OXFORD

Spatiotemporal behavior of predators and prey in an arid environment of Central Asia

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Handling editor: Zhi-Yun JIA

Abstract

The mechanisms of interactions between apex and smaller carnivores may range from competition to facilitation. Conversely, interactions between predators and prey are mainly driven by the prey reducing the likelihood of encounters with predators. In this study, we investigated (1) the spatiotemporal interactions between an apex (the snow leopard) and a meso-predator (the red fox), and (2) the temporal interactions between the snow leopard and its potential prey (Siberian ibex, argali, Asian wild ass, Tolai hare) through camera trapping in the Mongolian Great Gobi-A. The probability of occurrence for the red fox was higher in the presence of the snow leopard than in its absence. Moreover, the red fox activity pattern matched that of the snow leopard, with both species mostly active at sunset. This positive spatiotemporal interaction suggests that the presence of the snow leopard may be beneficial for the red fox in terms of scavenging opportunities. However, other explanations may also be possible. Amongst prey, the Siberian ibex and the argali were mainly active during the day, whereas the Asian wild ass and the Tolai hare were more nocturnal. These findings suggest that potential prey (especially the Siberian ibex and the argali) may shape their behavior to decrease the opportunity for encounters with the snow leopard. Our results have revealed complex interactions between apex and smaller predators and between apex predator and its potential prey.

Key words: avoidance, facilitation, Mongolia, *Panthera uncia*, ungulates, *Vulpes vulpes*.

Terrestrial carnivores tend to adapt their spatiotemporal behavior to minimize the opportunities for negative interactions, an ecological process called "niche partitioning" (e.g., Linnel and Strand 2000). Small predators may suffer from interspecific competition with larger species, not only from the depletion of some food resources, but also because of direct killing (Palomares and Caro 1999; Donadio and Buskirk 2006). In this sense, spatial and temporal avoidance may reduce competition and facilitate coexistence between sympatric carnivores of different sizes (Hearn *et al.* 2018; Massara *et al.* 2018; Hua *et al.* 2020). Conversely, small predators can benefit from scavenging carcasses left by apex predators (Ferretti *et al.* 2021; Krofel *et al.* 2021; Rossa *et al.* 2021). This concept is known as "facilitation hypothesis" which, in contrast to the "avoidance hypothesis," may explain why the less competitive smaller carnivores can coexist with larger predators (Ferretti *et al.* 2021; Rossa *et al.*

2021). Nevertheless, the spatiotemporal overlap or segregation among mammalian species (including apex and meso-predators) might also be driven by other factors (Niedballa *et al.* 2019) such as intra- and interspecific relationship (Zhao *et al.* 2020), species' endogenous clock (Kronfeld-Schor and Dayan 2003), and abiotic factors (Zielinski 2000). Although the presence of apex predators can lead to complex interactions with small- and medium-sized carnivores (Ritchie and Johnson 2009; Sivy *et al.* 2017; Prugh and Sivy 2020), effects on prey are primarily determined by direct predation (Sinclair *et al.* 2003; Fortin *et al.* 2005) which tends to shape their activity patterns to avoid direct encounters with larger predators (Rossa *et al.* 2021; Salvatori *et al.* 2021). In fact, limiting the temporal overlap with predators is a common antipredatory behavioral strategy adopted by prey species (Ross *et al.* 2013; Rossa *et al.* 2021; Salvatori *et al.* 2021).

Arid regions host highly specialized animal species which can stand scarcity or absence of water for long periods of time, together with other adaptations, for example, to regulate body temperature (Withers et al. 2016). Climatic changes may further affect the survival of desert-adapted species, imposing even more rigorous living conditions on them. Thus, monitoring the spatiotemporal activity patterns of animal communities in desert areas should deserve special attention. The Mongolian Gobi Desert hosts a unique mammal community adapted to this environment. Only recently, mammal communities in the Gobi ecosystem (Augugliaro et al. 2019; Mas-Carrió et al. 2021), as well as observations on their temporal activity patterns (Nasanbat et al. 2021), have been described overall. Previous studies conducted in the Gobi Desert were mainly focused on single species rather than on interactions between species (Sharma et al. 2014; Tumursukh et al. 2016). Nonetheless, information regarding the interaction between apex and meso-predators, as well as between apex predators and prey, remains scanty for this area.

Using camera-trapping data, we investigated the spatial and temporal interactions between mammalian species in the Great Gobi-A Strictly Protected Area (hereafter, GGA) with emphasis on the "Threatened" snow leopard *Panthera uncia* (McCarthy et al., 2017), local meso-predators, and potential prey species. Our purpose has been to gain preliminary insights into the interspecific interactions between mammalian species from an understudied arid part of the snow leopard range. In line with the "facilitation hypotheses" (Ferretti et al. 2021; Krofel et al. 2021; Rossa et al. 2021) we have assumed that the presence of larger predators may be beneficial for smaller ones in terms of scavenging opportunities, hence leading to both spatial and temporal overlap between species. We have also assumed that the presence of predators can be a disturbing event to potential prey, thus influencing its activity and spatial behavior (Rossa et al. 2021; Salvatori et al. 2021). The intra-guild predation theory dictates that the distribution of prey species is determined by food availability and dispersion, as well as safety from predation (Polis and Holt 1992). In the "Arms Race" between predators and prey, the prey must be 1 step ahead of the predator to make the system stable. In fact, the cost of a mistake is clearly greater for the prey which competes to survive (Krebs and Davies 1987). According to this theory, we expected a low temporal overlap of activity between predators and prey, assuming that the latter may adjust their behavior to minimize encounters with the former.

Materials and Methods

Study area

Our study area (N 42°89'; E 99°66'; datum WGS84) is located in the GGA (Mongolia) (Supplementary Material 1). The GGA extends over 44,190 km² and encompasses narrow valleys, mountains, dry riverbeds, and several waterholes (Nasanbat et al. 2021). Overall, the area is characterized by scarcely vegetated dales, in which elevations range from 525 to 2,683 m above sea level (Nasanbat et al. 2021). Climate is arid with just a few snowfalls during winter, while precipitations are scarce (on average 60 mm/year, with annual variations ranging from 30 to 140 mm) and mostly concentrated between July and August (Nasanbat et al. 2021).

