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Research article

Who's the boss? Understanding the spatial relationship between snow leopard and Eurasian lynx in southern Mongolia

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Interspecific competition, a fundamental ecological process characterized by negative interactions between species, plays a vital role in shaping ecological communities. Despite the co-occurrence of the snow leopard *Panthera uncia* and the Eurasian lynx *Lynx lynx* across vast landscapes in Asia, their interactions remain poorly understood. In this study, we investigated how the presence of snow leopards affected site-use by lynx and whether the presence of snow leopards resulted in behavioral adaptations by the lynx. Between 2017 and 2022, we conducted camera trap-based surveys across six sites in southern Mongolia and evaluated species co-occurrence by snow leopards and lynx using the occupancy framework. We assumed snow leopards to be the dominant species while using topographical and land cover variables as covariates. Our results show that the presence of snow leopards influenced site-use by lynx, leading to a shift in space use when snow leopards were present. Specifically, lynx used the entire range of ruggedness and did not select for shrubby areas in the absence of snow leopards, whereas they avoided rugged areas and had a strong preference for shrubby areas when snow leopards were present. Our findings emphasize the influence a larger predator can have on the space use of a smaller predator, and how the presence of snow leopards can alter the space-use of lynx. Understanding these interactions and behavioral adaptations can be useful for developing effective conservation strategies in the region.

Keywords: competition, intraguild predation, *Lynx lynx*, occupancy, *Panthera uncia*

Introduction

Interspecific competition, defined as the negative effects of one or both species on another, is one of the most important processes determining the structure of

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natural communities (Case and Gilpin 1974, Connell 1983). Competition can be direct (interference or predation) or indirect (utilization of the same resources) and affect both individuals and entire populations (Creel 2001, Caro and Stoner 2003). Interference competition can be reduced, facilitating the coexistence of morphologically similar species, through behavioral mechanisms, particularly by spatial or temporal segregation (Schoener 1974, Donadio and Buskirk 2006, Ritchie and Johnson 2009). Competition among carnivores can limit the density and distribution of subordinate carnivores by kleptoparasitism, partial exclusion from preferred habitats, and direct killing (Letnic et al. 2009, Ritchie and Johnson 2009).

Intraguild predation (interspecific killing) is common among mammalian carnivores and may occur to remove a source of mortality for the killer or its offspring, to increase access to resources (reduce indirect competition), or as a source of food (predation) (Palomares and Caro 1999, Donadio and Buskirk 2006, Helldin et al. 2006). Such lethal interactions among carnivores can commonly be predicted by differences in body size, where the larger carnivore typically kills the smaller unless the smaller has the benefit of numbers (e.g. lions *Panthera leo* versus spotted hyenas *Crocuta crocuta*) (Donadio and Buskirk 2006, Periquet et al. 2015). Interspecific killing is common among species that are similar enough to utilize the same food sources, and where the smaller species is not large enough to pose a substantial threat to the larger species (Donadio and Buskirk 2006). In a review of interspecific killing in carnivores, the average weight ratio of killer to victim was 2.5 (Ritchie and Johnson 2009). While interspecific killing occurs, especially in felids, mustelids and canids (Palomares and Caro 1999), the indirect effects caused by the presence of a dominant carnivore can be stronger than the actual risk of mortality through behavioral adaptations to avoid intraguild predation in the subordinate carnivore (Creel and Creel 1996). Examples of such behaviors include altering habitat use or activity patterns that may produce a landscape of fear where the subordinate carnivore select patches where they have the highest likelihood of avoiding the dominant carnivore (Ritchie and Johnson 2009, Di Bitetti et al. 2010).

The snow leopard *Panthera uncia* is listed as ‘Vulnerable’ by the IUCN and found across the mountain regions of 12 countries in Asia, covering approximately 2 million km^2. Snow leopards are habitat specialists that prefer rugged mountain habitats and occur at altitudes of 900–4500 m a.s.l. (Fox et al. 2024). The average weights for adult females and males are 36 and 42 kg, respectively (Johansson et al. 2022). Snow leopards are known to prey predominantly on wild sheep and goats such as ibex *Capra sibirica*, bharal *Pseudois nayaur* and argali *Ovis ammon*, but also prey on domestic goats *Capra hircus*, sheep *Ovis aries* and yaks *Bos grunniens* (Lyngdoh et al. 2014, Mallon et al. 2016)

The Eurasian lynx *Lynx lynx (*hereafter lynx) has one of the largest distribution ranges of any of the medium-sized felids and is found across Europe, West, Central and East Asia (Sunquist and Sunquist 2002). The ecology and behavior of lynx are not well known in many Asian countries and population status and trends are uncertain with density estimates available for Turkey only (Avgan et al. 2014). Despite this, the lynx conservation status is listed as ‘Least concern’ on the global scale by the IUCN Red List (Breitenmoser et al. 2015). Similar to many medium and large carnivores, lynx occur at low densities and have large home ranges (Herfindal et al. 2005). Lynx are habitat generalists found in deciduous, mixed and coniferous forests, mixed forest-steppes, rocky-steppes, and montane forest ecosystems and pastures (Breitenmoser and Breitenmoser-Wursten 2008, Nagl et al. 2022). The average weights for adult lynx are about 17 kg for females and 20 kg for males (Sunquist and Sunquist 2002). Through most of the distribution range, lynx co-occur with other, larger carnivores, such as wolves *Canis lupus* and brown bears *Ursus arctos*. Lynx in Europe primarily prey on small ungulates such as roe deer *Capreolus capreolus* and chamois *Rupicapra rupicapra*, but they also take smaller species such as hares (*Lepus* spp.), marmots (*Marmota* spp.), rodents and grouse and (Tetraonidae spp.), and livestock such as sheep and goat (Jędrzejewski et al. 1993, Jobin et al. 2000, Odden et al. 2006). However, lynx are capable of killing prey up to four times their own size such as red deer *Cervus elaphus*, reindeer *Rangifer tarandus*, and moose *Alces alces* (Okarma et al. 1997, Pedersen et al. 1999, Odden et al. 2006). Very little is known about lynx feeding behaviour in Asia but presumably they feed on similar prey as in Europe.

