


Factors affecting the spatial distribution and co-occurrence of two sympatric mountain ungulates in southern Mongolia

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Keywords

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Abstract

Co-occurrence of ungulates in multi-species assemblages has fascinated ecologists because these species seemingly belong to the same guild – feeding on plants. Across large parts of the high mountains of Central Asia, ibex (*Capra sibirica*) and argali (*Ovis ammon*), both predominantly grazers, co-occur at local and regional scales. However, little is known about the ecological and anthropogenic factors that influence their spatial distribution, co-occurrence and habitat use. We examined factors affecting the distribution and co-occurrence of these two sympatric species in Tost Tosonbumba Nature Reserve in southern Mongolia using an occupancy modeling approach. Specifically, we used single species occupancy models to examine the influence of road density, livestock density, terrain ruggedness and elevation on occupancy of these two species separately. We then assessed how these two species influence each other's distribution by using multi-species occupancy models. The model-averaged occupancy probabilities for ibex and argali were 0.64 ± 0.3 SE and 0.44 ± 0.2 SE, respectively. Terrain ruggedness positively influenced ibex distribution, while it negatively affected the occupancy of argali. We found limited evidence of relationship with factors associated with human disturbance. The species interaction factor, which indicates the level of co-occurrence, suggested that ibex and argali occurred independent of each other ($\phi = -0.72 \pm 0.3$ SE). Together, our results imply that there was limited co-occurrence between the two species and that this was largely driven by terrain ruggedness at the scale of the home range. These results suggest that topography plays an important role in enabling these two species to co-occur at the regional scale.

Introduction

Spatial variation in biotic and abiotic factors influences the distribution of species (Brown, 1984; Verberk, 2011). Although large scale distribution patterns of species may be determined by evolutionary history, resource distribution and connectivity of the landscape, fine scale distribution patterns are often explained by the interplay of abiotic (e.g. temperature, rainfall) and biotic factors (e.g. competitors, food availability) (Brown, 1984; Verberk, 2011). When sympatric species share similar ecological niches in resource limited systems, the interaction between them can be strongly competitive (Yoshihara *et al.*, 2008; Estevo *et al.*, 2017). In such cases, the dominant species may push the subordinate species to less suitable habitats or even local extinction (Namgail *et al.*, 2007; Singh *et al.*, 2010; Estevo *et al.*, 2017). This sparks the question of how

ungulates, dependent on similar species of plants, can co-occur as multi-species assemblages. Variation in body mass (Prins & Olf, 1998), species-specific feeding adaptations (Hofmann, 1989; Gordon & Prins, 2008), species-specific predator avoidance strategies (Sinclair, 1985), variation in use of micro-habitats (Namgail *et al.*, 2004; Ashraf *et al.*, 2014) have all been used to explain the co-occurrence of ungulates.

Larger-bodied herbivores are better able to process and survive on relatively low-quality forage, compared to smaller bodied ones (Peters & Peters, 1986). Also, by feeding on coarse grass and reducing its biomass, larger-bodied species can improve forage quality (Olf *et al.*, 2002). This can allow for some level of species co-occurrence based on differences in body mass – smaller species can benefit from the presence of larger species – however, if species are similar in body mass, they will tend to compete. Ibex *Capra sibirica* and argali *Ovis*

ammon are the largest and heaviest species in their respective genera. They differ in body size though with adult male argali weighing about 90 kg on average and adult male ibex weighing 75 kg on average (Reading *et al.*, 1997; Fedosenko & Blank, 2001; Mishra *et al.*, 2016). Although mean adult body mass of ibex and argali is different, there is significant overlap in body mass between different age and sex classes of these species and there is, therefore, a potential for both facilitation and competition between these two mountain ungulates (Bagchi *et al.*, 2004; Namgail *et al.* 2009; Wingard *et al.*, 2011). Ibex and argali are strictly diurnal and graze actively from early morning to late afternoon (Fox *et al.*, 1992; Bhatnagar, 1997; Xu *et al.*, 2012; Xue *et al.*, 2018). Ibex and argali are sympatric across large parts of their distribution and both species are predominantly grazers which suggest that interspecific competition may be at play (Fedosenko & Blank, 2001; Bagchi *et al.*, 2004; Fedosenko & Blank, 2005; Mishra *et al.*, 2016).