The area has been protected since 1975, mainly because of the presence of iconic and threatened mammals, such as

the wild Bactrian camel *Camelus ferus*, the brown bear *Ursus arctos*, the snow leopard, the goitered gazelle *Gazella sub-gutturosa*, the argali sheep *Ovis ammon*, and the Asian wild ass *Equus hemionus* (Nasanbat et al. 2021). Besides these globally threatened species, other mammalian species are the Eurasian lynx *Lynx lynx*, the gray wolf *Canis lupus*, the red fox *Vulpes vulpes*, and the Siberian ibex *Capra sibirica* (Nasanbat et al. 2021).

The area is almost uninhabited except for several family units, and the soldiers living in and around the customs bordering China. Livestock is bred by a few households and 2 soldiers' families living outside the customs precinct.

Data collection

From December 2018 to February 2019, that is, in the winter months, we deployed 94 camera traps (38 HCO Scout Guard, 37 Reconyx, 10n Browning, 5 IR Plus, 1 Bushnell, 1 Cuddleback, 1 Wild Vison, and 1 Big Blue) covering an area of 1,090 km². The size of the area was calculated through the Minimum Convex Polygon (MCP 100%) encompassing all camera-trap locations (Supplementary Material 1). Cameras were left unchecked for the duration of the study period to prevent human scent from being detectable by wildlife species. The sampling design was conceived specifically to detect carnivore species, with a special focus on the snow leopard. We paired 2 cameras on each site ($N = 47$), with a spacing of approximately 3 km between sites (Jackson et al. 2006). Cameras were placed at elevations spanning from 1,530 to 2,099 m and mainly along narrow passes and a few ridges, as we could find no clear sign of marking sites. Camera traps were stabilized with stones at a height of 30–50 cm above the ground. Neither baits nor lures were used at any site. Cameras were active over for 24 h and set to take a sequence of 5 pictures per capture, recording date, and time stamps. We sampled the area between the mountain foothills and higher elevations because wildlife trails were either absent or hardly detectable in the plains surrounding our study area (except for water sources), thus making it difficult the placement of camera traps. Furthermore, topographic gradients were too small to determine how these affect the species' presence.

Data analyses

Detection events and Relative Abundance Index

Mammal identifications, date, and time of detections from camera traps were managed through the open-access Software Wild.ID (Bolger et al. 2012). We filtered the images using 30-min intervals between pictures (hereafter, detection events) of the same species at the same site (Meek et al. 2014). The Relative Abundance Index (RAI) and the naïve occupancy for detected species (MacKenzie et al. 2002; O'Brien 2011) were calculated using the R Package "vegan" (Oksanen et al. 2019). We determined the RAI as the number of detection events per 100 trap nights and divided by the sampling effort:

$$RAI_i = detection\ events \times 100\ camera\ trap\ nights/sampling\ effort$$

where i is the ith species, detection events count the number of independent records for a given species, 100 camera trap nights represent the unit of standardization to compare data with other studies, and sampling effort is the total number of camera-trap days. Statistical analyses were all run using the Software R (v. 4.1) (R Development Core Team 2021).

Multi-species occupancy and co-occurrence models

To assess species occupancy and co-occurrence at a site, we ran multi-species occupancy and co-occurrence models (MSOMs) (Rota *et al.* 2016) implemented in the "unmarked" package (Fiske and Chandler 2011). An interval of 5 days was considered to define occasions in MSOMs. MSOM analyses were focused only on snow leopard and red fox. Due to their low detection rates, we excluded from our analyses the other carnivore species, that is, gray wolf, Eurasian lynx, and Pallas's cat (see Supplementary Material 2). When modeling different species in the same multi-species estimator, the estimator assumes that more species are expected to respond in similar ways to variations in the same covariate (Rota *et al.* 2016). Foxes are known to "follow" larger predators and take advantage from carcass remains. This was observed in both fox–wolf (e.g., Ferretti *et al.* 2021) and fox–snow leopard interactions (e.g., Krofel *et al.* 2021). Therefore, we believe that our assumption can be considered reasonable. Camera traps were placed mainly in locations where the probability to record snow leopards was the highest. Therefore, because these locations may be less suitable for prey species, we chose to discard their records from the occupancy analysis. Conversely, activity may be considered relatively independent from the terrain used and, therefore, indications on activity rhythms may be inferred (e.g., Salvatori et al. 2021, 2022).

Covariate layers were prepared using ArcGIS (v. 10.5). We downloaded the Digital Elevation Model (DEM) Shuttle Radar Topography Mission (SRTM v. 4.1) at 3-arc seconds resolution. Overall, we considered 5 metrics as suitable topographic covariates potentially affecting both snow leopard and red fox occupancy and co-occurrence at camera sites: (1) Topographic Position Index (TPI), defined as the difference between a central pixel and the mean of its surrounding cells (Salinas-Melgoza *et al.* 2018); (2) density of riverine areas; (3) Topographic Ruggedness Index (TRI), which express the amount of elevation difference between adjacent cells of a DEM (Riley *et al.* 1999); (4) Compound Topographic Index (CTI), which provides a measure of soil moisture (Moore *et al.* 1991); and (5) elevation.

From the DEM, we calculated TPI, CTI, and TRI using the Geomorphometry and Gradients Metrics Toolbox (Evans *et al.* 2014) in ArcGIS, applying a focal mean equal to the average length of the edges of the Minimum Spanning Tree connecting the sites (i.e., 2,840.75 m). The density of riverine areas was calculated starting from the shapefile of Mongolian rivers downloaded from Divagis (https://www.diva-gis.org/gdata), at the same focal radius.

Before being included in the MSOMs, multicollinearity among covariates was tested through the Variance Inflation Factor (VIF) (Fox and Monette 1992) using the "usdm" package (Naimi *et al.* 2014). We considered VIF ≥3 (Hair 2014) as a threshold value to define those covariates presenting collinearity problems. In our case, TPI showed a VIF >3 and hence was dropped from the model (Gareth *et al.* 2014; Peter and Bruce 2017).

