Received: 8 October 2025 | Revised: 15 January 2026 | Accepted: 13 February 2026

DOI: 10.1002/ecs2.70641

ECOSPHERE
AN ESA OPEN ACCESS JOURNAL

ARTICLE
Animal Ecology

Coexistence under constraint: Spatiotemporal co-occurrence in a dryland carnivore guild

Nicholas Pilaud[1] | **Atie Taktehrani**[2,3] | **Morteza Pourmirzai**[2,3] | **Mahsa Shahhosseini**[2,3] | **Mohammad Hossein Karimi**[2,3] | **Navid Gholikhani**[2,3] | **Kaveh Hobeali**[4] | **Fatemeh Hosseini-Zavarei**[4] | **Ugyen Penjor**[5] | **David W. Macdonald**[6] | **Mohammad S. Farhadinia**[7]

[1]School of Geography and the Environment, University of Oxford, Oxford, Oxfordshire, UK

[2]Iranian Cheetah Society (ICS), Tehran, Tehran Province, Iran

[3]Sarvin Wildlife Conservation (SWC), Tehran, Tehran Province, Iran

[4]Future4Leopards Foundation, Tehran, Tehran Province, Iran

[5]Fauna & Flora, The David Attenborough Building, Cambridge, Cambridgeshire, UK

[6]Department of Biology, University of Oxford, Oxford, Oxfordshire, UK

[7]Durrell Institute of Conservation and Ecology, School of Anthropology and Conservation, University of Kent, Canterbury, Kent, UK

Correspondence
Mohammad S. Farhadinia
Email: m.farhadinia@kent.ac.uk

Funding information
Stichting SPOTS; WWF INNO Program; People's Trust for Endangered Species; Prince Bernhard Nature Fund; La Palmyre Zoo; Parc des Félins & SOS; Association Française des Parcs Zoologiques; UNDP

Handling Editor: Jesse S. Lewis

Abstract

Interspecific competition plays a crucial role in shaping the structure and dynamics of large carnivore guilds. Extreme temperatures and heightened resource heterogeneity in drylands can present additional challenges to intraguild coexistence, potentially making dryland carnivore guilds particularly susceptible to climate change and anthropogenic stressors. We employed multispecies occupancy modeling to analyze data from 232 camera trap locations throughout eight reserves in Iran over 18,806 trapping days to investigate spatiotemporal co-occurrence within a guild of large dryland carnivores, including Asiatic cheetahs (*Acinonyx jubatus venaticus*), gray wolves (*Canis lupus*), Persian leopards (*Panthera pardus tulliana*), and striped hyaenas (*Hyaena hyaena*). Furthermore, we evaluated temporal overlap and differences in diel activity between Asiatic cheetahs and sympatric carnivores across seasons to assess seasonal shifts in temporal activity. We found evidence of spatial segregation between cheetahs and leopards and a negative association between cheetah occupancy and proximity to humans. Cheetahs displayed the highest temporal overlap with wolves, followed by leopards and hyaenas, while seasonality was not found to influence the temporal activity of any of the carnivores. Our findings highlight the risk of potential competition between cheetahs and wolves and underscore the need to maintain sufficient water sources and adequate ungulate prey diversity and abundance to diminish the risk of increased resource scarcity-induced competition in drylands. This study further reinforces the importance of mitigating anthropogenic disturbance for the last Asiatic cheetahs.

KEYWORDS
carnivore community, cheetah, competition, dryland, occupancy modeling, temporal overlap

---

INTRODUCTION

Competition plays a crucial role in shaping the structure of large carnivore guilds (Davis et al., 2021). Individuals can compete by directly interfering with resource access, a process known as interference competition (Case & Gilpin, 1974), or by indirectly reducing resource availability, referred to as exploitative competition (Schoener, 1983). To coexist and mitigate reductions in fitness caused by competition, different species of large carnivores often segregate their use of space, time, or food resources (Schoener, 1974).

Competition among large carnivore species is often asymmetrical, with some species being competitively dominant over others (Schoener, 1983). This dominance hierarchy influences niche differentiation, as dominant carnivores can overlap spatially and temporally with their preferred prey, while subordinate species must balance mitigating the threat posed by dominant carnivores and foraging for food (Polis & Holt, 1992). For example, cheetahs (*Acinonyx jubatus*) endure high levels of kleptoparasitism (Swanson et al., 2016). Lions (*Panthera leo*), spotted hyaenas (*Crocuta crocuta*), and leopards (*Panthera pardus*) are dominant over cheetahs (Hayward & Slotow, 2009; Mills & Mills, 2017). Cheetahs must find a trade-off through resource partitioning with more dominant carnivores to acquire resources while avoiding risks posed by these competitors (Hayward & Slotow, 2009).

However, bottom-up processes, such as those driven by landscape productivity and resource availability, can lead to complex changes in carnivore interactions (Burgos et al., 2023). Drylands, defined as areas with an aridity index (precipitation divided by potential evapotranspiration) of less than 0.65 (Middleton & Thomas, 1997), create landscapes with high levels of resource heterogeneity, primarily in the form of water resources and vegetation, and the prey that are predominantly dependent on them (Kluever et al., 2017). Extreme temperatures in drylands can present additional challenges for their inhabitants, particularly in the context of climate change, which could constrain niche partitioning, such as by shifting diel activity patterns (Rafiq et al., 2023). Therefore, given the projected effects of climate change and rising temperatures in the coming years, it is crucial to understand how species interactions within a community of large carnivores are impacted, especially if some species of concern are highly conservation-dependent.

This study aims to understand the spatial and temporal patterns of co-occurrence in a guild of several large carnivores in drylands based on a case study from various sites in Iran. Since 2001, Iran has been running an extensive conservation program to save the critically endangered Asiatic cheetahs (*A. j. venaticus*) (Farhadinia et al., 2017). However, these cheetahs share their dryland habitats with other large carnivores, such as Persian leopards (*P. p. tulliana*), gray wolves (*Canis lupus*), and striped hyaenas (*Hyaena hyaena*) throughout much of their range (Farhadinia et al., 2017). Unlike striped hyaenas, which primarily meet their dietary needs through scavenging (Kruuk, 1976), the other three large carnivores actively hunt medium-sized ungulates, while gray wolves and Persian leopards are also known to rely on opportunistic scavenging (Farhadinia et al., 2023; Hosseini-Zavarei et al., 2013). They are dependent on a limited diversity of wild prey, including goitered gazelles (*Gazella subgutturosa*), bezoar goats (*Capra aegagrus*), wild sheep (*Ovis orientalis*), and chinkara (*G. bennettii*), all of which occur at low densities throughout our study sites (Farhadinia et al., 2023; Khalatbari et al., 2022), potentially exacerbating interspecific competition.

Despite the possibility that resource scarcity could exacerbate interspecific competition in drylands (Astete et al., 2017), knowledge deficiencies remain regarding intraguild interactions among carnivores in these low-productivity landscapes. Drylands account for approximately 41% of the planet's terrestrial surface and are essential for global biodiversity (Safriel et al., 2005). Nonetheless, they are expected to expand due to climate change and face rapid changes, with many dryland vertebrates' habitats threatened by anthropogenic disturbance (Lewin et al., 2024), leading to additional scarcity of some carnivores (Dunford et al., 2024; Shams et al., 2025).

We assessed the potential niche partitioning across space and time between Asiatic cheetahs and other sympatric large carnivores, including Persian leopards, gray wolves, and striped hyaenas, across multiple dryland sites in Iran. To this end, we pursued the following three hypotheses:

> **Hypothesis 1.** Asiatic cheetahs reduce spatial overlap with dominant predators, such as Persian leopards and wolves, and reduce temporal overlap with these predators during the cold months, to avoid predation or competition risk (Cheraghi et al., 2019; Farhadinia et al., 2017; Mills & Mills, 2017). Conversely, in the hot months, they shift to nocturnal activity due to extreme temperatures, which increases their temporal overlap with other large carnivores (Belbachir et al., 2015; Rafiq et al., 2023).
>
> **Hypothesis 2.** Asiatic cheetahs do not exhibit spatial segregation from carnivores

more strictly specialized in scavenging, notably striped hyaenas, as these scavengers are less likely to pose a significant threat of kleptoparasitism or other adverse interactions (Panda et al., 2023).

Hypothesis 3. Spatial co-occurrence between cheetahs and sympatric large carnivores is influenced by conservation law enforcement and human presence. Areas benefiting from increased enforcement of wildlife laws are known to harbor greater prey availability in Iran (Ghoddousi et al., 2016), potentially creating a redoubt for carnivores given the relative scarcity of wild ungulate prey in these arid environments. Meanwhile, the prevalence of livestock herding near our study sites will likely influence carnivore spatial interactions (Farhadinia et al., 2023). Cheetahs exhibit lower tolerance to anthropogenic disturbance than their sympatric carnivores, hence influencing their spatial co-occurrence since contrasting responses to human presence can shape patterns of spatial overlap and avoidance among carnivores (Havmøller et al., 2024).

METHODS

Study areas

Our study was conducted across eight reserves in the eastern half of Iran (Figure 1), with annual rainfall ranging from 98.6 mm in Bafq, Ariz, and Dareh Anjir, the southernmost reserves, to 274.2 mm in Miandasht, the northernmost reserve (Khalatbari et al., 2022; Table 1). These reserves encompass mountainous landscapes, flat arid lowlands, and hilly terrain with vegetation primarily consisting of bean caper (*Zygophyllum* sp.) and wormwood (*Artemisia sieberi*). Wild ungulates in these areas include wild sheep, bezoar goats, chinkara,

