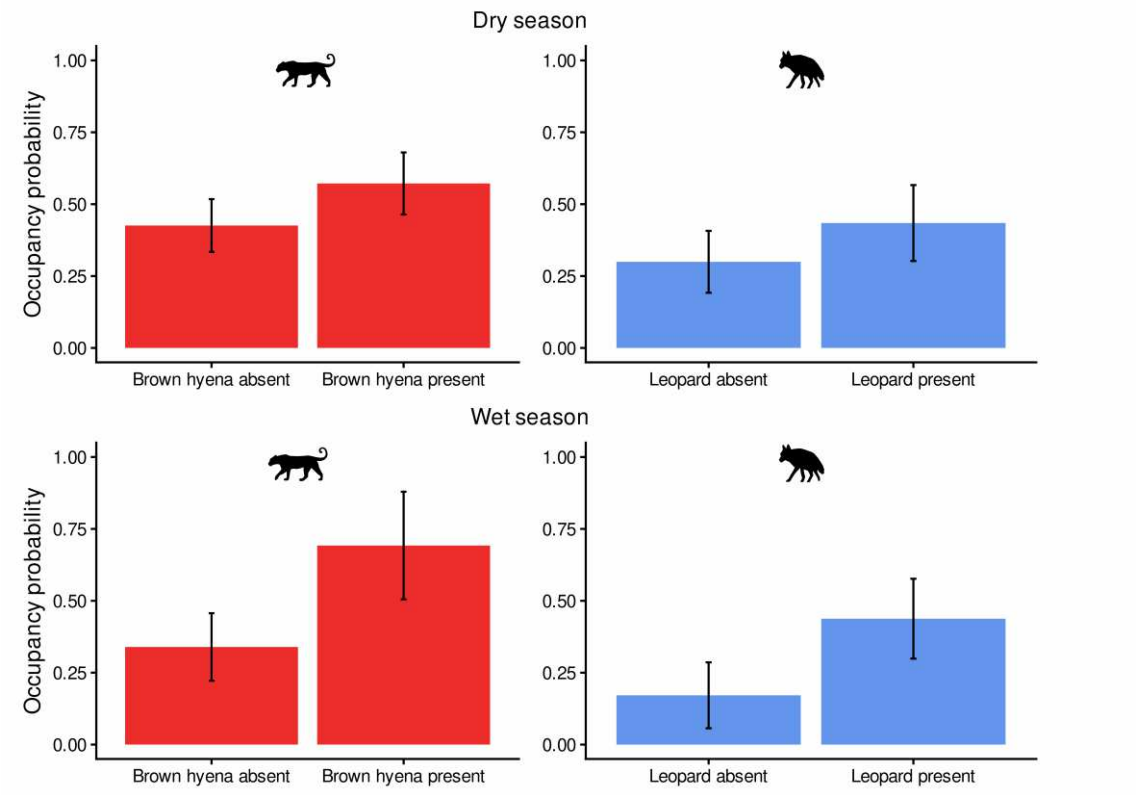


Fig. 6 Mean occupancy probability (± SE = standard error) predicted for leopard and brown hyena from environmental top-ranking models during both seasons, accounting for the presence/absence of one another

Discussion

In this study we investigated the seasonal spatio-temporal patterns of coexistence between leopards and brown hyenas in the hyper-arid inland of southern Namibia, in the absence of dominant apex predators, lion and spotted hyena. This carnivore assemblage represents one of the most widespread configurations across Namibia's unprotected and semi-protected landscapes, where historical eradication of lions and spotted hyenas has left subordinate species to occupy the apex predator niche across much of the country's farmlands and arid rangelands (Verschueren et al. 2024; NCE, LCMAN and MEFT 2022). Understanding the ecological dynamics within this simplified guild is not merely a site-specific question, but rather reflects a broader conservation reality across southern Africa. Through camera trapping, activity pattern analysis, and a multi-species occupancy framework, we documented how leopard and brown hyena partition their temporal and spatial niches in relation to environmental, biological, and anthropogenic drivers. Our results reveal a dynamic interplay consistent with mechanisms between competition and facilitation, shaped by seasonal resource availability, in which consistent temporal partitioning year-round is coupled with a seasonal shift from spatial independence during the DS, to resource-mediated spatial co-occurrence during the WS.