For both snow leopard and red fox, we formulated specific assumptions for the effects of covariates in terms of occupancy and detection (Table 1). Because of the complexity of MSOMs, which allow to express single-species occurrence and co-occurrence (Rota *et al.* 2016), we followed the method proposed by Twining *et al.* (2020) and divided the analysis into 2 steps. In the first step, we ran MSOMs to test the effect of each covariate on the occupancy probability while

maintaining the detection constant. In the second step, we ran 4 (1 per covariate) different single-species occupancy models (SSOMs) (MacKenzie *et al.* 2002) per carnivore species (i.e., snow leopard and red fox) and then calculated the outcome of the single covariates on detection probabilities while keeping the occupancy constant.

MSOMs were implemented considering the density of riverine areas, TRI, CTI, and elevation as site covariates influencing occupancy, with the sampling effort as detection covariate, to estimate carnivore species occupancy and co-occurrence. Before being included in the model, all site covariates were standardized to improve the maximum-likelihood estimates (Chandler 2017). We first created a maximal model using the function *occuMulti* (Rota *et al.* 2016) in which the additive effect of the selected covariates and the interaction between species (i.e., co-occurrence) were included. The goodness-of-fit (i.e., absence of overdispersion) of the most parametrized model was tested using the *parboot* function implemented in the "unmarked" package (Fiske and Chandler 2011), which reproduces the parametric bootstrap method for fitted models with 1,000 replicates. Afterwards, the c-hat value was calculated as the ratio between the observed chi-square statistic and the average of the statistics obtained from the simulations. If the resulting value is not markedly different from 1, then the absence of overdispersion can be inferred. Model simplification was done based on the *principle of parsimony*, which relies on the removal of those explanatory variables which do not produce a significant effect over the response variable. The selection of the best model was then done using the Akaike Information Criterion (Burnham and Anderson 2002). The significance of the co-occurrence between interacting species was assessed based on the *P*-value obtained from the best model.

With regards to the conditional occupancy, we considered four different scenarios: In the first and second scenarios, the red fox was the conditioning effect (i.e., presence of snow leopard vs. presence/absence of red fox), while in the third and fourth scenarios, the snow leopard was the conditioning effect (i.e., presence of red fox vs. presence/absence of snow leopard).

Activity patterns and temporal overlap

We used the Software Moonrise (v. 3.5) to determine the exact sunrise and sunset times. Given the small differences in sunrise times (approximately 1 h), we did not account for this minor bias which is negligible for a single-season data collection (Rowcliffe *et al.* 2014). Although 20–30 detection events have been previously recommended as a reliable lower detection threshold in studies of activity patterns (Ridout and Linkie 2009; Lashley *et al.* 2018), Lashley *et al.* (2018) have suggested that 14–15 detections may still be an acceptable low benchmark for this kind of analyses. We have analyzed the activity patterns and overlaps only in those species for which more than 10 detection events were recorded (thus including argali, 14 detections, and ibex, 15 detections). In fact, our aim has been to provide a preliminary picture of activity patterns on understudied species, in a remote environment.

Activity patterns were analyzed by fitting kernel density estimates (Linkie and Ridout 2011). For each species, we performed the Hermans–Rasson test (Landler *et al.* 2019) and used the function *HR_test* in the package "CircMLE" (Fitak and Johnsen 2020), to assess whether a random activity pattern was exhibited over a circadian cycle. Temporal overlaps

Table 1 Assumptions on the effects of the selected topographic covariates on the probability of occupancy (Ψ) and detection (P) for both snow leopard and red fox in the Great Gobi-A Strictly Protected Area (GGA)

Species	Topographic covariates	Predicted influence on Ψ and P	Rationale	Supporting literature
Panthera uncia	TRI	Neutral	Higher snow leopard's occupancy and detections are frequently associated to highly rugged terrain and higher elevations. However, wildlife trails were hardly detectable in the lowlands surrounding our study area. Therefore, cameras were placed between the mountain foothills and higher elevations (from 1,530 to 2,099 m), where the terrain ruggedness is mostly homogeneous along the elevation gradient.	McCarthy et al. (2005); Bai et al. (2018); Watts et al. (2019); Sing et al. (2020)
	Elevation	Neutral		
	Riverine	Positive	Stream availability is a determinant of snow leopard habitat selection. Moreover, because rainfalls in the GGA are rare and mostly concentrated from July to August water resources are of a special importance.	Atzeni et al. (2020); Din et al. (2021); Nasanbat et al. (2021)
	CTI	Positive		
Vulpes vulpes	TRI	Neutral	Rugged areas may constitute refuges for foxes to mitigate the effect of human hunting and/or interspecific competition. However, in our study site hunting is forbidden and the terrain ruggedness is mostly homogeneous along the elevation gradient.	Murdoch et al. (2007, 2016)
	Elevation	Neutral	Higher elevations may be detrimental for foxes especially during winter, where harsh climate conditions may limit the access to food resources. Nevertheless, in our study area snowfalls are rare.	Lindström (1994); Weber and Meia (1996); Cagnacci et al. (2004); Nasanbat et al. (2021)
	Riverine	Positive	Riparian zones are important ecological corridors and suitable areas for the red fox and its main prey (e.g., Tolai hare, micro-mammals). Moreover, because the red fox is not an arid-adapted species, the presence of water should be important for its survival.	Jędrzejewski and Jędrzejewska (1992); Murdoch et al. (2007); Sanchez-Montoya et al. (2016); Elmeros et al. (2018); Jackowiak et al. (2021); Nasanbat et al. (2021)
	CTI	Positive		

The effect of each covariate was simultaneously predicted on both Ψ and P following the method proposed by Twining et al. (2020). Because of the complexity of Multi-Species Occupancy and co-occurrence Models (MSOMs), they suggest dividing the analysis into two steps using Single-Species Occupancy Models (SSOMs) and testing the effect of each covariate on Ψ while maintaining p constant, and vice versa. Abbreviations: TRI, Topographic Ruggedness Index; Riverine, Density of riverine areas; CTI, Compound Topographic Index.

between carnivores and between carnivores and potential prey were estimated using the coefficient of overlap Δ, defined as the area under the 2 kernel density curves, varying between 0 and 1 (respectively, no overlap and full overlap; Ridout and Linkie 2009). We adopted the estimator Δ_1, which is considered as the most robust estimator for sample sizes lower than 50 detections (Meredit and Ridout 2021). The 95% confidence interval for the overlap coefficients was obtained by bootstrapping 1,000 samples from estimated probability density functions (Meredith and Ridout 2021). The analysis of species activity and the overlap between species pairs was performed using the R package "Overlap" (Linkie and Ridout 2011). Furthermore, to compare activity patterns between species pairs, we performed a probability test to assess whether 2 sets of circular observations belonged to the same distribution using the function *compareCkern* in the package "activity" (Rowcliffe 2019).