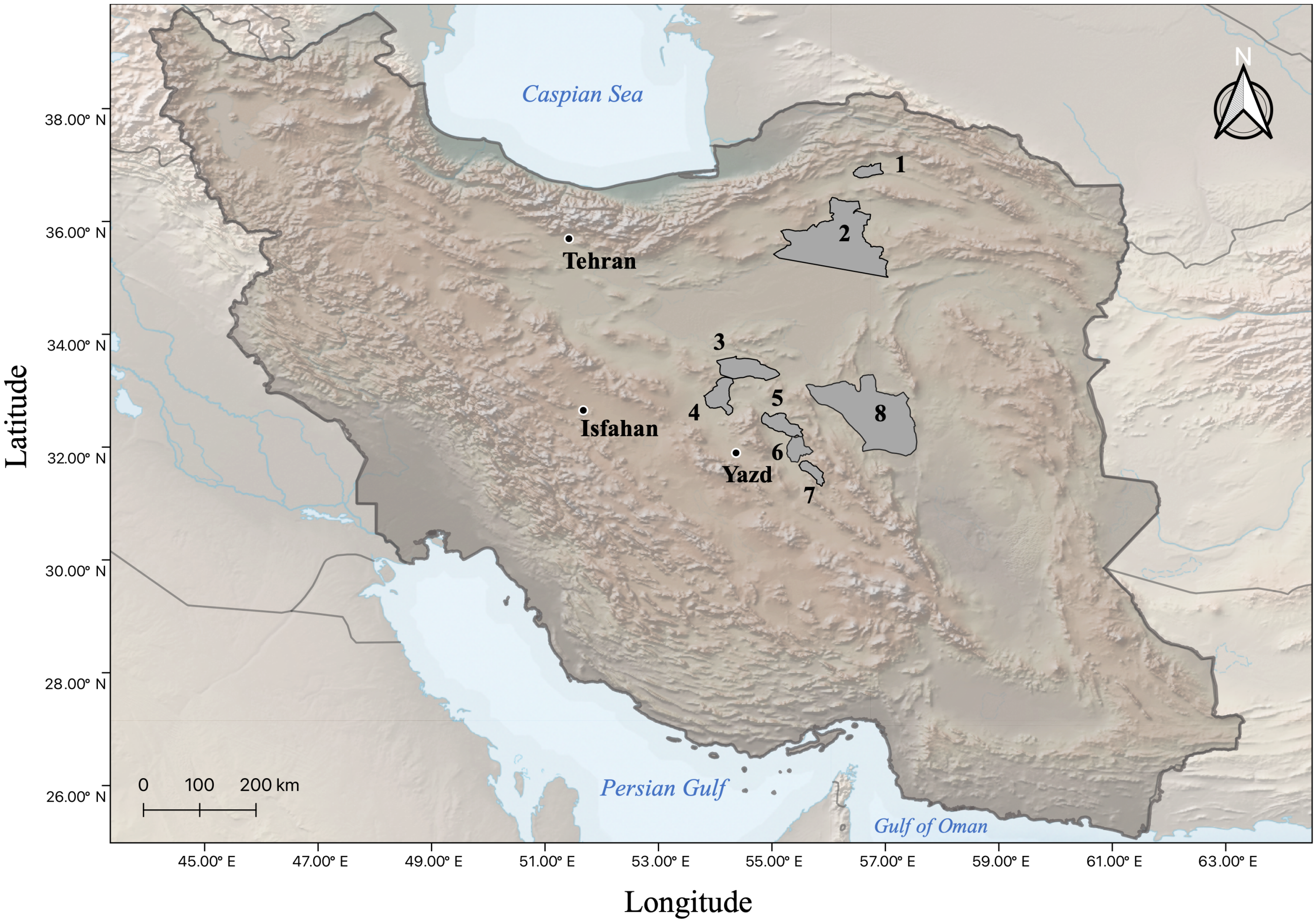

FIGURE 1 Location of the study sites in Iran. The study reserves are denoted by gray polygons and are labeled in the following manner: (1) Miandasht, (2) Touran, (3) Abbasabad, (4) Siahkouh, (5) Dareh Anjir, (6) Ariz, (7) Bafq, (8) Naybandan. Land coloring was derived from Natural Earth raster data.

TABLE 1 Dates of surveys, season, area, and potentially present ungulate and sympatric carnivore species for each study site.

Reserve	Area (km^2)	Prey species	Sympatric large carnivores	Sampling period	Locally interpreted season
Touran	3054	Goitered gazelle, bezoar goat, wild sheep, chinkara	Wolf, leopard, hyaena	05 Jun 2021–20 Oct 2021	Summer
Abbasabad	1313	Bezoar goat, wild sheep, chinkara	Wolf	12 Apr 2012–20 Jul 2012	Summer
Miandasht	1753	Goitered gazelle, wild sheep	Wolf, hyaena	16 Aug 2014–11 Nov 2014	Summer
Siahkouh	850	Bezoar goat, wild sheep, chinkara	Wolf	29 Dec 2011–05 Apr 2012	Winter
Bafq	15,169	Bezoar goat, wild sheep, chinkara	Leopard, occasionally wolf	26 Dec 2011–08 Apr 2012	Winter
Naybandan	14,415	Bezoar goat, wild sheep, chinkara	Hyaena	15 Nov 2012–22 Feb 2013	Winter
Ariz	885	Bezoar goat, wild sheep, chinkara	NA	24 Dec 2011–08 Apr 2012	Winter
Dareh Anjir	2040	Bezoar goat, wild sheep, chinkara	NA	30 Dec 2011–06 Apr 2012	Winter

Note: The terms "summer" and "winter" are used to refer to the warm and cooler periods within each study site based on the local context.

and goitered gazelle; however, not all prey species are found in each reserve (Table 1).

Sampling design

Camera traps were deployed in 232 stations between December 2011 and October 2021 (Table 1; Appendix S1: Table S1). Water sources were prioritized for placing camera traps during the warm season. Alternatively, cameras were positioned along trails and flood paths, consulting the expertise of the reserves' rangers. The Cuddeback C1 and Cuddeback X-Change Color 1279 (Green Bay, WI, USA) models were the dominant types of camera trap, while a few Cuddeback Capture (Green Bay, WI, USA), CamTrakker (CamTrak South Inc., Watkinsville, Georgia, USA), and Bushnell Trophy Cam HD (Bushnell Europe Ltd., Colchester, Essex, United Kingdom) models were also used. Camera traps were placed approximately 40 cm off the ground on natural features, such as trees or rock piles, or on post mounts. Camera trap functionality and downloading of captures were monitored by inspections every 5–10 days. When operating at night, there was a 20–30 s time lag following a photographic capture for the Xenon charge to flash. To avoid this lag, we used infrared and black infrared flash.

Sampling effort was approximated by using the number of days each camera was active as a detection covariate. Six occupancy covariates were delineated for each camera station using QGIS version 3.22 (QGIS Development Team, 2021). These covariates encompassed vegetation, topographic complexity, anthropogenic disturbance, and conservation law enforcement, as these are key predictors of the distribution of carnivores and essential prey species in Iran (Ghoddousi et al., 2016; Khosravi et al., 2018), as well as roads since they constitute a key source of fatalities for Asiatic cheetahs and sympatric carnivores (Mohammadi & Kaboli, 2016).

Topographic covariates encompassed topographic heterogeneity, using the Terrain Ruggedness Index (TRI) developed by Riley et al. (1999) and elevation. Elevation and terrain ruggedness were derived from the SRTM Digital Elevation Data Version 4 (Jarvis et al., 2008). Vegetation cover was approximated through the Modified Soil-adjusted Vegetation Index (MSAVI2) developed by Qi et al. (1994), which was calculated from Sentinel-2 image data with a 10-m resolution (ESA, 2022), as this metric is associated with essential food resources for prey species in arid environments (Funghi et al., 2020). Mean TRI and MSAVI2 were calculated at four different scales (with radii of 250, 500, 1000, and 2000 m) to account for the possibility that ruggedness and vegetation influence the occupancy of different species at different scales given the broad spatial range of the carnivores in this study (Khosravi et al., 2018).

The Euclidean distance from the nearest ranger station was calculated for each camera trap location, as a proxy for conservation law enforcement and prey availability as areas near these stations have been found to harbor a greater abundance of ungulate prey in Iran due to increased protection from hunting, a source of wild ungulate population decline across our study regions (Ghoddousi et al., 2016). The distance from the nearest human settlement was calculated to account for anthropogenic disturbance such as livestock grazing and hunting (Khosravi et al., 2018). Additionally, the distance from the nearest road was calculated for each camera trap location using the HOTOSM Iran Roads dataset (Humanitarian OpenStreetMap Team, 2020). In addition to these occupancy covariates, we included latitude and longitude as geographic control covariates to account for broadscale spatial variation in species occupancy across multiple study sites distributed over a large geographic area (Rota et al., 2016).

All statistical analyses were conducted using the *R* software version 4.1.2 (R Core Team, 2021). All occupancy covariates were examined for potential collinearity using Pearson's correlation matrix, with covariate pairs that displayed an $|r| \geq 0.7$ considered strongly correlated, and one of the covariates in such pairs would be removed prior to any subsequent analysis (Dormann et al., 2013). TRI at the 2000-m scale and elevation were excluded from occupancy modeling as they were found to be highly correlated ($|r| \geq 0.7$) to latitude, while elevation also showed high collinearity with multiple scales of TRI (Appendix S1: Figure S1). Moran's *I* Index was applied using the package "ncf" (Bjornstad, 2022) to test for spatial autocorrelation for each species detection, and the corresponding spatial correlograms were visually examined for patterns of correlations across the distance from the trap where each species was detected (Legendre & Legendre, 2012). Each covariate was standardized to have a mean of '0' and a standard deviation of '1' (Curveira-Santos et al., 2021).

Multispecies occupancy modeling

We employed a joint occupancy model for two or more interacting species (Rota et al., 2016), implemented through the package "unmarked" (Fiske & Chandler, 2011). Sampling days were grouped into 10 sampling occasions to minimize overdispersion in the data and increase the temporal independence of detections (Penjor et al., 2022). As a few sites had two camera traps set up, the spatial analyses only used the detection records from one camera trap to avoid skewing detection probability and to avoid pseudoreplication.

To obtain the most parsimonious set of multispecies occupancy models and reduce their complexity, a multistage modeling process was employed to select the most relevant covariates (Andrade-Ponce et al., 2022), in which we first used single-species occupancy models (Mackenzie et al., 2002) to inform covariate selection. First, a model with intercept-only occupancy parameters and detection modeled as a function of sampling effort and a null detection model were compared for each species to determine whether to include sampling effort in their detection formulae (Richmond et al., 2010). Then, the optimal scale of the multiscale covariates for each species was examined by fitting single-species models for each covariate scale. Finally, a set of models, including one model per covariate and a null model, was used to select occupancy covariates for each species.

All single-species models were ranked using the Akaike information criterion corrected for small samples (AIC_c), with the R package "AICcmodavg" (Mazerolle, 2023). Single-species models were selected at each stage based on the lowest AIC_c score, with models with a $\Delta\text{AIC}_c < 2.00$ considered to receive considerable support (Anderson, 2008). The covariates from the highest ranking single-species models were incorporated into candidate multispecies occupancy models, reflecting the following interactions:

1. No spatial interactions between cheetahs and sympatric carnivores.
2. Constant pairwise interactions (intercept-only second-order parameters).
3. Pairwise interactions as a function of geographic variation (latitude and longitude).
4. Pairwise interactions as a function of the distance from human settlements and the distance from ranger stations.