Throughout their distribution, ibex and argali co-occur alongside pastoralists who herd large number of livestock (Dulamtsuren, 1970; Nanmnandorj, 1976; Dulamtseren *et al.*, 1989). Bagchi *et al.*, (2004) found that livestock and herders have a negative impact on ibex through interference competition. Negative impacts of interference and scramble competition from livestock have also been seen on argali (Namgail *et al.*, 2007; Wingard *et al.*, 2011). For effective conservation and management of these species, it is important to understand the factors that influence their distribution and co-occurrence. The primary objectives of this study were to examine factors affecting the distribution and co-occurrence of ibex and argali, at the scale of their home range in southern Mongolia. Although the two species share the same food resources, and overlap in terms of body mass, they have a different evolutionary history where ibex evolved as climbers and argali evolved a cursorial behavior (Geist 1991; Schaller, 1983). These different evolutionary paths suggest a potentially different use of lands. Ibexiforms are known to be adapted to rugged and steep terrains, Ovis are known to be much more adapted to rolling hilly terrains. Given the ecology of the two species, we hypothesize that terrain ruggedness to be the most important determinant in habitat separation between these two species. We predict the distribution of ibex to be positively correlated with terrain ruggedness while the distribution of argali to be negatively correlated with ruggedness. We also hypothesize that human disturbances associated with livestock grazing and roads would have a negative influence on the distribution of both the species. We used the occupancy framework (Mackenzie *et al.*, 2002) which accounts for imperfect detection and we assessed the potential direct impact that these two species have on the distribution of each other by using the novel multi-species co-occurrence occupancy models.

Materials and methods

Study area

We conducted this study in the Tost Mountains (43.10°N, 100.40°E) in the Tost Tosonbumba Nature Reserve in South

Gobi, Mongolia (Fig. 1). The elevation of the Tost Mountains ranges from 1900 to 2500 m above sea level and the average annual precipitation ranges from 50 to 150 mm with the majority of precipitation falling in summer. Average snowfall in winter ranged from 2 to 4 cm. The temperature range from as low as −35°C in winter to up to +40°C in summer. Major wildlife species found in the Tost Mountains include ungulates such as argali, ibex, and goitered gazelle *Gazella subgutturosa* and carnivores such as the snow leopard *Panthera uncia*, wolf *Canis lupus* and red fox *Vulpes vulpes*. Ibex and argali constitute about two thirds of the snow leopard diet in this area and are important prey species for the snow leopard across the distribution (Johansson *et al.*, 2015; Suryawanshi *et al.*, 2017).

Nearly 7000 km² of the area around Tost Tosonbumba Mountains were declared a local protected area in 2012. The status of the Tost Tosonbumba Mountains was upgraded to Nature Reserve in 2016 and the reserve was extended and now covers a total area of 8430 km². About 20% of the reserve is mountainous, whereas the rest (80%) is steppe. We conducted our study in 945 km² at the center of the nature reserve which consisted of a mixture rugged and more gentle mountains with about equal representation by these two habitats in the study area (Fig. 1).

Data collection

We surveyed ungulates in the Tost Mountains between December 2017 and February 2018. We overlaid the Tost mountain range with 63 grid cells that were 5 × 3 km in size using QGIS 3.3 (QGIS Development Team, 2014), encompassing an area of 945 km² across all the grids cells (Fig. 1). We chose this area because previous surveys showed that ibex and argali were both present in this region (Tumursukh *et al.*, 2016). Argali and ibex home range size in south-central Mongolia is estimated to range between 15 and 20 km², but in winter decreasing to some extent (Reading *et al.*, 2007). We chose a grid size of 15 km² to approximate the home range size of both species during the winter, ensure that we were able to sufficiently represent it with our 6–7 km long surveys, and avoid concerns of non-independence between grid cells even though from a species-level perspective it is immaterial whether neighboring units are occupied by the same or different individuals (Mackenzie *et al.* 2018). Within each grid cell, we identified one transect along the main ridgeline or valley in order to maximize the visual coverage of the area using viewshed in QGIS. The length of the transects ranged from 6 to 10 km (average 7.8 km) where the length of the transects varied in relation to the topography of the grid cells. One observer walked the transect and recorded all sightings of ibex and argali. The observer walked at a constant speed of *c.* 2–3 km per hour. Our grid cells covered a total 492 km with a mean of 7.8 km (SE = 0.58) walked per grid cell.