Results

Species detection and Relative Abundance Index values

The sampling effort was 3,274 camera-trap days (mean ± *SE* = 69.66 ± 1.33 per camera) recording a total of 331 detection events of wild mammals. Among carnivores, the red fox was the most frequently detected species (RAI = 5.71) followed by the snow leopard (RAI = 0.77) (Supplementary Material 2). Among herbivores, the Tolai hare was the most frequently detected species (RAI = 1.64), followed by the Asian wild ass (RAI = 0.86), the Siberian ibex (RAI = 0.46), and the argali (RAI = 0.43) (Supplementary Material 2).

Occupancy and co-occurrence between snow leopard and red fox

Considering the overall number of monitoring sites (*N* = 47), the snow leopard was detected at least once on 11 sites (with a minimum of 9 individuals identified through their coat patterns, cf. Jackson *et al.*, 2006), whereas the red fox was detected at least once on 23 sites. From MSOM selection, the best model was the one in which the additive effect of all the topographic covariates was considered per each species (Table 2). The c-hat value of the most complex model was equal to 1.02, which in turn indicates the absence of overdispersion.

The predicted snow leopard occupancy was not affected by any covariate: density of riverine areas ($\beta = -45.10 \pm 38.71$ *SE*, $z = -1.16$, $P = 0.24$), TRI ($\beta = 44.15 \pm 44.50$ *SE*, $z = 0.99$, $P = 0.32$), CTI ($\beta = -81.01 \pm 67.79$ *SE*, $P = 0.23$), and elevation ($\beta = -92.12 \pm 79.34$ *SE*, $P =$

0.24) (Table 3). However, the snow leopard detection probability was affected by both the density of riverine areas ($\beta = 0.77 \pm 0.29$ *SE*, $z = 2.60$, $P = 0.009$) and TRI ($\beta = 0.92 \pm 0.26$ *SE*, $z = 3.58$, $P < 0.001$) (Table 3). The predicted red fox occupancy was affected by the TRI ($\beta = -1.11 \pm 0.52$ *SE*, $z = -2.16$, $P = 0.03$) (Table 3, Figure 1) while the detection probability was influenced by both the density of riverine areas ($\beta = 0.39 \pm 0.10$ *SE*, $z = 4.00$, $P < 0.001$) and elevation ($\beta = -0.86 \pm 0.11$ *SE*, $z = -7.65$, $P < 0.001$) (Table 3).

Estimates of covariate coefficient from the MOSM and SSOMs have been summarized in Table 3. Despite the MSOM showing weakly significant pairwise co-occurrence ($\alpha = 2.12 \pm 1.11$ *SE*, $z = 1.90$, $P = 0.06$; Table 3) between snow leopard and red fox, the results obtained from the predicted conditional occupancy of each species, based on the presence/absence of the interacting species, showed that the presence/absence of the red fox (i.e., first and second scenarios) did not affect the probability of occupancy of the snow leopard (red fox present: $\beta = 0.47 \pm 0.34$ *SE*, CI95% = 1.74e–03 – 0.99; red fox absent: $\beta = 0.46 \pm 0.34$ *SE*, CI95% = 2.78e–05 – 0.99) (Supplementary Material 3). Conversely, the presence/absence of the snow leopard (i.e., third and fourth scenarios) determined a higher occupancy probability of the red fox when the snow leopard is present ($\beta = 0.71 \pm 0.15$ *SE*, CI95% = 0.34 – 0.90) than in its absence ($\beta = 0.30 \pm 0.16$ *SE*, CI95% = 0.11 – 0.68) (Supplementary Material 3).

Overlap of activity patterns

The snow leopard showed a nonsignificant 3-modal activity pattern (Hermans–Rasson test, $P = 0.33$), with 2 smaller peaks before sunrise, and falls around mid-day and 10:00 PM (Supplementary Material 4). Conversely, the red fox showed activity patterns significantly different ($P < 0.001$) from a random distribution, according to the Hermans–Rasson test (Supplementary Material 4). This canid exhibited a low activity in the early noon, with a peak slightly after the activity peak of the snow leopard, just once dark started (7 PM) (Supplementary Material 4). Amongst the potential prey, the Siberian ibex and the argali were mainly diurnal with peaks of activity around mid-day, whereas the Asian wild ass and the Tolai hare were more nocturnal (Supplementary Material 4).

The use of the diel cycle did not differ significantly between snow leopard and red fox (Figure 2). In fact, the index of overlap was moderate for these carnivores (Figure 2). The activity rhythms of the snow leopard and that of any potential prey were all significantly different, hence suggesting no significant temporal overlap between species (Figure 3). Indeed, both the

Table 2 MSOMs with relative topographic covariates considered per species

Model ID	Covariates considered per species		-2logLik	K	AIC	ΔAIC	*ωi*
	Panthera uncia	*Vulpes vulpes*					
1	Ψ(~*Riverine+TRI+CTI+Elevation*), p(~1, ~1)	Ψ(~*Riverine+TRI+CTI+Elevation*), p(~1, ~1)	1,195.46	13	1,221.46	0.00	0.88
2	Ψ(~CTI+Elevation), p(~1, ~1)	Ψ(~*Riverine+TRI*), *p*(~1, ~1)	1,208.6	9	1,226.62	5.16	0.07
3	Ψ(~Elevation), p(~1, ~1)	Ψ(~*TRI*), *p*(~1, ~1)	1,213.5	7	1,227.45	5.99	0.04
4	Ψ(~*Riverine+CTI+Elevation*), p(~1, ~1)	Ψ(~*Riverine+TRI+Elevation*), *p*(~1, ~1)	1,207.8	11	1,229.75	8.29	0.01

The interaction between species was denoted by *p*(~1, ~1) and the best model was *italicized*.
Abbreviations: Riverine, Density of riverine areas; TRI, Topographic Ruggedness Index; CTI, Compound Topographic Index; *logLik*, log-likelihood; *K*, number of parameters; AIC, Akaike Information Criterion, *ωi*, Akaike's weight.