Two null models were also included, one of which holds all first-order parameters constant with no interactions and another that also assumes constant interactions between cheetahs and each of the other sympatric carnivores. None of the candidate models incorporated pairwise interactions that did not involve cheetahs, as we were specifically interested in discerning potential spatial partitioning between cheetahs and each of the carnivores. Higher order parameters (i.e., more than two species interacting) were also excluded from all models to avoid overparameterization. Each multispecies occupancy model (except null models) incorporated latitude and longitude to control for geographic variation, given the broad spatial scope of this study (Rota et al., 2016). These candidate models were ranked based on their respective AIC scores, with those having $\Delta\text{AIC} < 2.00$ considered to carry substantial support and used to make predictions regarding marginal and conditional occupancy. The *p* values of the model estimates were used to determine the significance of a covariate's effect on marginal and conditional occupancy. Beta-coefficients and mean conditional occupancy probabilities were presented with their corresponding SE. The goodness-of-fit of the highest-ranked single-species and multispecies occupancy models was evaluated using a parametric bootstrap approach to calculate the sum of squared errors, Freeman–Tukey, and χ^2 statistics, with the observed χ^2 statistic being used to calculate the dispersion parameter ($\hat{c}$ or c-hat) as a measure of model fit (Andrade-Ponce et al., 2022; Fiske & Chandler, 2011).

Temporal activity

To limit pseudoreplication, only one image was used for the temporal analysis when the time of capture was within 30 min of another photographic detection of the same species at the same location (Davis et al., 2021). In addition to analyzing temporal activity patterns with the entire combined data set, temporal data from six of the eight reserves were grouped into two regions which are known to harbor the same cheetah subpopulations: (1) The northern landscape: Touran and Miandasht, and (2) the southern landscape: Ariz, Dareh Anjir, Bafq and Naybandan, with data from the first three reserves and Naybandan being pooled separately to compare subregions where leopards and hyaenas are the only sympatric carnivores, respectively. Siahkouh and Abbasabad were excluded from these analyses as they contained insufficient cheetah detections ($n = 3$). To account for the seasonality effect, temporal data were then pooled into locally interpreted seasons, representing summer (April–September) and winter (October–March), as they differ significantly in their temperatures (Table 1).

We used the package "insol" (Corripio, 2020) to calculate the sunset and sunrise times for the date of each detection. This approach was also used to calculate the average sunrise and sunset time across detection dates within each landscape or season, except the total combined data since it spans multiple seasons, and obtaining an average sunrise and sunset time for these data would likely misrepresent the actual timing of these events. The average sunrise and sunset times were 06:39 and 17:15 for winter and 06:00 and 18:54 for summer (Appendix S1: Table S2).

We then defined the crepuscular periods as 1.5 h before and after sunrise and sunset (Gómez et al., 2005); the diurnal period spanned from the end of the first crepuscular period (around dawn) until the beginning of the second (around dusk), whereas the nocturnal period spanned from the end of the second crepuscular period until the beginning of the first (Appendix S1: Table S2). When classifying detections within these categories, we employed the sunset and sunrise times of the specific date of that detection rather than the averaged sunrise and sunset times for its corresponding landscape or season to avoid misclassifying the event's timing within the diel cycle.

We applied the Hermans–Rasson test for circular uniformity to test the null hypothesis that a species' temporal activity was distributed in a uniform distribution over 24 h for each species within every temporal data category, using the "HR_test" function from the "CircMLE" package in R (Landler et al., 2018). We compared the overlap in daily activity patterns through nonparametric kernel density estimations for circular data through the package "overlap" (Meredith & Ridout, 2021; Ridout & Linkie, 2009). Detection times were converted to sun time before analysis using the "sunTime" function, as clock times are prone to misrepresent the actual timing of the diel cycle (Nouvellet et al., 2012). Temporal overlap between cheetahs and sympatric carnivores was estimated using the coefficient of overlap (Δ), with $\Delta = 0$ representing no overlap and $\Delta = 1$ representing complete overlap. $\Delta \leq 0.5$ was considered to represent low overlap, $0.5 < \Delta \leq 0.75$ was considered to represent moderate overlap, and $\Delta > 0.75$ was interpreted as representing high overlap (Monterroso et al., 2014).

We used estimator Δ_1 when the number of detections was lower than 50 and employed estimator Δ_4 when the number of detections was greater than 75 (Meredith & Ridout, 2021). For each overlap estimate, 95% CIs were calculated through smooth bootstraps with 10,000 permutations (Meredith & Ridout, 2021). We assessed pairwise differences in activity levels between species using a Wald test applied using the "compareAct()" function from the "activity" package in R (Rowcliffe et al., 2014), comparing the fitted activity models based on bootstrapped CIs.

RESULTS

A total of 18,806 trapping days throughout 232 camera stations in eight reserves resulted in a total of 809 detections of the four carnivores (Table 2). After excluding photographic detections which failed to record a specific time due to technical issues with the camera trap or that occurred less than 30 min from another detection for the same site and animal (as above), the temporal analyses comprised 180 cheetah detections, 304 hyaena detections, 127 wolf detections, and 96 leopard detections. As many of these detections occurred during the same day or within the same occupancy modeling sampling occasion, the spatial analyses comprised 148 cheetah detections, 185 hyaena detections, 91 wolf detections, and 59 leopard detections (Appendix S1: Table S1). No evidence of

TABLE 2 Number of photographic detections for each of the four large carnivores focal to this study across eight protected areas in Iran.

	Species			
Study area	**Asiatic cheetah**	**Gray wolf**	**Persian leopard**	**Striped hyaena**
Abbasabad	0	9	0	0
Ariz	23	0	0	0
Bafq	4	0	30	0
Dareh Anjir	42	0	0	0
Miandasht	14	50	0	26
Touran	98	70	82	287
Naybandan	18	0	0	32
Siahkouh	3	21	0	0
Total	202	150	112	345

spatial autocorrelation was found for any species (Appendix S1: Figure S2).

Hyaenas were the most detected species with a naïve occupancy of 32.8% ($n = 76$ sites), followed by cheetahs ($n = 69$; 29.7%), wolves ($n = 41$; 17.7%), and leopards ($n = 27$; 11.6%). The single-species models for the detection probability revealed that models incorporating sampling effort ranked highest for all species except wolves, where the null detection model ranked marginally higher than the sampling effort detection model (sampling effort: $\Delta\text{AIC}_c = 0.19$). Since the sampling effort detection model for wolves ranked only slightly lower than the null detection model in terms of AIC_c, sampling effort was incorporated as a detection covariate for subsequent occupancy models to facilitate model convergence. For TRI, the 1000-m scale ranked highest for hyaenas (Appendix S1: Table S3). However, all other carnivores had multiple scales that received considerable support through the model selection for TRI and MSAVI2, so while the highest ranking scales were incorporated in the multispecies occupancy models, they cannot be considered to represent the only optimal scale (Appendix S1: Table S3).

The second stage of single-species modeling revealed multiple plausibly relevant predictors for cheetah occupancy, as the models that incorporated TRI, distance from human settlements, MSAVI2, distance from roads, and distance from ranger stations all ranked highly ($\Delta\text{AIC} < 2.00$; Appendix S1: Table S4). Therefore, these covariates were included in separate models in the multispecies occupancy modeling stage. TRI was the highest ranking covariate for hyaenas and wolves, while MSAVI2 ranked highest for leopards among the single-species candidate models (Appendix S1: Table S4). All the highest ranking single-species models fitted the data relatively well, with a dispersion parameter close to 1 (Appendix S1: Figures S1 and S4).

Multispecies occupancy modeling

We evaluated 22 candidate multispecies occupancy models: two null models, five without interspecific interactions, five with constant interactions, five with interactions parameterized by latitude and longitude, and five with interactions parameterized by distance to human settlements and ranger stations (Appendix S1: Table S5). The highest ranking multispecies model incorporated the distance from human settlements as a covariate for cheetah occupancy and modeled pairwise interactions as a function of latitude and longitude (AIC mass = 0.99). This model fitted the data well, based on the goodness-of-fit test results with a dispersion parameter relatively close to 1 ($\hat{c} = 1.08$; Appendix S1: Figure S5). Sampling effort was positively associated with the detectability of all species (Appendix S1: Table S6).

Cheetah occupancy was positively associated with the distance from human settlements ($\beta = 1.14 \pm 0.35$ [SE], $p = 0.001$; Figure 2a), while leopard occupancy was positively associated with MSAVI2 ($\beta = 1.67 \pm 0.39$, $p < 0.001$; Figure 2b). The second highest ranking multispecies occupancy model (AIC mass = 0.007) incorporated MSAVI2 for cheetah marginal occupancy and only included geographic control covariates in the second-order parameters; this model's outputs present a marginal negative relationship between this vegetation covariate and cheetah marginal occupancy ($p = 0.06$; Appendix S1: Table S7).

The mean conditional probability of cheetahs and leopards co-occurring was lower ($\psi_{\text{cheetah}} = 0.20 \pm 0.02$; $\psi_{\text{leopard}} = 0.07 \pm 0.01$) than that of one of these carnivores occurring in the absence of the other ($\psi_{\text{cheetah}} = 0.58 \pm 0.02$; $\psi_{\text{leopard}} = 0.32 \pm 0.02$; Figure 3). However, no discernible spatial interactions were found for cheetahs and any of the other carnivores based on model outputs, while the co-occurrence between cheetahs and wolves was positively associated with longitude (Appendix S1: Tables S7–S9).