Here we investigate co-occurrence of snow leopards and lynx in a large landscape across southern Mongolia (Fig. 1) and examine if snow leopards affect the space use of lynx. We assumed that snow leopards were the dominant species and lynx were the subordinate species and predicted that snow leopards excluded lynx from mountainous landscapes.

Material and methods

Study area

The study took place in the Bayankhongor, Gobi-Altai and South Gobi Provinces (46°N, 96°E) along part of the Khangai and Gobi Altai mountain ranges of southern Mongolia (Fig. 1). Our sampling areas included the Khuvd and Khurshuut Oasis (229 km^2) and the Tost Mountains (1450 km^2) in the Tost-Tosonbumba Nature Reserve, the Atas Bogd Mountains (2651 km^2) in the Great Gobi A Strictly Protected Area, the Khurkh Mountains (2853 km^2) in the Small Gobi A Strictly Protected Area, the Nemegt Mountains (1248 km^2) in the Gobi Gurvansaikhan National Park, and the Gurvan Agit Mountains (1259 km^2) in Bayankhongor (Fig. 1). These mountains are surrounded by desert and semi-desert steppe with a few isolated rugged hillocks potentially creating narrow corridors for animals to move between the mountains. The nearest mountains to the south of our study are separated by the fenced border with China and approximately 400 km of steppe of the Alashan Gobi Desert, impeding animals from dispersing to and from the south (Johansson et al. 2024). The mountains in which we worked were 1600–2600 m a.s.l.,

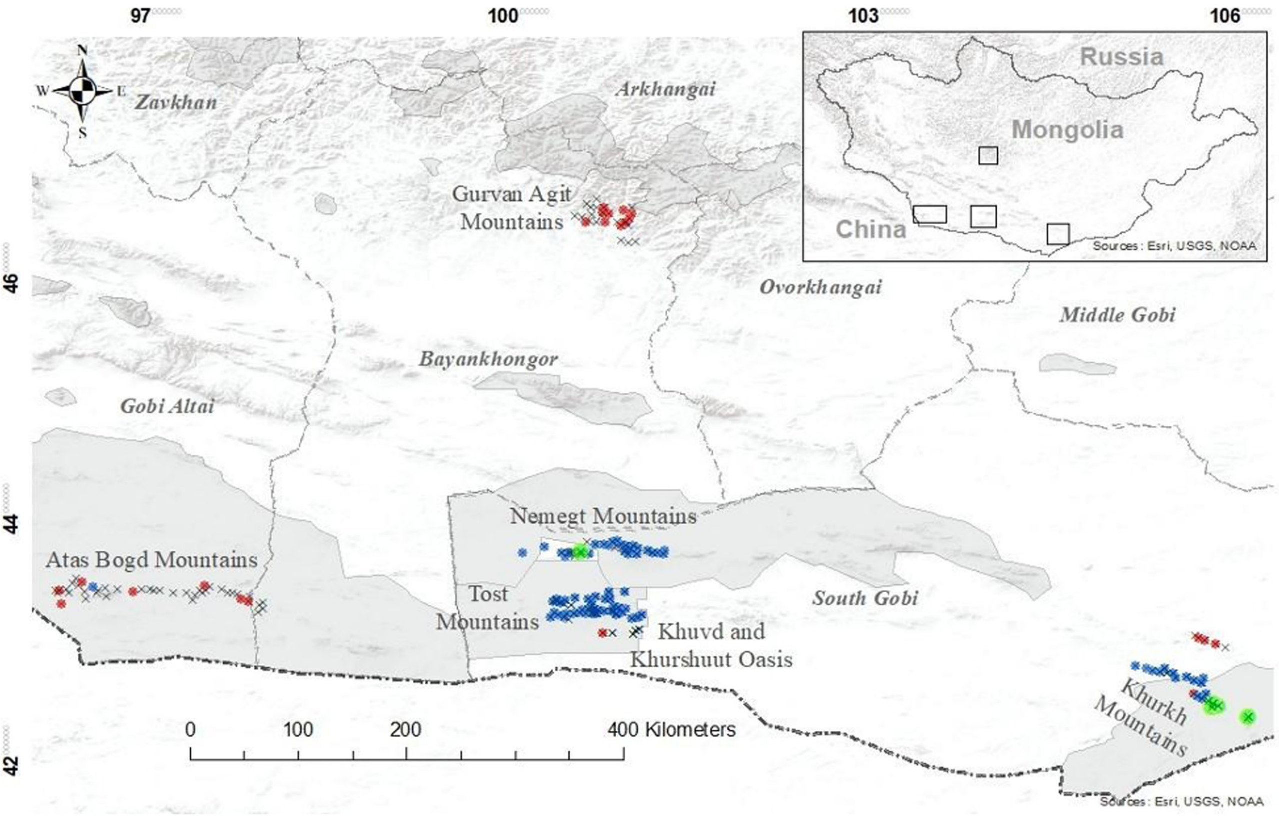

Figure 1. Spatial distribution of sampling locations for monitoring of snow leopards and lynx in southern Mongolia where dots represent camera sites where snow leopards and lynx were encountered (blue = snow leopards, red = lynx, green = both species), and gray crosses sites where none of the two species were encountered. Protected areas are outlined in gray and province names in bold italic.