Each transect was divided into one km segments and the presence of ibex and argali were recorded for each segment. For each observation, we recorded information on group size, age class and sex of all individuals of the group, and GPS location and distance from the observer. We used the one km segments within each grid cell as spatial replicates for each

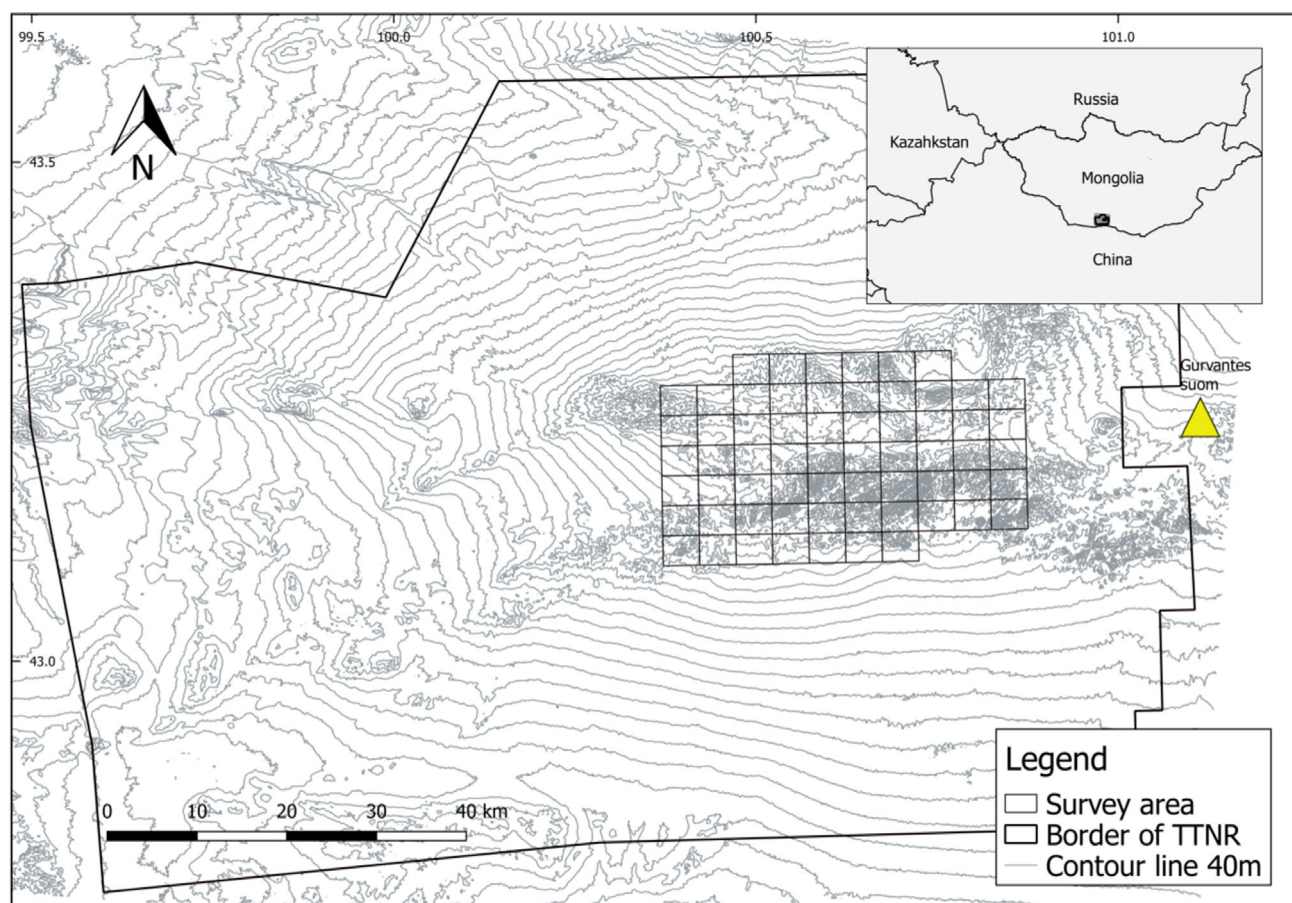


Figure 1 Map of Tost Tosonbumba Nature Reserve with survey area overlaid with 63 grids of 5 × 3 km each. Thin gray lines are 40 m elevation contour lines. Also shown on the map is the town of Gurvantes, South Gobi, Mongolia.

grid cell in our occupancy modeling (Mackenzie *et al.*, 2002; Mackenzie *et al.*, 2004; Hines *et al.*, 2010). We tested for independence of the spatial replicates within each grid cell following Hines *et al.*, (2010). The spatial replicates were independent for both species (details in section Single species single season models) so we used non-correlated models in our final analyses. Finally, we developed encounter histories for each grid cell that consisted of detection (1) and non-detection (0) for each one km segment within the grid cells.

Sampling of covariates

We recorded information on five covariates that could potentially affect the detection and occupancy of ibex and argali. We expected weather (especially snow fall) to influence our ability to detect ibex and argali. We therefore recorded if it was snowing while walking the transects. Previous studies have shown that livestock can have a negative impact on the distribution of ungulates (Bagchi *et al.*, 2004; Wingard *et al.*, 2011; Berger *et al.*, 2013) therefore we recorded the number of livestock grazing in each grid cell at the time of the survey.

