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Factors influencing the diurnal spring distribution of sympatric urial and Siberian ibex in the Hindu Kush Mountains of Wakhan National Park, Afghanistan

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ABSTRACT

Patterns of habitat selection for sympatric urial *Ovis vignei* and Siberian ibex *Capra sibirica* are poorly known, in part because there are few places where such overlap exists. Using envelope modeling methodology, we analyzed location data of these species in the Hindu Kush range along the Wakhan Valley of the Wakhan National Park (10,950 km²) in northeastern Afghanistan, recorded during field surveys in April-May of 2011, 2015, and 2018. Distribution models showed significant ecological niche differences (P 0.05) between urial (a true sheep species) and ibex (a true goat species) for most variables. Urial stayed at lower elevations compared to ibex, both species tended to avoid flat areas, but urial avoided slopes above 60 %.

Urial used southeast-facing slopes more, and west-facing slopes less, than available, whereas ibex had a slightly more than expected use of southwest-facing slopes. Urial preferred terrains with ruggedness index (\sim 20–40) of the values available (15–60), whereas ibex were more generalist in terrain preference. Urial utilized habitats closer to human activity areas compared to ibex. Both species utilized the higher quality vegetation areas (NDVI > 0) and showed the same avoidance of lower quality areas. Understanding selection criteria of habitat use by urial and ibex in Wakhan Valley, inhabited by over 14,000 people and their livestock (ca. 78,000), will enable adjustments to the protection schemes regarding the requirements of two key mountain ungulate species critical to the sustainability and conservation of this unique ecosystem. This type of information is very scarce in the literature for the sympatric mountain ungulates in Asia.

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1. Introduction

Mountain ungulates play key roles in the functionality of mountain ecosystems throughout south, central, and northeastern Asian mountain ranges (Bagchi and Ritchie, 2010; Lyngdoh et al., 2014). For example, the density and distribution of mountain ungulates are positively related with the density of large carnivores in such areas (Oli, 1994; Suryawanshi et al., 2017; Leki et al., 2018), and these species live in sympatry with other species including other caprids (Odonjavkhlan et al., 2021). The behavior, and thus the distribution, of sympatric and ecologically similar species is shaped by competition relative to the species' niche overlap, community composition, and resource availability (Schoener, 1974). Species coexistence, and thus niche separation, among Asian mountain ungulates has been related to topography (Namgail, 2006; Odonjavkhlan et al., 2021), vegetation (Bragin et al., 2017), and anthropogenic factors, including livestock (Yang et al., 2021), but such relationships have been studied in relatively few places or for few species assemblages.

The geographic range of urial *Ovis vignei* extends over limited mountainous areas in Afghanistan, India, Iran, Kazakhstan, Pakistan, Tajikistan, Turkmenistan, and Uzbekistan, and the species is listed as Vulnerable (VU) by the International Union for Conservation of Nature (IUCN) (Michel and Ghoddousi, 2020). Unlike urial, Siberian ibex *Capra sibirica*, (later named as 'ibex') listed as Near Threatened (NT; Reading et al., 2020), has a wider distribution and occurs throughout the mountainous regions of Central Asia including Tajikistan, the northwest Himalayas including Afghanistan and Pakistan, northern and western China, south and western Mongolia, and southern Russia (Shackleton, 1997; Fedosenko and Blank, 2001; Raza et al., 2015; Moheb et al., 2018). These two species coexist in relatively few places mainly because urial populations have suffered population declines and local extinction due to poaching (Michel and Ghoddousi, 2020) and competition with livestock (Khan and Zahler, 2004).

Afghanistan has been engaged in war and civil unrest for several decades, which impaired its biological exploration (Smallwood et al., 2011). As a consequence, the distribution of many large mammal species, including urial and ibex, remains poorly known, although both species have been reported to occur in sympatry in the Wakhan (Michel, 2010; Moheb et al., 2022). In this area urial and ibex coexist with herders and their livestock (sheep, goats, cattle, yaks, donkeys, horses and Bactrian camels) within the Wakhan National Park (hereafter referred to as WNP), where these mountain ungulates are thought to play an important role in maintaining the functionality of rangeland and mountain ecosystems (Manier and Hobbs, 2007; Li et al., 2022).

Although urial and ibex live in sympatry with each other, ibex are found throughout the park at higher density, whereas urial occur only in the Hindu Kush part and at lower density (Moheb et al., 2022). In theory, ibex (as a true goat species) are likely to occupy more steep areas and slightly higher elevations, whereas urial (as a true sheep species) are expected to occur in more undulating lower areas



Fig. 1. Location of ungulate survey areas and sites in the Hindu Kush Mountains of Wakhan National Park in northeastern Afghanistan.

(Schaller, 1977). However, little is known about the habitat selection by these species where they are sympatric and this ambiguity is an important challenge for conserving them for the benefit of the ecosystem (Moheb, 2020). The present study helps fill this knowledge gap by comparing the diurnal habitat use for urial and ibex during spring in WNP.