Table 3 Covariate coefficient estimates from the MSOM, and SSOMs for snow leopard *Panthera uncia* and red fox *Vulpes vulpes* from camera-trap surveys in the Great Gobi-A Strictly Protected Area (GGA)

Species	Function	Parameter	Estimate	SE	z	P (>|z|)	
Panthera uncia	Ψ	(Intercept)	–22.89	17.95	–1.28	0.20	
		(Riverine)	–45.10	38.71	–1.17	0.24	
		(TRI)	44.15	44.50	0.99	0.32	
		(CTI)	–81.01	67.80	–1.20	0.23	
		(Elevation)	–92.12	79.34	–1.16	0.25	
	P	*(Intercept)*	–4.67	0.40	–11.50	< 0.001	***
		(Riverine)	0.77	0.30	2.60	< 0.01	**
		(Intercept)	–4.67	0.39	–11.89	< 0.001	***
		(TRI)	0.92	0.26	3.58	< 0.001	***
		(Intercept)	–4.16	0.35	–11.96	< 0.001	***
		(CTI)	–0.52	0.54	–0.95	0.34	
		(Intercept)	–4.13	0.48	–8.61	< 0.001	***
		(Elevation)	–0.20	0.39	–0.51	0.61	
Vulpes vulpes	Ψ	(Intercept)	–1.03	0.61	–1.69	0.09	•
		(Riverine)	0.93	0.59	1.59	0.11	
		(TRI)	–1.12	0.52	–2.16	0.03	*
		(CTI)	0.06	0.43	0.14	0.89	
		(Elevation)	1.03	0.68	1.52	0.13	
	P	*(Intercept)*	–2.74	0.11	–24.80	< 0.001	***
		(Riverine)	0.39	0.10	4.00	< 0.001	***
		(Intercept)	–2.64	0.10	–25.67	< 0.001	***
		(TRI)	–0.25	0.15	–1.74	0.08	•
		(Intercept)	–2.65	0.10	–25.57	< 0.001	***
		(CTI)	–0.32	0.18	–1.85	0.06	•
		(Intercept)	–3.03	0.14	–21.96	< 0.001	***
		(Elevation)	–0.86	0.11	–7.65	< 0.001	***
Panthera uncia–Vulpes vulpes		Pairwise co-occurrence	2.12	1.11	1.90	0.06	•

Occupancy probability was indicated with Ψ while detection probability with *P*.
Levels of significance: • = 10%, * = 5%, ** = 1%, *** = 0.1%.
Abbreviations: Riverine, Density of riverine areas; TRI, Topographic Ruggedness Index; CTI, Compound Topographic Index.

Siberian ibex and the argali showed a sharp peak of activity around noon, when the snow leopard was mainly inactive (Figure 3).

Discussion

The RAI analyses revealed that the snow leopard was the apex predator most frequently detected in our sampling area, showing a consistently higher number of detections compared to other carnivores such as the grey wolf and the Eurasian lynx. Nasanbat *et al.* (2021) recorded higher detection rates of wolves, but their study was oriented toward the whole mammal community and covered a wider variety of habitats across the GGA. Conversely, our sampling design was mainly tailored to detect the snow leopard in its prime habitat within the same environment, which in turn may have affected our results. The red fox was the most frequently detected meso-predator, thus confirming the ecological flexibility which allows this species to colonize even harsh habitats (Hoffmann and Sillero-Zubiri 2021), including one of the most arid environments in the world such as the Gobi Desert (Nasanbat *et al.* 2021). On the contrary, the Pallas's cat was recorded only once, thus confirming its low detection rate previously suggested for the GGA (Nasanbat *et al.* 2021). The desert environment may not be an optimal habitat for this species, because of the local scarcity of prey or, rather, a sampling design aimed specifically at detecting this elusive species may be required (Anile *et al.* 2021).