The terrain ruggedness and elevation were included as predictors of ibex and argali occurrence in each cell. We

calculated ruggedness using the terrain ruggedness index (Riley 1999) in QGIS using a digital elevation model (DEM) with 90 m spatial resolution downloaded from Landsat Shuttle Radar Topography Mission (SRTM) (Jarvis *et al.*, 2008). We estimated the mean of elevation and ruggedness for each grid to be used as site covariates.

The disturbance caused by vehicles on well-marked gravel roads was also expected to influence the distribution of ungulates. Therefore, we included road density (calculated as the total length of road in each grid cell) as one of the explanatory variables for site occupancy in our analyses.

All continuous covariates (Table 1) were standardized to z-scores before analysis. We also examined the correlation between all covariates using the Pearson correlation test. All correlation values were <0.13.

Data analyses

Single species single season models

First, we tested whether the correlated or non-correlated versions of the single species models fitted our data better (Mackenzie *et al.*, 2002; Hines *et al.*, 2010). For ibex, the

Table 1 Description of covariates used in the occupancy analyses of ibex and argali in the Tost Mountains

| Covariate and abbreviation | Description of covariate | Expected influence on occupancy and detection |
|----------------------------|---|--|
| Terrain ruggedness (rugg) | Mean of ruggedness for each grid | Positive effect on ibex' occupancy Negative effect on argali' occupancy |
| Elevation (elev) | Mean of elevation above mean sea level for each grid | Positive effect on ibex' occupancy Negative effect on argali' occupancy |
| Precipitation (snow) | Whether it was snowing or not when walking the transect | Negative effect on detection probability of ibex and argali |
| Livestock density (livst) | Livestock number in each site divided by the size of the site | Negative effect on both occupancy and detection probability of ibex and argali |
| Road density (road) | Length of roads per site divided by the size of the site | Negative effect on occupancy and detection probability of both species |
| Effort (effort) | Walking distance for each grid | Positive effect on occupancy and detection probability of both species |

delta AIC difference between the correlated and non-correlated model was 5.41 AIC units, but the correlated model failed to converge (Table 2). For argali, the non-correlated model was 3.84 AIC units lower than correlated model (Table 2), and it was the only model that converged for ibex, and hence it was used for all further analyses (Burnham & Anderson, 2002).

We developed 10 candidate models (see Table 3) each for ibex and argali where we included four covariates for occupancy [Ψ] (*terrain ruggedness + elevation + livestock + road density*) and one covariate for detection probability [p] (*snow*) in the global model. We ran our analyses in program Presence version 12 (Hines, 2006) and we ranked the candidate models by using Akaike's Information Criterion (AIC) (Burnham & Anderson, 2002). We used model-averaged estimates in cases where the top models were within two AIC units.

Model fitting was assessed for over-dispersion by running a bootstrap goodness of fit tests for the best-fitting model of occupancy ($n = 1000$, bootstrapped samples). We used model weights to estimate the model-averaged estimates of probability of occupancy at each sampling unit, and probability of detection at each segment.

Co-occurrence models

To examine the potential impact that one species has on the other, we used multi-species occupancy models (Mackenzie *et al.*, 2004). We used the alternative parameterization in program Presence which estimates species interaction factors (SIF) to infer how each of the species affected the distribution of the other species (Richmond *et al.*, 2010). SIF values >1 mean that two species occur together more than expected by chance alone, and values <1 imply that two species occur together less than expected by chance. SIF equal to one indicates that the two species occur independently and do not impact the distribution of each other. We ran the models with both ibex and argali as the dominant species but the models converged only when using ibex as the dominant species.

Result

Single species single season model

Ibex and argali were detected in 70 and 27 of the 492 one km segments and in 35 and 25 of the 63 grid cells, respectively. Mean group size of ibex and argali was 4.6 (range: 1–18) and 5 (range: 1–16) individuals, respectively. Naïve occupancy estimates, without accounting for imperfect detection of ibex and argali were 0.55 and 0.25, respectively.

Single season single species occupancy models for ibex

Snow did not influence the detection of ibex (Table 3). We therefore used the constant detection model in our final analyses. The top ranked model for ibex included terrain ruggedness ($B_{\text{rugg}} = 3.7$; 95% SE = 1.5) and livestock ($B_{\text{livst}} = -0.85$; SE = 0.5) but the slope estimate for livestock overlapped with zero and the impact of livestock was thus unclear (Table 3). Since the difference in AIC values between the top models was small, we used model-averaged estimates of occupancy and detection probability. The model-averaged detection probability for ibex was 0.22 (SE = 0.03) per grid cell and the model-averaged occupancy probability was 0.64 (SE = 0.3) per grid cell (Fig. 2a).