2. Study area

This study occurred in the Hindu Kush mountains along the Wakhan Valley in the western half of WNP in the northeastern province of Badakhshan, Afghanistan. We surveyed areas along the northern drainages of the Hindu Kush range from Fetur Valley (c. 2500 m) in the west to upper Dehqankhana Valley (c. 3500 m) in the middle of Wakhan (c. 2500–7490 m). The Wakhan and Panj rivers, and the drainages of the mountain ridges and glaciers in the Hindu Kush Mountains, limited the boundaries of the study area to the north and south, respectively (Fig. 1). The Hindu Kush Mountain ridge in Wakhan also marks the international border with Pakistan in the south. The Wakhan River, an upper tributary of the Panj River, separates the Hindu Kush from the Pamir Mountain range in the north, whereas the Panj River constitutes the northern international border with Tajikistan in the western half of the park (Fig. 1). The Hindu Kush range in Afghanistan is dominated by the highest and steepest peaks and associated glaciers that stream out into the Panj River at the bottom of the Wakhan Corridor. The northern offshoots of this range are composed of less steep slopes and alluvial fans.

Yearly average temperatures range between 1 °C and 3 °C, and annual precipitation totals around 200 mm in the valleys (Zandler et al., 2019). Absolute extremes across the landscape may reach 60 °C in winter and 26 °C in summer (Zandler et al., 2019). Average vegetation cover shows large differences, with values mostly below 20 % in steppe communities and above 20 % in riparian alpine grasslands (Zandler et al., 2022). Along the northern drainages of the Hindu Kush range vegetation is dominated by woody shrubs such as *Artemisia* spp. and low scrub composed of *Rosa* spp. and *Barberis* spp., with limited growth due to poor soil conditions, short summers, and cold temperatures (Fig. 2).

Wakhan Valley has 42 permanent villages, occupied by > 14,000 people grouped in 1706 households, and seasonal nomadic camps (Moheb, 2020). Most people living in this area subsist in an agro-pastoral economy, using meager arable lands for wheat and legume-based agriculture. They tend around 78,000 livestock belonging to the following seven species: sheep, goats, cattle, donkeys, yaks, horses, and Bactrian camels (from the highest to lowest number, respectively; Moheb, 2020).

The biological significance of the area is illustrated by a high diversity of flora, with about 20 % endemic species (Soelberg and Jäger, 2016), and fauna, with several rare species such as (in addition to urial and ibex) snow leopards *Panthera uncia*, Eurasian lynx *Lynx lynx*, brown bears *Ursus arctos*, Marco Polo argali *Ovis ammon polii*, and large-billed reed warblers *Acrocephalus orinus* (Smallwood and Shank, 2019).

3. Methods

3.1. Data collection

To explore the diurnal habitat use and distribution of urial and ibex, we used observations of locations recorded during a spring (April-May) total count survey in 2011 over a broad survey area (~1303 km²) that was later sub-sampled and re-surveyed in 2015 and 2018, during the same season (Moheb, 2020; Moheb et al., 2022; Table 1). We conducted these field surveys in teams of 3 persons,



Fig. 2. Pamir (up front with the snow caped peaks) and Hindu Kush (where the photo has been taken) Mountains in Wakhan National Park, northeastern Afghanistan, rising \sim 5000 m from the valley floor. Z.Moheb@WCS Afghanistan.

Table 1

Sample sizes of he	erds recorded during	g ungulate surveys i	n the Hindu Kusł	Mountains of the	Wakhan Valley	of northeastern Afghanistan.
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			Number of herds	
Survey type	Year	Location	Urial	Ibex
Total Count	2011	Entire study area	62	130
Double Observer	2015	10 survey units within the study area	19	37
Double Observer	2018	Repeat of 2015 survey	12	38
			93	205

mostly during 0630–1320 h before animals moved to higher elevations (e.g., Ladakh urial in India; Mallon, 1983). In 2015 and 2018, each subunit (range = 14–33 km², calculated as a "viewshed" area; Moheb et al., 2022) was surveyed in a single day to avoid duplicate counts. In all surveys, observers usually walked at a pace of ~ 1 km/hr and also stopped every 20–30 min at vantage points to scan the terrain. For all surveys we recorded herd actual locations with GPS unit either at the location site (if animals were close-by and easily located on a map), or through triangulation by marking GPS locations and compass bearings of the herd obtained from two observation sites on the map and drawing the herd's actual location (see Moheb et al., 2022 for details). We acknowledge that, like many other habitat-use studies on mountain ungulates, our data only represent the daytime habitat use of ibex and urial in the spring season. The habitat use of ibex and urial may show different patterns if survey tools such as camera traps are used to monitor habitat use continuously throughout the year.

3.2. Data preparation

To understand urial and ibex habitat use with respect to each other's presence, we tested their point location spatial features (clustering or segregation) using point pattern analysis. Once the factors were selected and prepared, the values for every factor were added to the herd location points by extracting the value of the raster cells over which each herd location fell. The Euclidean distances were calculated for every herd location points to the nearest polygon edge of the human activity areas. For the herd locations, the query points were the coordinates recorded in the field; however, for the random points from the study area, null raster layers were built using the elevation layer as a template in which the raster cell values represented the distance to the nearest polygon edge for the factor.

A 'concave hull' (Moreira and Santos, 2007) was constructed around the herd locations from the survey data (Park and Oh, 2012) using the R package 'concaveman' (Gombin et al., 2020). The default concavity factor of 2.0 was used to build the hull, to produce a hull that contained all the points but did not capture large areas outside the survey area. We then buffered the concave hull by 100 m to ensure that all raster cells containing survey points were within the hull, and to avoid the inclusion of large areas outside the survey area, which can artificially inflate the Maximum Entropy (MAXENT) model evaluation measure.