Among herbivore species, the Tolai hare showed the highest number of detections, in contrast to Nasanbat *et al.*'s (2021) who recorded it for the Asian wild ass. This inconsistency may depend on the fact that Nasanbat *et al.*'s study (2021) was conducted at waterholes, which could have favored the detection of species strictly dependent on water availability such as the Asian wild ass (Kaczensky *et al.* 2010; Payne *et al.* 2020). Not surprisingly, the lowest number of detections was recorded for the Bactrian camel and the goitered gazelle, which are not mountain-dwelling species (cf. Nasanbat *et al.* 2021). In contrast to our results revealing almost the same number of detections for both species, Nasanbat *et al.* (2021) found a considerably higher number of records for the Bactrian camel. In fact, placing cameras near waterholes may favor the detection of camel groups forming there to drink. Furthermore, in our study, the sites where camera traps were placed do not correspond to the optimal habitat for these ungulates (Schaller 2020), especially during the cold months.
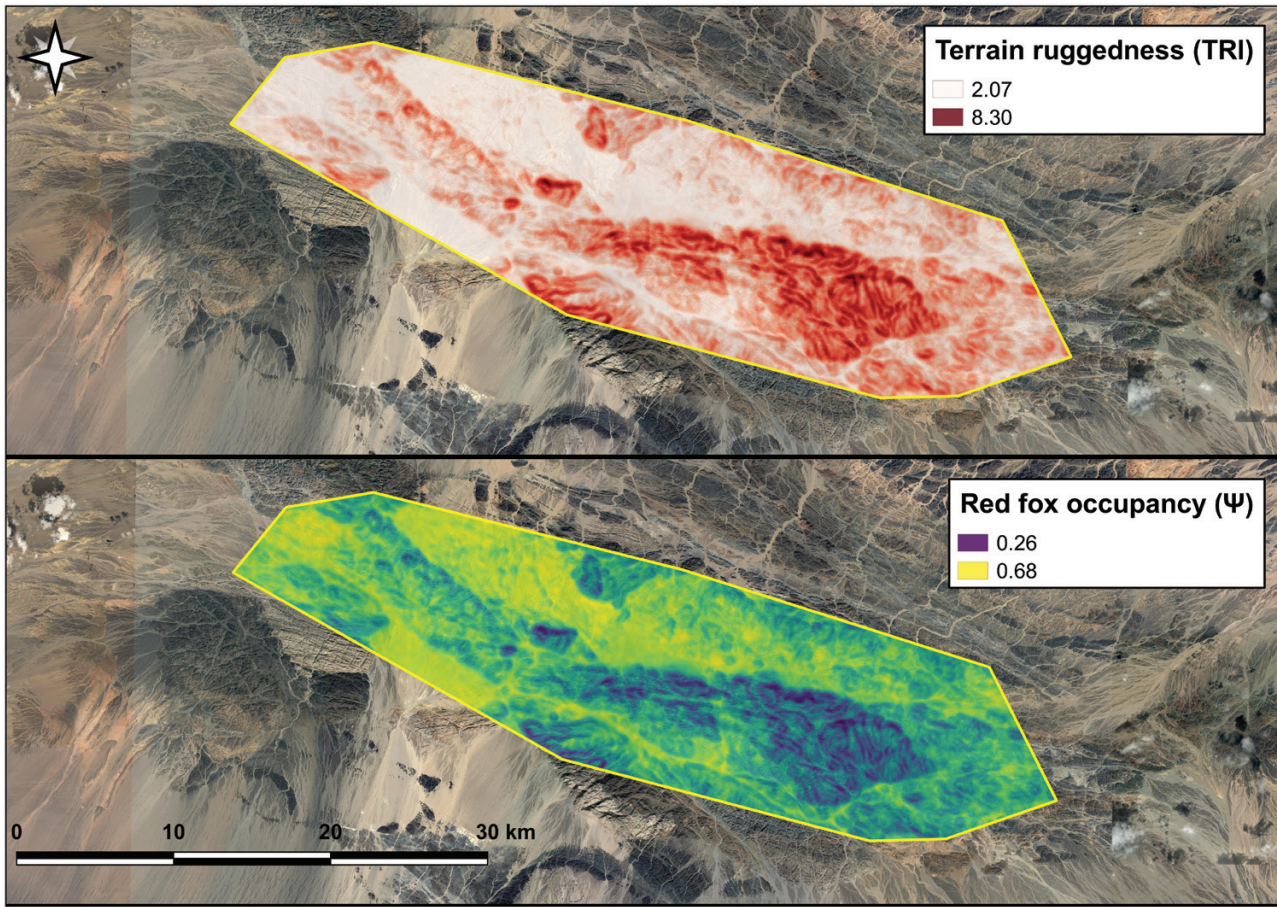
Figure 1 Predicted occupancy probability (Ψ) for the red fox in relation to the terrain ruggedness, expressed through the Topographic Ruggedness Index (TRI). The MCP identifies the area covered by camera trap locations.
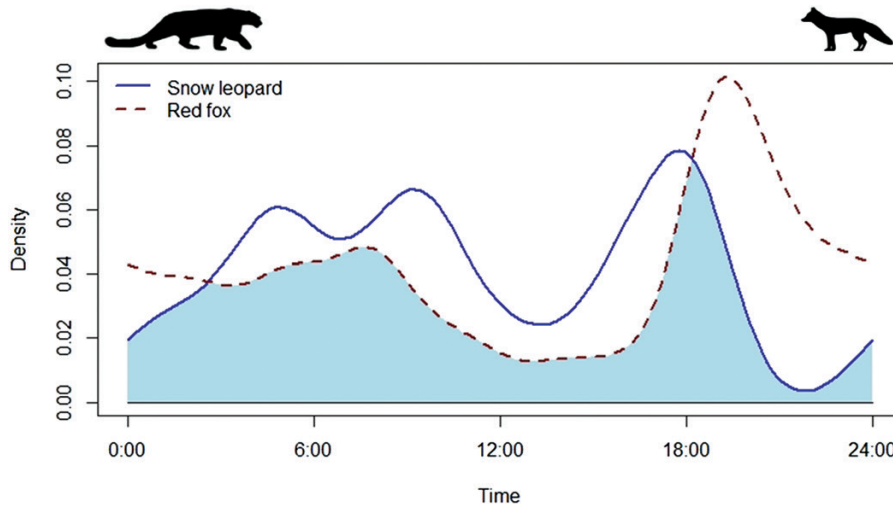

Figure 2 Activity overlap of snow leopard and red fox.