Even though livestock was part of the top model, the slope estimate for livestock overlapped with zero for all models and the impact of livestock on occupancy was thus unclear (Table 3). Delta AIC of the models that included road density and elevation was greater than two (Table 3) and the impact of these variables on occupancy by ibex was thus limited.

Single season single species occupancy results for Argali

The top ranked model for argali included snow and effort as a covariate for detectability (Table 3). In all top models, the

Table 2 Model comparison for correlated and non-correlated occupancy models for Ibex and argali in the Tost mountains

| Species name | Model | AIC | delta | | Model Likelihood | K | Maximum Likelihood |
|--------------|--|--------|-------|---------|------------------|---|--------------------|
| | | | AIC | AIC wgt | | | |
| Ibex | psi,th0(),th1(),p(),th0pi() ^a | 386.28 | 0 | 0.9373 | 1 | 5 | 376.28 |
| | psi(.),p(.) | 391.69 | 5.41 | 0.0627 | 0.0669 | 2 | 387.69 |
| Argali | psi(.),p(.) | 200.49 | 0 | 0.8721 | 1 | 2 | 196.49 |
| | psi,th0(),th1(),p(),th0pi() | 204.33 | 3.84 | 0.1279 | 0.1466 | 5 | 194.33 |

AIC, Akaike's information criteria; delta AIC, difference in AIC; K, Akaike weight, number of parameters.

^aModel failed to converge.

Table 3 Model selection for covariates affecting occupancy and detection probability of ibex *Capra sibirica* and argali *Ovis ammon* in the Tost Mountains

| Species | Model | AIC | Delta AIC | AIC weight | Model Likelihood | K | Maximum Likelihood |
|---------|--|--------|-----------|------------|------------------|---|--------------------|
| Ibex | Psi (rugg + livst), p (.) | 370.33 | 0 | 0.2722 | 1 | 4 | 362.33 |
| | Psi (rugg + livst + road), p (.) | 370.98 | 0.65 | 0.1967 | 0.7225 | 5 | 360.98 |
| | Psi (rugg), p (.) | 372.07 | 1.74 | 0.114 | 0.419 | 3 | 366.07 |
| | Psi (rugg + livst + elev), p (.) | 372.11 | 1.78 | 0.1118 | 0.4107 | 5 | 362.11 |
| | Psi (rugg + livst + elev + road), p (.) | 372.51 | 2.18 | 0.0915 | 0.3362 | 6 | 360.51 |
| | Psi (rugg + livst + elev + road), p (snow) | 372.64 | 2.31 | 0.0858 | 0.3151 | 7 | 358.64 |
| | Psi (rugg + road), p (.) | 372.77 | 2.44 | 0.0804 | 0.2952 | 4 | 364.77 |
| | Psi (rugg + road + elev), p (.) | 373.82 | 3.49 | 0.0475 | 0.1746 | 5 | 363.82 |
| Argali | Psi, th0 (), th1 (), p (), th0pi () | 386.28 | 15.95 | 0.0001 | 0.0003 | 5 | 376.28 |
| | Psi (rugg), p (snow) | 190.06 | 0 | 0.3343 | 1 | 4 | 182.06 |
| | Psi (rugg + elev), p (snow) | 191.27 | 1.21 | 0.1826 | 0.5461 | 5 | 181.27 |
| | Psi (rugg + livst), p (snow) | 191.92 | 1.86 | 0.1319 | 0.3946 | 5 | 181.92 |
| | Psi (rugg + road), p (snow) | 192.06 | 2 | 0.123 | 0.3679 | 5 | 182.06 |
| | Psi (rugg + elev + livst), p (snow) | 193.27 | 3.21 | 0.0672 | 0.2009 | 6 | 181.27 |
| | Psi (rugg + elev + road), p (snow) | 193.27 | 3.21 | 0.0672 | 0.2009 | 6 | 181.27 |
| | Psi (rugg + livst + road), p (snow) | 193.92 | 3.86 | 0.0485 | 0.1451 | 6 | 181.92 |
| | Psi (rugg + elev + livst + road), p (snow) | 195.27 | 5.21 | 0.0247 | 0.0739 | 7 | 181.27 |
| | Psi (elev), p (snow) | 196.62 | 6.56 | 0.0126 | 0.0376 | 4 | 188.62 |
| | Psi (road), p (snow) | 199.33 | 9.27 | 0.0032 | 0.0097 | 4 | 191.33 |
| | Psi (livst), p (snow) | 199.42 | 9.36 | 0.0031 | 0.0093 | 4 | 191.42 |
| | Psi (rugg + elev + livst + road), p (.) | 200.82 | 10.76 | 0.0015 | 0.0046 | 6 | 188.82 |
| | Psi, th0 (), th1 (), p (), th0pi () | 204.33 | 14.27 | 0.0003 | 0.0008 | 5 | 194.33 |

