



Co-occurrence of snow leopard, wolf and Siberian ibex under livestock encroachment into protected areas across the Mongolian Altai

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ABSTRACT

In countries such as Mongolia, where globalization of the cashmere market has spurred herders to massively increase their livestock numbers, an important conservation concern is the effect of livestock encroachment on wildlife. This is especially important inside protected areas (PAs), which often represent the last refugia for threatened large mammals. We used camera-traps to sample four areas with different protection status across the Mongolian Altai Mountains, and targeted a predator-prey system composed of livestock, one large herbivore, the Siberian ibex, and two large carnivores, the snow leopard and the wolf. To determine the effect of livestock on habitat use by the wild species and their spatio-temporal co-occurrence we applied an occupancy framework explicitly developed for modelling interacting species. We recorded a widespread presence of domestic animals in the PAs, and observed avoidance of sites used by livestock by snow leopard and ibex, while wolves tended to co-occur with it. Snow leopard and ibex showed clear mutual co-occurrence, indicating a tight predator-prey relationship. Results provide evidence that, at the scale of sites sampled primarily to maximise snow leopard detections, grazing livestock interferes with wild species by inducing avoidance in snow leopards, and attraction in wolves. We suggest that (1) PAs management should enforce real grazing limitations on the ground, especially in the core areas of the parks; (2) new policies incorporating wildlife conservation into government subsidies to pastoralists should be envisaged, to prevent increasing displacement of snow leopards and ibex; (3) as wolves co-occurred with livestock, with the potential for human-wildlife conflicts, we encourage the use of a set of prevention techniques to mitigate livestock depredation.

1. Introduction

Demand for livestock products has more than doubled in the last forty years globally (FAO, 2009), and as a result 30% of the terrestrial surface is currently used for pastures and fodder crops, making the livestock industry the largest land-use sector on the planet (Herrero et al., 2013). As the biomass of domestic animals has concomitantly increased (currently estimated at 60% of the total global mammalian biomass; Bar-On et al., 2018), there is growing concern for the impact that animal farming exerts on wildlife and ecosystems (Reid et al., 2009; Machovina et al., 2015; Ripple et al., 2015). In this context, an important

conservation issue is the encroachment of free-ranging livestock inside protected areas (PAs), where livestock can outcompete wild mammals for space and resources and trigger human-wildlife conflicts (e.g., Mishra et al., 2004; Gandiwa et al., 2011). Yet, PAs often represent the last refugia for many threatened and rare species of mammals around the globe (Pacifi et al., 2020).

Across central Asia, highlands and mountains host a unique grassland ecosystem that has been used as rangeland for centuries. However, in recent decades livestock numbers have strongly increased, mainly because of the rapid growth of the global cashmere trade market (Berger et al., 2013). As a result, the biomass of wild ungulates in many regions

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of central Asia is currently between one and two orders of magnitude lower than that of domestic animals (Berger et al., 2013; Tumursukh et al., 2016), and free-ranging livestock often encroaches into PAs (e.g., Rovero et al., 2020). Several studies have shown the negative effects of high livestock densities on wild ungulate populations, mainly attributed to competitive exclusion due to the similar diets (Bagchi and Mishra, 2006; Sharma et al., 2015; Siraj-ud-Din et al., 2016). Pastoralism also threatens large carnivores in the region, through a complex, but still poorly documented cascade of effects (Ekernas et al., 2017), with reduction of wild prey and predation of livestock, triggering human-carnivore conflicts and retaliatory killings, being considered the main processes involved (Snow Leopard Network, 2014; Mishra et al., 2016; Ali et al., 2016). However, and in spite of the plausible link between prey reduction and livestock predation by carnivores, it remains poorly understood how the pervasive presence of livestock influences the occurrence of the whole large carnivore-wild herbivore system (Gordon, 2018). This question is of both ecological and conservation relevance especially within PAs, because knowledge on how mutually interacting wild species respond spatially and temporally to livestock encroachment informs on the vulnerability of these wild species. It can also give insights on strategies to increase the efficiency of PAs and harmonize their protection with pastoralism, hence mitigating human-wildlife conflicts. Here, we aim to provide a contribution to address this question using data from the Mongolian Altai Mountains.

In Mongolia more than one third of the land is devoted to pastures and 40% of the gross domestic product comes from livestock farming (Mijiddorj et al., 2018). The country has become the world's second exporter of cashmere after China (Lecraw et al., 2005), with total livestock numbers estimated at 71 million in 2019 (National Statistics Office of Mongolia, 2020), of which 29 million were goats. We focused on four areas in the Altai Mountains in the western part of the country, where snow leopard (*Panthera uncia*) and wolf (*Canis lupus*) are the top predators, and both are known to prey on domestic animals (Mijiddorj et al., 2018). However, there are key relevant differences between these two predators: the snow leopard is a strict mountain-dweller felid considered as Vulnerable by the IUCN and has a fragmented distribution and declining global population. Habitat degradation, decline of wild prey and retaliatory killing are considered to be the major threats faced by the snow leopard globally (McCarthy et al., 2017). However, knowledge on the effects of livestock on snow leopard remains scant. Evidence from the Indian Himalaya indicates increased intensity in snow leopard site use with increasing livestock numbers, and a decrease beyond a threshold of livestock densities (Sharma et al., 2015). The wolf, on the contrary, is relatively widespread across Mongolia, typically preying on plains-dwelling wild ungulates but reported to frequently raid livestock (Chetri et al., 2017). Wolves were reported to prey on livestock more often than snow leopards (Shrestha et al., 2019) and a recent study in our study region found that predation by wolves accounts annually for 4.1% of the total livestock holdings, while predation by snow leopards accounts for 0.2% (Augugliaro et al., 2020). A similar study in the Tost Mountains in Southern Mongolia reports higher proportions of livestock depredation attributed to wolves than snow leopards (Mijiddorj et al., 2018). Among wild prey, the Siberian ibex (*Capra sibirica*; hereafter, ibex) is the only mountain and cliff-adapted ungulate that we consistently recorded across the study areas and it is also the main prey for snow leopards in the region (Shehzad et al., 2012). Similar to snow leopard, mountainous PAs protect optimal habitat for the ibex, yet data from one of the four PAs we targeted showed that encroaching livestock may displace ibex (Rovero et al., 2020).

We used camera-trapping data from systematic sampling at 216 sites in four areas across the Mongolian Altai, representing a gradient from a Strictly Protected Area where livestock grazing is not allowed and two National Parks (NPs) where livestock grazing is allowed with limitations, to an area that was not protected at the time of our survey. We analysed the data using a multi-species, co-occurrence occupancy model (Rota et al., 2016), and aimed to assess how livestock encroaching into

PAs influences the spatio-temporal occurrence of snow leopard, wolf and ibex, and their spatial interactions. We analysed species occurrences at the scale of camera trap sites that we selected primarily within habitat deemed suitable to snow leopards, hence we framed our hypotheses and interpretation of results based on such spatial scale. Relative to a previous study based on data from the first of the four areas here considered (Rovero et al., 2020), our study provides for a novel assessment of the targeted ecological system, in view of the wider area and gradient of protection sampled, the inclusion of the wolf, and the use of an unconditional relationship between species. Specifically, by relaxing the dominant-subordinate assumption and focusing on a wider pool of species over a wider area we aimed to address the following questions: (1) does the presence of livestock herds decrease ibex habitat use spatially and/or temporally? We expected a decrease in ibex occurrence probability in the presence of livestock, but no major segregation in diel activity pattern given the diurnal/crepuscular habits of ibex (Xu et al., 2012). (2) Do wolves and snow leopards avoid or co-occur with livestock in space and time? Main hypotheses were that (i) both predators occur with lower probabilities at sites where livestock is also present, and their diel activity peaks at times of lower livestock activity. Alternatively, (ii) we hypothesised that wolf shows more neutral or even positive co-occurrence with livestock than snow leopard given the evidence of greater livestock depredation by the former. (3) Is there a co-occurrence pattern between snow leopard and ibex? We hypothesised a positive co-occurrence probability given the marked dependence of snow leopard on wild prey (McCarthy et al., 2016). (4) Is there a spatial segregation of the two carnivores as a result of competition? Our main hypothesis was that their co-occurrence is neutral given that they have different focal wild prey, and assuming that their propensity to predate on livestock, which may drive their use of space, is also different (Mijiddorj et al., 2018; Augugliaro et al., 2020). 5) Is there a co-occurrence pattern between wolves and ibex? We expected a neutral pattern, given the low suitability of ibex as a wolf prey (Chetri et al., 2017).