Temporal activity

The Hermans–Rasson test for circular uniformity revealed considerable variation in the strength of temporal patterning across species, seasons, and regions. We did not reject the null hypothesis of uniform activity for cheetahs in Naybandan, leopards in Bafq, Ariz, and

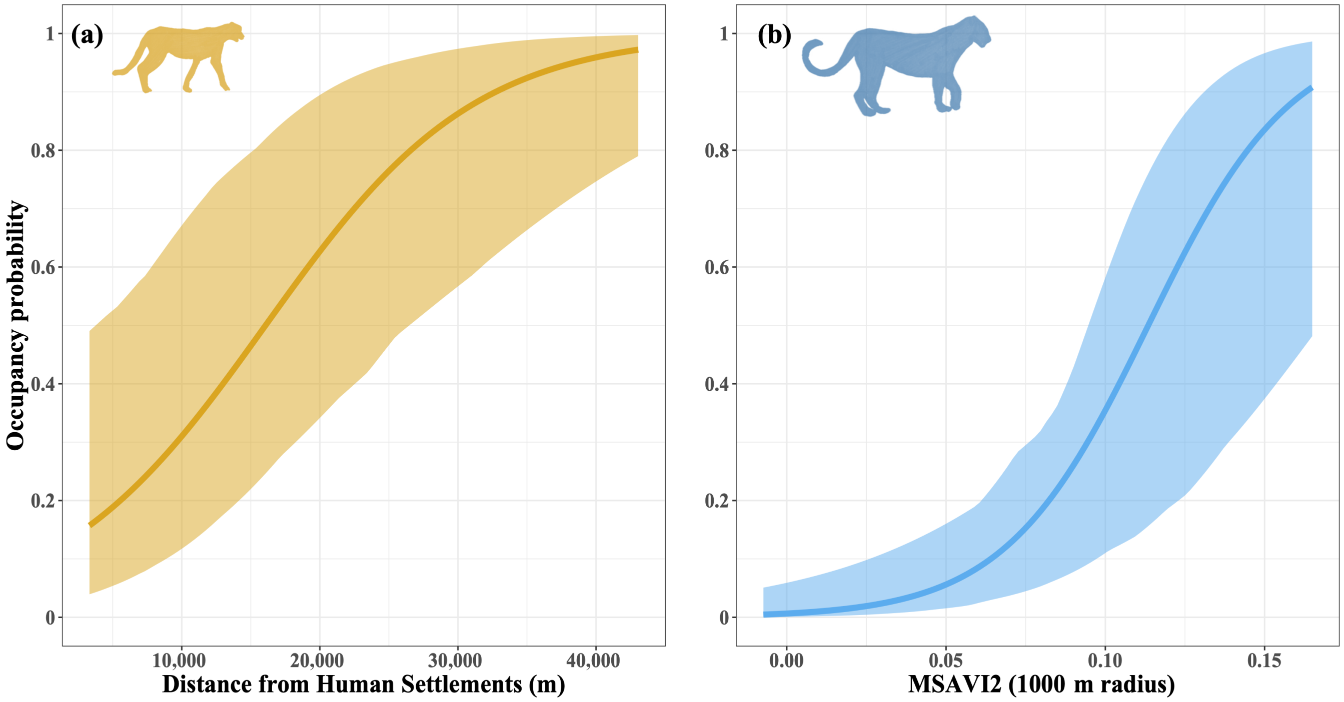

FIGURE 2 Plotted marginal occupancy probabilities of (a) cheetahs in relation to the distance from human settlements and (b) leopards in relation to vegetation (MSAVI2), with values for other covariates held constant. Ribbons indicate bootstrapped 95% CIs with 100 samples. Illustration credit: Nicholas Pilaud.

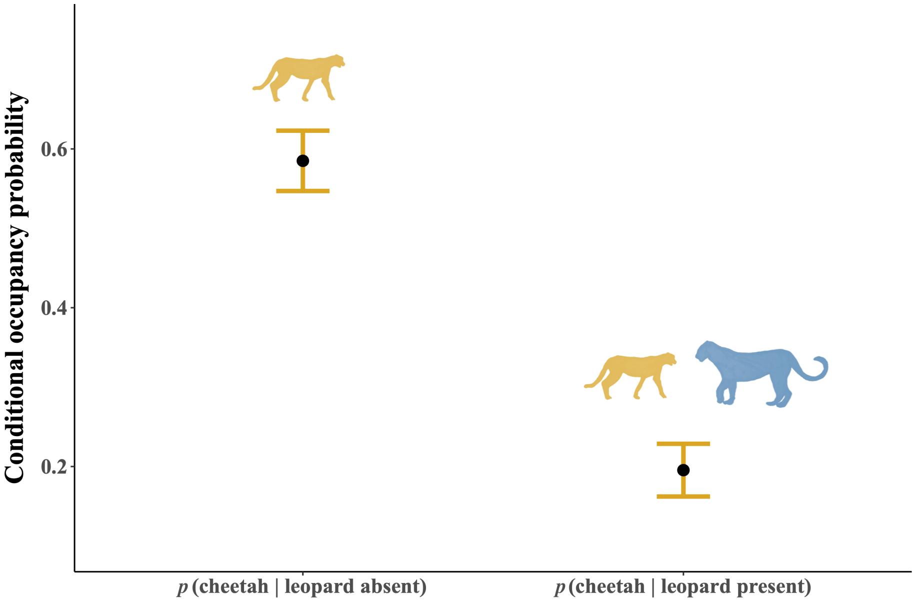

FIGURE 3 Plotted mean occupancy probability (p) and 95% CIs of cheetahs conditional on the absence and presence of leopards. Illustration credit: Nicholas Pilaud.

Dareh Anjir, and both leopards and wolves during winter (all $p > 0.05$; Appendix S1: Table S10), suggesting no clearly distinguishable activity pattern throughout the 24-h cycle for these species within the southern landscapes and during the cooler months, respectively. In contrast, hyaenas exhibited consistently nonuniform activity across all regions and seasons (all $p < 0.001$; Appendix S1: Table S10). All species displayed significant deviation from uniform activity for the northern region and summer, as well as when temporal activity was examined for each species for the entire combined dataset (all $p < 0.001$; Appendix S1: Table S10).

Wald tests comparing seasonal activity levels indicated no significant differences between winter and summer for any species (all $p > 0.05$; Appendix S1: Table S11). In analyses of the northern landscape and summer data, cheetahs exhibited diel activity patterns that differed from those of leopards ($p = 0.002$ for both) and hyaenas (northern: $p = 0.045$, summer: $p = 0.050$; Appendix S1: Table S12). The crepuscular period accounted for the largest proportion of cheetah detections for the northern landscape and summer (58% for both) with cheetahs displaying defined bimodal crepuscular peaks of activity (Figure 4), and 29% of cheetah detections occurred at night. In contrast, hyaena detections were mostly nocturnal (77%), as were those of leopards (56%), a distinction that appears to be reflected by the medium to low temporal overlap between cheetahs and these species (Table 3; Figure 4). However, hyaenas appeared to display more pronounced nocturnal activity peaks than leopards and displayed the lowest temporal overlap with cheetahs of any of the sympatric large carnivores.

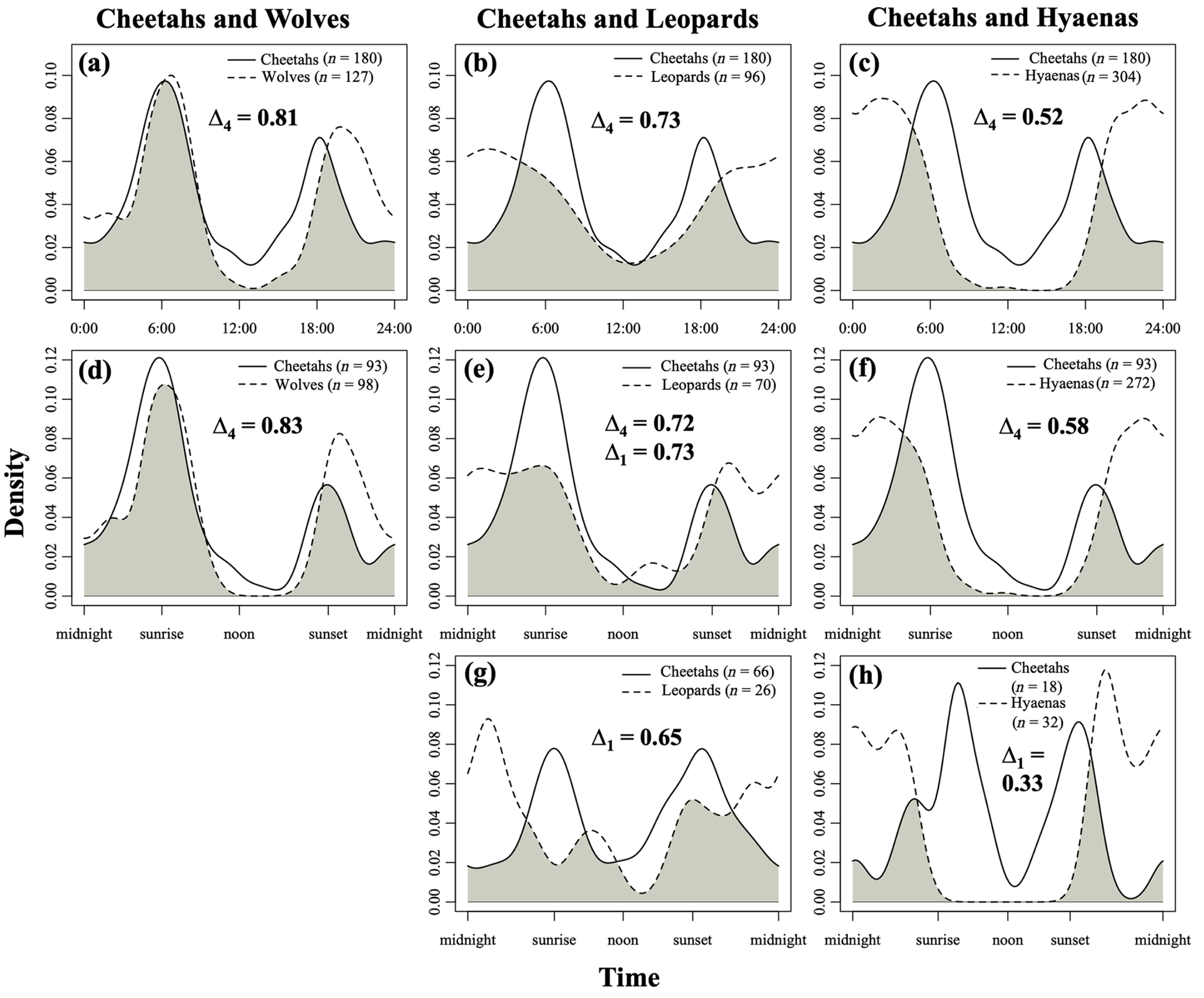

FIGURE 4 Temporal activity overlap plots of cheetahs (solid lines) and sympatric carnivores (dashed lines) for (a–c) combined data from all reserves and (d–f) the northern landscape, and (g, h) the southern landscape. The shaded areas underneath the curves represent temporal overlap. The coefficient of overlap estimators (Δ_4 and Δ_1) are displayed on each plot.

TABLE 3 Temporal overlap with 95% CIs and Wald test p values for the temporal activity curves of cheetahs and sympatric carnivores.

