Environmental niche overlap between snow leopard and four prey species in Kazakhstan

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The snow leopard Panthera uncia has declined due to habitat loss, habitat fragmentation and human persecution. Predator distribution is heavily dependent on prey species availability and distribution. With increasing pressures from farming practices encroaching into native species range and persecution of snow leopards in response to livestock depredation, it is vital to assess current predator and prey species distribution to highlight sensitive areas of overlap for protection. This study uses MaxEnt, a presence-only Species Distribution Model (SDM) to assess snow leopard and four prey species habitat suitability along the southern and eastern borders of Kazakhstan using environmental data. This area is considered an important corridor between snow leopard populations in the north and south of their range. Each of the five SDM’s produced models of ‘good’ discriminating abilities. We then compared the potential niche overlap between snow leopard and four prey species using ENMTools to highlight areas of important niche overlap within the corridor. The results indicated a very high degree of overlap between snow leopard and Siberian ibex Capra sibirica and high degrees with red deer Cervus elaphus, argali Ovis ammon and urial Ovis orientalis. The snow leopard population in this region is also found to be using forested areas below 2500 m, much lower than recorded in other areas of their range. The results highlight areas needed for protection but also pose additional conservation questions regarding the importance of prey species to transitory individuals.

1. Introduction

Land use change due to human modification is a global issue that is not restricted to the local environment where the change occurs (Foley et al., 2005). Changes to forests, farmland, waterways and air are driven by human need for resources and are causing considerable losses to biodiversity (Foley et al., 2005; WWF, 2016). Human activities, geographical barriers and ecological processes, competition and predation impact animal populations and can force populations out of their fundamental niche (all suitable habitat) into a much smaller area (Phillips et al., 2006; Pulliam, 2000; WWF, 2016); the realised niche (Hutchinson, 1957). Many studies have used species distribution models (SDM also known as habitat suitability models HSM and climate envelopes) to estimate the relationship between species records and the characteristics of the landscape (Aryal et al., 2016; Elith et al., 2011; Lamsal et al., 2018a; Lamsal et al., 2018b; Su et al., 2015; Ward, 2007). SDM models require a set of known species locations and predictor variables such as land cover, elevation and climate data to train the model and predict species distribution (Phillips and Dudík, 2008). By identifying suitable habitat, SDM models can produce starting points for further discussion and research in particular areas, for example, highlighting the fundamental niche for a species and comparing it to the realised niche and assessing what impact human activity is having upon distribution.

The snow leopard Panthera uncia is one species that has declined due to habitat loss, human persecution and reduction in prey species distribution (Jackson et al., 2014). Until recently the snow leopard was listed as an endangered species but has now been down listed to vulnerable (Aryal, A. 2017). This has occurred despite much debate by experts as to the current populations size, with experts believing that many animals are poached and deaths are unreported (Aryal, A. 2017). The estimated population size published in 2003 was between 4080 and 6590 individuals (Jackson et al., 2008). It is suggested that snow leopards are found between 2500 and 5500 m in alpine and sub-alpine areas (Aryal et al., 2016) in habitats such as grassland, bare areas and agricultural mosaic (Forrest et al., 2012). The current population

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inhabit the mountainous regions of the Himalaya, thorough the Quighai-Tibet Plateau and central Asia to southern Siberia (Jackson et al., 2008). Human wildlife conflict occurs when these animals depredate domesticated species in farmed areas, unless there are conservation incentives in place to dissuade hunting (Bagchi and Mishra, 2006). There is no one singly important prey species for snow leopard survival, as prey varies in different areas of the snow leopards range (Lyngdoh et al., 2014). Wild goat and sheep species are commonly taken by snow leopards with Siberian ibex Capra ibex, Himalayan tahr Hemitragus jemlahicus, blue sheep Pseudois nayaur and argali Ovis ammon being the four favoured species (Lyngdoh et al., 2014). However, domesticated goat and sheep species are also taken (Aryal et al., 2014a; Aryal et al., 2014b; Aryal et al., 2014c; Lyngdoh et al., 2014). These domesticated species are often farmed within the same areas of the landscape that the wild goat and sheep species occur and in some areas the density of livestock is higher than the native wild ungulates (Aryal et al., 2014a; Aryal et al., 2014b; Aryal et al., 2014c; Bagchi and Mishra, 2006). In areas of the snow leopards range in Pakistan, livestock out compete wild species for food and have caused dramatic declines in wild species such as the urial Ovis orientalis which is now classed as vulnerable (Siraj-ud-Din et al., 2016; Valdez, 2008). The decline in some native prey species forces snow leopard to prey on livestock, behaviour that can cause human wildlife conflict with the local farming population (Bagchi and Mishra, 2006).