Temporal activity patterns and temporal segregation

The moderate temporal overlap, together with significant differences in activity patterns between the two species, supported temporal partitioning as one of the main likely strategies for reducing interference competition (Carothers and Jaksić 1984; Hayward and Slotow 2009), validating our hypothesis of competition-driven behavioral adaptations facilitating coexistence in CNP. However, temporal niche partitioning was observed year-round, partially contradicting our prediction on seasonal variation in competition dynamics (Wiens 1993). Although previous studies described a higher degree of temporal overlap between co-occurring large carnivores (Krag et al. 2023; Vissia et al. 2022; Say-Sallaz et al. 2026; Périquet et al. 2015), direct comparisons are difficult given crucial differences in environmental conditions and community structure compared with our study site. Our findings are, however, consistent with other studies (Havmøller et al. 2020; Edwards et al. 2015; Ramello et al. 2025) comparing activity overlap of leopard and competitor species in a simplified large carnivore guild, suggesting the two species consistently could compete for resource access, adapting their temporal niche to minimize negative encounters (Dröge et al. 2017; Vanak et al. 2013).

Brown hyenas were consistently nocturnal, in accordance with literature (Mills 1994), while leopards exhibited more diurnal activity than expected (Martins and Harris 2013; Vissia et al. 2022), suggesting leopards may have adjusted their temporal niche to reduce interference competition (Karanth et al. 2017; Hayward and Slotow 2009). In arid environments, brown hyenas represent a dominant competitor (Mills 2015), known to scavenge leopard kills, increasing kleptoparasitism risk (Stein et al. 2013). A shift toward a more diurnal activity could therefore allow leopards to mitigate these interactions by targeting smaller, diurnal species such as rock hyrax (Stander et al. 1997). This interpretation is consistent with findings in arid environments where leopards are smaller and rely more on small-bodied prey compared to populations from mesic environments (Mills 2015; Martins and Harris 2013; Judas et al. 2006) and is supported by our marginal occupancy results (see below).

Alternatively, leopard's cathemeral activity may be explained as a consequence of mesopredator release (Prugh et al. 2009). Leopards can be considered mesopredators when co-existing with lions and spotted hyena, which dominate the apex-predator niche (Périquet et al. 2015). Conversely, when apex carnivores are absent, top-down pressure is released, allowing leopards to exploit a broader temporal and dietary niche (Estes et al. 2011; Dröge et al. 2017; Prugh et al. 2009).

Spatial overlap and co-occurrence

The positive reciprocal spatial association observed during the WS suggests that the interaction between leopard and brown hyena extends beyond simple competitive coexistence, aligning more closely with a facilitation-competition continuum. Critically, the reciprocal nature of this association whereby also leopard occupancy increased conditional on brown hyena presence is difficult to reconcile with a purely competitive framework and instead points toward a degree of mutual resource-tracking, where both species independently concentrate in areas of high prey biomass and productivity. In contrast, during the DS both species likely concentrate around fixed resource hotspots such as waterholes, riverbeds, and restricted foraging areas, reducing the need for spatial co-occurrence at the scale detectable by our camera array, and instead promoting fine-scale avoidance mechanisms, as documented by Augugliaro et al. (2026, unpubl. data). Under this interpretation, positive spatial co-occurrence emerges not despite competition but as an emergent property of shared resource tracking during productive periods, while seasonal spatial independence during the DS reflects heightened exploitative competition for scarce and localized resources

491 rather than avoidance *per se*. During these resource-scarce periods, both species may need to increase
492 foraging efforts and diversify their habitat use and diet, thus indirectly reducing competitive interactions
493 (Mills 2015; Owen-Smith 2008).