and characterized by steep cliffs and crevices. The climate is arid continental with temperatures ranging from −35°C in winter to 40°C in summer. Annual precipitation ranges from 56 to 150 mm, with most of the precipitation falling in the form of rain in summer and fall. Water is a limiting resource during summer as most water-holes dry up, leaving only a few perennial springs accessible to wildlife. Ibex is the primary prey of snow leopards in this region, followed by domestic goats and sheep, and argali (Johansson et al. 2015). The lynx diet in the study area is unknown, but based on the feeding behaviors of lynx from other areas (Fedosenko and Blank 2001, Odden et al. 2006), black-tailed gazelle *Gazella subgutturosa*, Mongolian gazelle *Procapra gutturosa*, argali, ibex, tolai hare *Lepus tolai*, chukar partridge *Alectoris chukar* and domestic animals are likely common prey. Other predators include wolves and red foxes *Vulpes vulpes*.

The flora for the southern study sites of southern Mongolia is dominated by low shrubs such as littleleaf peashrub *Caragana microphylla*, fringed sagebrush *Artemisia frigida* and virgate wormwood *Artemisia scoparia*, herbaceous plants including shrubby ajania *Ajania fruticulosa*, Pamirian winterfat *Krascheninnikovia ceratoides*, *Scorzonera capito*, and sparsely distributed grasses *Stipa gobica* and *Stipa glareosa* (Ulziibadrakh et al. 2023). The bushes Mongolian almond *Prunus mongolica* and Saxaul *Haloxylon ammodendron* are prominent in most valleys and small gullies (Wesche et al. 2005). The Gurvan Agit Mountains, part of the Khangai Ridge mountain range to the north, differ from the remaining study area in that coniferous trees such as the Siberian larch *Larix sibirica* grow there (Gunin et al. 2013).

Data collection

Between 2017 and 2022, we sampled six sites across southern Mongolia aiming to cover both protected and non-protected areas (Fig. 1). The sites were sampled using a camera trap design that aimed to assess snow leopard abundance (Sharma et al. 2014). The locations of the camera stations were chosen based on natural pathways for snow leopards (such as ridges and valleys) and the presence of snow leopard marking signs. Each camera station consisted of one camera trap where we used a combination of Reconyx RM45, Reconyx HP2x, Bushnell Trophy Cam, Stealth Cam STC-G26NG, and Wild View sp cameras. Camera traps were set up approximately 2–3 km apart on various types of topography (ridges, valleys, slopes). Camera traps were deployed for a mean of 97 days (SD = 43, range = 90–388 days). We used 270 camera trap sites (13–88 cameras per study site) with the trapping frame covering an area of approximately 9692 km^2 (Table 1).

Table 1. Sampling effort (number of active camera trap-days) and number of encounters of snow leopards and lynx across six study areas in southern Mongolia in 2017–2022.

Study site	Deployment date	Removal date	Survey effort (days)	n cameras	Size of study site (km²)	n cameras with only snow leopard	n cameras with only lynx	n cameras with both species
Khurkh Mountains	Sep 2017	Jan 2018	139	14	2897	21	8	2
Khurkh Mountains	Oct 2018	Mar 2019	151	22	2324	50	9	1
Khurkh Mountains	Oct 2019	Feb 2020	141	25	2785	89	10	2
Atas Bogd Mountains	Jun 2020	Sep 2020	106	43	2792	1	10	0
Tost Mountains	Sep 2019	Dec 2019	96	42	1219	190	0	0
Tost Mountains	Sep 2020	Dec 2020	95	46	1209	153	0	0
Gurvan Agit Mountains	May 2020	Aug 2020	96	27	868	0	26	0
Nemegt Mountains	Oct 2020	Jan 2021	68	38	938	115	1	1
Khuvd and Khurshuut Oasis	Oct 2021	Jan 2022	84	13	56	0	4	0
Total			96	270		619	68	6

Data preparation

To minimize the effect of camera malfunction, battery drain and memory running out of space, adding unexplained variance, we truncated all camera trapping datasets at a maximum of 150 days. We used each camera trap as a detector representing a circular area of 20 km² (radius ca 2.5 km) around it and defined this area as a sampling unit. We assumed that given their large ranges, the space used by snow leopard or lynx within this area remained fairly homogenous during a season represented by 150 days. The probability that these sampling units were used by snow leopard and lynx during the 150-day sampling period was estimated within an occupancy framework (MacKenzie et al. 2017). We used the normalized difference vegetation index (NDVI) estimated from Landsat imagery (https://lpdaac.usgs.gov/products/mod13q1v006) for the entire landscape. A forest surface prepared by the Ministry of Environment and Tourism of Mongolia (2018) was used as binary data denoting the presence or absence of saxaul and Mongolian almond bushes. We estimated terrain ruggedness index (Riley et al. 1999) ranging between 1 and 100 using the Shutter Radar Topography Mission data on elevation (CGIAR-CSI SRTM – SRTM 90m DEM Digital Elevation Database). While the NDVI and forest cover datasets were prepared with satellite imagery available at 30 m resolution, the ruggedness surface was prepared from data available at 90 m resolution. We averaged the values of elevation, forest presence, NDVI and ruggedness for each sampling unit (Ghoshal et al. 2017). These averaged values were then used as covariates to test for their effect on the probability of the sampling unit being used by snow leopards and lynx during the sampling period. For lynx, we additionally included the presence of snow leopards as a covariate.