To characterize habitat use, we used landscape-, environmental-, and human-related factors (Table 2). Geographic Information System (*ArcGIS vr. 10.3 and later,* Esri, Redlands, USA), and R (R Core Team, 2022) software were used to extract data from the relevant geographic, environmental, and anthropogenic factors (cf. Bragin et al., 2017; Ahmad et al., 2022).

Slope, aspect, and terrain ruggedness index (TRI) layers were all derived from the Digital Elevation Model (DEM) obtained from the Shuttle Radar Topography Mission (SRTM) using the *terrain()* function in R package 'raster' (Hijmans, 2020). The DEM data were resampled from the original Shuttle Radar Topography Mission (SRTM) to a resolution of approximately 90 m at the equator. We used

Table 2	
Different factors used in the species habitat analysis.	
Types of	

Types of	
Factors used in data analysis	Source of the data
Topographic ^a	
Elevation	CGIAR SRTM version 4.0, tile 51_05.
Slope	Calculated in R using terrain () 'raster' package
Aspect	Calculated in R using terrain () 'raster' package
Terrain Ruggedness	Calculated in R using terrain () 'raster' package
Anthropogenic ^b	
Human activity areas	Sketched the human activity areas using the Google Earth machine
Environmental ^c	
NDVI	Calculated from the Landsat 8 data for the study area

^a Elevation, slope, aspect and ruggedness are all factors that can affect habitat selection, and forage availability and growth (especially in the spring), as well as escape habitat (Han et al., 2021). These needs are likely different for each species.

^b These include human settlement agricultural fields and other human activity areas that serve as the base for potential encounter between human and wild ungulates, which should have negative population effects (Stankowich, 2008; Brown et al., 2012).

^c This is a measure of vegetation productivity and "greenness" that should affect wild ungulate distribution and foraging behavior (Pettorelli, and et al., 2005, 2011).

the *terrain()* function in the R raster package to generate layers for slope, aspect, and TRI. Slopes were measured in percentages from zero (no slope) to 100 (i.e., vertical). Aspect was measured from 0° (north-facing areas) to 180° (south-facing areas), and 360° back to the north (Horn, 1981). Terrain Ruggedness Index, a combination of slope, aspect, and elevation (Nellemann and Reynolds, 1997), was calculated as the absolute value of the mean difference between a central pixel with its surrounding neighbors (Wilson et al., 2007).

Normalized Difference Vegetation Index (NDVI) values (Pettorelli et al., 2005) were calculated from Landsat 8 images sourced from the U.S. Geological Survey Earth Resources Observation and Science (USGS EROS, https://eros.usgs.gov/usa) as a recent vegetation cover layer was lacking for all the study area. We downloaded three Landsat layers corresponding to the time of our field research (2015 and 2018) with a minimum (1–10%) cloud cover. We calculated the NDVI according to Pettorelli et al. (2005), using the raster calculator in ArcGIS Toolbox.

We digitized the human activity areas across the survey area in 2019 using the Google Earth online resources. Given the traditional lifestyle of local communities in Wakhan, it was difficult to distinguish, from the Google Earth map, between villages and agricultural areas; therefore, we lumped all the likely human activity areas under a single layer of human activities and made a GIS readable layer using Google Earth. Euclidean distances were calculated from the herd locations to the nearest polygon edge of the human activity areas.

3.3. Data analyses

To determine correlation among the variables, we used the correlation coefficients and pairwise scatterplots for each pair of the covariates (elevation, slope, aspect, TRI, NDVI, distance to human activity areas; Fig. 3).

A kernel density estimation algorithm was used to calculate a density curve at 512 points along the range of each covariate using function *density()* in R. Resampling simulations were used to estimate 95 % sampling envelopes for each factor. This provides a null hypothesis against which the observed covariate values at the ungulate sample points could be compared. A set of 200 points randomly placed within the study area was generated in each simulation. The values of each factor at the simulated points were extracted using



Fig. 3. Covariate pairplot and correlation coefficients for variables used to model the distribution of urial and ibex in the Hindu Kush Mountains of Wakhan National Park. The plots below the diagonal represent bivariate scatterplots for each pair of covariates: elevation, slope, aspect, Terrain Roughness Index (TRI), Normalized Difference Vegetation Index (NDVI) and distance to the nearest human disturbance. The corresponding numbers above the diagonal are the corresponding Pearson correlation coefficients.

the same procedure as for the survey points. Kernel density estimates were created for each factor as described above. To estimate sampling envelopes for each factor, 1000 simulations were performed (generating 1000 kernel density estimates of randomly chosen points). The upper and lower bounds of the envelope were calculated as the upper and lower 2.5 percentiles at each of the 512 values for which densities were estimated.

To quantify the amount of niche overlap between the two species, environmental niche models (ENMs) were constructed and compared using MAXENT as implemented in the ENMTools package in R (Warren and Dinnage, 2022). MAXENT models for both species were created using 10,000 background points. The numbers of presence points in the models were 93 and 205 for urial and ibex, respectively (Table 1). MAXENT models used the covariates elevation, slope, aspect, TRI, distance to disturbance, and NDVI. (Fig. 3). The performance of the MAXENT models was evaluated using the receiver-operator area under the curve (AUC) metric (Araújo et al., 2005). The same concave hull used for the envelope analysis was used to constrain the locations of background points. By using a conservative buffer width, we aimed to avoid the artificial inflation of the model evaluation metric (receiver-operator area under the curve), which can be misleadingly high when background points from outside the species' range are included (Lobo et al., 2008).