494 Here, we found *P. capensis* to positively affect leopard's occupancy during the DS, whereas the most
495 abundant mid-sized ungulate had no detectable effect. Although the detectability of rock hyrax by CT is
496 low due to the sampling design, the species is widespread in the area (Olds and Shoshani 1982; Brown
497 2006). Studies in the Western Cape (South Africa) and the rocky deserts of the Arabian Peninsula have
498 recorded *P. capensis* as one of the main prey items for leopards (Mills 2015; Martins and Harris 2013;
499 Judas et al. 2006; Puls et al. 2021), despite its body mass being considerably smaller than the felid's
500 preferred prey weight range (10 – 40 kg; Hayward et al. 2006). Hunting *P. capensis* may provide multiple
501 advantages, including high accessibility, rapid consumption, and easy transportation and caching, reducing
502 the likelihood of carcass loss to scavengers (Balme et al. 2017; Stander et al. 1997; see Supplementary Fig.
503 S4). This is supported by leopard's preference for rugged terrain across seasons, offering hunting cover for
504 the predator and denning sites for rock hyrax colonies (Pitman et al. 2017; Olds and Shoshani 1982). Diet
505 analysis through DNA metabarcoding on feces would be the most reliable follow-up study to elucidate the
506 putative key role of rock hyrax in shaping this large carnivore community.

507 Another possible indication of increased competition during the DS came from the relationship between
508 distance from water and marginal occupancy probability for both species. Water is a limited, localized
509 resource, and although both species are defined as water-independent, they regularly drink when surface
510 water is available (Mills 1994; Bothma 1998; Owens and Owens 1978). Both species were found to prefer
511 areas closer to water, suggesting the importance of this resource in determining species habitat use in desert
512 ecosystems (Edwards et al. 2016; Krag et al. 2023). During the WS, the distance from water remained
513 inconsistent in influencing leopard occupancy, but appeared important for the brown hyena. This aligns
514 with the increase in hunting during the summer months, as leopards supplement water intake from fresh
515 kills, thereby reducing reliance on surface water (Bothma 1998).

516 Marginal occupancy analysis also showed both carnivores responded positively to large ungulate
517 abundance year-round, indicating shared attraction to areas offering greater prey biomass. During the WS,
518 increased prey availability likely enhances leopard hunting success; as prey are more evenly distributed,

519 hunting opportunities increase, and carcass generation becomes more frequent and widespread, making
520 leopard-derived carrion a diffuse and relatively accessible resource for brown hyenas (Smit et al. 2007;
521 Pereira et al. 2014). This form of indirect facilitation mediated by carrion is increasingly recognized within
522 large-carnivore communities and may help explain the positive association detected during the WS (Selva
523 and Fortuna 2007; Moleón et al. 2014; Pereira et al. 2014). Contrarily, the absence of this pattern during
524 the DS could be explained by differences in carcass spatial detectability, rather than resource incentive
525 alone, as hunting opportunities are reduced and leopard-driven carrion is less reliable. However, natural
526 mortalities during dry periods are common (Owen-Smith 2008), with large carcasses persisting long in arid
527 environments, representing key localized resources for both species in periods of reduced hunting
528 opportunities (Moleón et al. 2014; Pereira et al. 2014). These mortality events create spatially fixed nutrient
529 hot-spots attracting both opportunistic and obligate scavenger species competing for access to this
530 ephemeral resource (Wilson and Wolkovich 2011). Both leopards and brown hyenas are known to engage
531 in scavenging behaviors, with brown hyenas often described as unskilled hunters, heavily relying on other
532 predators to access large-bodied carcasses (Stein et al. 2013); whereas leopards are generally considered
533 opportunistic scavengers (Balme et al. 2017), and may visit the same carcass multiple times when
534 undisturbed (R.V. pers. obs.). Augugliaro et al. (2026, unpubl. data) analyzed photographic evidence of the
535 two species feeding on the same carcass for several days, recording vigilance behavior for both species, as
536 well as fine-scale temporal avoidance mechanisms to reduce direct competition.