For the occupancy analysis, we pooled the data into ten-day periods for a total of up to 15 survey periods for the sites that were followed for 150 days. The encounter histories for the two species were constructed such that for each survey period zero represented non-detection of either species, one represented detection of snow leopard, two represented detection of lynx, and three represented detection of both species (MacKenzie et al. 2002, Mackenzie and Royle 2005).

Occupancy modelling

To estimate occupancy, we used the Richmond et al. (2010) and Waddle et al. (2010) parameterization to examine the co-occurrence between snow leopards and lynx, where we assumed snow leopards to be the dominant species and lynx the subordinate species. This parameterization allowed us to estimate the probability of occupancy (site use in our case) of the lynx conditional on the presence and absence of the snow leopard. The parameterization also allowed us to estimate occupancy of each species independent of each other. We also tested how topography and land cover affected the distribution of these two carnivores within southern Mongolia.

Probability of site use (occupancy) for the two species is estimated such that:

ψ^{SL} Unconditional probability that snow leopard is present
$\psi^{EL|SL}$ Probability that lynx is present given the presence of snow leopard
$\psi^{EL|sl}$ Probability that lynx is present given the absence of snow leopard

We estimated detection probabilities for cases when only one of the two species was present at a sampling unit (p); and when both species were present at a sampling unit (r). This parameterization, under the assumption that snow leopard was the dominant species, allowed the detection probability of lynx to be dependent on whether the sampling unit was occupied by snow leopard. It also allowed us to hypothesize that the probability of detecting lynx might have been lower if the snow leopard was detected in the sampling unit during that survey (represented by ten days of camera trap operation, defined as sampling occasion). Specifically, we estimated:

p_j^{SL} Probability of detecting snow leopard during a survey (j), given only snow leopard is present
p_j^{EL} Probability of detecting lynx during a survey (j), given only lynx is present
r_j^{SL} Probability of detecting snow leopard during a survey, given both snow leopard and lynx were present
$r_j^{EL|SL}$ Probability of detecting lynx during a survey, given snow leopard and lynx were present and snow leopard was also detected during the survey

$r_j^{EL|sl}$ Probability of detecting lynx during a survey, given snow leopard and lynx were present and snow leopard was NOT detected during the survey

We also estimate the level of dependence by using the estimates of $\psi^{EL|SL}$ and $\psi^{EL|sl}$ where, if the two species occurred independently, these two parameters would have been the same, i.e. presence (site-use) or absence (non-use of the site) of snow leopard has no effect on the probability of lynx being present (site-use) in the sampling unit. We defined events for the same species to be independent if they were separated by more than 30 minutes following (Mackenzie and Royle 2005, Meek and Pittet 2014)

In total we developed 15 candidate models to test the above hypotheses using an information theoretic approach (Burnham and Anderson 2002). Out of the fifteen candidate models, two models did not converge and were discarded before comparing the rest of the models using AIC for the most parsimonious model with the best possible fit.

Results

Sampling effort

Between 2017 and 2022, we recorded 619 independent captures of snow leopards across 142 camera trap sites and 68 independent captures of lynx on 31 camera trap sites (Table 1). Of these encounters, both snow leopards and lynx were encountered on the same camera at six different camera trap sites. The remaining 105 camera trap sites did not detect either species.

Occupancy modelling

The model that described the spatial distribution of snow leopards and lynx the best, carried 99% of the model weight and was 13 AIC units better than the second-best model (Table 2). According to this model (Table 3), the probability of site use (Ψ) was species-specific with the probability of site use for lynx depending on the probability of site use by snow leopards. Snow leopard used sites with low shrub cover ($\beta(\psi^{SL}_{Shrub}) = -2.28$, SE = 0.59) and was agnostic to rugged habitats ($\beta(\psi^{SL}_{Rgd}) = 0.03$, SE = 0.33). Lynx used sites with low ruggedness when snow leopard was present ($\beta\left(\psi^{EL|SL}_{Rgd}\right) = -1.04$, SE = 0.49), but was agnostic to ruggedness as a covariate when snow leopard was absent ($\beta\left(\psi^{EL|sl}_{Rgd}\right) = 0.15$, SE = 0.76). Lynx restricted themselves to habitat with high shrub cover in the presence of snow leopards ($\beta\left(\psi^{EL|SL}_{Shrub}\right) = 23.48$, SE = 2.72), but were agnostic to them in the absence of snow leopards ($\beta\left(\psi^{EL|sl}_{Shrub}\right) = 0.96$, SE = 3.81).