			Temporal overlap with cheetahs			Wald test
Data pooling	**Reserves**	**Sympatric carnivore**	**Estimator**	**Estimate**	**95% CI**	p
Northern	Touran, Miandasht	Wolf	Δ_4	0.83	0.73–0.92	>0.05
		Leopard	Δ_4	0.72	0.60–0.84	**<0.05**
			Δ_1	0.73	0.61–0.84	
		Hyaena	Δ_4	0.58	0.49–0.67	**<0.05**
Southern	Bafq, Ariz, Dareh Anjir, Naybandan	Leopard	Δ_1	0.65	0.49–0.80	>0.05
		Hyaena	Δ_1	0.33	0.15–0.51	>0.05
Winter	Bafq, Ariz, Dareh Anjir, Naybandan, Siahkouh	Wolf	Δ_1	0.75	0.58–0.90	>0.05
		Leopard	Δ_1	0.64	0.48–0.79	>0.05
		Hyaena	Δ_1	0.42	0.31–0.54	>0.05
Summer	Touran, Miandahst, Abbasabad	Wolf	Δ_4	0.82	0.72–0.90	>0.05
		Leopard	Δ_4	0.72	0.60–0.84	**<0.05**
			Δ_1	0.73	0.61–0.84	
		Hyaena	Δ_4	0.58	0.48–0.67	**<0.05**
Total	All reserves	Wolf	Δ_4	0.81	0.74–0.88	>0.05
		Leopard	Δ_4	0.73	0.63–0.82	>0.05
		Hyaena	Δ_4	0.52	0.45–0.60	>0.05

Note: Wald test p values less than 0.05 are demarcated in bold typeface. The choice of estimator based on sample size is displayed, with both estimators included for sample sizes between 50 and 75.

Meanwhile, no evidence of differences in activity patterns was found between cheetahs and wolves for any landscape or season ($p > 0.10$ for all). The crepuscular period accounted for the largest proportion of activity of both species, with the exception of winter when wolves displayed a higher proportion of nocturnal detections (50%) while cheetahs remained most active during the crepuscular period (49%; Appendix S1: Table S12). Further, both species exhibited pronounced crepuscular activity peaks, displaying the highest temporal overlap of any dyad with high overlap between wolves and cheetahs evident for the northern landscape and combined southern and northern landscapes (Table 3; Figure 4). This general trend in temporal overlap remained consistent across seasons, with wolves displaying the highest temporal overlap with cheetahs, followed by leopards, and, lastly, hyaenas (Figure 5).

DISCUSSION

Asiatic cheetahs displayed varied spatial and temporal relationships with sympatric carnivores in dryland ecosystems. Our findings reveal temporal partitioning with hyaenas, both spatial and temporal separation from leopards, but no clear evidence of pronounced partitioning with wolves. Notably, 24% of cheetah detections occurred at night, a level of nocturnality comparable to African populations (Broekhuis et al., 2014; Cozzi et al., 2012). This adds to the growing body of evidence that cheetahs are more nocturnal than previously assumed, suggesting that temporal segregation from other nocturnal carnivores may be less distinct than earlier proposed (Hayward & Slotow, 2009).

Hypothesis 1: Asiatic cheetahs versus sympatric predators

Consistent with our first hypothesis, Asiatic cheetahs and Persian leopards exhibited clear spatial and temporal segregation. This pattern is expected, given the lethal threat leopards pose to cheetahs in arid landscapes (Cheraghi et al., 2019; Mills & Mills, 2017). Persian leopards tend to be less diurnal than cheetahs (Cheraghi et al., 2019; Rouse et al., 2021) and typically occupy distinct habitat types such as montane landscapes which are less frequented by cheetahs (Khosravi et al., 2018). Although both species rely heavily on the same spectrum of ungulate prey (Farhadinia et al., 2023; Khalatbari et al., 2022), they appear to select different environments to optimize their hunting strategies: cheetahs predominantly hunt at lower altitudes, while leopards are better adapted to higher elevations (Farhadinia et al., 2020, 2023). This ecological divergence likely facilitates spatial separation and reduces the risk of intraguild predation. Equally

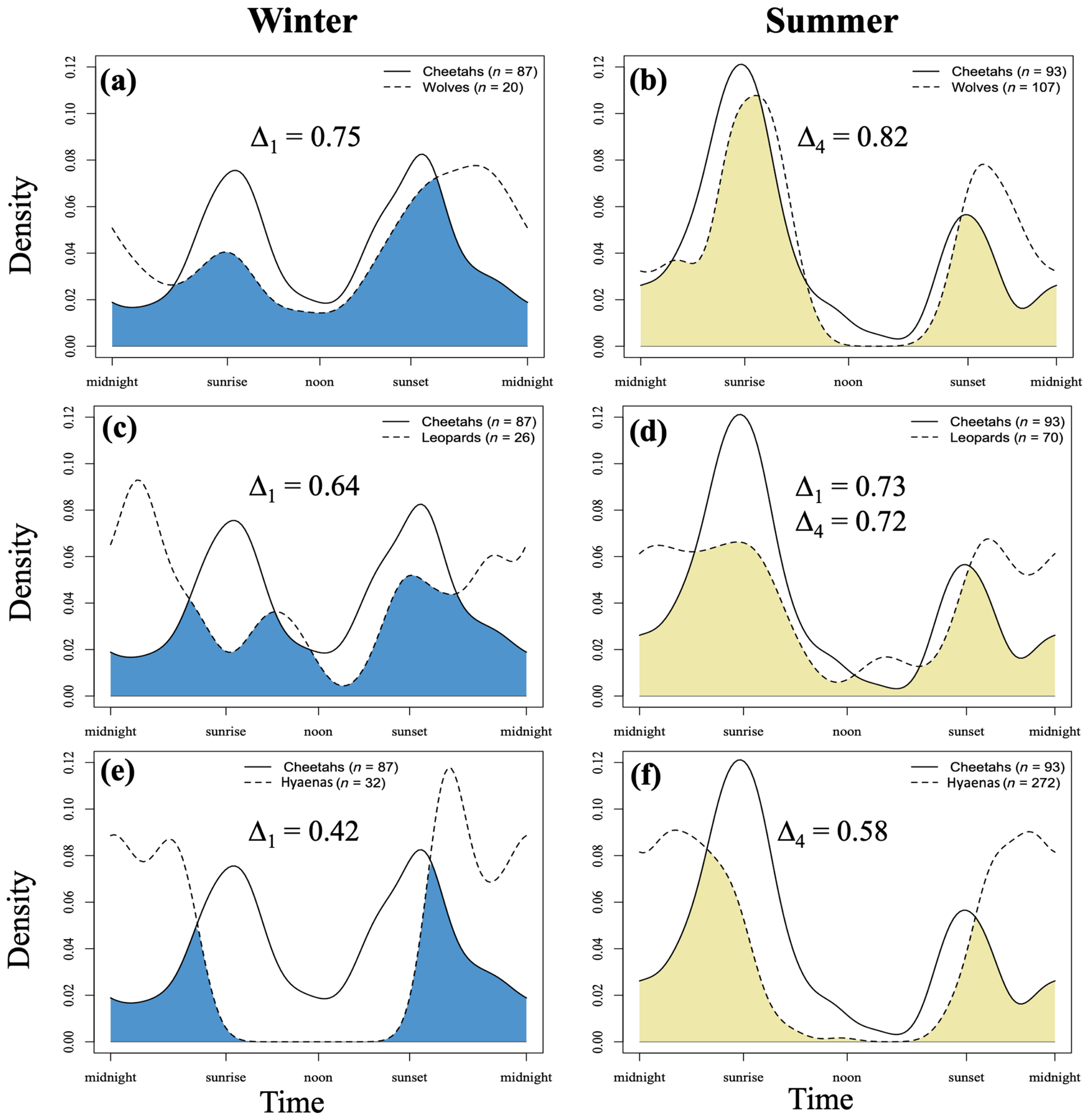

FIGURE 5 Temporal activity overlap plots of cheetahs (solid lines) and sympatric carnivores (dashed lines) for the (a, c, e) winter and (b, d, f) summer data. The shaded areas underneath the curves represent temporal overlap. The coefficient of overlap estimators (Δ_4 and Δ_1) are displayed on each plot.

important, cheetahs may employ behavioral avoidance mechanisms similar to those observed in African ecosystems, where they tolerate spatial overlap with leopards by responding to sensory cues rather than actively avoiding areas of high leopard activity (Cornhill et al., 2023; Gigliotti et al., 2021). Such strategies may further reduce direct encounters and enhance coexistence in resource-limited drylands.

Contrary to our first hypothesis, we found no evidence of spatial or temporal partitioning between wolves and cheetahs. This dyad consistently exhibited high temporal overlap, with no marked differences in activity patterns across the 24-h cycle, while it displayed no pronounced spatial segregation or overlap. Two factors may explain this pattern. First, wolves were present in Abbasabad and Siahkouh, two reserves with little to no cheetah detections (Abbasabad: $n = 0$, Siahkouh: $n = 3$), as well as in Miandasht and Touran, which yielded markedly more cheetah detections (Appendix S1: Table S1). These regional differences are supported by the positive association between longitude and spatial interactions between wolves and cheetahs since Abbasabad and Siahkouh were the westernmost reserves whereas Touran and Miandasht were the easternmost reserves in this study (Figure 1; Appendix S1: Table S9). Consequently, the broad spatial scale of this study may obscure more local patterns of spatial overlap or segregation between these two species.

Second, our data indicated that Asiatic cheetahs tend to avoid areas near human settlements, whereas gray wolves are partially reliant on anthropogenic food sources such as livestock and waste (Hosseini-Zavarei et al., 2013; Mohammadi et al., 2019). Our surveys in Miandasht and Touran were conducted during the hottest period of the year, when extreme temperatures dissuade herders from grazing their livestock in more remote areas, perhaps rendering wolves more likely to forage near human settlements while cheetahs remain farther away from these sites of anthropogenic disturbance. This anthropogenically mediated divergence in habitat use may promote coexistence between these sympatric predators by reducing spatial overlap. However, as both species likely share similar use for open habitat that supports cursorial hunting strategies (Mech & Boitani, 2003; Wilson et al., 2013), they may still display higher spatial overlap when hunting wild ungulates. Such opposing habitat use pressures may account for the lack of pronounced broadscale spatial attraction or avoidance between wolves and cheetahs.

Hypothesis 2: Asiatic cheetahs versus scavengers

Consistent with our second hypothesis, we found no evidence of spatial partitioning between Asiatic cheetahs and striped hyaenas. While cheetahs exhibited a bimodal crepuscular activity pattern with notable nocturnal activity, striped hyaenas were more strictly nocturnal. Consequently, hyaenas showed the lowest temporal overlap with cheetahs among all sympatric carnivores, a finding aligned with their well-documented nocturnal behavior (Panda et al., 2023).

Our results also suggest a potentially symbiotic dynamic between the two species. Striped hyaenas may partially fulfill their dietary needs by scavenging prey remains left by cheetahs, perhaps accounting for the lack of spatial partitioning between the two species. However, the low temporal overlap implies limited direct interaction and a reduced likelihood of kleptoparasitism, which may occur only occasionally between striped hyenas and large felids (Yosef & Kumbhojkar, 2025).