537 The interpreted framework emerging from our results describes leopard-brown hyena interactions as
538 dynamically shifting along the competition-facilitation axis depending on resource availability, consistent
539 with theoretical predictions for intraguild interactions under variable resource regimes (Chesson 2000;
540 Périquet et al. 2015).

541 *Conclusions*

542 This study underlined the likely spatial and temporal mechanisms enabling coexistence between two large
543 carnivores in the arid landscapes of southern Namibia. Specifically, our findings highlight the role of desert
544 environments in driving species interactions, allowing opportunistic species to dominate the apex-predator
545 niche left vacant by the lion and the spotted hyena, establishing highly competitive conditions that require
546 adaptive spatial and temporal responses to ensure coexistence.

Our results did not reveal the presence of a clear dominant species. Conversely, they revealed coexistence mechanisms that may moderate competitive interactions. The competitive relationship between the two species is case-dependent in literature, with studies defining leopards as a key species for brown hyena's presence (Stein et al. 2013) and others highlighting the kleptoparasitic impact of hyenas (Owens and Owens 1978). The harsh environmental conditions of the Fish River area, the generalist behavior of both species, the low prey densities, and large home ranges allow both predators to reduce competitive interactions. During the DS, both species exploit carcasses and diversify their diet by using areas independently; while, in the WS, as competition eases with higher resource availability, they utilize similar areas and resources. Year-round, competition is mitigated by temporal partitioning and fine-scale avoidance (Dröge et al. 2017; Hayward and Slotow 2009).

Our results challenge studies that define drier conditions as beneficial to carnivores hunting success, driven by prey's increased vulnerability from worsened body conditions (Owen-Smith 2008; Creel et al. 2016). In this scenario, prey availability increases during the DS, which in turn would reduce intraguild competition. However, considering the prey species that populate the Fish River Canyon, most herbivores have evolved to sustain the harsh climate by reducing water needs and adopting physiological and behavioral adaptations to heat and water scarcity (Estes 2012). Additionally, such studies explored drought events in mesic areas, intrinsically different from regular seasonal variability in desert ecosystems. Therefore, the weakened conditions expected for ungulates during the DS would not apply here. In conclusion, we suggest that in hyper-arid environments, leopard and brown hyena compete for limited resources, and coexistence is mediated by consistent temporal partitioning throughout the year, coupled with a seasonal shift in spatial relationship, from independence under resource scarcity to facilitation-driven co-occurrence during productive periods.

Our interpretations should be considered in light of the study limitations. The lack of evidence on covariates' effects on the co-occurring patterns may reflect the opportunistic and generalist nature of the two species (Stander et al. 1997; Hayward et al. 2006; Mills 1994). Both carnivores have broad diets and habitat tolerance, and are capable of adapting to different environmental conditions (Hayward et al. 2006; Mills 1994). These characteristics make them highly adaptable to challenging environments such as CNP. The detected niche partitioning could additionally be explained by variables unaccounted for in our study or by

575 species-specific intrinsic evolutionary constraints (Kronfeld-Schor and Dayan 2003). Therefore, we invite
576 future research to include methodologies that can account for different aspects of species interaction, such
577 as scat analysis (as previously mentioned), GPS collaring, and time-to-event analysis including all levels
578 of the carnivore community. This will allow a more comprehensive analysis of the community structure
579 and define large-scale and fine-scale interaction patterns.