Detection probabilities were also species-specific as per the top model (Table 2). The probability of detecting snow leopards was lower in sites that were not used by lynx ($\beta(p_j^{SL}) = -0.43$, SE = 0.1) than the sites used by lynx ($\beta(r_j^{SL}) = -1.98$, SE = 0.32). Lynx (β(p_EL) = −1.68, SE = 0.36) on the other hand were less detectable than the snow leopards when only one of the two species was present, as compared to where snow leopards were present but not detected (β(r_EL|sl) = −0.14, SE = 0.78), and where snow leopards were present and got detected (β(r_EL|SL) = 0.58, SE = 0.87).

Discussion

Our study investigated the spatial interactions between snow leopards and lynx in southern Mongolia, aiming to understand the factors influencing their coexistence and potential implications for conservation. Snow leopards clearly tend to use habitat patches with fewer shrubs irrespective of the ruggedness across the study area. As for the lynx, in absence of shrubs, the presence of snow leopards impacted the former's habitat use where lynx avoided rugged habitat when snow leopards were present, but were indifferent to ruggedness when snow leopards were absent (Fig. 2B, C, yellow curves). Areas with shrubs were consistently used by lynx where snow leopards were present irrespective of ruggedness (Fig. 2C), but were not used more than areas without shrubs where snow leopards were absent (Fig. 2B). This indicates that lynx used habitats irrespective of their ruggedness in absence of snow leopards. The presence of snow leopards appears to push lynx into flatter areas and areas with more shrubs, possibly to avoid encounters with snow leopards. This shift indicates a possible behavioral adaptation to reduce direct competition, and potential negative interactions with snow leopards that could lead to injury and even mortality. The spatial separation between snow leopards and lynx likely facilitated their coexistence. Such separation could reduce the negative effects of direct competition, such as the threat of predation, which can favor the persistence of both predator species in the same landscape. This finding aligns with the patterns observed in other ecosystems, where larger predators influence the space use of smaller predators such as lions affecting the space use of cheetahs and wild dogs in Africa (Creel and Creel 1996, Mills and Gorman 1997, Broekhuis et al. 2013). We acknowledge that our cameras were deployed to monitor snow leopards and that this may have resulted in a possible unmodeled heterogeneity beyond what we were able to test. However, we believe that the modeling approach should have largely taken care of the heterogenous detectability of lynx specifically for sites where the snow leopards were present and/or detected. Whether lynx responds to snow leopard marking behavior per se is beyond the scope of this study, but something of interest and will require more detailed studies.

Coexistence of carnivore species within the same guild is generally facilitated through partitioning of diet and/or by differential use of time or space (Hayward and Slotow 2009, Karanth et al. 2017). While lynx diets in southern Mongolia are largely unknown, based on the species diet in other areas we assume that the lynx will feed on ibex, argali, black-tailed gazelle, hares, chukar and domestic sheep and goat. Because

Table 2. Parameterization for p: SP+INT: species- specific with interaction, INT_o: interaction effect of occupancy on detection ((p? ! = r?), INT_d: interaction effect of detection of one species on detection of other species (rB ! = rA), SP X INT_o: interaction effect of occupancy and detection of one species on detection of the other species (rBa! = rBA). Parameterization for ψ: SP (in case of psi): species effect on occupancy (psiBA, and psiBa ! = psiA)), INT (in case of psi: Interaction effect of occupancy of species A on species B (psiBa ! = psiBA),Model selection for site use (occupancy) and detection probability of snow leopards and lynx in southern Mongolia in 2017–2022. Ψ: Probability of site use, p: probability of detection, Rgd: ruggedness, Forest: bush cover, DEM: mean altitude above sea level, DAIC: delta Akaike information criteria between the corresponding model and the top model, wgt: model weight, npar: number of parameters used, neg2ll: negative likelihood of the model.