Hypothesis 3: Effects of environmental covariates

Asiatic cheetah occupancy was inversely related to anthropogenic disturbance, that is, the proximity to sites of human habitation and activity. Asiatic cheetahs widely suffer from anthropogenic mortality (Farhadinia et al., 2017) and tend to avoid human presence (Khosravi et al., 2019), likely confining cheetah occurrence by pushing them farther away from human settlements. However, contrary to our predictions, we found no evidence that co-occurrence between cheetahs and sympatric carnivores is influenced by anthropogenic disturbance, suggesting that sympatric carnivores such as leopards, hyaenas, and wolves may display greater flexibility to occur both near human presence and in more remote areas.

Although wolves, leopards, and striped hyaenas may be attracted to anthropogenic food sources such as livestock (Khosravi et al., 2024; Mohammadi et al., 2019; Mwebi et al., 2024), we found no evidence that the cheetah's presumably lower tolerance for human disturbance drives spatial partitioning with these species. This contrasts with previous findings that differences in tolerance to human presence among sympatric carnivores can shape anthropogenically mediated competitive relationships (Havmøller et al., 2024). However, this lack of association could also reflect insufficient representation of human presence in the detection data for other carnivores.

We initially envisaged that the scarcity of food resources in these arid landscapes would lead to increased spatial overlap between cheetahs and sympatric carnivores around resource-rich patches, particularly near ranger stations. These areas often coincide with higher prey availability, likely due to more effective enforcement of conservation laws (Ghoddousi et al., 2016). However, our findings do not support this bottom-up mechanism.

Two supplementary explanations may account for this pattern. First, elevated prey densities near ranger posts are frequently linked to greater access to water, a critical limiting factor, especially during the hot summer months in dryland ecosystems. Consequently, multiple predators, including subordinate cheetahs, are compelled to visit these sites to obtain both water and food (Farhadinia et al., 2023). These locations function as spatially fixed resources and can become hotspots for competitive interactions unless mediated by temporal partitioning or short-term spatiotemporal avoidance (Edwards et al., 2015; Krag et al., 2023; Morin et al., 2024; Valeix et al., 2010). However, not all water sites are concentrated near ranger stations, a consideration that may explain why we found no evidence of a pronounced relationship between the proximity to ranger stations and carnivore co-occurrence. Second, cheetahs exhibit behavioral adaptations that allow them to balance optimal hunting conditions with the risks of encountering dominant predators. Wherever they are sympatric with larger carnivores, cheetahs mitigate intraguild competition by employing strategies such as heightened vigilance and fine-scale behavioral avoidance (Broekhuis et al., 2013; Swanson et al., 2016), enabling them to access prey-rich areas even in the presence of dominant competitors.

Limitations

Our study faced two primary limitations. First, despite an extensive sampling effort, the scarcity of large carnivores in dryland ecosystems resulted in relatively small sample sizes, limiting the statistical power of our analyses. To meet the detection thresholds required by multispecies occupancy models (Kéry & Royle, 2021), we pooled data across multiple reserves and landscapes. While this approach was necessary for robust model performance, we acknowledge that the broader spatial scale may obscure finer scale patterns of co-occurrence. This issue is particularly relevant for leopards and cheetahs, as previous studies suggest low spatial overlap at broadscales (Khosravi et al., 2018), but higher overlap at more localized levels (Cheraghi et al., 2019).

The second limitation, closely tied to the first, concerns the sensitivity of the Rota et al. (2016) model under conditions of limited sample size or weak co-occurrence signals (Cowans et al., 2025). Similarly, the Wald test used to assess differences in temporal activity may lack statistical power when sample sizes are low, as was evident in our winter dataset, which yielded far fewer carnivore detections compared to summer. Although we found no evidence of spatial segregation between wolves and cheetahs, it remains possible that subtle spatial co-occurrence or segregation patterns went undetected due to these methodological constraints. Moreover, we cannot rule out the possibility that elevated temperatures may hinder temporal partitioning between cheetahs and their competitors. As the most diurnal large carnivore in our study system (Cheraghi et al., 2019), cheetahs are expected to exhibit diel activity patterns that are particularly sensitive to high daytime temperatures. This thermal sensitivity may increase temporal overlap with more nocturnal species, as previously reported (Rafiq et al., 2023).

To address this limitation, we recommend that future research directly investigate the role of daily temperature variability, especially maximum daytime temperatures, in shaping spatiotemporal co-occurrence. This approach is particularly relevant for cheetahs and wolves, which already show high temporal overlap and no evidence of spatial segregation, and inhabit desert landscapes where extreme temperatures are common. Additionally, while this work was aimed at examining spatial and temporal patterns of segregation or overlap to assess the potential for partitioning or competition, we recommend that future research more directly investigate the dominance relationship between these species by examining patterns of short-term spatiotemporal avoidance. Similarly, we recommend investigating possible finer scale attraction or avoidance between wolves and cheetahs as the broad spatial extent of this study may obfuscate such interactions. Recent methodological developments provide robust ways to assess whether a species avoids or is attracted to a site following the presence of another species, providing further options for studying these finer scale spatiotemporal interactions (Ferry et al., 2024; Kellner et al., 2022).

CONCLUSIONS

Our study advances understanding of the spatial and temporal dynamics within an understudied dryland carnivore guild and provides three conservation implications:

First, our findings indicate that Asiatic cheetahs avoid human disturbance, highlighting the need for targeted conservation measures in areas with high human density to minimize anthropogenic disturbance.

Second, the absence of clear partitioning between cheetahs and wolves raises concerns about competition in resource-rich patches, particularly near water resources. To mitigate co-occurrence around scarce water, we recommend restoring natural springs and developing artificial water points with broad spatial coverage. As climate change reduces water availability, understanding the role of water provisioning during peak heat periods becomes increasingly critical (Allan & Douville, 2024). Reduced access to water may intensify competition as carnivores converge around limited sources (Edwards et al., 2015; Morin et al., 2024; Valeix et al., 2010), especially in the absence of temporal separation.

Finally, the lack of spatial or temporal partitioning between cheetahs and wolves, coupled with competitive pressure from leopards and limited anthropogenic niche separation, highlights the need to sustain diverse and abundant prey to enable coexistence. In degraded drylands, conservation-dependent carnivores like the Asiatic cheetah face intensified competition and survival challenges. As prey populations decline and habitats deteriorate, restoring prey populations and habitats becomes critical to easing competitive pressures and securing the future of vulnerable dryland carnivores.

AUTHOR CONTRIBUTIONS

Nicholas Pilaud and Mohammad S. Farhadinia conceived the ideas and designed the methodology in conjunction with Ugyen Penjor for the spatial analyses. Atie Taktehrani, Morteza Pourmirzai, Mahsa Shahhosseini, Mohammad Hossein Karimi, Navid Gholikhani, Kaveh Hobeali, and Fatemeh Hosseini-Zavarei carried out the data collection and preparation. Nicholas Pilaud analyzed the data and led the writing of the manuscript under the supervision of Mohammad S. Farhadinia. David W. Macdonald reviewed an earlier draft of the paper. All authors reviewed the results and approved the final version of the manuscript.

ACKNOWLEDGMENTS

We thank the Iranian Department of the Environment, Conservation of Asiatic Cheetah Project, and our donors, the Iran UNDP, La Palmyre Zoo, the Association Française des Parcs Zoologiques, the Prince Bernhard Nature Fund, Stichting SPOTS, the People's Trust for Endangered Species, Parc des Félins & SOS and the WWF INNO Program. Mohammad S. Farhadinia was supported by Research England's Expanding Excellence in England (E3) Fund, UK Research and Innovation. Finally, we are grateful to game wardens for field assistance and data collection in the surveyed reserves.

CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

The photographic detection data analyzed in this study are not publicly available due to the ongoing threats to Asiatic cheetahs and their critically endangered conservation status. To obtain these sensitive data, contact Atie Taktehrani, email a.taktehrani@gmail.com.

REFERENCES

Allan, R. P., and H. Douville. 2024. "An Even Drier Future for the Arid Lands." *Proceedings of the National Academy of Sciences* 121(2): e2320840121. https://doi.org/10.1073/pnas.2320840121.

Anderson, D. R. 2008. *Model Based Inference in the Life Sciences: A Primer on Evidence*. New York: Springer.

Andrade-Ponce, G. P., S. Mandujano, W. Dáttilo, V. Farías-González, J. Jiménez, K. Velásquez-C, and A. Zavaleta. 2022. "A Framework to Interpret Co-Occurrence Patterns from Camera Trap Data: The Case of the Gray Fox, the Bobcat, and the Eastern Cottontail Rabbit in a Tropical Dry Habitat." *Journal of Zoology* 318(2): 91–103. https://doi.org/10.1111/jzo.13002.

Astete, S., J. Marinho-Filho, M. Kajin, G. Penido, B. Zimbres, R. Sollmann, A. T. A. Jácomo, N. M. Tôrres, and L. Silveira. 2017. "Forced Neighbours: Coexistence between Jaguars and Pumas in a Harsh Environment." *Journal of Arid Environments* 146: 27–34. https://doi.org/10.1016/j.jaridenv.2017.07.005.

Belbachir, F., N. Pettorelli, T. Wacher, A. Belbachir-Bazi, and S. M. Durant. 2015. "Monitoring Rarity: The Critically Endangered Saharan Cheetah as a Flagship Species for a Threatened Ecosystem." *PLoS One* 10(1): e0115136. https://doi.org/10.1371/journal.pone.0115136.

Bjornstad, O. N. 2022. "ncf: Spatial Covariance Functions." R Package. https://CRAN.R-project.org/package=ncf

Broekhuis, F., G. Cozzi, M. Valeix, J. W. McNutt, and D. W. Macdonald. 2013. "Risk Avoidance in Sympatric Large Carnivores: Reactive or Predictive?" *Journal of Animal Ecology* 82(5): 1098–1105. https://doi.org/10.1111/1365-2656.12077.

Broekhuis, F., S. Grünewälder, J. W. McNutt, and D. W. Macdonald. 2014. "Optimal Hunting Conditions Drive Circalunar Behavior of a Diurnal Carnivore." *Behavioral Ecology* 25(5): 1268–75. https://doi.org/10.1093/beheco/aru122.

Burgos, T., J. Salesa, J. M. Fedriani, G. Escribano-Ávila, J. Jiménez, M. Krofel, I. Cancio, J. Hernández-Hernández, J. Rodríguez-Siles, and E. Virgós. 2023. "Top-Down and Bottom-Up Effects Modulate Species Co-Existence in a Context of Top Predator Restoration." *Scientific Reports* 13(1): 4170. https://doi.org/10.1038/s41598-023-31105-w.

Case, T. J., and M. E. Gilpin. 1974. "Interference Competition and Niche Theory." *Proceedings of the National Academy of Sciences of the United States of America* 71(8): 3073–77. https://doi.org/10.1073/pnas.71.8.3073.