Akaike's information criteria (AIC), difference in AIC (delta AIC), Akaike weight, number of parameters (K) and deviance (Maximum likelihood) are included in the table. Abbreviation of covariates: terrain ruggedness (rugg), elevation (elev), livestock density (livst) and road density (road).

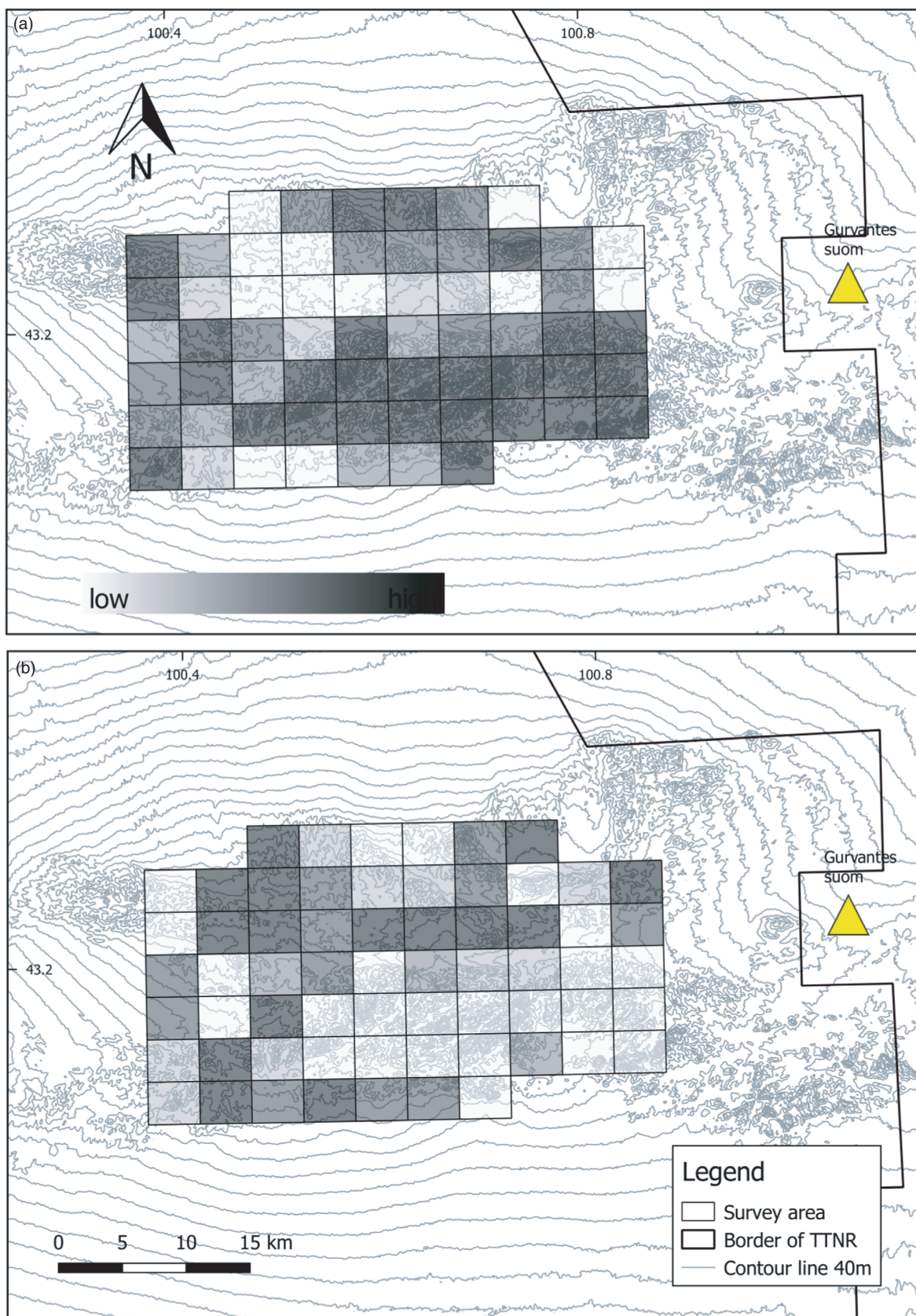
probability of detecting argali was predicted to be lower during surveys when it was snowing ($B_{\text{snow}} = -1.72$; $SE = 0.6$, Table 4). In the subsequent analysis, we used snow as a detection covariate and varied occupancy covariates. Among the candidate set of models, the model that included only ruggedness ranked as the top model with the lowest AIC (Table 3). Argali occupancy decreased with increasing ruggedness ($B_{\text{rugg}} = -1.67$; $SE = 1.0$). Average overall detection probability of argali was 0.13 ($SE = 0.06$). The model-averaged detection probability for argali was 0.22 ($SE = 0.03$) per grid cell and the model-averaged occupancy probability was 0.44 ($SE = 0.2$) per grid cell (Fig. 2b). Delta AIC of the models that included road density and elevation was greater than two (Table 3); the occupancy of