Model	Model Description	DAIC	wgt	npar	neg2ll
ψ((SP + INT) X (Rgd + Bush)) p(SP + INT_o + INT_d + SP X INT_o)	Occupancy: species-specific, interaction, and a function of ruggedness and bush cover (Ψ^{SL} ! = Ψ^{EL}, $\Psi^{EL} \mid \Psi^{SL}$) ~ (Rgd + Bush); Detection: species-specific, interaction ($p^{SL}! = p^{EL}! = r^{SL}! = r^{EL}$, $p^{EL} \mid p^{SL}$, $p^{EL} \mid \Psi^{SL}$, $r^{EL} \mid p^{SL}$, $r^{EL} \mid \Psi^{SL}$)	0.0	1.0	14.0	2449.4
ψ((SP + INT) X Bush) p(SP + INT_o + INT_d + SP X INT_o)	Occupancy: species-specific with interaction, and a function of bush cover (Ψ^{SL} ! = Ψ^{EL}, $\Psi^{EL} \mid \Psi^{SL}$) ~ (Bush); Detection: species-specific, interaction ($p^{SL}! = p^{EL}! = r^{SL}! = r^{EL}$, $p^{EL} \mid p^{SL}$, $p^{EL} \mid \Psi^{SL}$, $r^{EL} \mid p^{SL}$, $r^{EL} \mid \Psi^{SL}$)	11.3	0.0	11.0	2466.7
ψ((SP P INT) X DEM) p(SP + INT_o + INT_d + SP X INT_o)	Occupancy: species-specific with interaction, and a function of DEM (Ψ^{SL} ! = Ψ^{EL}, $\Psi^{EL} \mid \Psi^{SL}$) ~ (DEM); Detection: species-specific, interaction ($p^{SL}! = p^{EL}! = r^{SL}! = r^{EL}$, $p^{EL} \mid p^{SL}$, $p^{EL} \mid \Psi^{SL}$, $r^{EL} \mid p^{SL}$, $r^{EL} \mid \Psi^{SL}$)	12.4	0.0	11.0	2467.8
ψ((SP + INT + Rgd + Forest)) p(SP + INT_o + INT_d + SP X INT_o)	Occupancy: species-specific with interaction, and an additive effect of Rgd or Forest (Ψ^{SL} ! = Ψ^{EL}, $\Psi^{EL} \mid \Psi^{SL}$) ~ (Bush + DEM); Detection: species-specific, interaction ($p^{SL}! = p^{EL}! = r^{SL}! = r^{EL}$, $p^{EL} \mid p^{SL}$, $p^{EL} \mid \Psi^{SL}$, $r^{EL} \mid p^{SL}$, $r^{EL} \mid \Psi^{SL}$)	28.8	0.0	10.0	2486.3
ψ((SP + INT) X Rgd) p(SP + INT_o + INT_d + SP X INT_o)	Occupancy: species-specific with interaction, and a function of Rgd (Ψ^{SL} ! = Ψ^{EL}, $\Psi^{EL} \mid \Psi^{SL}$) ~ (DEM); Detection: species-specific, interaction ($p^{SL}! = p^{EL}! = r^{SL}! = r^{EL}$, $p^{EL} \mid p^{SL}$, $p^{EL} \mid \Psi^{SL}$, $r^{EL} \mid p^{SL}$, $r^{EL} \mid \Psi^{SL}$)	42.0	0.0	11.0	2497.5
ψ(SP X Rgd) p(SP + INT_o + INT_d + SP X INT_o)	Occupancy: species-specific and a function of Rgd; detection: species-specific, interaction ($p^{SL}! = p^{EL}! = r^{SL}! = r^{EL}$, $p^{EL} \mid p^{SL}$, $p^{EL} \mid \Psi^{SL}$, $r^{EL} \mid p^{SL}$, $r^{EL} \mid \Psi^{SL}$)	44.4	0.0	9.0	2503.8
ψ(SP + INT) p(SP + INT_o + INT_d + SP X INT_o)	Occupancy: species-specific with interaction; detection: species-specific, interaction ($p^{SL}! = p^{EL}! = r^{SL}! = r^{EL}$, $p^{EL} \mid p^{SL}$, $p^{EL} \mid \Psi^{SL}$, $r^{EL} \mid p^{SL}$, $r^{EL} \mid \Psi^{SL}$)	50.8	0.0	8.0	2512.2
ψ(SP + INT + DEM.z) p(SP + INT_o + INT_d + SP X INT_o)	Occupancy: species-specific with interaction and an additive effect of DEM; detection: species-specific, interaction ($p^{SL}! = p^{EL}! = r^{SL}! = r^{EL}$, $p^{EL} \mid p^{SL}$, $p^{EL} \mid \Psi^{SL}$, $r^{EL} \mid p^{SL}$, $r^{EL} \mid \Psi^{SL}$)	51.5	0.0	9.0	2510.9
ψ(SP + INT + Rgd.z) p(SP + INT_o + INT_d + SP X INT_o)	Occupancy: species-specific with interaction and an additive effect of Rgd; detection: species-specific, interaction ($p^{SL}! = p^{EL}! = r^{SL}! = r^{EL}$, $p^{EL} \mid p^{SL}$, $p^{EL} \mid \Psi^{SL}$, $r^{EL} \mid p^{SL}$, $r^{EL} \mid \Psi^{SL}$)	52.7	0.0	9.0	2512.2
ψ(SP + INT)p(SP)	Occupancy: species-specific with interaction; detection: species-specific	70.2	0.0	5.0	2537.7
ψ(SP)p(SP)	Occupancy: species-specific; detection: species-specific	88.3	0.0	4.0	2557.8
ψ(SP)p()	Occupancy: species-specific; detection: constant	134.2	0.0	3.0	2605.6
ψ()p()	Occupancy: constant; detection: constant	244.8	0.0	2.0	2718.3

snow leopards prey on the same species, except for hares, this limited availability of suitable prey species might constrain the ability of lynx and snow leopards to partition their resource use. In addition, the high visibility in the vegetation-sparse landscapes of southern Mongolia could be a critical factor influencing the spatial interactions between snow leopards and lynx. The high visibility might hinder lynx from effectively avoiding snow leopards at a fine scale, explaining why lynx did not use rugged mountains much when snow leopards were present. Similar findings have been reported for dholes *Cuon alpinus*, and leopards *Panthera pardus* not being able to adjust spatial behaviour to avoid interactions with tigers *Panthera tigris* within open woodland habitat, while adjusting their behaviour in closed habitats, thereby facilitating coexistence (Karanth et al. 2017). Similarly, African wild dogs *Lycaon pictus* were not able to adjust space use to avoid lions and hyenas in open landscapes (Creel and Creel 1996, Droge et al. 2017).

Additionally, the presence of large scavenging birds in the study area, capable of revealing a subordinate predator at a kill in open, vegetation-sparse areas (Creel 2001), might increase the risk of kleptoparasitism and predation, further influencing habitat selection by the lynx. Conversely, the cover provided by shrubs, i.e. lower visibility as well as vegetation to cover the carcass, may allow lynx to avoid encounters with snow leopards, which could explain why snow leopards and lynx co-occurred more in shrubby areas. While we have no data on kleptoparasitism of snow leopards on lynx kills, we have recorded several instances where a GPS-collared snow leopard has scavenged from the kill of another GPS-collared snow leopard still present at the kill, indicating that snow leopards are able to locate kills with relative ease (Snow Leopard

Table 3. Coefficients of covariates from the top model chosen by minimum AIC.