Cheraghi, F., M. R. Delavar, F. Amiraslani, K. Alavipanah, E. Gurarie, H. Jowkar, L. T. B. Hunter, S. Ostrowski, and W. F. Fagan. 2019. "Inter-Dependent Movements of Asiatic Cheetahs *Acinonyx jubatus venaticus* and a Persian Leopard *Panthera Pardus Saxicolor* in a Desert Environment in Iran (Mammalia: Felidae)." *Zoology in the Middle East* 65(4): 283–292. https://doi.org/10.1080/09397140.2019.1632538.

Cornhill, K. L., G. A. Balme, L. T. B. Hunter, and G. I. H. Kerley. 2023. "Cheetah Spatiotemporal Overlap with Other Large Carnivores and Prey at Camera-Trap Sites: Do They Fit the Niche-Complementarity Hypothesis?" *Mammalian Biology* 103(5): 505–517. https://doi.org/10.1007/s42991-023-00368-1.

Corripio, J. G. 2020. "insol: Solar Radiation." R Package Version 1.2.2. https://meteoexploration.com/R/insol/

Cowans, A., A. B. Bigatà, and C. Sutherland. 2025. "Sample Size Considerations for Species Co-Occurrence Models." *Ecology* 106(8): e70175. https://doi.org/10.1002/ecy.70175.

Cozzi, G., F. Broekhuis, J. W. McNutt, L. A. Turnbull, D. W. Macdonald, and B. Schmid. 2012. "Fear of the Dark or Dinner by Moonlight? Reduced Temporal Partitioning among Africa's Large Carnivores." *Ecology* 93(12): 2590–99. https://doi.org/10.1890/12-0017.1.

Curveira-Santos, G., C. Sutherland, M. Santos-Reis, and L. H. Swanepoel. 2021. "Responses of Carnivore Assemblages to Decentralized Conservation Approaches in a South African

Landscape." *Journal of Applied Ecology* 58(1): 92–103. https://doi.org/10.1111/1365-2664.13726.

Davis, R. S., R. W. Yarnell, L. K. Gentle, A. Uzal, W. O. Mgoola, and E. L. Stone. 2021. "Prey Availability and Intraguild Competition Regulate the Spatiotemporal Dynamics of a Modified Large Carnivore Guild." *Ecology and Evolution* 11(12): 7890–7904. https://doi.org/10.1002/ece3.7620.

Dormann, C. F., J. Elith, S. Bacher, C. Buchmann, G. Carl, G. Carré, J. R. García Marquéz, et al. 2013. "Collinearity: A Review of Methods to Deal with it and a Simulation Study Evaluating their Performance." *Ecography* 36(1): 27–46. https://doi.org/10.1111/j.1600-0587.2012.07348.x.

Dunford, C. E., J. P. B. Faure, M. D. Ross, J. A. Spalton, M. Drouilly, K. J. P. Pryce-Fitchen, R. De Bruin, et al. 2024. "Searching for Spots: A Comprehensive Survey for the Arabian Leopard *Panthera pardus nimr* in Saudi Arabia." *Oryx* 58(3): 351–362. https://doi.org/10.1017/S0030605323000807.

Edwards, S., A. C. Gange, and I. Wiesel. 2015. "Spatiotemporal Resource Partitioning of Water Sources by African Carnivores on Namibian Commercial Farmlands." *Journal of Zoology* 297(1): 22–31. https://doi.org/10.1111/jzo.12248.

European Space Agency (ESA). 2022. *Copernicus Sentinel Data*. Paris: ESA. https://earthengine.google.com/.

Farhadinia, M. S., D. R. Heit, R. A. Montgomery, P. J. Johnson, K. Hobeali, L. T. B. Hunter, and D. W. Macdonald. 2020. "Vertical Relief Facilitates Spatial Segregation of a High Density Large Carnivore Population." *Oikos* 129(3): 346–355. https://doi.org/10.1111/oik.06724.

Farhadinia, M. S., L. T. B. Hunter, A. Jourabchian, F. Hosseini-Zavarei, H. Akbari, H. Ziaie, G. B. Schaller, and H. Jowkar. 2017. "The Critically Endangered Asiatic Cheetah *Acinonyx jubatus venaticus* in Iran: A Review of Recent Distribution and Conservation Status." *Biodiversity and Conservation* 26(5): 1027–46. https://doi.org/10.1007/S10531-017-1298-8.

Farhadinia, M. S., B. Nezami, A. Ranjbaran, and R. Valdez. 2023. "Animal Behavior Informed by History: Was the Asiatic Cheetah an Obligate Gazelle Hunter?" *PLoS One* 18(4): e0284593. https://doi.org/10.1371/journal.pone.0284593.

Ferry, N., P. Dupont, A. Bender, and M. Heurich. 2024. "Introducing Recurrent Event Analyses to Assess Species Interactions Based on Camera-Trap Data: A Comparison with Time-to-First-Event Approaches." *Methods in Ecology and Evolution* 15(7): 1233–46. https://doi.org/10.1111/2041-210X.14338.

Fiske, I. J., and R. B. Chandler. 2011. "Unmarked: An R Package for Fitting Hierarchical Models of Wildlife Occurrence and Abundance." *Journal of Statistical Software* 43(10): 1–23. https://doi.org/10.18637/jss.v043.i10.

Funghi, C., R. H. J. Heim, W. Schuett, S. C. Griffith, and J. Oldeland. 2020. "Estimating Food Resource Availability in Arid Environments with Sentinel 2 Satellite Imagery." *PeerJ* 8: e9209. https://doi.org/10.7717/peerj.9209.

Ghoddousi, A., A. K. Hamidi, M. Soofi, I. Khorozyan, B. H. Kiabi, and M. Waltert. 2016. "Effects of Ranger Stations on Predator and Prey Distribution and Abundance in an Iranian Steppe Landscape." *Animal Conservation* 19(3): 273–280. https://doi.org/10.1111/acv.12240.

Gigliotti, L. C., R. Slotow, C. Sholto-Douglas, C. de Vos, and D. S. Jachowski. 2021. "Short-Term Predation Risk and Habitat Complexity Influence Cheetah Antipredator Behaviours." *Animal Behaviour* 178: 175–184. https://doi.org/10.1016/j.anbehav.2021.06.003.

Gómez, H., R. B. Wallace, G. Ayala, and R. Tejada. 2005. "Dry Season Activity Periods of some Amazonian Mammals." *Studies on Neotropical Fauna and Environment* 40(2): 91–95. https://doi.org/10.1080/01650520500129638.

Havmøller, R. W., A. W. Parsons, L. W. Havmøller, and R. Kays. 2024. "Sex and Size Matter: Intricate Dominance Relationships in an East African Large Carnivore Guild." *Ecosphere* 15(6): e4913. https://doi.org/10.1002/ecs2.4913.

Hayward, M. W., and R. Slotow. 2009. "Temporal Partitioning of Activity in Large African Carnivores: Tests of Multiple Hypotheses." *South African Journal of Wildlife Research* 39(2): 109–125. https://doi.org/10.3957/056.039.0207.

Hosseini-Zavarei, F., M. S. Farhadinia, M. Beheshti-Zavareh, and A. Abdoli. 2013. "Predation by Grey Wolf on Wild Ungulates and Livestock in Central Iran." *Journal of Zoology* 290(2): 127–134. https://doi.org/10.1111/jzo.12022.

Humanitarian OpenStreetMap Team. 2020. "Iran Roads Dataset." Humanitarian Data Exchange. https://data.humdata.org/dataset/hotosm_irn_roads

Jarvis, A., H. I. Reuter, A. Nelson, and E. Guevara. 2008. "Hole-Filled SRTM for the Globe Version 4." CGIAR-CSI SRTM 90m Database. https://srtm.csi.cgiar.org

Kellner, K. F., A. W. Parsons, R. Kays, J. J. Millspaugh, and C. T. Rota. 2022. "A Two-Species Occupancy Model with a Continuous-Time Detection Process Reveals Spatial and Temporal Interactions." *Journal of Agricultural, Biological and Environmental Statistics* 27: 321–338. https://doi.org/10.1007/s13253-021-00482-y.

Kéry, M., and J. A. Royle. 2021. "Modeling Interactions among Species." In *Applied Hierarchical Modeling in Ecology: Analysis of Distribution, Abundance and Species Richness in R and BUGS, Vol. 2: Dynamic and Advanced Models* 455–526. Amsterdam: Academic Press. https://doi.org/10.1016/b978-0-12-809585-0.00008-9.

Khalatbari, L., B. Egeter, H. Abolghasemi, E. Hakimi, T. Ghadirian, A. H. Khaleghi Hamidi, H. Jowkar, U. Breitenmoser, and J. C. Brito. 2022. "Assessing Asiatic Cheetah's Individual Diet Using Metabarcoding and its Implication for Conservation." *Scientific Reports* 12: 11403. https://doi.org/10.1038/s41598-022-15065-1.

Khosravi, R., M.-R. Hemami, and S. A. Cushman. 2018. "Multispecies Assessment of Core Areas and Connectivity of Desert Carnivores in Central Iran." *Diversity and Distributions* 24(2): 193–207. https://doi.org/10.1111/ddi.12672.

Khosravi, R., M.-R. Hemami, and S. A. Cushman. 2019. "Multi-Scale Niche Modeling of Three Sympatric Felids of Conservation Importance in Central Iran." *Landscape Ecology* 34: 2451–67. https://doi.org/10.1007/s10980-019-00900-0.

Khosravi, R., L. Julaie, G. Fandos, T. Kuemmerle, and A. Ghoddousi. 2024. "Determinants of Livestock Depredation Risk by Persian Leopards in Southern Iran." *Biological Conservation* 291: 110510. https://doi.org/10.1016/j.biocon.2024.110510.

Kluever, B. M., E. M. Gese, and S. J. Dempsey. 2017. "Influence of Free Water Availability on a Desert Carnivore and Herbivore." *Current Zoology* 63(2): 121–29. https://doi.org/10.1093/cz/zow071.

Krag, C., L. W. Havmøller, L. Swanepoel, G. Van Zyl, P. R. Møller, and R. W. Havmøller. 2023. "Impact of Artificial Waterholes on Temporal Partitioning in a Carnivore Guild: A Comparison of Activity Patterns at Artificial Waterholes to Roads and Trails." *PeerJ* 11: e15253. https://doi.org/10.7717/peerj.15253.

Kruuk, H. 1976. "Feeding and Social Behaviour of the Striped Hyaena (*Hyaena vulgaris* Desmarest)." *African Journal of Ecology* 14(2): 91–111. https://doi.org/10.1111/j.1365-2028.1976.tb00155.x.