There are a number of commonly used statistics to quantify niche overlap in MAXENT models, each having a set of advantages, disadvantages, and assumptions (Warren et al., 2008; Rödder, and Engler, 2011). We chose to use three common statistics: Warren's I (Warren et al., 2008), Schoener's D (Schoener, 1968), and the Spearman correlation coefficient (Warren et al., 2021). These three statistics were reported because of their history of use in ENM literature and their ease of interpretation: 0 = no overlap, 1 = complete niche overlap (Warren et al., 2008). We used the *identity.test()* function in R to examine the niche equivalency between the two species. To perform a significance test, the function *identity.test()* was used where a random relabeling technique in which empirical models are first created, and the niche overlap statistics calculated. We used this function to create 1000 replicate resampled models, each using 10,000 background points.

Since MAXENT models use a randomly selected set of background points, the empirical values of the three overlap statistics can vary (Sillero and Barbosa, 2021). To account for the variance in these statistics, we created 100 pairs of models, calculated the statistics, and used the mean values to calculate approximate p-values. To calculate approximate significance, we plotted histograms of the null distribution of the three statistics and compared the mean values of the empirical models. In addition, we used the *ecdf()* function in R to create empirical cumulative distribution functions of the null distributions of the three statistics, and computed the p-values using the mean values of the empirical statistics.



Fig. 4. Kernel density plots of urial and ibex habitat use in the Hindu Kush Mountains compared to 95 % H₀ density envelope for terrain variables (elevation, slope, aspect, TRI), NDVI, and distance to nearest disturbance. The red and blue lines correspond to the observed kernel densities for urial and ibex, respectively, while the lower and upper bounds of the gray region represent the 2.5 % and 97.5 % percentiles of kernel densities.

4. Results

4.1. Envelope analysis

Urial and ibex showed significant elevational differences (p-value 0.001) in their habitat use. Ibex stayed at relatively higher elevations (mean = 3651 m, range = 2826-4642) as compared to urial (mean = 3406, range = 2842-4246). Both the species used areas from 3000 to 4200 m elevation the most, above which there was a sharp decline in their elevational use (Fig. 4).

Ibex seem to be less selective than urial in using slopes across their habitats; the distribution of slopes at ibex herd locations mostly fell within the confidence envelope of slopes at randomly-selected locations for the study area. Both species avoided flat areas, particularly valley bottoms, with slopes less than 22 %, but urial also avoided slopes above 60 % and tended to occur at mid-range slopes (Fig. 4).

The distribution of slope direction (aspect) in the study area were primarily North, Northwest, West, Southwest, with South-facing areas, reflecting the directional orientation of the glacial river valleys. Both urial and ibex mostly used areas in proportions that were available as shown by the curves primarily falling within the 95 % confidence envelope (Fig. 4). Urial used southeast-facing slopes more, and west-facing slopes less than available. Ibex, on the other hand, were mostly within the 95 % envelope with a slightly more than expected use of southwest-facing slopes (much more than did urial; Fig. 4).

Most of the study area consisted of areas with TRI in the range of \sim 15–60. Similar to the pattern with elevation, urial seem to be relatively selective compared to a more generalist use of terrains by ibex (Fig. 4). Both species avoided areas of low TRI (approximately 15 or less). Urial were most concentrated in areas with TRI of approximately 20–40, being found in these areas much more frequently than expected by chance. The ibex curve fell almost entirely within the confidence envelope, illustrating their generalist nature with regard to terrain roughness.

Habitat use with respect to distance to human activity areas (e.g., villages and agricultural lands) were different for ibex and urial (Fig. 4). Ibex seemed to utilize locations in proportion to what was available, except for areas 500 m from human activity areas that,



Fig. 5. MAXENT variable importance diagrams for the ibex and urial models. The histograms show the distributions of variable importance for 1000 permutations. 'tri' = Terrain Ruggedness Index, and 'dist_to_disturb' = Distance to Human Disturbance.

like urial, were used little. In contrast to ibex, urial seemed to be much more selective and mostly utilized habitats less far from human activity areas and showed a sharp decline at distances > 3500 m from human activity areas (Fig. 4).

Urial and ibex interaction with the vegetation cover in their habitats, as indicated by the Normalized Difference Vegetation Index (NDVI), were very similar to each other (Fig. 4). Both species utilized the higher quality vegetation areas (areas above zero values for NDVI) and showed the same avoidance of lower quality areas.

4.2. Environmental niche models and overlap

The environmental niche models for both urial and ibex performed better than random, with area under the receiver-operator curve (AUC) values of 0.80 (ibex) and 0.91 (urial) indicating good and excellent model fits, respectively (Araújo et al., 2005). For the ibex model, the most important predictor was elevation, followed by slope, while for urial the most important predictor was slope, followed by elevation (Fig. 5). The empirical values of Warren's I (Monte Carlo p-value 0.001), Schoener's D (p 0.001), and the rank



Fig. 6. MAXENT niche overlap significance for urial and ibex in the Hindu Kush Mountains of Wakhan National Park, Afghanistan. Histograms show the distribution of the three niche overlap statistics under a random relabeling null hypothesis. The dotted lines are the empirical values of the test statistics.

Warren's I

correlation (p 0.001) were all much lower than most of the values under the null hypothesis of no niche differentiation (Fig. 6). This indicates that the two species occupy significantly different niches in spring during the day in WNP.