Source	Parameter	Beta	SE
Estimated	ψ^{SL}	1.26	0.44
	$\psi^{EL\|SL}$	−1.66	0.46
	$\psi^{EL\|sl}$	−0.63	0.69
	ψ^{SL}_{Rgd}	0.03	0.33
	ψ^{SL}_{Shrub}	−2.28	0.59
	$\psi^{EL\|SL}_{SP2:Rgd}$	−1.07	0.36
	$\psi^{EL\|SL}_{Sp2:Shrub}$	25.76	2.65
	$\psi^{EL\|sl}_{Int:Rgd}$	1.20	0.58
	$\psi^{EL\|sl}_{Int:Shrub}$	−22.52	2.67
Derived	$\psi^{EL\|SL}_{Rgd}$	−1.04	0.49
	$\psi^{EL\|SL}_{Shrub}$	23.48	2.72
	$\psi^{EL\|sl}_{Rgd}$	0.15	0.76
	$\psi^{EL\|sl}_{Shrub}$	0.96	3.81
Estimated	p^{SL}	−0.43	0.10
	p^{EL}	−1.67	0.36
	r^{SL}	−1.98	0.32
	$r^{EL\|sl}$	−0.14	0.79
	$r^{EL\|SL}$	0.58	0.87

ψ^{SL} Unconditional probability of snow leopard presence.

ψ_k^{SL} Probability of snow leopard presence as a function of covariate k.

$\psi^{EL|SL}$ Probability that lynx is present given the presence of snow leopard.

$\psi_k^{EL|SL}$ Probability that lynx is present given the presence of snow leopard as a function of covariate k.

$\psi_k^{EL|sl}$ Probability that lynx is present given the absence of snow leopard as a function of covariate k.

p_j^{SL} Probability of detecting snow leopard during a survey (j), given only snow leopard is present.

p_j^{EL} Probability of detecting lynx during a survey (j), given only lynx is present.

r_j^{SL} Probability of detecting snow leopard during a survey, given both snow leopard and lynx were present.

$r_j^{EL|SL}$ Probability of detecting lynx during a survey, given snow leopard and lynx were present and snow leopard was also detected during the survey.

$r_j^{EL|sl}$ Probability of detecting lynx during a survey, given snow leopard and lynx were present and snow leopard was NOT detected during the survey.

Trust, unpubl.). Conservation efforts for lynx in Mongolia should consider the potential role of mountains as refuges from human persecution. While lynx appear to have less specific habitat requirements than snow leopards as they occur in many different habitats throughout large parts of Europe and Asia, they require that the habitats offer enough concealment to ambush prey and to avoid dominant predators and human persecution (Breitenmoser and Breitenmoser-Wursten 2008). Lynx were extinct from most of Europe in the 20th century, with only small populations remaining in mountains and large forested areas of Scandinavia, the Carpathian mountains and the Balkans (Breitenmoser 1998). Here, the mountains likely served as a refuge from human persecution. Perhaps the situation is similar also in southern Mongolia where wildlife has declined dramatically from the steppe areas since the early 1990s (Zahler et al. 2004, Berger et al. 2013). While lynx are not adapted to mountains per se, it may be that the mountains provide refuge from humans and dogs while at the same time harboring higher prey density than the surrounding steppe. The mountains, on the other hand, expose lynx to snow leopards and thus may force lynx to select less preferred habitats within the mountains when snow leopards are present. To gain insights in lynx ecology and behaviour, it would be important to conduct a telemetry study in central Asia. Understanding the specific ecological requirements of lynx and the mechanisms of competition with snow leopards is crucial for devising effective conservation strategies.

While snow leopards are known to prefer rugged habitats (Fox et al. 2024), we could not detect any effect of ruggedness on snow leopard space use within the range of ruggedness that was sampled. We propose that this may be attributed to our sampling scheme, which focused predominantly on mountainous areas, similar to the findings of Franchini et al. (2023). Specifically, in our case most of the cameras were placed in mountains while steppe and rolling hills were underrepresented. Also, because we used the average ruggedness for each sampling unit (20 km^2) as covariate, sampling units that were predominantly rugged but also included flat areas could achieve a low ruggedness score. Furthermore, the higher detection probabilities of snow leopards and lynx at sites used by both species likely stem from specific microhabitat characteristics, as these cameras may have been placed along natural travel routes shared by both predators. We do not expect lynx to adjust space use beyond the scale of our sampling unit between seasons to minimize encounter risk with snow leopards and assume that small scale microhabitat level shifts in space use reflected in changes in detection probability that averaged out for the two species. However, the small sample size prevented us from splitting the data into multiple seasons to assess seasonal change in site use by the two carnivores . Similarly, as observed in other subordinate carnivores (Hayward and Slotow 2009, Bischof et al. 2014), it is possible that lynx adjust their behavior by modifying their activity patterns to avoid encounters with snow leopards in overlapping areas. However, investigating temporal partitioning often requires at least 100 independent detections of each species (Havmøller et al. 2020) and due to our limited sample size, we were unable to explore for temporal partitioning between the two felids, emphasizing the need for future studies to address these important questions.