Landler, L., G. D. Ruxton, and E. P. Malkemper. 2018. "Circular Data in Biology: Advice for Effectively Implementing Statistical Procedures." *Behavioral Ecology and Sociobiology* 72(8): 128. https://doi.org/10.1007/s00265-018-2538-y.

Legendre, P., and L. Legendre. 2012. "Chapter 13 – Spatial Analysis." In *Developments in Environmental Modelling, Numerical Ecology*, Vol. 24, 785–858. Amsterdam: Elsevier. https://doi.org/10.1016/B978-0-444-53868-0.50013-7.

Lewin, A., G. Murali, S. Rachmilevitch, and U. Roll. 2024. "Global Evaluation of Current and Future Threats to Drylands and their Vertebrate Biodiversity." *Nature Ecology & Evolution* 8: 1448–58. https://doi.org/10.1038/s41559-024-02450-4.

Mackenzie, D. I., J. D. Nichols, G. B. Lachman, S. Droege, J. A. Royle, and C. A. Langtimm. 2002. "Estimating Site Occupancy Rates When Detection Probabilities Are Less than One." *Ecology* 83(8): 2248–55. https://doi.org/10.1890/0012-9658(2002)083[2248:esorwd]2.0.co;2.

Mazerolle, M. J. 2023. "AICcmodavg: Model Selection and Multimodel Inference Based on (Q)AIC(c)." R Package. https://CRAN.R-project.org/package=AICcmodavg

Mech, L. D., and L. Boitani. 2003. *Wolves: Behavior, Ecology, and Conservation*. Chicago: University of Chicago Press.

Meredith, M., and M. S. Ridout. 2021. "Overview of the Overlap Package."

Middleton, N., and D. Thomas. 1997. *World Atlas of Desertification*. London: Arnold.

Mills, M. G. L., and M. E. J. Mills. 2017. *Kalahari Cheetahs: Adaptations to an Arid Region*. Oxford: Oxford University Press. https://doi.org/10.1093/oso/9780198712145.001.0001.

Mohammadi, A., and M. Kaboli. 2016. "Evaluating Wildlife-Vehicle Collision Hotspots Using Kernel-Based Estimation: A Focus on the Endangered Asiatic Cheetah in Central Iran." *Human-Wildlife Interactions* 10(1): 103–9. https://doi.org/10.26077/0xjd-az08.

Mohammadi, A., M. Kaboli, V. Sazatornil, and J. V. López-Bao. 2019. "Anthropogenic Food Resources Sustain Wolves in Conflict Scenarios of Western Iran." *PLoS One* 14(6): e0218345. https://doi.org/10.1371/journal.pone.0218345.

Monterroso, P., P. C. Alves, and P. Ferreras. 2014. "Plasticity in Circadian Activity Patterns of Mesocarnivores in Southwestern Europe: Implications for Species Coexistence." *Behavioral Ecology and Sociobiology* 68(9): 1403–17. https://doi.org/10.1007/S00265-014-1748-1.

Morin, A., O. Gimenez, L. L. Sousa, J. Seymour-Smith, H. O'Donnell, M. L. Delignette-Muller, D. Madhlamoto, A. J. Loveridge, and M. Valeix. 2024. "Response of a Carnivore Community to Water Management in a Semi-Arid Savanna." *Biological Conservation* 299: 110777. https://doi.org/10.1016/j.biocon.2024.110777.

Mwebi, O., W. Ogara, T. Adhola, J.-B. Fourvel, and J.-P. Brugal. 2024. "Striped Hyena *Hyaena hyaena* (Linnaeus 1758): Feeding Ecology Based on Den Prey Remains in a Pastoralist Landscape, Southern Kenya." *Mammalia* 88(5): 384–399. https://doi.org/10.1515/mammalia-2024-0008.

Nouvellet, P., G. S. A. Rasmussen, D. W. Macdonald, and F. Courchamp. 2012. "Noisy Clocks and Silent Sunrises: Measurement Methods of Daily Activity Pattern." *Journal of Zoology* 286(3): 179–184. https://doi.org/10.1111/j.1469-7998.2011.00864.x.

Panda, D., S. Mohanty, M. L. Allen, A. Dheer, A. Sharma, P. Pandey, H. Lee, and R. Singh. 2023. "Competitive Interactions with Dominant Carnivores Affect Carrion Acquisition of Striped Hyena in a Semi-Arid Landscape of Rajasthan, India." *Mammal Research* 68(2): 129–141. https://doi.org/10.1007/s13364-022-00663-1.

Penjor, U., C. Astaras, S. A. Cushman, Ż. Kaszta, and D. W. Macdonald. 2022. "Contrasting Effects of Human Settlement on the Interaction among Sympatric Apex Carnivores." *Proceedings of the Royal Society B: Biological Sciences* 289(1973): 20212681. https://doi.org/10.1098/rspb.2021.2681.

Polis, G. A., and R. D. Holt. 1992. "Intraguild Predation: The Dynamics of Complex Trophic Interactions." *Trends in Ecology & Evolution* 7(5): 151–54. https://doi.org/10.1016/0169-5347(92)90208-S.

QGIS Development Team. 2021. *QGIS Geographic Information System, Version 3.22 (Białowieża)*. Laax: QGIS Association. http://www.qgis.org.

Qi, J., A. Chehbouni, A. R. Huete, Y. H. Kerr, and S. Sorooshian. 1994. "A Modified Soil Adjusted Vegetation Index." *Remote Sensing of Environment* 48(2): 119–126. https://doi.org/10.1016/0034-4257(94)90134-1.

R Core Team. 2021. *R: A Language and Environment for Statistical Computing, Version 4.1.2*. Vienna: R Foundation for Statistical Computing. http://www.R-project.org.

Rafiq, K., N. R. Jordan, K. Golabek, J. W. McNutt, A. Wilson, and B. Abrahms. 2023. "Increasing Ambient Temperatures Trigger Shifts in Activity Patterns and Temporal Partitioning in a Large Carnivore Guild." *Proceedings of the Royal Society B: Biological Sciences* 290(2010): 20231938. https://doi.org/10.1098/rspb.2023.1938.

Richmond, O. M. W., J. E. Hines, and S. R. Beissinger. 2010. "Two-Species Occupancy Models: A New Parameterization Applied to Co-Occurrence of Secretive Rails." *Ecological Applications* 20(7): 2036–46. https://doi.org/10.1890/09-0470.1.

Ridout, M. S., and M. Linkie. 2009. "Estimating Overlap of Daily Activity Patterns from Camera Trap Data." *Journal of Agricultural, Biological, and Environmental Statistics* 14(3): 322–337. https://doi.org/10.1198/jabes.2009.08038.

Riley, S. J., S. D. DeGloria, and R. Elliot. 1999. "A Terrain Ruggedness Index that Quantifies Topographic Heterogeneity." *Intermountain Journal of Sciences* 5: 23–27.

Rota, C. T., M. A. R. Ferreira, R. W. Kays, T. D. Forrester, E. L. Kalies, W. J. McShea, A. W. Parsons, and J. J. Millspaugh. 2016. "A Multispecies Occupancy Model for Two or More Interacting Species." *Methods in Ecology and Evolution* 7(10): 1164–73. https://doi.org/10.1111/2041-210x.12587.

Rouse, S., P. Behnoud, K. Hobeali, P. Moghadas, Z. Salahshour, H. Eslahi, M. Ommatmohammadi, et al. 2021. "Intraspecific Interactions in a High-Density Leopard Population." *Ecology and Evolution* 11(23): 16572–84. https://doi.org/10.1002/ece3.8227.

Rowcliffe, J. M., R. Kays, B. Kranstauber, C. Carbone, and P. A. Jansen. 2014. "Quantifying Levels of Animal Activity Using Camera Trap Data." *Methods in Ecology and Evolution* 5(11): 1170–79. https://doi.org/10.1111/2041-210X.12278.

Safriel, U., Z. Adeel, D. Niemeijer, J. Puigdefabregas, R. White, R. Lal, M. Winslow, et al. 2005. "Dryland Systems." In *Ecosystems and Human Well-Being: Current State and Trends*, Vol. 1, edited by R. Hassan, R. Scholes, and N. Ash, 623–662. Washington: Island Press.

Schoener, T. W. 1974. "Resource Partitioning in Ecological Communities." *Science* 185(4145): 27–39. https://doi.org/10.1126/science.185.4145.27.

Schoener, T. W. 1983. "Field Experiments on Interspecific Competition." *The American Naturalist* 122(2): 240–285. https://doi.org/10.1086/284133.

Shams, A., M. S. Farhadinia, M. J. O'Riain, A. Gaylard, M. Smit, C. Fraticelli, M. Koutou, et al. 2025. "Perilous State of Critically Endangered Northwest African Cheetah (*Acinonyx jubatus hecki*) across the Sudano-Sahel." *Animal Conservation* 28(2): 208–223. https://doi.org/10.1111/acv.12974.

Swanson, A., T. Arnold, M. Kosmala, J. Forester, and C. Packer. 2016. "In the Absence of a 'Landscape of Fear': How Lions, Hyenas, and Cheetahs Coexist." *Ecology and Evolution* 6(23): 8534–45. https://doi.org/10.1002/ece3.2569.

Valeix, M., A. J. Loveridge, Z. Davidson, H. Madzikanda, H. Fritz, and D. W. Macdonald. 2010. "How Key Habitat Features Influence Large Terrestrial Carnivore Movements: Waterholes and African Lions in a Semi-Arid Savanna of North-Western Zimbabwe." *Landscape Ecology* 25: 337–351. https://doi.org/10.1007/s10980-009-9425-x.

Wilson, J. W., M. G. L. Mills, R. P. Wilson, G. Peters, M. E. J. Mills, J. R. Speakman, S. M. Durant, N. C. Bennett, N. J. Marks, and M. Scantlebury. 2013. "Cheetahs, *Acinonyx jubatus*, Balance Turn Capacity with Pace When Chasing Prey." *Biology Letters* 9(5): 20130620. https://doi.org/10.1098/rsbl.2013.0620.

Yosef, R., and S. Kumbhojkar. 2025. "Kleptoparasitism and Coexistence: Resource Competition between Indian Leopards and Striped Hyenas." *Animals* 15(6): 784. https://doi.org/10.3390/ani15060784.

SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

How to cite this article: Pilaud, Nicholas, Atie Taktehrani, Morteza Pourmirzai, Mahsa Shahhosseini, Mohammad Hossein Karimi, Navid Gholikhani, Kaveh Hobeali, et al. 2026. "Coexistence under Constraint: Spatiotemporal Co-Occurrence in a Dryland Carnivore Guild." *Ecosphere* 17(5): e70641. https://doi.org/10.1002/ecs2.70641