A recent camera trap study has identified individual snow leopards within a reserve in south Kazakhstan in lower elevations with tree cover (Convery et al., 2015). Snow leopard distribution in the mountainous areas of Kazakhstan is suggested to be between 750 m and 5500 m (Jackson et al., 2014). This is much lower than Aryla et al.’s (2016) suggestion of a lower limit of 2500 m, though in one of the earliest papers on snow leopard ecology, Hemmer (1973) reports that ‘seasonal migration from higher to lower elevations may depend on climatic conditions and the movements of ungulate herds, and during winter, it may descend to the lower zones.’ Riordan et al. (2015) least-cost connectivity study suggested that the Tian Shan mountain range, which runs through Kyrgyzstan and borders south Kazakhstan and north China, is a potentially sensitive corridor between southern and northern snow leopard populations (Riordan et al., 2015). The use of lower elevations seen in Convery et al. (2015) and Jackson et al. (2008) could potentially be in response to prey species distribution and the functional connectivity of habitat in this area acting as a movement corridor. The movement patterns suggested by Convery et al. (2015) suggest that snow leopards frequently crossed valley bottoms when moving between alpine mountain ridges or from ridges to forested areas. This will bring them closer to areas of human activity and habitation and make them susceptible to anthropogenic disturbance, potential poaching and increase the likelihood of livestock depredation.

Recent SDM studies have focused primarily on snow leopard distribution in the Himalayan portion of the species range and how habitat may shift in response to climate change altering population distribution (Aryal et al., 2013; Aryal et al., 2016; Forrest et al., 2012). However, Aryal et al., 2016 suggests that predator species distribution models should be compared to prey species distribution due to the influence prey availability has on predator distribution. There are still gaps in our current knowledge of global, national and local snow leopard population sizes and fine scale species distribution modelling is needed to aid conservation and help map current distribution (Jackson et al., 2014). Forrest et al.’s (2012) SDM suggests that climate change will effect snow leopard distribution through changes in habitat loss and fragmentation rather than temperature and precipitation. We suggest that habitat type, elevation and movement of prey species is important to snow leopard distribution. As elevation and temperature co-vary, in this study, elevation was chosen as an environmental layer to represent changes in mountainous areas. Previous studies have used Maxent, a

Fig. 1. Current suggested range of the snow leopard highlighted study area along the southeast border of Kazakhstan. * Snow leopard range shaped file courtesy of The Snow Leopard Trust.
SDM, to assess snow leopard distribution (Li et al., 2014; Li et al., 2016) and to assess prey species in the Himalayan area (Aryal et al. (2016). However, this study aims to use MaxEnt (Elith et al., 2011) to assess snow leopard habitat suitability along the Kazakhstan south and eastern border, which has been highlighted by Riordan et al. (2015) least-cost connectivity study as part of a potentially sensitive corridor between southern and northern snow leopard populations. Due to the importance of prey species presence on snow leopard distribution (Aryal et al. (2016), we will then compare the potential niche overlap between snow leopard and four prey species to highlight areas of importance within this dispersal corridor.