Our study provides valuable insights into the spatial interactions between snow leopards and lynx in southern Mongolia. It allowed us to present a number of hypotheses that may explain their coexistence. However, limited sample size and a relatively course study design restrained us from exploring potential behavioral adjustments by lynx in response to snow leopards and more intricate details of the interactions between these species. Future studies with larger sample sizes and detailed behavioral observations are

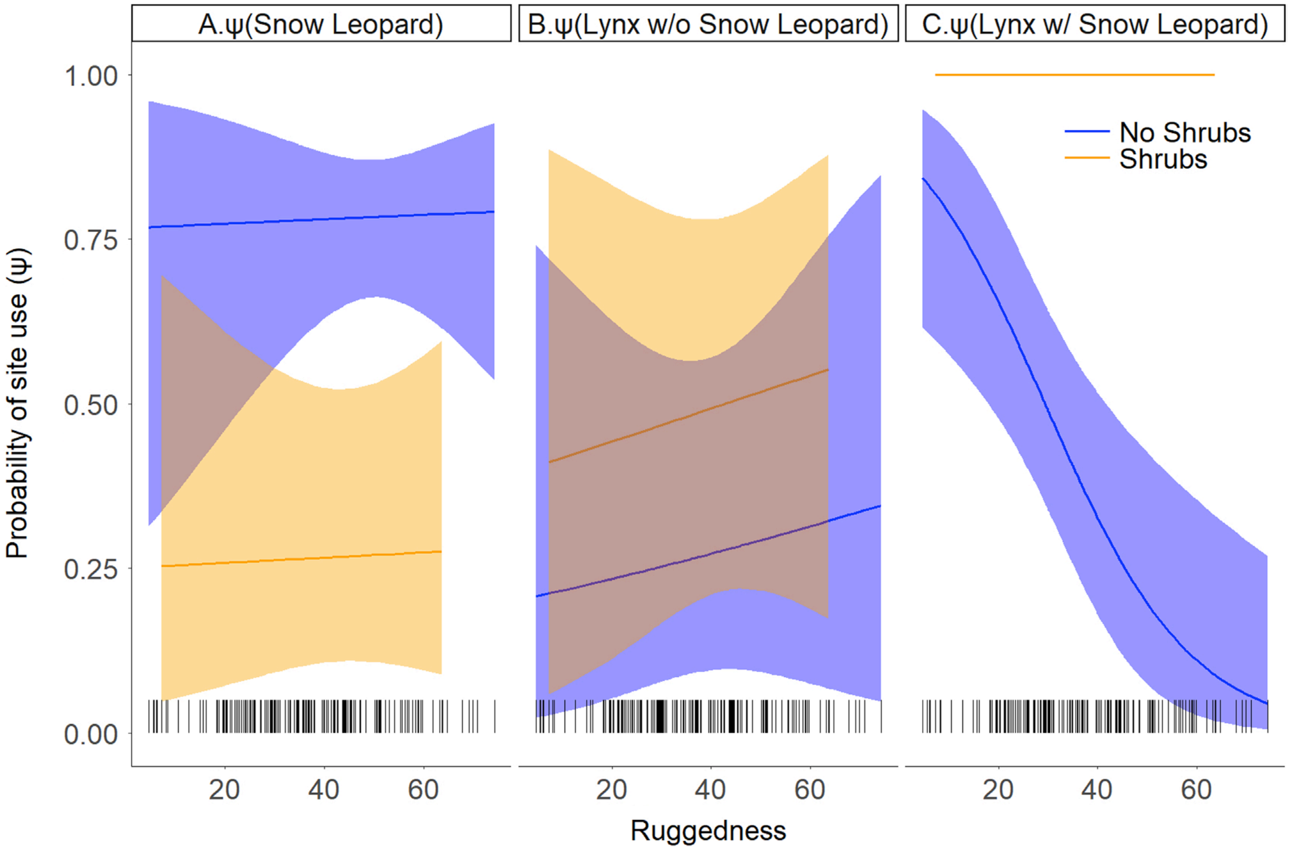

Figure 2. Probabilities of site-use (Ψ) estimated from the top model as a function of ruggedness (x-axis) and shrub-cover (yellow denotes shrubs, blue denotes no shrub-cover). (A) probability of site-use by snow leopards; (B) probability of site use by lynx in areas that were not used by snow leopards; (C) probability of site use by lynx in sites that were used by snow leopards. Tick-marks denote the value of ruggedness that was sampled with camera traps.

necessary to gain a more comprehensive understanding of the coexistence dynamics between these predator species. Such knowledge will aid in the successful conservation of both snow leopards and lynx in the region.

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Choidogjamts Byambasuren: Data curation (lead); Investigation (equal); Visualization (supporting); Writing – original draft (supporting). **Örjan Johansson**: Conceptualization (equal); Writing – original draft (lead); Writing – review and editing (lead). **Justine Shanti Alexander**: Conceptualization (equal); Methodology (supporting); Resources (supporting); Writing – original draft (supporting). **Purevjav Lkhagvajav**: Project administration (equal); Resources (supporting). **Gustaf Samelius**: Project administration (supporting); Writing – original draft (supporting); Writing – review and editing (supporting). **Koustubh Sharma**: Conceptualization (supporting); Formal analysis (lead); Methodology (lead); Visualization (lead); Writing – original draft (supporting); Writing – review and editing (supporting).

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Data availability statement

Data are available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.pnvx0k6x0 (Byambasuren et al. 2024).

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