2. Material and methods

2.1. Study areas

The Altai Mountains of Mongolia stretch over 900 km from the north-western part of the country to the south, through the provinces of Bayan Olgii and Hovd. The area has cold semi-arid continental climate with long cold winters and short summers during which most precipitation falls, and supports alpine meadows and tundra. High plateaus extend for hundreds of square kilometres with desert-steppe vegetation, lichens and mosses being the principal ground cover, while peaks host a rugged, rocky and steep environment; valley bottoms are sparsely covered by coniferous forest and shrubs.

During 2015 and 2017–2019 we surveyed one area per year in the spring (March–June). Study sites (Fig. 1) include: (1) Siilkhem-B National Park (49°49' N; 89°44' E) in north-western Mongolia bordering Russia, with highest elevation up to 3900 m a.s.l. The park is characterized by steep, rocky and dry habitat, with grassland as main vegetation cover and scattered larches *Larix sibirica* along valley bottoms. (2) Tavan Bogd National Park (48°33' N; 88°37' E), in western Mongolia bordering Russia and China; this is the largest PA in Mongolia, reaching the highest elevation in the country (4374 m a.s.l.). The northern part that we surveyed presents large portions of alpine and glacial habitat, with lower elevation covered with grasslands. (3) Khork Serkhe Strictly Protected Area (47°93' N; 90°99' E) located in western Mongolia and reaching 4127 m a.s.l. It is mainly represented by steep grasslands and valleys. (4) Sutai massif (46°37' N; 93°35' E) was surveyed in 2019, when it had no legal protection, but was declared a Natural Reserve shortly after the end of our study. Sutai holds the highest mountain of the Gobi-Altai chain, with elevations reaching 4220 m a.s.l. at the main peak, which is permanently covered by the southernmost glacier of the region. Overall, the four study areas present very similar environmental



Fig. 1. Map of the four study areas across the Altai range, western Mongolia. From upper right to bottom left: Siilkhem-B National Park, Tavan Bogd National Park, Khork Serkhe Strictly Protected Area and Sutai Massif. The locations of camera-trap sites within each area are indicated by black dots and the borders of protected areas are shown with green lines (not shown for Sutai, since this area was not protected at the time of the survey). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

characteristics relevant to our analysis, with mountainous grassland as the dominant vegetation type and broadly consistent elevation range. Details on sampling areas and efforts are provided in [Appendix A](#).

Pastoralism is the main livelihood in all four study areas. The herders inhabiting the Bayan Olgii province (where Siilkhem-B, Tavan Bogd and Korkh Serkhe are located) belong to the ethnic group of the Kazakhs, professing Islam, while in the Sutai massif they belong to the ethnic group of the Mongols, which profess Buddhism. In the Bayan Olgii province alone, 2.2 million livestock were reported in 2018, of which 1.9 million were sheep and goats ([National Statistics Office of Mongolia, 2020](#)). Herder families move seasonally to change the grazing areas. Goats and sheep are guarded by herders and dogs during the day and held in corrals at night, except in summer (July–August), where often no corral is used, while horses, camels, cattle and yaks are mostly free ranging ([Augugliaro et al., 2020](#)). According to the Mongolian law, the NPs are subdivided into three zones: special zone, travel and tourism zone, and limited use zone. Traditional pastoralism is only allowed in the latter, whereas it is not allowed in the Strictly Protected Areas.

2.2. Data collection

For each area, our sampling design was based on a regular grid with cells of 4 km² that aimed to cover at least the minimum extent of 500 km² recommended for snow leopard population estimate studies ([Jackson et al., 2005](#)). Within each cell we located in the field one camera-trap site. The number and locations of sites sampled were constrained by accessibility (conditioned mainly by terrain morphology and snow cover) and the number of camera-traps available for sampling (see [Table A.1](#)). Thus, in the two PAs that were too large for complete coverage, we selected portions that we considered optimal snow leopard habitat according to the literature and local knowledge. Specifically, in Siilkhem-B we did not sample the southern end of the PA as this is lower elevation and least suitable habitat, and in Tavan Bogd we targeted the north-eastern portion of the PA. In Khork Serkhe we sampled the whole PA and surrounding suitable areas, and in Sutai we sampled the whole mountain massif. Overall, the area sampled ranged in size from 513 to 1110 km² ([Table A.1](#)). At the selected sampling locations, we fitted camera-traps on small rock piles c. 50 cm above the ground at approx. 2–4 m from the target trail, and set them to record photos in continuous

mode, with no delay between consecutive triggers. We maintained a minimum distance between contiguous sites of approximately 1.5 km. We did not use baits or lures. Camera-trap models were of 3 different manufacturers, characterized by high (Reconyx) and medium (Cuddeback and Bushnell) trigger speed. Camera-traps ran on average for 65 days (SD = 20.7; see Table A.1). Camera-trapping sites were mainly set on narrow passing trails, ridges and valley bottoms, to maximise detections of the rarest and most elusive species, the snow leopard. While we are aware that such design may under-sample the other focal species (such as livestock or ibex), our preliminary study (Rovero et al., 2020) and the results of this study indicate that the selected sites were also widely used by the other species (in 79.2% of sites in which snow leopard was detected we also detected at least one of the other three focal species). However, we acknowledge that inference from our findings should be interpreted as co-occurrence patterns within expected snow leopard habitat. Environmental covariates included camera-trap site elevation, terrain slope and distance from the closest herders' settlement, and were derived from a Digital Elevation Model and satellite maps through the software Quantum Gis (QGIS, 2018). The chosen covariates were not correlated according to Spearman's correlation test ($\rho < 0.5$).

2.3. Spatial analyses

Given our aim of assessing the overall effects of livestock on selected wild species, and that herds of grazing livestock most often grouped multiple domestic species, we merged detections of all domestic animals and humans (which were all of herders or other local community members) into a single entity, henceforth referred to as 'livestock'. For snow leopard, wolf, ibex and livestock, we then arranged detections into matrices of sites i by sampling occasions j , using five days as the resolution, as such interval outperformed occasions of 1 or 2 days in terms of model convergence and precision of estimates.

We modelled detection/non-detection data of the $S = 4$ species (including the category livestock) collected in the four areas using the multi-species co-occurrence model developed by Rota et al. (2016), which is a generalization for two or more interacting species of the single-species occupancy model by MacKenzie et al. (2002). The modelling framework includes a latent occupancy state (Z_i) for each of the $s = 1, \dots, S$ species at site $i = 1, \dots, I$, where Z_i is represented by a sequence of 0/1 values indicating whether each species is present (1) or absent (0) at site i . The latent state is modelled using a multivariate Bernoulli distribution, $Z_i \sim \text{MVB}(\psi_i)$, where ψ_i is a vector of length $2^S = 16$ probabilities for each possible absence/presence combination of $S = 4$ species, with $\sum_k \psi_{ik} = 1$. These probabilities are modelled on the logit scale, as log odds of occupancy, also referred to as natural parameters (f). The vector of natural parameters for each site (f_i) can have maximum length $2^S - 1$, depending on the number of species and the nature of the interactions included in the model. In our case, we used a model with four interacting species, and considered only pairwise interactions between species (i.e., we did not consider three-species and four-species interactions), resulting in ten natural parameters being modelled. Four natural parameters f represented the log odds a single species individually occurs at a site, and the other six natural parameters were the log odds of the probabilities that two species occur together: $f_i = \{f_{1,i}, f_{2,i}, f_{3,i}, f_{4,i}, f_{12,i}, f_{13,i}, f_{14,i}, f_{23,i}, f_{24,i}, f_{34,i}\}$, with numbers from 1 to 4 denoting species identity. The single-species natural parameters $f_{1,i}, f_{2,i}, f_{3,i}$ and $f_{4,i}$ were modelled as a linear function of covariates while co-occurrence parameters $f_{12,i}, f_{13,i}, f_{14,i}, f_{23,i}, f_{24,i}$ and $f_{34,i}$ were kept constant across sites, since we did not expect inter-specific interactions to vary along covariates gradients. The observation model relates the true underlying occupancy states (z_{si}) to the observed detection data (y_{sij}) for species s , at site i , and sampling occasion $j = 1, \dots, J_i$: $y_{sij} \sim \text{Bernoulli}(z_{si} p_{sij})$, with detection probability p_{sij} independent for each species.