2. Materials and methods

2.1. Species distribution data

This study focuses on snow leopard distribution along a potential corridor on the southern and eastern border of Kazakhstan. This area includes the Western Tian Shan and Kyrgyz Alatau mountain ranges, which run along part of the southern border with Kyrgyzstan, the Bororo, Junggar Alatau, Saur, and Tarbagatai ranges, which are on the border of Kazakhstan and China, and the Altai which is on the border with Mongolia, China and Russian (Jackson et al., 2014; Fig. 1). Often there is limited systematic survey data available on the presence/absence of elusive animals in the environment (Elith et al., 2011). In many cases only presence data is available which has either been collected systematically during surveys, or in the majority of cases, is acquired from natural history museums and databases (Elith et al., 2011). Ideally using data that has been systematically collected over the survey area would be best, however often this data is not available and data from museums and databases are used instead. One fundamental limitation of this data is sample selection bias, where some areas of the study area are sampled more intensively that others, but at times this is the only data available (Elith et al., 2011). Snow leopard sightings (N = 125) data was obtained from WWF. These data were collected by multiple specialists over 50 years for WWF using multiple survey techniques within different studies, due to the different techniques used it is acknowledged there may be biases present within the data such as sample selection bias. Four prey species were also selected from data available from WWF, two of these, the Siberian ibex (N = 194) and argali (N = 317), are favoured prey species (Lyngdoh et al., 2014). The two other species were the threatened urial (N = 49) and the red deer Cervus elaphus (N = 129), both of which are known prey species (Jackson et al., 2014). Within the study area, no data was recorded for the favoured prey species the blue sheep or the Himalayan tahr therefore species distribution model cannot be constructed for these species in this area currently.

2.2. Environmental Layer

Land cover data was obtained from the European Space Agency GloCover data set (Medis-France 2008). These data are divided into 22 land cover categories and are in raster (gridded data) format at a resolution of 300 m as used in Forrest et al. (2012). It is acknowledged that these data have biases in what classes they differentiate.

Global Multi-resolution Terrain Elevation data (GMTED2010) was obtained from United States Geological Service (USGS) Earth Explorer at a resolution of 250 m. Aspect and slope were calculated from the elevation data using ArcGIS (ESRI, Redlands, CA) Spatial Analysis extension toolbox and the slope and aspect tools. The elevation, slope and aspect raster data sets were resized using the Spatial Analysis Extract by Mask tool using nearest neighbour to 300 m resolution (this was done to match the land cover extend which is the largest resolution). MaxEnt requires all environmental layers to have the same co-ordinate systems, map extent and raster cell size, all of which can be altered using the Extract by Mask tool. All environmental layers must also be converted to an Ascii file type using the Conversion Tools Raster to Ascii tool for modelling purposes.

2.3. MaxEnt Modelling

The models for all species were run in MaxEnt Version 3.3.3k, using primarily default settings (regularisation multiplier = 1; duplicate occurrences removed; maximum number of background points = 10,000, as used in Kramer-Schadt et al. (2013). MaxEnt can select a proportion of random points to be used as test data or this can be defined by the user. In this study, the distribution data was split so that 25% of the distribution locations were used for testing the model and 75% for model training. Five-fold cross validation was used to calculate mean Area Under Receiver Operating Characteristic (ROC) Curve or AUC and extrinsic omission rates (the average proportion of test points that fall outside the area predicted to be suitable), following use of the occupancy threshold rule that maximises the sum of test sensitivity and specificity (as recommended by Liu et al., 2013). AUC is used to assess model performance with values of 0.5 and below indicating the model is no better than random and values closer to 1.0 indicating better model performance. Hawlitschek et al. (2011) define AUC > 0.9 as having ‘very good’ discriminating abilities, > 0.8 are ‘good’ and > 0.7 is ‘useful’ (based on the definition of Swets, 1988). The 10% minimum training logistic threshold found in the MaxEnt results table was used to define suitable and unsuitable habitat for each species (Aryal et al., 2016; Warren et al., 2010). The ENMTools software (Warren et al., 2010) was then used to compare the ecological niche of the snow leopard and their prey species using the niche overlap tool. Schoener (1968) and the I statistic (Warren et al., 2008) were the statistics used to measure niche overlap.