argali and the impact of these variables on occupancy by argali was thus limited.

Co-occurrence occupancy model

The estimated SIF was 0.72 ($SE = 0.3$). Since this is not statistically different from one, it suggests that both species occurs independent of each other. The results of the co-occurrence model show that the probability of occupancy of ibex was higher than that of argali 0.72 ($SE = 0.1$). The estimated occupancy of argali given presence of ibex (ψ^{BA}) was 0.4 ($SE = 0.3$), and estimated occupancy of argali where ibex was absent (ψ^{BA}) was 0.9 ($SE = 0.5$).

Figure 2 Ibex (a) and argali (b) distribution map in Tost Tosonbumba Nature Reserve, South Gobi, Mongolia based on model-averaged site-specific occupancy estimates. Darker colors indicated higher occupancy probabilities. Thin gray lines represent 40 m elevation contour.



Discussion

Co-occurrence of ungulates has puzzled scientists since the infancy of ecology. In this study, we found that ibex and argali – both predominantly grazers – used different parts of the mountains and that there was limited evidence of them affecting the distribution of each other at the local scale.

We found that ibex preferred the rugged areas of the mountains, whereas argali preferred gentler slopes of the mountains which is consistent with space use of these species in other areas (Fox *et al.*, 1992; Bhatnagar, 1997). Nomadic livestock herders of this region tend to herd their goats in the valley bottoms and on mountainsides in the steeper parts of the mountains during the winter to avoid strong winds of the steppe and more gentle parts of the mountains (Mijiddorj *et al.*, 2019). Their overlap with ibex is therefore likely greater than their overlap with argali that occupied the more open and less rugged areas of the mountains. Some of our models failed to converge. We suspect it was due to over-parameterization or sheer lack of a plausible relationship when attempting to model certain effects, including correlated detections. Given the limited dataset, we chose to limit our models to include a core set of covariates that were most likely to affect occupancy and detection, than manually seek convergence for more complex models. While it is unlikely to affect the overall results of our study, it is an area for improvement for future work.

Unlike some of the previous studies (e.g. Berger *et al.*, 2013; Ito *et al.*, 2013; Buuveibaatar *et al.*, 2016), we did not find evidence of the impact of human disturbances such as road density and livestock grazing on the distribution of ibex and argali. Although livestock was part of the top model for ibex occupancy, the coefficient value was not significant. Domestic goats – the predominant livestock of this region – are closely related to the ibex, and their diets have a significant overlap (Tumursukh, 2013). With increasing global demand for Pashmina wool, the goat population in the Tost bag (the smallest administrative unit in Mongolia) increased from about 30 000 in 2012 to about 60 000 in 2019 (Mongolian Statistical

Information Service) and is expected to increase and reduce the wild ungulate population (Berger *et al.*, 2013).

In our study, the lack of any significant effect of livestock and road density on ibex and argali's occurrence could be related to our study assessing the impacts of these variables at the scale of home ranges whereas potentially negative impacts of these variables may occur at different scales such as foraging patches as observed by Bagchi *et al.* (2004). Moreover, the human and road densities in our study area were very low which may explain differences in the impacts of these variables between our and previous studies that found negative impacts of human activity and livestock grazing (Bagchi *et al.*, 2004; Namgail *et al.*, 2007; Wingard *et al.*, 2011). The herders in the Tost Mountains are dispersed across the landscape with only about 90 families (owning on average one motorcycle and one four-wheel vehicle to move camps) in the entire study area and most of these families use the mountains only during winter (Mijiddorj *et al.*, 2018). Our results suggest that there was limited effect of humans and livestock on the distribution of ibex and argali in the Tost Mountains in winter. The majority of the herders move out of the mountains to the steppe habitat during the summer months and hence we expect the impact of human activity and livestock grazing to be less or equally low in summer. These results are likely to be specific to our study sites. The snow cover in the Tost Mountains is very limited and we therefore do not expect snow cover to have much impact on the distribution of these two species. We suggest that studies that evaluate the impact of factors such as distribution and amount of vegetation may provide further detail in the factors that affect how ibex and argali are distributed in space. In other words, at the scale of the grid cells represented by 15 km², we anticipated ibex to use more rugged areas that are typically represented by higher mountains. The rolling terrain preferred by argali on the other hand is typically represented by lower elevation in the study area.