Given the complexity of the multi-species co-occurrence model, that allows to express both single-species occurrence and co-occurrence

parameters f as a function of covariates, we used a two-step approach following Twining et al. (2020). In the first step we selected the most supported covariates for each species using single-species occupancy models, on the basis of the Akaike Information Criterion (AIC, Burnham and Anderson, 2002). For each species, we formulated specific hypotheses for the effects of covariates on occupancy and detection probability (Table A.2). We first tested the distance to the closest herders' settlement and the camera performance (high trigger speed for Reconyx models versus medium trigger speed for Cuddeback and Bushnell models) as covariates on detection probability while modelling occupancy with all relevant covariates (i.e., a full model for occupancy, following MacKenzie et al., 2017), resulting in four models being compared. We then tested the distance to the closest settlement, terrain slope, elevation, and the sampling area as categorical variable, on occurrence probability while keeping the best encounter structure previously selected, resulting in 16 models being compared. In the second step, the most supported covariates from single-species occupancy models were included as predictors of occurrence and detectability of single species in the multi-species model. The multi-species model included six co-occurrence parameters f , one for each species pair. These six co-occurrence parameters represented our six specific hypotheses on co-occurrence of species pairs described in the Introduction (see also Table A.3), and we judged their significance according to the 95% confidence intervals. We implemented the models using the R (R Development Core Team, 2019) package 'unmarked' (Fiske and Chandler, 2011). In view of the large home ranges of the studied species and the fact that co-occurrence dynamics may vary with the spatial scale sampled, we acknowledge that our occupancy estimates should be interpreted as metrics of site use rather than occupancy sensu stricto.

2.4. Temporal analyses

In addition to modelling co-occurrence, we investigated the diel activity pattern for the three wild species and livestock. We subsampled the detection data considering consecutive detections within a 30 min interval as a single event and created temporal activity curves (Zimmermann et al., 2016). Then we performed pairwise comparisons of activity patterns between all the three wild species and livestock by estimating the overlap coefficient Δ (ranging from 0, no overlap, to 1, complete overlap) and its confidence interval using the package 'overlap' (Meredith and Ridout, 2016).

3. Results

Overall, livestock was detected at 110 out of 216 sites, resulting in a naïve occupancy of 0.51, snow leopard was detected at 81 sites (0.37), wolf at 49 (0.23), ibex at 54 (0.25; Table B.1.). Livestock encroachment occurred in all the four areas, with livestock detected at 29% of sites in Tavan Bogd, 44% in Siilkhem-B, 60% in Khork Serkhe and 62% in Sutai (see also Appendix B). Livestock site use was negatively associated with elevation ($\beta = -0.56 \pm 0.20$ SE, Fig. 2) and distance to the closest settlement ($\beta = -0.67 \pm 0.21$). This latter variable was also negatively related to livestock detection probability ($\beta = -0.51 \pm 0.08$), together with camera-trap sensitivity ($\beta = -0.49 \pm 0.13$, Fig. D.1). Snow leopard site use was significantly different among study areas, with the highest estimated site use probability in Sutai ($\beta = 2.62 \pm 0.55$) and the lowest in Tavan Bogd ($\beta = -2.07 \pm 0.85$). Its detection probability was positively correlated with camera-trap sensitivity ($\beta = 1.46 \pm 0.35$). The best model for wolves did not include any covariates for detection probability ($p = 0.08 \pm 0.12$), while site use probability increased with increasing distance from settlements ($\beta = 0.51 \pm 0.22$) and decreased with increasing elevation ($\beta = -0.11 \pm 0.21$). Finally, ibex site use was positively related to terrain slope ($\beta = 0.39 \pm 0.17$) and site elevation ($\beta = 0.20 \pm 0.21$). It was lower in Siilkhem-B compared to the other areas ($\beta = -1.41 \pm 0.66$), and its detectability was lower at sites with camera-traps with higher sensitivity ($\beta = -0.84 \pm 0.29$; see also Table C.1 for

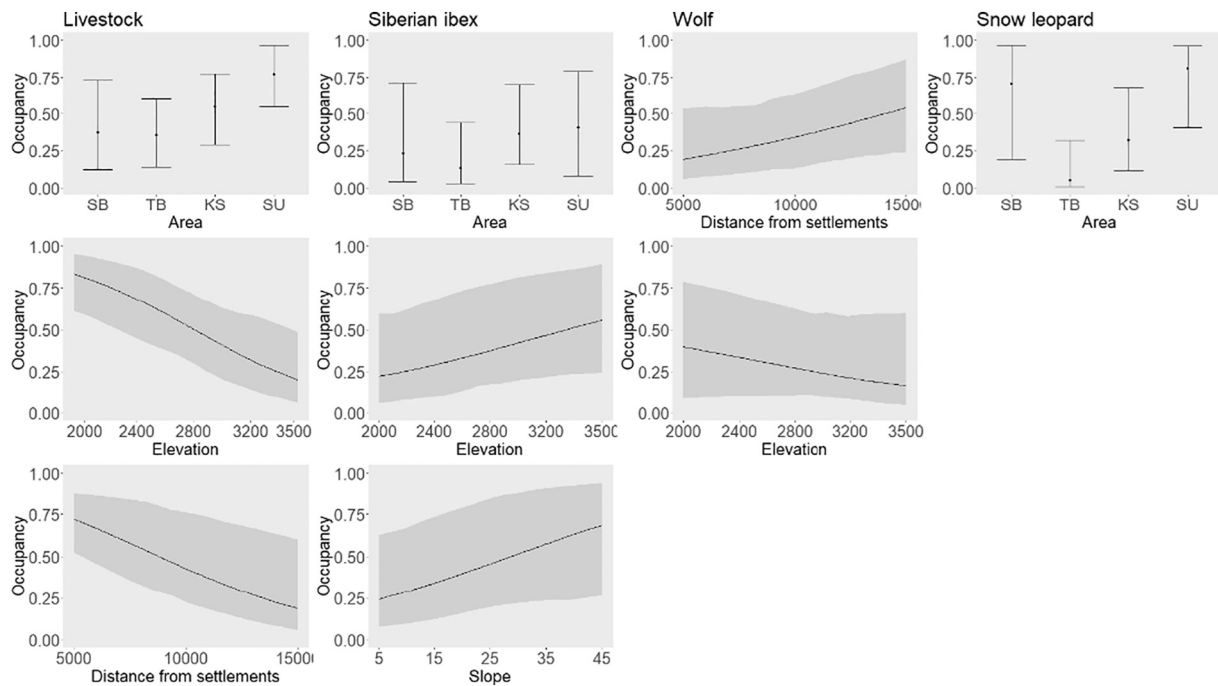


Fig. 2. Bivariate plots of the relationships between each species occurrence probability, extracted from the multi species co-occurrence model, and the selected covariates from camera-trapping surveys in four areas of western Mongolia. SB stands for Siikhem-B NP, TB for Tavan Bogd NP, KS for Khork Serkhe SPA, and SU for Suta Massif. The error bars and bands represent 95% confidence intervals. To extract predicted probability of occurrence for one covariate all other covariates were set to their mean (i.e. zero). Bivariate plots for the effects on detectability are reported in [Appendix D](#).

single-species model selection and C.2 for the multi-species model output on covariate coefficients).