2.4. Accounting for pseudoabsences

Within MaxEnt background samples, known as pseudoabsences can be randomly selected within the programme to create absence points (Elith et al., 2011). The background samples used can have significant effects on the model outputs (Elith et al., 2011). In MaxEnt points are selected typically from a large rectangular area that may contain suitable habitat where no species sightings have been recorded (Brown, 2014). When models select background points from these areas it causes false positives (Brown, 2014). To overcome this bias Brown (2014) and Elith et al. (2011) suggest reducing the area where background points can be selected by using a minimum convex polygon (MCP) based on the presence data. In this study the SDMtoolbox was added in to ArcGIS and a background file was created using the Sample by Buffered MCP tool. This creates a bias file which can then be used within the MaxEnt interface. MaxEnt will then only select background sample points from within the designated 1 km buffered MCP. Therefore in this study, the background point selection is limited to the areas where sightings have occurred and are assumed to have been surveyed for snow leopards.

3. Results

3.1. Predicted snow leopard habitat

The results from the MaxEnt five-fold cross-validation test showed that the model for snow leopard distribution has ‘good’ discriminating abilities (Table 1) with a mean AUC of 0.817. The predicted areas of suitable habitat for the snow leopard along the Kazakhstan southern border included areas that are currently designated as within the snow leopards range (Fig. 2). However, the MaxEnt model also highlighted additional areas (shown in green in Fig. 4) within the fundamental niche that are potentially suitable for snow leopards. Mainly these areas are on the border between Kazakhstan and Kyrgyzstan and Kazakhstan and China. The study area contains multiple areas of suitable habitat,
Table 1
MaxEnt results for snow leopard and prey species.

<table>
<thead>
<tr>
<th>Species</th>
<th>Train set</th>
<th>Test set</th>
<th>Train AUC</th>
<th>Test AUC</th>
<th>Test gain</th>
<th>Test omission</th>
</tr>
</thead>
<tbody>
<tr>
<td>Snow leopard</td>
<td>79</td>
<td>20</td>
<td>0.858 ± 0.005</td>
<td>0.817 ± 0.010</td>
<td>0.763 ± 0.763</td>
<td>0.010*</td>
</tr>
<tr>
<td>Siberian ibex</td>
<td>117</td>
<td>29</td>
<td>0.801 ± 0.009</td>
<td>0.736 ± 0.020</td>
<td>0.939 ± 0.124</td>
<td>0.020*</td>
</tr>
<tr>
<td>Argali</td>
<td>124</td>
<td>31</td>
<td>0.850 ± 0.009</td>
<td>0.808 ± 0.020</td>
<td>0.619 ± 0.232</td>
<td>0.038*</td>
</tr>
<tr>
<td>Urial</td>
<td>30</td>
<td>7</td>
<td>0.826 ± 0.018</td>
<td>0.740 ± 0.084</td>
<td>0.338 ± 0.514</td>
<td>0.082</td>
</tr>
<tr>
<td>Red deer</td>
<td>78</td>
<td>19</td>
<td>0.913 ± 0.002</td>
<td>0.898 ± 0.003</td>
<td>1.485 ± 0.129</td>
<td>0.031*</td>
</tr>
</tbody>
</table>

Train set = the average number of training samples, Test set = average number of test samples, Test omission = Balance training omission, predicted area and threshold value test. Asterisk = p < .05, ± = Standard deviation from mean.

![Fig. 2. The probability of presence based on the effect of each variable for each species.](image)

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![Fig. 3. Partial dependency plot from MaxEnt displaying the partial effect elevation has on the probability of presence of the snow leopard.](image)

Fig. 3. Partial dependency plot from MaxEnt displaying the partial effect elevation has on the probability of presence of the snow leopard.

which vary in size and are surrounded by less suitable areas of the landscape (less suitable areas of the landscape shown in blue in Fig. 4). The current predicted range does also include some areas where the MaxEnt model has not highlighted as highly suitable. Based on jackknife estimates assessing the importance of each environmental layer added into the MaxEnt model (land cover, elevation, slope and aspect), elevation is seen as a significant factor in defining the predicted area. Elevation influences the suitable habitat by contributing 74.1% to the model, slope is second but with a much lower 17.6% contribution, land cover is third (6.7%) and aspect forth (1.6%) (Fig. 2). The partial dependency plots also indicates that probability of snow leopard presence is highest at an elevation of 2500 m (Fig. 5).