580 Overall, our results can aid management programs aimed at preserving stable arid ecosystems to understand
581 the implications for predator reintroduction or removal. As the establishment of rigorous protection areas
582 is relatively recent in southern Namibia, wildlife populations, especially previously persecuted carnivores,
583 are expected to naturally expand, also supported by possible reintroduction programs (Brown 2006). Thus,
584 investigating the interspecific dynamics within the carnivore community and their evolution in time can
585 help monitor species population status and identify shifts in community composition and its impact on the
586 ecosystem. Finally, as many of these predators are listed in risk categories of the IUCN, maintaining these
587 'lion-free' areas could help boost subordinate carnivore populations, while preserving key ecosystem
588 functions.

589 ***Statements and Declarations***

590 **Competing interests***:* The authors have no competing interests to declare that are relevant to the content
591 of this article.

592 **Data and/or Code availability:** The datasets generated during and/or analysed during the current study
593 are available from the corresponding author on reasonable request.

594 **Funding**: The authors have no relevant financial or non-financial interests to disclose

595

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Tables

Table 1 Model selection for environmental covariates fitted by season on the conditional occupancy of leopard and brown hyena. In grey = competitor model, in bold = best model, italic = intercept model. Abbreviations: DS = dry season; WS = wet season; p = detection probability; ψ = occupancy probability; co = conditional occupancy; env = environmental covariates retained on marginal occupancy; TRI = Topographic Ruggedness Index; Elev = elevation; Dist.W = distance from water sources; leo = leopard; bh = brown hyena; TPI = Topographic Position Index; NDVI = Normalized Difference Vegetation Index;

818 AICc = second-order Akaike Information Criterion; ModelLik = model likelihood; ωi = Akaike weight; LL
819 = log-likelihood

DS environmental models	***K***	***AICc***	***ΔAICc***	***ModelLik***	***ωi***	***LL***
p(effort), ψleo(env), ψbh(env)	***9***	***974.09***	***0.00***	***1.00***	***0.49***	***-475.68***
p(effort), ψleo(env), ψbh(env), ψco(.)	*10*	*976.04*	*1.95*	*0.38*	*0.18*	*-475.05*
p(effort), ψleo(env), ψbh(env), ψco(TPI)	11	976.84	2.75	0.25	0.12	-473.75
p(effort), ψleo(env), ψbh(env), ψco(TRI)	11	977.89	3.80	0.15	0.07	-474.28
p(effort), ψleo(env), ψbh(env), ψco(NDVI)	11	978.48	4.39	0.11	0.05	-474.57
p(effort), ψleo(env), ψbh(env), ψco(Elev)	11	978.80	4.72	0.09	0.05	-474.74
p(effort), ψleo(env), ψbh(env), ψco(Dist.W)	11	979.42	5.33	0.07	0.03	-475.04
WS environmental models						
p(effort), ψleo(env), ψbh(env), co(.)	***10***	***507.07***	***0.00***	***1.00***	***0.30***	***-240.56***
p(effort), ψleo(env), ψbh(env)	*9*	*507.47*	*0.40*	*0.82*	*0.24*	*-242.37*

p(effort), ψleo(env), ψbh(env), ψco(TRI)	11	508.82	1.75	0.42	0.12	-239.74
p(effort), ψleo(env), ψbh(env), ψco(Elev)	11	508.90	1.83	0.40	0.12	-239.78
p(effort), ψleo(env), ψbh(env), ψco(TPI)	11	509.10	2.03	0.36	0.11	-239.88
p(effort), ψleo(env), ψbh(env), ψco(NDVI)	11	510.33	3.26	0.20	0.06	-240.50
p(effort), ψleo(env), ψbh(env), ψco(Dist.W)	11	510.36	3.29	0.19	0.06	-240.52

Table 2 Model selection for biological covariates fitted by season on the conditional occupancy of leopard and brown hyena. In grey = competitor model, in bold = best model, italic = intercept model. Abbreviations: DS = dry season; WS = wet season; p = detection probability; ψ = occupancy probability; co = conditional occupancy; bio = biological covariates retained on marginal occupancy; LargeUng = large ungulates; Hare = Cape hare; Dist.W = distance from water sources; leo = leopard; bh = brown hyena; AICc = second order Akaike Information Criterion; ModelLik = model likelihood; ωi = Akaike weight; LL = log-likelihood