The co-occurrence parameter for the species pair ibex – livestock was estimated as $\alpha = -0.30 \pm 0.44$ (Fig. 3 and Table C.2). The co-occurrence estimate for snow leopard and livestock was $\alpha = -0.94 \pm 0.54$. Wolf and livestock co-occurrence had an estimated parameter of $\alpha = 0.98 \pm 0.49$. The species pair with the highest co-occurrence parameter was ibex – snow leopard, with an estimate of $\alpha = 1.70 \pm 0.61$. The two predators showed an estimated co-occurrence of $\alpha = 1.03 \pm 0.51$. Lastly, the pair wolf – ibex had a parameter estimate of $\alpha = -0.97 \pm 0.54$. The predictions of each species site-use probability conditional on the presence or absence of the interacting species, derived from the multi-species co-occurrence model, are shown in Fig. 4.

Domestic animals and humans showed a markedly diurnal activity pattern, with activity peak around midday. Ibex were also mainly active during daylight, with two peaks in the early morning and in the late afternoon. The pattern of the two carnivores differed: snow leopards showed a crepuscular and nocturnal activity pattern with two peaks at dusk and dawn and a higher activity level during night than day, while wolves had a more constant activity pattern with no marked difference between daylight and night hours (Fig. 5). The maximum coefficient of overlap between activity patterns was between ibex and livestock ($\Delta = 0.80$; 95% CI: 0.74–0.87), followed by snow leopard and wolf ($\Delta = 0.79$; 0.70–0.88). An intermediate level of overlap was shown by wolf and ibex ($\Delta = 0.69$; 0.59–0.79) and wolf and livestock ($\Delta = 0.62$; 0.53–0.71). The lowest values were recorded for the pairs snow leopard – ibex ($\Delta = 0.51$; 0.43–0.58) and snow leopard – livestock ($\Delta = 0.44$; 0.39–0.49).

4. Discussion

By modelling the co-occurrence of snow leopard, wolf, Siberian ibex and livestock in the Mongolian Altai, at the scale of sites selected to maximise snow leopard detections, we provided a contribution to understand how livestock encroaching into PAs affects wildlife. We

recorded the presence of livestock in large portions of all the areas sampled, with an estimated average occurrence of 0.52. This diffused presence of livestock clearly points to a lack of protection effectiveness of target PAs, as according to the Mongolian law grazing is not allowed within Strictly Protected Areas and only allowed in “limited use zones” within NPs. Surprisingly, despite a high occurrence of livestock in Suta, we also found the highest occurrence of the three wild species in this area that had no legal protection when surveyed. Reasons for these differences among areas are not readily apparent, however we qualitatively observed skins and traps in the herders' houses in all areas except Suta (F.R., unpublished data), suggesting that wildlife poaching might be more practiced by the Kazakhs than Mongols, as their different religious beliefs are reported to influence the attitude of local communities towards wildlife (Bhatia et al., 2017). Besides these general observations, our modelling results reveal a number of patterns on spatial occurrence of target species within the areas sampled, that generally point to a potentially negative effect of livestock on snow leopard presence, while to a positive effect on wolf, possibly mediated by the hunting prohibition in PAs and its persecution outside PAs.

The positive co-occurrence of snow leopard and ibex support the hypotheses of a predator-prey relationship that apparently holds regardless of livestock presence. Given that no environmental covariates had significant effects on snow leopard site use, this result suggests that the abundance of wild prey might be a key driver of snow leopard habitat use (Suryawanshi et al., 2017). Moreover, we found a potential indication of a negative effect of livestock on snow leopard as revealed by the negative spatial co-occurrence parameter, that yet had a 95% confidence interval that slightly overlapped zero. Moreover, snow leopard temporal activity was markedly nocturnal, meaning that the co-occurrence of this predator with livestock was low both spatially and temporally, given the distinctly diurnal pattern of domestic animals. This is a valuable result, as knowledge on whether livestock represents an additional food resource and hence ‘attracts’ snow leopards or displaces them through direct disturbance remains limited, yet Sharma et al. (2015) found evidence of negative effects of high livestock density

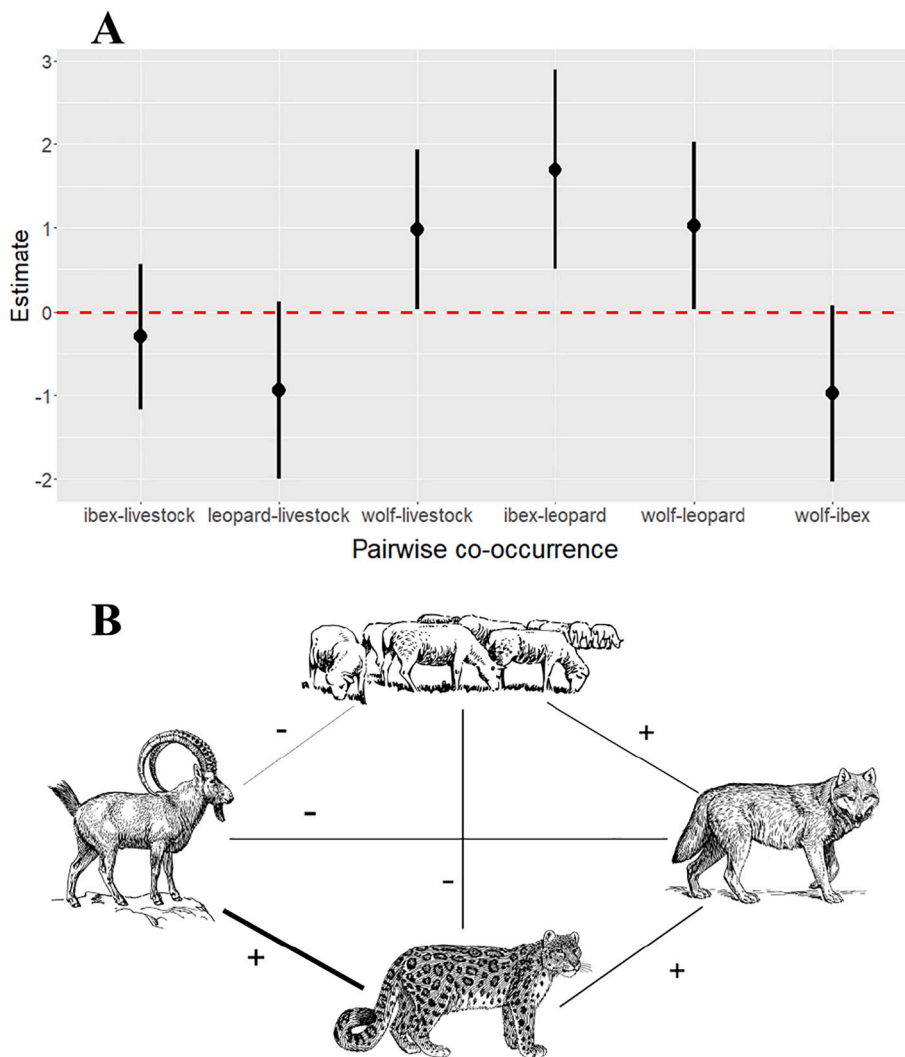


Fig. 3. (A) Mean co-occurrence parameter estimates from the multi species co-occurrence model. Bars show 95% confidence intervals. The red dotted line stands for a co-occurrence parameter estimate equal to zero. Values above the line indicate positive co-occurrence, while values below indicate negative co-occurrence. (B) Schematic representation of the sign of co-occurrence relationships between species pairs. The line width is proportional to the magnitude of the co-occurrence estimate. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

on snow leopard's habitat use in the Indian Himalayas. The higher site use probability of snow leopard in absence of livestock might also derive from a relatively low livestock depredation rate by the snow leopard in the target areas, as suggested by other studies in Mongolia (Mijiddorj et al., 2018; Augugliaro et al., 2020). However, data on snow leopard diet and prey selection will be necessary to assess the validity of this interpretation (e.g., Johansson et al., 2015; Hacker et al., 2021).