3.2. Comparison of predicted habitat suitability for snow leopard and prey species

The results from the MaxEnt five-fold cross-validation test for the four prey species, Siberian ibex, argali, urial and red deer, indicated that the models varied in performance but all performed better than random and are classed as having ‘good’ discriminating abilities (Table 1, Fig. 5). Red deer had the highest mean test AUC of all models with a value of 0.898, argali had a lower value of 0.808, and urial and Siberian ibex test AUC values were 0.740 and 0.736, respectively. The highest degree of niche overlap using the mean Schoener’s D index value and the I-statistic was between snow leopard and Siberian ibex with a value of $D = 0.716$ and I = 0.921. Values of 0 represent little overlap and values closer to 1 represent high degree of overlap and I-statistic values are generally higher than D values (Hawlitschek et al., 2011). A lower degree of niche overlap was seen between the snow leopard and red deer ($D = 0.665$ and I = 0.889) and argali ($D = 0.629$ and I = 0.876) and the lowest overlap is seen between snow leopard and urial ($D = 0.452$ and I = 0.751).

At elevation of 2500 m – 5500 m there is highly suitable habitat for snow leopard (2.826, df = 2, p = .01) and Siberian ibex (2.529, df = 2, p < .05), whereas argali (2.396, df = 2, p < .05), urial (chi 61.69, df = 2, p < .05) and red deer (2.364, df 2, p < .05) highly suitable habitat is lower than 2500 m.

4. Discussion and conclusions

MaxEnt SDM has been used to assess the habitat suitability for the snow leopard in south and east Kazakhstan. The results provided a model of ‘good’ discriminatory abilities that indicated that there is a substantial amount of highly suitable habitat for the snow leopard along the Kazakhstan border. These habitats are connected to other highly suitable habitats in Kyrgyzstan, China, Mongolia and Russia. The habitat along the Kazakhstan border forms part of an important narrow corridor between snow leopard populations in the north and south of their range (Riordan et al., 2015) and could potentially have both resident and dispersing individuals using the habitat in these areas. Kazakhstan is thought to have a population of 100–110 snow leopards (2.5% of the global population) (Jackson et al., 2008) and two stable populations are thought to inhabit Almaty State Nature Reserve (area = 915 km², population of 30–35 individuals) and Aksu Zhagaby State Reserve (area = 744 km²) both situated near the Kazakhstan and Kyrgyzstan border (Convery et al., 2015; Jackson et al., 2014; Saparbayev and Woodward, 2008). Individuals with these reserves are protected, but can potentially disperse into unoccupied areas of highly suitable habitat shown in the SDM. The unsuitable habitat indicated in the SDM are seen at lower elevations and are mainly comprised of urban and agricultural land cover types. However, MaxEnt jackknife analysis identified elevation is the key variable in determining areas that are highly suitable for snow leopards (contributing 74.1% to the SDM) not land cover type. In this study, snow leopard and Siberian ibex are shown to have the highest degree of niche overlap. The SDM indicates that the majority of the landscape is shared by these two species, with a small amount of the landscape highlighted as prey only. This overlap suggests that the environmental space for both predator and prey is similar and they can potentially inhabit similar areas (Lyngdoh et al., 2014). This is consistent with other studies that have found that the main prey species are blue sheep and the Siberian ibex, both of
which are found in higher elevations (Aryal et al., 2016; Lyngdoh et al., 2014). The snow leopard sightings locations in this study were located between 1188 m to 4799 m, 1312 m lower than Aryal et al. (2016) suggestion of a lower threshold of 2500 m for the Himalaya population, though within the range suggested by Jackson et al. (2008) for Kazakhstan, where snow leopard can be found in the mountain ranges between 750 m to 5500 m (Jackson et al., 2014; Saparbayev and Woodward, 2008). Although, there were significantly more distribution points above 2500 m indicating a preference, 46 individual points were seen below 2500 m.