5. Discussion

The Siberian ibex is typically found in areas characterized by steep slopes, precipitous terrains and rocky screes either above the tree line (Ahmad et al., 2022), or at lower elevations such as foothills to high mountain ridges and sometimes far from higher mountains (Peterson, 2016; Reading et al., 2020). The present study confirms that in Wakhan during daytime the species can use areas with steepest slopes, but is also present in areas of less rugged terrains relatively distant from human settlements and where it can benefit from good forage conditions. The flexibility of the species at using a variety of habitats, including amongst the harshest as escape grounds, might explain its persistence in areas where it is exposed to significant poaching pressure (Bradfield and Rajabi, 2018).

In contrast, the urial in Wakhan seems to prefer areas of moderate roughness and is particularly averse to steepest slopes, a characteristic common to all species of the genus *Ovis*. A similar pattern of habitat use was noticed in Ladakh, India, where the species occupies high-altitude, semi-desert habitats consisting of open, stony hillsides lying between the bottom of the river valleys and the high mountain peaks on the lowest and most accessible slopes (Mallon, 1983; Khara et al., 2021). In Gilgit-Baltistan, Pakistan, urial also prefer intermediate slopes versus gentle or steep slopes (Siraj-ud-Din et al., 2018). Inevitably this habitat preference coupled to the fact that the species is not reluctant to use areas closer to human settlements makes the species particularly vulnerable to poaching, one of the major causes of population decline and local extinction observed across its distribution range (Michel and Ghoddousi, 2020).

The comparative study of niche ecology of ibex and urial in spring in Wakhan parallels observations concerning the general distribution of sympatric wild sheep and goats in mountains of Asia. Schaller (1977) suggested from his field observations an ecological separation between sympatric wild sheep and goats of similar size, with sheep occupying more undulating terrain and goats the precipices. Such habitat use pattern was confirmed in sympatric argali sheep and ibex, for which limited co-occurrence between the two species is largely driven by terrain ruggedness, which positively influences ibex and negatively affects argali occupancy (Odonjavkhlan et al., 2021). Similarly, in Nepal blue sheep *Pseudois nayaur* occur in areas that are less rugged with rolling mountains, whereas sympatric ibex occur in areas with more rugged and steeper mountains (Namgail, 2006; Ghoshal et al., 2019).

Like in the other parts of the world (e.g., Schaller, 1977; Fox et al., 1991; Siraj-ud-Din et al., 2018), seasonality may also affect the distribution of ibex and urial in Wakhan. We recognize that our work only occurred in spring when, for example, others reported that "ibex use lower, south facing slopes" (Reading et al., 2020). Distribution of blue sheep as related to elevation, slope, and distance to nearest cliffs, for example, varied with season and whether or not they were sympatric with urial and/or ibex (Namgail et al., 2009). Snow cover in higher elevations push urial and ibex to lower areas and south facing slopes in spring in Wakhan where it is relatively warmer with no or relatively less snow cover and early arise of fresh forage (Moheb et al., 2022). Descending to lower and rather concentrated areas close to human settlements exposes these mountain ungulates to livestock encounters and diseases transmission (Richomme et al., 2006). It also increases the urial and ibex vulnerability to poachers when they concentrate in relatively smaller areas favored by poachers (Ghoddousi et al., 2022).

Urial in Wakhan have a restricted and patchy distribution compared to more uniformly distributed ibex (Moheb et al., 2022). Urial as a true sheep species, utilizes relatively lower elevation and more undulating terrain that overlaps with livestock range in Wakhan. The presence of excessive number of livestock around urial populations in Wakhan (Moheb, 2020) is likely to expose urial to an uneven competition over resource. Although competition over resources among mountain ungulates and livestock is not the focus of this research, we believe such relationship is important for conservation of the mountain ungulates and it needs to be studied in the future.

In Afghanistan, urial populations near major urban centers appeared to have declined significantly due to indiscriminate poaching pressure (Habibi, 1997). Urial suffer excessive poaching across their distribution range within and outside Afghanistan which is considered as a major cause of the species' local extinction in some parts of its range (Michel and Ghoddousi, 2020). While urial poaching has not been explicitly studied in Wakhan, circumstantial facts supported by monitoring results (e.g., Moheb et al., 2022) suggest that the species suffers excessive poaching. The present study findings - that urial occupy lower areas, easily accessible to poachers - will guide geographically more focused surveillance and thus strengthen conservation measures on flatter areas near human settlements where the species forages in spring, shortly before lambing.

Similar to urial, ibex are also exposed to poaching in Wakhan (Rajabi, 2018); however, given the nature of ibex as a cliff species, they tend to be more resilient than sympatric urial. Our results suggest that ibex utilize steep slopes that are relatively hard to access and farther away from human habitations, which enable the species to avoid poaching to some extent. Even though ibex habitat use seems more protective, our results suggest that ibex would also likely use flatter areas if poaching and competition over resources with domestic stock were controlled.

Ultimately the current distribution of ibex and urial will likely be affected by changing climate conditions over the relative near future. Elsen et al. (2022) predicted that the range size of mountain ungulate species (including ibex and urial) in north-east Afghanistan will decrease by the end of century with a larger decrease of priority habitat under higher carbon emission scenarios. Similarly, Ali et al. (2021) hypothesized that both ibex and blue sheep will lose a significant part of their habitats, particularly in the Himalayan and Hindu Kush ranges. We hypothesize that this distribution range will result mainly from resource scarcity. Because ibex seem to be less specialized in their habitat preferences compared to urial, it is possible that the latter species would be less successful at accessing rarified forage and prove less resilient to climate change than the former. The recently observed decline of urial in Wakhan versus a relatively stable population of ibex is aligned with this hypothesis (Moheb et al., 2022).