Our hypothesis on the negative effect of livestock presence on ibex was not supported, since the 95% confidence interval of the co-occurrence parameter largely overlapped zero. However, the sign of the species co-occurrence was negative, indicating that either a negative effect was present but weak or that our sample size was not sufficient to resolve the nature of this potential inter-specific interaction. The dietary niche composition of ibex and domestic goats and sheep largely overlaps, and previous studies have generally found detrimental effects of livestock on wild mountain ungulates in central Asia and Himalaya (e.g. Bagchi and Mishra, 2006; Sharma et al., 2015; Siraj-ud-Din et al., 2016). Opposite to the spatial interaction patterns observed in the snow leopards, wolves positively co-occurred with livestock while there was an indication of a possible negative co-occurrence with ibex. The negative, though non-significant, co-occurrence of wolf and ibex agrees with our hypothesis on the low suitability of this cliff-adapted ungulate as wolf prey, as well as findings from previous studies in Central Asia (e.g. Chetri et al., 2017). That wolf site-use probability was higher in presence of livestock bears potential implications in view of the human-wildlife

conflicts documented in the study areas. Indeed, results from Augugliaro et al. (2020) show that wolf predation of livestock increases in PAs, as wolf hunting is not allowed and hence wolves' numbers within PAs might be higher compared to non-protected areas where they are persecuted. Thus, even though the interior portion of PAs may not represent optimal wolf habitat, PAs seemingly provide both protection from poaching (Clark et al., 2006) and livestock as a food source for this carnivore. The fact that wolves were active throughout the day, with no evidence of temporal avoidance of livestock and humans, further corroborates this hypothesis, and points to its lower sensitivity to disturbance than snow leopard. However, the site-use probability of the wolf significantly increased at greater distances from human settlements, an opposite pattern compared to livestock. The higher site-use probability of wolves far from herders' houses and where livestock is also present matches evidence that most predations take place when herds are not supervised (Mijiddorj et al., 2018). The positive co-occurrence we found between wolf and snow leopard might reflect a lack of direct competition through interference. However, this is also likely contributed by the sampling design, whereby sites chosen to maximise snow leopard detection may also have been suitable to wolf.

4.1. Conclusions and conservation recommendations

This study shows that recently developed co-occurrence modelling that relaxes the dominant-subordinate assumption is a useful approach

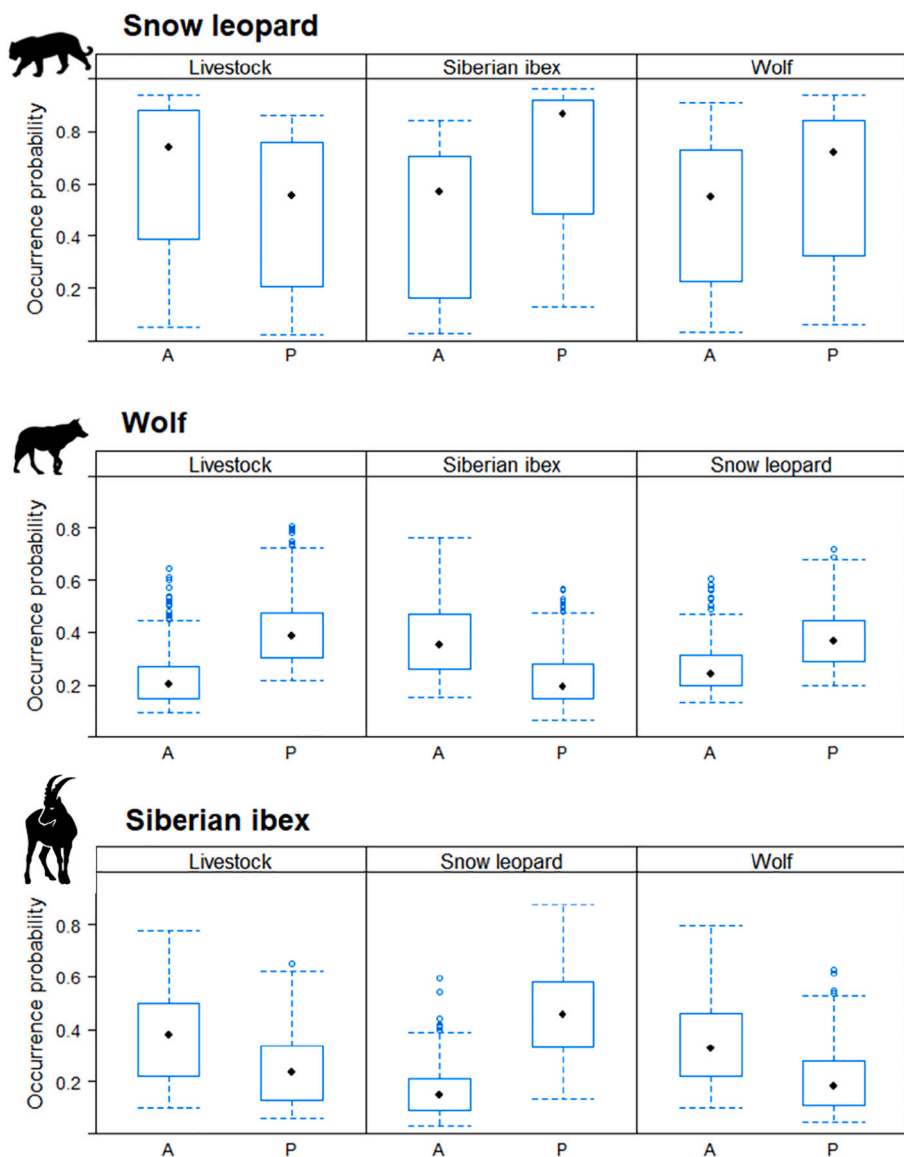


Fig. 4. Predicted occurrence probabilities from the multi species co-occurrence model, developed on camera-trapping data from four areas of western Mongolia. Each species occupancy (y axis) is predicted conditional on the presence (P) or absence (A) of another (x axis), reported in each box title. Black dots and lines indicate median and mean value respectively, the light blue boxes show first and third quartiles and the horizontal dashed lines indicate minimum and maximum values. Predictions were extracted at the real covariate values for our 216 sampling sites. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

to determine the effects of grazing livestock on multiple wild species. It allowed us to assess both the effects on single species and on their spatial interactions while accounting for preferences in habitat use, which provides for a more comprehensive understanding of how the interacting prey-predator system responds to anthropogenic influence. Within PAs, our sampling design targeted the presumed optimal snow leopard habitat, and therefore the inference on spatio-temporal interactions between species should be primarily related to such areas within the wider landscape. Our findings bear several conservation implications: (1) the diffuse presence of livestock inside PAs, even within core wildlife habitats, calls for more effective protection and the establishment of sustainable grazing regimes. We found no evidence on the ground of the existence of the supposed “special zone” in the two NPs, and our data on livestock occurrence do not seem compatible with such limitations. (2) The possible avoidance of livestock by snow leopard could mirror the sensitivity of this threatened species to grazing herds. This is particularly worrying when considering that the number of goats in the region has more than tripled in the last 30 years (National Statistics Office of Mongolia, 2020) and that most herders in our study areas seemingly aim for increasing the size of their herds (Augugliaro et al., 2020). Currently the Mongolian government is encouraging pastoralists to increase livestock numbers (Endicott, 2012), and this policy does not seem

compatible with the conservation of the snow leopard – Siberian ibex predator-prey system in the Altai Mountains. We advise for including wildlife conservation into government support schemes, enhancing compatibility between livestock rearing and biodiversity. (3) The positive co-occurrence of wolf with livestock draws attention on the potential for human-wildlife conflicts. Indeed, Augugliaro et al. (2020) found that wolves were responsible for most livestock depredations taking place in western Mongolia. Since wolf predation occurs mostly when herds are left unattended, limiting wolf-human conflicts may require a more constant guarding of herds (Mijiddorj et al., 2018). Corrals are generally not used in summer, and this might increment the amount of free-ranging livestock within PAs in this season and increase the risk of nocturnal depredation by predators. We therefore advise for promoting the use of predator-proof corrals year-round.