Despite we obtained a higher number of detections in response to terrain ruggedness, our occupancy analysis has revealed that neither the terrain roughness nor elevation significantly affected the snow leopard terrain use, thus matching our initial hypotheses. Terrain ruggedness is widely considered as an important landscape attribute influencing snow leopard habitat use (e.g., McCarthy *et al.* 2005; Bai *et al.* 2018; Watts *et al.* 2019; Sing et al. 2020). In spite of this consideration, in our study area, the lack of statistical significance may be attributable to the homogeneity in terms of terrain ruggedness, from foothills to higher elevations, which may allow the snow leopard to occur across different elevations. Furthermore, also the apparently low local wolf density may exert a key role. In fact, a study conducted in Kyrgyzstan
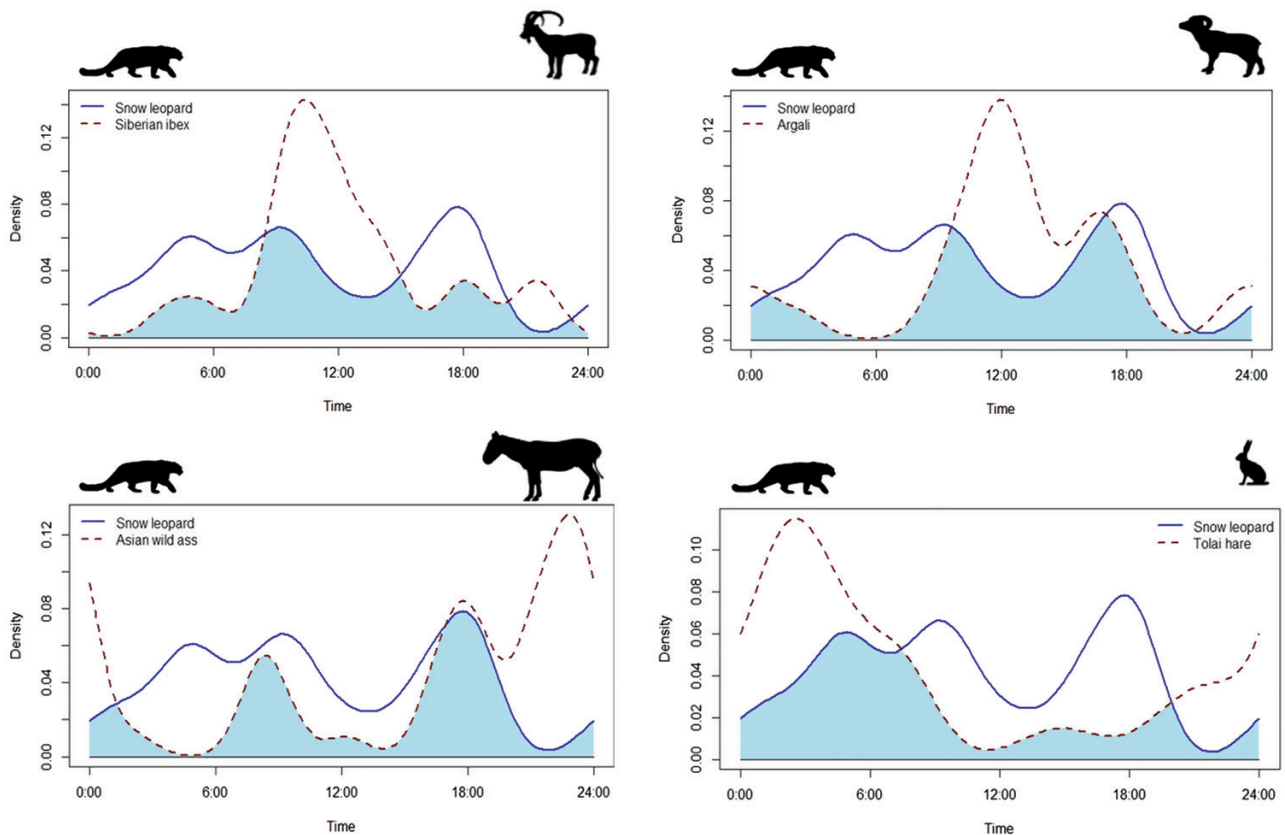
Figure 3 Activity overlap of snow leopard and potential prey species.

showed a clear difference in terms of terrain used by snow leopards (ridges and ledges) and wolves (valley bottoms), with the latter probably affecting the habitat selection of the former: In fact, a pack of wolves should be able to easily kill a snow leopard on a flat or undulating terrain (Lovari *et al.* In press).

In spite of the higher snow leopard detections in response to the density of riverine areas, our initial assumption on the snow leopard positive selection (in terms of occupancy probability) of river density and/or wet areas (cf. Din *et al.* 2021) was not met, suggesting that this species used these areas in proportion to their availability (as postulated in Atzeni *et al.* 2020). In fact, our data were collected over the winter period, with frequent snowfalls recorded by our camera traps. The presence of snow may thus have fulfilled the snow leopard's water requirements (Schaller 2012; Kikuchi *et al.* 2020). Second, water is generally scarce in riverbeds, because of the arid environment. Thus, snow leopards may have used alternative water sources as observed previously in this arid environment (e.g., waterholes; Nasanbat *et al.* 2021).

Our hypothesis on the neutral effect of terrain ruggedness on red fox presence was confirmed only for what concerns the number of detections. In fact, our results have revealed that terrain ruggedness influences negatively the red fox terrain use. In some Mongolian areas, this species has faced a strong hunting pressure (Wingard and Zahler 2006). Where intense human hunting occurs, rugged and/or rocky areas may increase the red fox occupancy as refuge areas (Murdoch et al. 2007, 2016). Furthermore, a fair availability of hiding places could be beneficial to the red fox as these decrease the risk of being killed by larger predators (e.g., wolves and snow leopards; Murdoch et

al. 2007, 2016; Samelius *et al.* 2022). However, because hunting is forbidden in the GGA and we obtained a poor number of wolf detections, the negative effect exerted by the rugged terrain on red fox presence may depend on some other local factors, perhaps a low prey density (Murdoch *et al.* 2016). Rugged areas may benefit the red fox only in contexts characterized by high human pressure and/or high densities of competitors. Our initial hypothesis on the neutral effect of elevation on the presence of this meso-predator is supported, as no significant effects were obtained for this environmental covariate. This result is in contrast with other studies (Lindström 1994; Weber and Meia 1996; Cagnacci *et al.* 2004) postulating that higher elevations (especially during the coldest seasons) might be avoided by the red fox. In fact, a deep snow cover could hamper the species movements and possibly determine the scarcity of food resources. In our study area, mild snowfalls in the coldest season may have played a key role. In fact, a thin snow layer in winter could have allowed the red fox to use higher elevations. Contrary to our initial assumption, the red fox occupancy was not influenced by the presence of high riverine density and/or wet areas, despite red foxes being reported to depend on water resources (Murdoch *et al.* 2007). Our results are in contrast with those presented by Roshier *et al.* (2021), who suggested that the red fox habitat selection was significantly affected by distance to water bodies. In our study area, foxes may have satisfied their water intake by utilizing waterholes (Nasanbat *et al.* 2021) as the arid environment determines scarce water presence in riverbeds. Additionally, foxes inhabiting this arid terrain might have used water-rich food items (e.g., insects) to compensate for water limitations (Dell'Arte and Leonardi 2009; Misher and Vanak 2021).