6. Conclusions

This research indicates that there are some differences in daytime habitat use of Siberian ibex and urial occupying the Hindu Kush range in Wakhan National Park. Ibex utilizes not just the steepest slopes but it is also found in less rugged terrains far from human activity areas. The generalist habitat use of ibex increases its persistence against poaching and makes it relatively safer compared to sympatric urial that utilizes a more specific habitat type and areas relatively closer to human activity areas. This study focused only on the habitat use of ibex and urial in spring where these animals are driven to lower areas to get warmer weather and fresh forage. This season is just before the parturition period and therefore it is of high biological significance for urial and ibex; climate models predict low habitat quality that could lead to fetus absorption and less yearly population increase. Understanding that urial occupy lower areas, easily accessible to poachers will inform a more focused spatio-temporal protection of the species and thus strengthen conservation measures on flatter areas near human activity areas where the species forages in spring, before lambing. Findings of this study suggest that urial would be less successful at accessing needed forage and prove less resilient to climate change than the sympatric ibex.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data Availability

Data will be made available on request.

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References

- Ahmad, S., Strelnikov, I.I., Ahmad, A., Rajpar, M.N., Khan, M.Z., Wanghe, K., Ahmad, I.M., Nabi, G., Li, D., 2022. Recent advances in ecological research on Asiatic ibex (*Capra sibirica*): a critical ungulate species of highland landscapes. Glob. Econ. Conserv. 35, e02105.
- Ali, H., Din, J.U., Bosso, L., Hameed, S., Kabir, M., Younas, M., Nawaz, M.A., 2021. Expanding or shrinking? Range shifts in wild ungulates under climate change in Pamir-Karakoram Mountains, Pakistan. PLoS One 16 (12), e0260031.
- Araújo, M.B., Pearson, R.G., Thuiller, W., Erhard, M., 2005. Validation of species-climate impact models under climate change. Glob. Change Biol. 11, 1504–1513. https://doi.org/10.1111/j.1365-2486.2005.01000.x.
- Bagchi, S., Ritchie, M.E., 2010. Herbivore effects on above- and belowground plant production and soil nitrogen availability in the Trans-Himalayan shrub-steppes. Oecologia 164, 1075–1082.
- Bradfield, D., Rajabi. A.M., 2018. Winter operational plan for community rangers in the Wakhan National Park, Afghanistan (2018–2019). Wildlife Conservation Society, Kabul, Afghanistan. 7pp.
- Bragin, N., Amgalanbaatarb, S., Wingard, G., Reading, R.P., 2017. Creating a model of habitat suitability using vegetation and ruggedness for *Ovis ammon* and *Capra sibirica* (Artiodactyla: Bovidae) in Mongolia. J. Asia-Pac. Biodivers. 10, 390–395.
- Brown, C.L., Hardy, A.R., Barber, J.R., Fristrup, K.M., Crooks, K.R., Angeloni, L.M., 2012. The effect of human activities and their associated noise on ungulate behavior. PLoS One 7 (7), e40505.
- Elsen, P.R., Faryabi, S.P., Surya, G.S., Grantham, H.S., 2022. Climate Change Vulnerability Assessment for the Panj-Amu River Basin, Afghanistan. WCS unpublished report, New York, 456pp.

Fedosenko, A.K., Blank, D.A., 2001. Capra sibirica. Mamm. Spec. 675, 1–13.

- Fox, J.L., Nurbu, C., Chundawat, R.S., 1991. The mountain ungulates of Ladakh. India Biol. Conserv. 58, 167–190.
- Ghoddousi, A., Van Cayzeele, C., Negahdar, P., Soofi, M., Hamidi, K.H., Bleyhl, B., Fandos, G., Khorozyan, I., Waltert, M., Kuemmerle, T., 2022. Understanding spatial patterns of poaching pressure using ranger logbook data to optimize future patrolling strategies. Eco. Applications. p.e2601.
- Ghoshal, A., Bhatnagar, Y.V., Pandav, B., Sharma, K., Mishra, C., Raghunath, R., Suryawanshi, K., 2019. Assessing changes in distribution of the Endangered snow leopard *Panthera uncia* and its wild prey over 2 decades in the Indian Himalaya through interview-based occupancy surveys. Oryx 53, 620–632.
- Gombin, J., Vaidyanathan, R., Agafonkin, V., 2020. Concaveman: A very fast 2D concave 627 hull algorithm. (https://CRAN.R-project.org/package=concaveman). Habibi, K., 1997. Afghanistan. Pp. 202–211 In Shackleton, D.M. (ed.) and the IUCN/SSC Caprinae Specialist Group. Wild Sheep and Goats and their Relatives. Status Survey and Conservation Action Plan for Caprinae. IUCN, Gland, Switzerland and Cambridge, UK. 390 + vii pp.

Han, L., Wang, Z., Blank, D., Wang, M., Yang, W., 2021. Different environmental requirements of female and male Siberian ibex, *Capra sibirica*. Sci. Rep. 11, 1–9. Hijmans, R.J., 2020. raster: geographic data analysis and modeling. R. Package Version 3, 0–12. (https://CRAN.R-project.org/package=raster). Horn, B.K.P., 1981. Hill shading and the reflectance map. Proc. IEEE 69, 14–47.