CRediT authorship contribution statement

Marco Salvatori: Conceptualization, Methodology, Software, Formal analysis, Data Curation, Writing – Original Draft, Visualization.

Simone Tenari: Conceptualization, Methodology, Writing – Review & Editing.

Valentina Obersoler: Investigation, Methodology, Writing – Review &

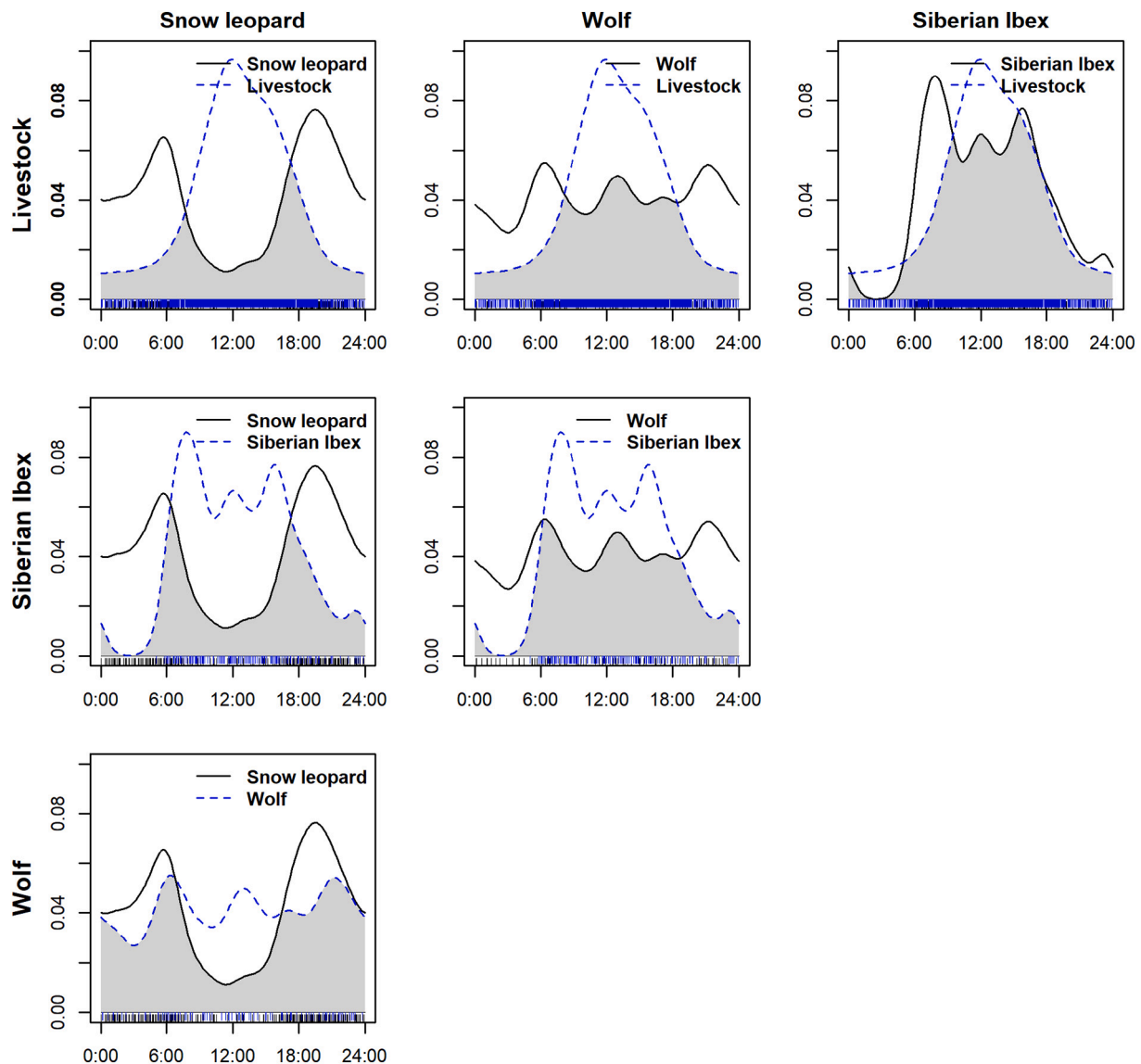


Fig. 5. Curves of the activity pattern for each species and their temporal overlap with the other species from camera-trapping detections in four areas of western Mongolia. The overlap in activity between species is highlighted in grey. The y axis shows the density in activity and the x axis indicates the hour. Different species in each pair are denoted with a solid black line and a blue dotted line. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Editing.

Claudio Augugliaro: Resources, Investigation, Writing – Review & Editing.

Philippe Christe: Resources, Writing – Review & Editing.

Claudio Groff: Investigation, Writing – Review & Editing.

Miha Krofel: Investigation, Writing – Review & Editing.

Fridolin Zimmermann: Investigation, Writing – Review & Editing

Francesco Rovero: Conceptualization, Methodology, Writing – Review & Editing, Supervision, Funding acquisition, Project administration.

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.

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Appendix A

Table A.1

Summary of the sampling design and effort of systematic camera-trapping surveys in four areas of western Mongolia. Effort is expressed as mean number of sampling days per camera \pm standard deviation. The area sampled is calculated as the minimum convex polygon around the camera-trap sites.

Area	Year	Protection status (PA extent)	Area sampled (km ²)	Elevation range sampled (m a.s.l.)	Number of camera-trapping sites	Survey period	Effort (camera days)
Siilkhem-B	2015	National Park (760 km ²)	513	2231–3123	48	19/03–23/06	46.5 \pm 6.6
Tavan Bogd	2017	National Park (3600 km ²)	720	2488–3489	44	07/04–2/06	48.2 \pm 1.6
Khork Serkhe	2018	Strictly Protected Area (750 km ²)	1110	1965–3072	63	18/03–20/06	65.2 \pm 5.8
Sutai	2019	Not protected	843	2115–3527	61	18/03–29/06	92.1 \pm 15.3

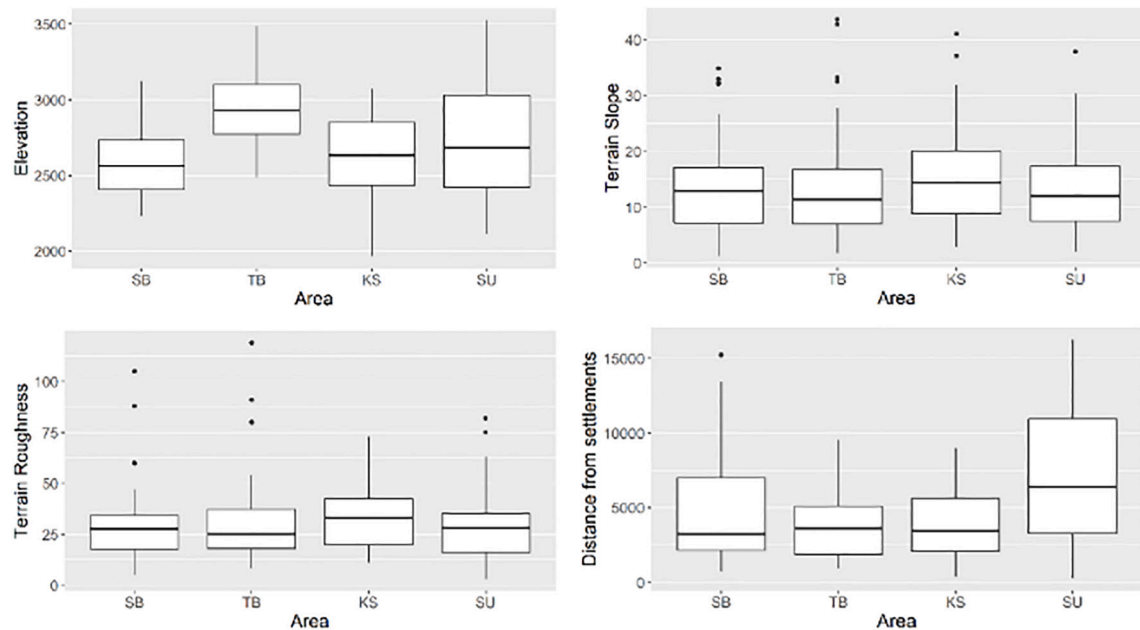


Fig. A.1. Boxplots summarising elevation, terrain slope, terrain roughness and distance from closest herder settlement, at the camera-trapping site level in the four study areas (SB: Siilkhem-B, TB: Tavan Bogd, KS: Khork Serkhe, SU: Sutai).