Assessing co-occurrence of species distribution is often challenging (MacKenzie *et al.*, 2004; Richmond *et al.*, 2010). Here, we used two species occupancy modeling to incorporate

Table 4 Models specific beta estimates and model-averaged estimates for the site covariates from the top four models for ibex and argali

| Species | Model | B_0 (SE) | B_{rugg} (SE) | B_{elev} (SE) | B_{road} (SE) | B_{livst} (SE) | AIC weight |
|---------|--|-------------|------------------------|------------------------|------------------------|-------------------------|------------|
| Ibex | Psi (rugg + livst), p (.) | 1.85 (1.4) | 3.7 (1.5) | | | −0.85 (0.5) | 0.2722 |
| | Psi (rugg + livst + road), p (.) | 1.68 (0.8) | 3.7 (1.4) | | 0.47 (0.4) | −0.89 (0.5) | 0.1967 |
| | Psi (rugg), p (.) | 1.55 (0.9) | 3.0 (1.3) | | | | 0.114 |
| | Psi (rugg + livst + elev), p (.) | 1.85 (1.0) | 3.69 (1.5) | −0.22 (0.4) | | −0.8 (0.4) | 0.1118 |
| | Psi (rugg + livst + elev + road), p (.) | 1.7 (0.9) | 3.79 (1.5) | −0.3 (0.4) | 0.5 (0.4) | −0.85 (0.5) | 0.0915 |
| | Psi (rugg + livst + elev + road), p (snow) | 2.2 (1.3) | 4.4 (1.9) | −0.4 (0.5) | 0.55 (0.54) | −0.9 (0.5) | 0.0858 |
| | Psi (rugg + road), p (.) | 1.7 (1.1) | 3.34 (1.6) | | 0.52 (0.5) | | 0.0804 |
| Argali | Psi (rugg), p (snow) | −0.4 (0.5) | −1.67 (0.8) | | | | 0.3343 |
| | Psi (rugg + elev), p (snow) | −0.45 (0.5) | −1.41 (0.7) | 0.52 (0.6) | | | 0.1826 |
| | Psi (rugg + livst), p (snow) | −0.41 (0.5) | −1.72 (0.8) | | | 0.13 (0.3) | 0.1319 |
| | Psi (rugg + road), p (snow) | −0.4 (0.5) | −1.67 (0.8) | | 0.05 (0.3) | | 0.123 |
| | Psi (rugg + elev + livst), p (snow) | −0.45 (0.5) | −1.41 (0.7) | 0.52 (0.6) | | −0.0009 (0.3) | 0.0672 |
| | Psi (rugg + elev + road), p (snow) | −0.45 (0.5) | −1.41 (0.7) | 0.52 (0.6) | −0.01 (0.3) | | 0.0672 |
| | Psi (rugg + livst + road), p (snow) | −0.41 (0.5) | −1.73 (0.8) | | −0.003 (0.3) | 0.13 (0.3) | 0.0485 |

Abbreviation of covariates: terrain ruggedness (rugg), elevation (elev), livestock density (livst), road density (road) and elevation (elev).

detection probability while examining co-occurrence patterns. There was no evidence that ibex presence affected the occupancy of argali. The SIF did not suggest direct competition or facilitation between the two species. The results showed that ibex are more widespread occupying two-thirds of the 945 km² study area and are found more commonly in rugged habitat. Argali occur in one-third of the landscape and seem to prefer the rolling hills.

Together the single species occupancy models and two-species occupancy models suggest that terrain ruggedness played an important role in the niche separation of these two ungulates at the scales of home ranges. Such differences in space use at the scale of home ranges may reduce the competition between these two species and thereby enable them to co-occur regionally across the high mountains of south and central Asia.

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Author contributions

CO, JSA, CM and KRS: involved in conceptualization. CO: collected the data. CO, KRS, CM, JSA and GS: designed the methods. CO, KRS and KS: analyzed the data. CO: involved in writing the first draft. All authors reviewed and edited the manuscript. GS, KS and PL helped logistically for this study.

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