Khan, M., Zahler, P., 2004. Status and new records of Ladakh urial (*Ovis orientalis vignei*) in northern Pakistan. Newsl. IUCN/SSC Caprinae Spec. Group 1–3. Khara, A., Khanyari, M., Ghoshal, A., Rathore, D., Pawar, U.R., Bhatnagar, Y.V., Suryawanshi, K.R., 2021. The forgotten mountain monarch? Understanding conservation status of the vulnerable Ladakh urial in India. Eur. J. Wildl. Res. 67, 62. Leki, Thinley, P., Rajaratnam, R., Shrestha, R., 2018. Establishing baseline estimates of blue sheep (Pseudois nayaur) abundance and density to sustain populations of the vulnerable snow leopard (Panthera uncia) in Western Bhutan. Wildl. Res. 45, 38–46.

Li, J., Xue, Y., Liao, M., Dong, W., Wu, B., Li, D., 2022. Temporal and spatial activity patterns of sympatric wild ungulates in Qinling Mountains, China. Animals 12, 1666. https://doi.org/10.3390/ani12131666.

Lobo, J.M., Jimenez-Valverde, A., Real, R., 2008. AUC: A misleading measure of the performance of predictive distribution models. Glob. Econ. Biogeogr. 17, 145–151. https://doi.org/10.1111/j.1466-8238.2007.00358.x.

Lyngdoh, S., Shrotriya, S., Goyal, S.P., Clements, H., Hayward, M.W., Habib, B., 2014. Prey preferences of the snow leopard (*Panthera uncia*): regional diet specificity holds global significance for conservation. PLoS One 9 (2), e88349.

Mallon, D., 1983. The status of Ladakh urial Ovis orientalis vignei in Ladakh. India Biol. Conserv. 27, 373-381.

Manier, D.J., Hobbs, N.T., 2007. Large herbivores in sagebrush steppe ecosystems: livestock and wild ungulates influence structure and function. Oecologia 152, 739–750.

Michel, S., 2010. Conservation of Tajik markhor (*Capra falconeri heptneri*) and urial (*Ovis vignei*) in Tajikistan and adjacent Afghanistan. Galemys 22, 407–419. Michel, S., Ghoddousi, A., 2020. Ovis vignei. The IUCN Red List of Threatened Species2020: e.T54940655A54940728.

Moheb, Z., 2020. Livestock Predation and Snow-leopard-human Conflict in the Wakhan Valley of Wakhan National Park, Northern Afghanistan (PhD thesis). University of Massachusetts, Amherst, USA.

Moheb, Z., Mostafawi, S.N., Zahler, P.I., Fuller, T.K., 2018. Markhor and Siberian ibex occurrence and conservation in northern Afghanistan. Caprinae N. 4–7. Moheb, Z., Rajabi, A.M., Jahed, N., Ostrowski, S., Zahler, P.I., Fuller, T.K., 2022. Using double-observer surveys to monitor urial and ibex populations in the Hindu

Kush of Wakhan National Park, Afghanistan. Oryx 1–7. https://doi.org/10.1017/S0030605322000412. Moreira, A., Santos, M.Y., 2007. Concave Hull: A K-nearest neighbors approach for the computation of the region occupied by a set of points. International Conference on Computer Graphics Theory and Applications.

Namgail, T., 2006. Winter habitat partitioning between Asiatic ibex and blue sheep in Ladakh, northern India. J. Mt. Ecol. 8, 7-13.

Namgail, T., Mishra, C., De Jong, C.B., Van Wieren, S.E., Prins, H.H., 2009. Effects of herbivore species richness on the niche dynamics and distribution of blue sheep in the Trans-Himalaya. Diver. Distrib. 15, 940–947.

Nellemann, C., Reynolds, P.E., 1997. Predicting late winter distribution of muskoxen using an index of terrain ruggedness. Arct. Alp. Res. 29, 334–338.

Odonjavkhlan, C., Alexsander, J.S., Mishra, C., Samelius, G., Sharma, K., Lkhagvajav, P., Suryawanshi, K.R., 2021. Factors affecting the spatial distribution and cooccurrence of two sympatric mountain ungulates in southern Mongolia. J. Zool. 314, 266–274.

Oli, M.K., 1994. Snow leopards and blue sheep in Nepal: densities and predator: prey ratio. J. Mammal. 75, 998-1004.

Park, J.S., Oh, S.J., 2012. A new concave hull algorithm and concaveness measure for n-dimensional datasets. J. Info Sci. Eng. 28, 587-600.

Peterson, E.C., 2016. Modeling Siberian ibex (*Capra sibirica*) Occupancy in Ikh Nart Nature Reserve, Mongolia (M.S. Thesis). University of Vermont, USA. Pettorelli, N., Vik, J.O., Mysterud, A., Gaillard, J.M., Tucker, C.J., Stenseth, N.C., 2005. Using the satellite-derived NDVI to assess ecological responses to environmental change. Trends Ecol. Evol. 20, 503–510.

Pettorelli, N., Ryan, S., Mueller, T., Bunnefeld, N., Jędrzejewska, B., Lima, M., Kausrud, K., 2011. The Normalized Difference Vegetation Index (NDVI)- unforeseen successes in animal ecology. Clim. Res. 46, 15–27.

R Core Team., 2022. R: A Language and Environment for Statistical Computing, Vienna, Austria.