Table A.2

Hypothesised effects of environmental covariates on single-species detection probability and occupancy, for snow leopard, wolf, Siberian ibex and livestock in four areas of western Mongolia.

Species	Submodel	Elevation	Slope	Distance from settlement	Camera sensitivity (high)	Area
Snow leopard	Occupancy	Positive	Positive	Positive		Neutral
	Detectability			Positive	Positive	
Wolf	Occupancy	Negative	Negative	Positive		Neutral
	Detectability			Positive	Positive	
Siberian Ibex	Occupancy	Positive	Positive	Positive		Neutral
	Detectability			Positive	Positive	
Livestock	Occupancy	Negative	Negative	Negative		Neutral
	Detectability			Negative	Neutral	

Table A.3

Hypothesised co-occurrence relationships between the six species pairs considered in the modelling, in four areas of western Mongolia.

Species pair	Hypothesised co-occurrence	Hypothesis
Siberian ibex - Livestock	Negative	Disturbance of the large grazing herds
Snow leopard - Livestock	Negative	Disturbance of the large grazing herds
Wolf - Livestock	Negative or neutral	Disturbance or tolerance of the large grazing herds
Siberian ibex - Snow leopard	Positive	Tight predator-prey relationship
Wolf - Snow leopard	Neutral	Absence of direct competition
Wolf - Siberian ibex	Neutral	Ibex do not represent optimal prey for wolves

Appendix B

Table B.1

Summary of naïve and predicted site use in each study area, estimated from the multi-species co-occurrence model, for snow leopard, wolf, ibex and livestock, in four areas of western Mongolia from systematic camera-trapping data. Values of predicted site use were extracted at the real covariate values for our 216 sampling sites, and are shown with corresponding standard errors.

	Siilkhem-B		Tavan Bogd		Korkh Serkhe		Sutai	
	Naïve ψ	ψ	Naïve ψ	ψ	Naïve ψ	ψ	Naïve ψ	ψ
Snow leopard	0.27	0.69 ± 0.23	0.05	0.05 ± 0.09	0.27	0.31 ± 0.18	0.80	0.83 ± 0.14
Wolf	0.17	0.37 ± 0.15	0.20	0.20 ± 0.08	0.16	0.27 ± 0.12	0.36	0.46 ± 0.17
Siberian ibex	0.19	0.21 ± 0.15	0.11	0.16 ± 0.13	0.30	0.36 ± 0.14	0.34	0.41 ± 0.18
Livestock	0.44	0.45 ± 0.17	0.29	0.31 ± 0.13	0.60	0.62 ± 0.12	0.62	0.66 ± 0.15

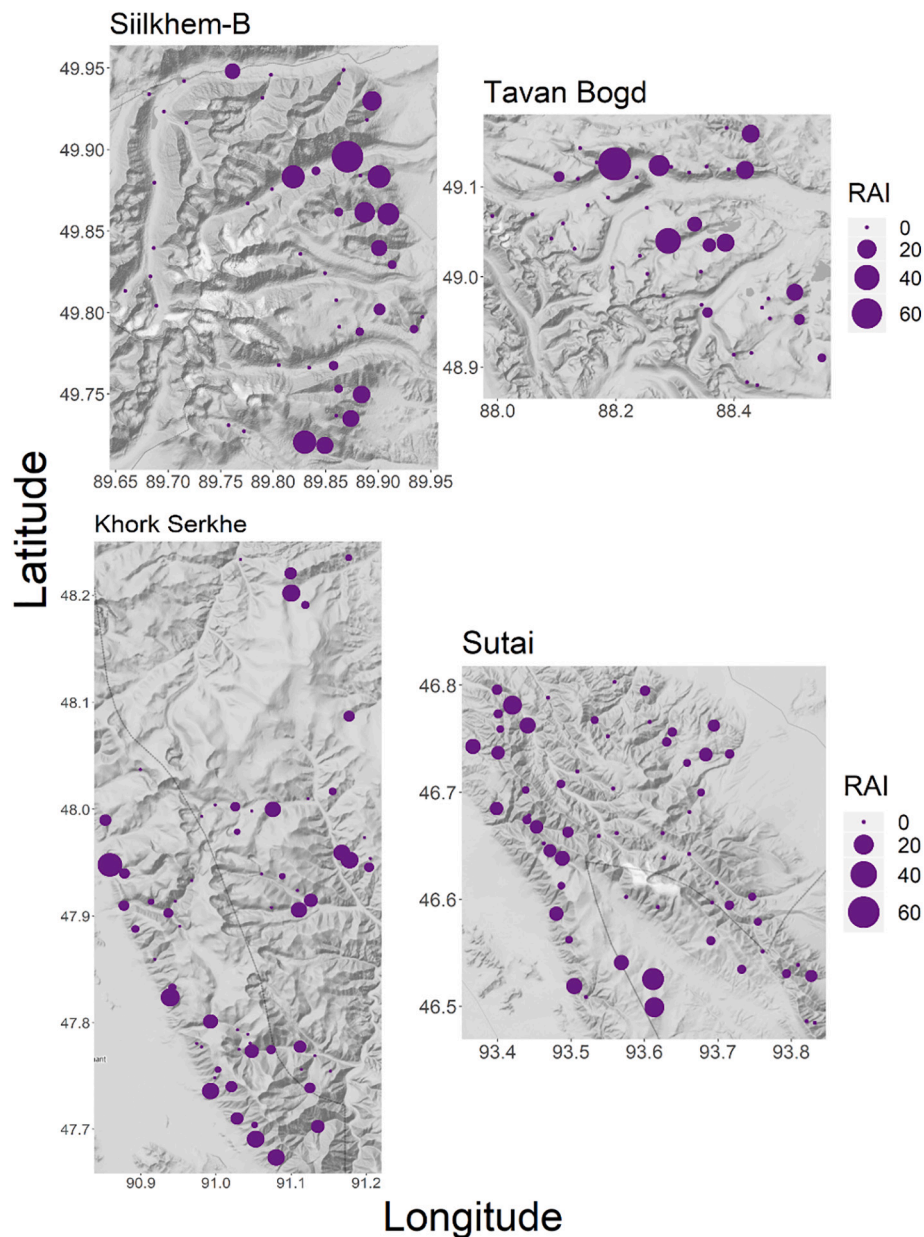


Fig. B.1. Maps of the Relative Abundance Index (number of camera-trapping detection events normalized by sampling effort) of livestock in the four study areas. RAIs have been calculated from daily detection events (i.e. temporal resolution equal to one day).

Appendix C

Table C.1

List of the most supported (with $\Delta AIC < 2$) single-species occupancy models for systematic camera-trapping data from four areas of western Mongolia for snow leopard, wolf, Siberian ibex and livestock. The null model, with constant detectability and occupancy, is shown as a reference for each species.