DS biological models	***K***	***AICc***	***ΔAICc***	***ModelLik***	***ωi***	***LL***
p(effort), ψleo(bio), ψbh(bio)	**9**	**966.45**	**0.00**	**1.00**	**0.70**	**-471.86**
p(effort), ψleo(bio), ψbh(bio), ψco(.)	*10*	*969.65*	*3.20*	*0.20*	*0.14*	*-471.85*

p(effort), ψleo(bio), ψbh(bio), ψco(Hare)	11	971.99	5.53	0.06	0.04	-471.33
p(effort), ψleo(bio), ψbh(bio), ψco(Dist.W)	11	972.61	6.16	0.05	0.03	-471.64
p(effort), ψleo(bio), ψbh(bio), ψco(Spring)	11	972.91	6.45	0.04	0.03	-471.79
p(effort), ψleo(bio), ψbh(bio), ψco(Dassie)	11	972.95	6.49	0.04	0.03	-471.81
p(effort), ψleo(bio), ψbh(bio), ψco(LargeUng)	11	972.95	6.50	0.04	0.03	-471.81
WS biological models						
p(effort),ψleo(bio), ψbh(bio)	***9***	***508.73***	***0.00***	***1.00***	***0.48***	***-243.00***
p(effort), ψleo(bio), ψbh(bio), ψco(.)	*10*	*510.00*	*1.27*	*0.53*	*0.25*	*-242.03*
*p(effort), ψleo(*bio), ψbh(bio), ψco(Spring)	11	511.97	3.24	0.20	0.09	-241.32
*p(effort), ψleo(*bio), ψbh(bio), ψco(LargeUng)	11	512.21	3.48	0.18	0.08	-241.44
*p(effort), ψleo(*bio), ψbh(bio), ψco(Hare)	11	513.31	4.58	0.10	0.05	-241.99

*p(effort), ψleo(*bio), ψbh(bio), ψco(Dist.W)	11	513.36	4.63	0.10	0.05	-242.01

827

828 **Table 3** Model selection for anthropogenic covariates fitted for the DS and WS on the conditional
829 occupancy of leopard and brown hyena. In grey = competitor model, in bold = best model, italic = intercept
830 model. Abbreviations: DS = dry season; WS = wet season; p = detection probability; ψ = occupancy
831 probability; co = conditional occupancy; ant = anthropogenic covariates retained on marginal occupancy;
832 Homo = Homo sapiens; leo = leopard; bh = brown hyena; AICc = second order Akaike Information
833 Criterion; ModelLik = model likelihood; ωi = Akaike weight; LL = log-likelihood

DS anthropogenic models	***K***	***AICc***	***ΔAICc***	***ModelLik***	***ωi***	***LL***
p(effort), ψleo(ant), ψbh(ant)	***8***	***987.68***	***0.00***	***1.00***	***0.60***	***-484.00***
p(effort), ψleo(ant), ψbh(ant), ψco(.)	9	990.23	2.54	0.28	0.17	-483.75
p(effort), ψleo(ant), ψbh(ant), ψco(Vehicle)	10	990.59	2.90	0.23	0.14	-482.32
p(effort), ψleo(ant), ψbh(ant), ψco(Homo)	10	991.38	3.70	0.16	0.09	-482.72
WS anthropogenic models						
p(effort), ψleo(ant), ψbh(ant), ψco(.)	***9***	***508.09***	***0.00***	***1.00***	***0.44***	***-242.68***
p(effort), ψleo(ant), ψbh(ant)	*8*	*508.13*	*0.04*	*0.98*	*0.43*	*-244.22*

p(effort), ψleo(ant), ψbh(ant), ψco(Homo)	10	510.47	2.38	0.30	0.13	-242.26

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