Rajabi, A.M., 2018. Report on environmental violations (poaching of wild species) in Pikut Valley. Original report in Dari. WCS unpublished report pp. 2.
Raza, G., Mirza, S.N., Anwar, M., Hussain, I., Khan, S.W., Ahmad, K., Nawaz, M.A., Ahmad, N., 2015. Population and distribution of Himalayan ibex, *Capra ibex sibrica*, in Hushe Valley, Central Karakoram National Park, Pakistan. Pak. J. Zool. 47, 1025–1030.

Reading, R., Michel, S., Suryawanshi, K., Bhatnagar, Y.V., 2020. Capra sibirica. The IUCN Red List of Threatened Species 2020:e.T42398A22148720.

Richomme, C., Gauthier, D., Fromont, E., 2006. Contact rates and exposure to interspecies disease transmission in mountain ungulates. Epidemiol. Infect. 134, 21–30.
Rödder, D., Engler, J.O., 2011. Quantitative metrics of overlaps in Grinnellian niches: advances and possible drawbacks. Glob. Ecol. Biogeogr. 20 (6), 915–927.
https://doi.org/10.1111/i.1466-8238.2011.00659.x.

Schaller, G.B., 1977. Mountain Monarchs. Wild sheep and goats of the Himalaya. University of Chicago Press, Chicago, Illinois, USA.

Schoener, T.W., 1968. Anolis lizards of Bimini: resource partitioning in a complex fauna. Ecology 49, 704–726.

Schoener, T.W., 1974. Resource partitioning in ecological communities: research on how similar species divide resources helps reveal the natural regulation of species diversity. Science 185, 27–39.

Shackleton, D.M., 1997. Wild sheep and goats and their relatives. Status survey and conservation action plan for Caprinae, IUCN/SSC Caprinae Specialist Group, Gland, Switzerland and Cambridge, UK. IUCN.

Sillero, N., Barbosa, A.M., 2021. Common mistakes in ecological niche models. Int. J. Geogr. Info Sci.. 35, 213-226.

Siraj-ud-Din, M., Minhas, R.A., Ali, U., Khan, M., Awan, M.S., Shafi, N., Ahmad, B., 2018. Habitat and feeding ecology of Ladakh urial (Ovis vignei vignei) in Gilgit-Baltistan. Pak. J. Zool. 50, 197–206.

Smallwood, P., Shank, C., 2019. "From Buffer Zone to National Park: Afghanistan's Wakhan National Park," in Collateral Values Landscape Series. Editors T. R. Lookingbill and P. D. Smallwood (Cham: Springer International Publishing), 213–233. https://doi:10.1007/978–3-030–18991-4_10.

Smallwood, P., Shank, C., Dehgan, A., Zahler, P., 2011. Wildlife conservation... in Afghanistan? Conservation projects multitask in conflict zones, blending development and conservation goals. BioScience 61, 506–511.

Soelberg, J., Jäger, A.K., 2016. Comparative ethnobotany of the Wakhi agropastoralist and the Kyrgyz nomads of Afghanistan. J. Ethnobiol. Ethnomed. 12 https://doi: 10.1186/s13002-015-0063-x.

Stankowich, T., 2008. Ungulate flight responses to human disturbance: a review and meta-analysis. Biol. Conserv. 141, 2159–2173.

Suryawanshi, K.R., Smout, S.C., Chaturvedi, V., Bhatnagar, Y.V., Redpath, S.M., Ramakrishnan, U., Mishra, C., 2017. Impact of wild prey availability on livestock predation by snow leopards. R. Soc. Open Sci. 4, 170026.

Warren, D., Dinnage, R., 2022. ENMTools: Analysis of niche evolution using niche and distribution models. R package version 1.0.6. (https://CRAN.R-project.org/package=ENMTools).

Warren, D.L., Glor, R.E., Turelli, M., 2008. Environmental niche equivalency versus conservatism: quantitative approaches to niche evolution. Evolution 62, 2868–2883.

Warren, D.L., Matzke, N.J., Cardillo, M., Baumgartner, J.B., Beaumont, L.J., Turelli, M., Glor, R.E., Huron, N.A., Simoes, M., Iglesias, T.L., Piquet, J.C., Dinnage, R., 2021. ENMTools 1.0: an R package for comparative ecological biogeography. Ecography 44, 504–511.

Wilson, M.J., O'Connell, B., Brown, C., Guinan, J.C., Grehan, A.J., 2007. Multiscale terrain analysis of multibeam bathymetry data for habitat mapping on the continental slope. Mar. Geodesy. 30, 3–35.

Yang, C., Zhang, P., Wu, Y., Dai, Q., Luo, G., Zhou, H., Zhao, D., Ran, J., 2021. Livestock limits snow leopard's space use by suppressing its prey, blue sheep, at Gongga Mountain, China. Glob. Econ. Conserv. 29, e01728 https://doi.org/10.1016/j.gecco.2021.e01728.

Zandler, H., Haag, I., Samimi, C., 2019. Evaluation needs and temporal performance differences of gridded precipitation products in peripheral mountain regions. Sci. Rep. 9, 15118. https://doi.org/10.1038/s41598-019-51666-z.

Zandler, H., Faryabi, S.P., Ostrowski, S., 2022. Contributions to satellite-based land cover classification, vegetation quantification and grassland monitoring in Central Asian Highlands using Sentinel-2 and MODIS data. Front. Environ. Sci. 1–19. https://doi.org/10.3389/fenvs.2022.684589.