Model	logLike	No. parameters	AIC	ΔAIC	AICwt
Snow leopard					
ψ (Area), p (Camera sens.)	-724.48	6	1460.96	0.00	0.21
ψ (Area + Distance), p (Camera sens.)	-723.59	7	1461.18	0.21	0.19
ψ (Area + Slope), p (Camera sens.)	-723.66	7	1461.32	0.35	0.17
ψ (Area + Slope + Distance), p (Camera sens.)	-722.80	8	1461.60	0.64	0.15
ψ (Area + EL), p (Camera sens.)	-724.48	7	1462.90	1.99	0.08
ψ (.), p (.)	-758.72	3	1523.45	8	0.00
Wolf					
ψ (Elevation + Distance), p (.)	-355.90	4	719.80	0.00	0.25
ψ (Distance), p (.)	-356.95	3	719.89	0.09	0.23
ψ (Slope + Elevation + Distance), p (.)	-355.84	5	721.67	1.87	0.10
ψ (Slope + Distance), p (.)	-356.90	4	721.79	1.98	0.09

(continued on next page)

Table C.1 (continued)

Model	logLike	No. parameters	AIC	Δ AIC	AICwt
ψ (.), p (.)	-359.65	2	723.31	3.50	0.04
Siberian ibex					
ψ (Area + Elevation + Slope), p (Camera sens.)	-437.10	8	890.20	0.00	0.20
ψ (Area + Slope), p (Camera sens.)	-438.23	7	890.46	0.27	0.18
ψ (Slope), p (Camera sens.)	-441.70	4	891.44	1.24	0.11
ψ (Area + Slope + Distance), p (Camera sens.)	-438.08	8	892.14	1.94	0.08
ψ (.), p (.)	-444.40	3	894.80	4.6	0.02
Livestock					
ψ (Area + Elevation + Distance), p (Camera sens. + Distance)	-1062.77	9	2143.54	0.00	0.65
ψ (Area + Elevation + Slope + Distance), p (Camera sens. + Distance)	-1062.54	10	2145.08	1.54	0.30
ψ (.), p (.)	-1082.92	4	2173.84	30.3	0.00

Table C.2

Covariate coefficient estimates from the multi-species co-occurrence model for snow leopard, wolf, Siberian ibex and livestock from camera-trap surveys in four areas of western Mongolia. Dots and asterisks indicate significance levels: a dot stands for a significance level of 10%, one asterisk stands for 5%, two asterisks indicate 1% and three asterisks indicate 0.1%.

Species	Parameter	Estimate	SE	Z	P (> z)	
Snow leopard	ψ Area KS	-1.31	0.59	-2.2	0.02	*
	ψ Area SB	1.95	1.01	1.9	0.05	.
	ψ Area SU	2.62	0.55	4.7	<0.001	***
	ψ Area TB	-2.07	0.85	-2.4	0.01	*
	p Intercept	-1.5	0.08	-18.9	<0.001	***
	p Camera sens. (medium)	-1.46	0.35	-4.2	<0.001	***
Wolf	ψ Intercept	-1.56	0.47	-3.3	<0.001	***
	ψ Distance from settlement	0.51	0.22	2.3	0.02	*
	ψ Elevation	-0.11	0.21	-0.5	0.62	.
	p Intercept	-2.44	0.16	-15.2	<0.001	***
Siberian ibex	ψ Area KS	-0.74	0.48	-1.5	0.12	.
	ψ Area SB	-1.41	0.66	-2.1	0.03	*
	ψ Area SU	-0.44	0.60	-0.7	0.46	.
	ψ Area TB	-1.02	0.67	-1.5	0.13	.
	ψ Slope	0.39	0.17	2.2	0.02	*
	ψ Elevation	0.20	0.21	0.9	0.34	.
	p Intercept	-2.15	0.14	-15.7	<0.001	***
	p Camera sens.(medium)	0.84	0.29	2.9	<0.01	**
	ψ Area KS	0.35	0.39	0.9	0.36	.
Livestock	ψ Area SB	-0.52	0.52	-1.0	0.30	.
	ψ Area SU	1.43	0.57	2.5	0.01	*
	ψ Area TB	-1.13	0.451	-2.2	0.02	*
	ψ Elevation	-0.56	0.20	-2.8	<0.01	**
	ψ Distance from settlement	-0.67	0.21	-3.2	<0.01	**
	p Intercept	-1.20	0.07	-16.6	<0.001	***
	p Camera sens. (medium)	0.49	0.13	3.7	<0.001	***
	p Distance from settlement	-0.51	0.08	-6.4	<0.001	***
	Pairwise co-occurrence	-0.30	0.44	-0.7	0.49	.
	Pairwise co-occurrence	-0.94	0.54	-1.7	0.08	.
Ibex - Livestock	Pairwise co-occurrence	0.98	0.49	2.0	0.04	*
Snow leopard - Livestock	Pairwise co-occurrence	1.70	0.61	2.8	<0.01	**
Wolf - Livestock	Pairwise co-occurrence	1.03	0.51	2.0	0.04	*
Ibex - Snow leopard	Pairwise co-occurrence	-0.97	0.54	-1.8	0.07	.
Wolf - Snow leopard	Pairwise co-occurrence					
Wolf - Ibex	Pairwise co-occurrence					

Appendix D

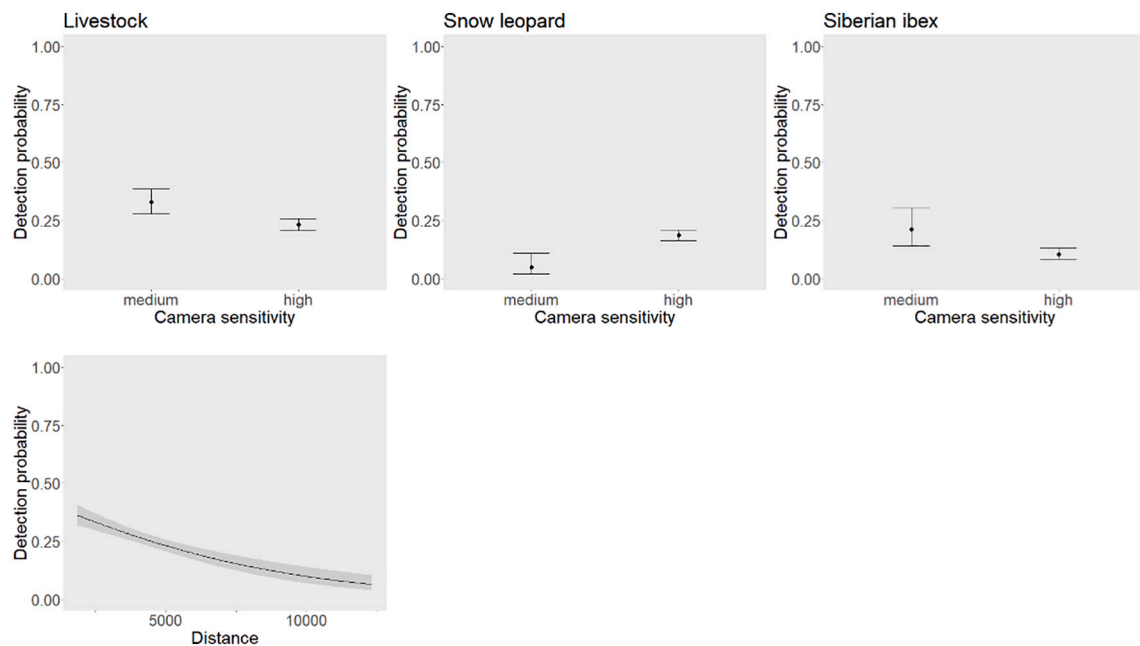


Fig. D.1. Bivariate plots of the relationships between each species detection probability, extracted from the multi species co-occurrence model, and the selected covariates from camera-trapping surveys in four areas of western Mongolia. To extract predicted probability of occurrence for one covariate all other covariates were set to their mean (i.e., zero). Error bars and bands indicate 95% confidence intervals.

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