With regards to the co-occurrence of snow leopard and red fox, our findings revealed a difference in terms of site use, for example, the red fox occupancy was strongly and negatively influenced by terrain ruggedness. Conversely, terrain ruggedness did not influence the snow leopard habitat use. Low-productivity landscapes generally host less biodiversity (Mann *et al.* 2015). Arid environments, such as the Gobi Desert, should be included in this category since the harsh climate and unfavorable geo-ecological conditions can negatively influence species abundance, at least for several mammalian species (Augugliaro *et al.* 2019). We speculate that species inhabiting these areas (including apex and meso-predators) may adopt comparable behavioral strategies to best cope with the challenges imposed by the environment. In this sense, both the snow leopard and the red fox have shown similar spatiotemporal habits according to their ecological needs (e.g., search for food) and to best cope with unfavorable terrain conditions. Nevertheless, the positive spatiotemporal relationship between snow leopard and red fox may also be linked to the advantages that the latter may obtain overlapping with the former. In fact, the red fox may meet its dietary requirements by scavenging carcasses of larger predators' kills (Murdoch *et al.* 2010; Wang *et al.* 2014; Ferretti *et al.* 2021; Rossa *et al.* 2021), although this strategy may be a "high risk, high gain" one (Samelius *et al.* 2022; Vipin et al. 2022).

The snow leopard was the only species showing an apparently nonsignificant 3-modal activity pattern. This result is in contrast with those found by Salvatori *et al.* (2021) in the Mongolian Altai, who observed that snow leopards were mainly active during the night. Different levels of anthropogenic disturbance between the Altai (Augugliaro *et al.* 2020) and the GGA, where human presence is negligible, may have determined these differences in activity patterns. However, Salvatori *et al.* (2021) monitored a larger number of sites (*N* = 216) and the snow leopard was detected in 81 of them. Therefore, the different number of detections suggests that more data are needed to allow a proper comparison between studies.

The "Arms Race" hypothesis dictates that the evolution of improved abilities of predators to catch prey triggers a co-evolutionary response in prey, which, in turn, improves their abilities to escape from predators. Similarly, the evolution of improved escape abilities in prey determines increased capture abilities in predators (Abrams 1986; Wilson *et al.* 2018). Following this evolutionary concept, prey species can modify their behavior to reduce the likelihood of encounters with predators (Rossa *et al.* 2021). Our findings suggest that both the ibex and the argali showed 1 sharp peak of activity around mid-day, when the snow leopard was the least active. The diet of the snow leopard is mainly composed of mountain ungulates (Lovari *et al.* 2013) and, among these, the Siberian ibex is the most frequently reported prey in Mongolia (Mallon *et al.* 2016). As to the argali, Shezad et al. (2012) reported the presence of this species in snow leopard scats in Mongolia. Our data would suggest that these herbivores may have learned to be the most active when the probability of meeting a snow leopard is the least (cf. Salvatori *et al.* 2021). Accordingly, Nasanbat *et al.* (2021) found a low temporal overlap between these species in the use of waterholes, in the GGA. As far as the Tolai hare is concerned, this lagomorph showed no temporal overlap with the snow leopard. However, snow leopard predation on Tolai hares has been rarely reported (Chundawat and

Rawat 1994; Lhagvasuren and Munkhtsog 2000; Bagchi and Mishra 2006). Furthermore, the preferred prey species for the snow leopard weights on average 55 kg, while the preferred weight range spans from 36 to 76 kg (Lovari *et al.* 2013; Lyngdoh *et al.* 2014), although the second prey mass category ranges between 2 and 26 kg (Lovari *et al.* 2013), which would include the Tolai hare although barely (Supplementary Material 2). We suggest that the absence of temporal overlap between snow leopard and Tolai hare may depend on the Tolai hare modulating its activity to reduce encounters with other potential predators (e.g., red fox and Eurasian lynx), rather than with the snow leopard (Murdoch *et al.* 2010). Mallon *et al.* (2016) reported 2 studies (Bannikov 1954; Dash *et al.* 1977) indicating that the Asian wild ass may occasionally fall prey to the snow leopard. Nevertheless, considering the snow leopard's preferred weight range for prey species (i.e., 36–76 kg) (Lovari *et al.* 2013; Lyngdoh *et al.* 2014) and since the Asian wild ass is far beyond that (Supplementary Material 2), it seems unlikely that the Asian wild ass may adjust its activity rhythms to avoid direct encounters with the snow leopard. Nasanbat *et al.* (2021) recorded a temporal overlap between Asian wild ass and snow leopard, although these results were affected by camera-trap sites close to water holes. Conversely, in the Great Gobi B (GGB), the Asian wild ass is reported to fall prey to the wolf (Feh *et al.* 2001) and it also happens in the GGA (Nasanbat *pers. comm.*). In spite of the few detections we obtained, the wolf is present in the region (Nasanbat *et al.* 2021) and one could assume that the Asian wild ass tends to reduce the risk of encounters with wolves, a cursorial predator who lives in packs, rather than with the solitary snow leopard.

Our data suggest that Siberian ibex and argali may modulate their behavioral activity to avoid direct encounters with the snow leopard. At the same time, the inconsistency in terms of activity overlap between snow leopard and both Asian wild ass and Tolai hare is most likely driven by the tendency of prey to modulate their activity rhythms to avoid other predators (e.g., wolf for the Asian wild ass; Eurasian lynx and red fox for the Tolai hare), since both species are far from the preferred snow leopard's weigh range for prey species (Lovari *et al.* 2013; Lyngdoh *et al.* 2014). Our findings also have suggested that the presence of an apex predator may not be a necessarily negative event for a meso-predator, for example, through the latter scavenging from the former's prey, which may turn crucial in a poorly productive habitat such as the GGA. In spite of these considerations, we are aware that the number of detections (especially for some prey species) was low compared to the minimum suggested to obtain reliable results (Lashley *et al.* 2018). Predators may have adopted similar behavioral strategies to best cope with their ecological needs and the harsh environmental conditions imposed by the Gobi Desert. Further research based on a longer time period, estimation of local abundance of wild prey, as well as diet analyses of local predators, should provide further insights.

Acknowledgments

Conflict of interest

The authors declare they have no conflict of interests.

Author contributions

MF, LA, SL, and CA conceived the work; CA supervised the research and acquired funding; CA and BN collected the data in the field; MF, LA, CA, and GB analyzed the data and produced figures; MF wrote the first draft of the manuscript; CA, LA, SL, and FC revised and edited the first draft; all authors contributed to review the final version of the manuscript.

Supplementary Material

Supplementary material can be found at https://academic.oup.com/cz.

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