In the Almaty Nature Reserve, south Kazakhstan, snow leopards use elevations lower than 2500 m in winter months as they are following their main prey species, the Tibetan ibex, to sheltered forested areas (Saparbayev and Woodward, 2008, Altynbek, (2015) pers. com). This is supported by anecdotal evidence from the ranger team at Almaty State Nature Reserve (ASNR), and in particular the head ranger Jany-spayer Altynbek, who has over 30 years experience of working within ASNR. Aryal et al. (2016) suggest that climate change will reduce the degree of overlap between blue sheep and snow leopard in the Himalaya regions with prey species shifting their current range. The snow leopard population in Kazakhstan are showing levels of adaptability in that they are currently seen to use lower elevations at certain times of the year (Saparbayev and Woodward, 2008). Once in these lower areas, snow leopards are sharing a niche with other potential prey species such as the argali, urial and red deer which are seen in this study to have a ‘good’ degree of niche overlap with the snow leopard. Pilot studies using Fuzzy Logic modelling to assess the impact of climate change on snow leopard distributions in ASNR (Convery et al., 2015) suggest that changes in the elevation at which seasonal snow pack accumulates will have a strong driving influence on elevational range occupied. Snow leopards are seen to prey upon different species in different regions depending upon what is available (Lyngdoh et al., 2014). The potential snow leopard niche area in Kazakhstan as indicated in the SDM suggests that snow leopard have opportunities to prey on a range of species, particular at lower elevations. However, this will bring the snow leopard in to areas of the landscape that are farmed and may have the potential to cause human-wildlife conflicts.

To conserve the snow leopard population in Kazakhstan there are areas of research that must be prioritised. First, it is essential that presence/absence of snow leopards is ascertained for all areas in the landscape that have been highlighted as highly suitable in the SDM. A key assumption of SDM is that sightings data are reliable and collected in a systematic way (Elith et al., 2011). Although the data used in this study was collected over the last 50 years by WWF, it is acknowledged that there may be biases and subjectivity within the sightings data. Investigating presence/absence and population data for snow leopards globally has been highlighted as a current research priority by the Snow Leopard Network (Jackson et al., 2014). Previous studies have used methods such as questionnaires and interviews with the general public and farming communities to establish presence/absence (Taubmann et al., 2016), while others have relied on tracks and signs in the environment and more recently using camera traps to assess presence and population size (Convery et al., 2015). By gathering this information, it will aid conversation efforts by highlighted areas that are currently inhabited by snow leopard but not protected and areas that are highly suitable but where snow leopards are missing.

Secondly, it is imperative to understand the predator/prey relationship in Kazakhstan. The areas highlighted in green in Fig. 4 identify where the snow leopard share a niche with the four prey species. These areas need to be studied to see whether prey distribution is correctly predicted within the SDM and to determine the viability and health of the current prey population. A decline in prey species has been listed as one of the main causes of snow leopard population declines (Jackson et al., 2014). Although species like the markor and urial are seen as unimportant to snow leopards current diet (Lyngdoh et al., 2014), this may change in the future with the effects of increased pressure from agriculture and due to climate change. It is clear from the impact farming practices has had on the urial population in Pakistan, that presence of domesticated animals can severely impact wild species populations size and niche area (Siraj-ud-Din et al., 2016). Also if
regularly using lower elevations the snow leopards are potentially coming in to regular contact with the farming community which may cause human/wildlife conflicts. As the SDM has highlighted a high degree of overlap between the snow leopard and red deer, argali, urial and, particularly, Siberian ibex, it is vital that studies are undertaken to understand population dynamics and seasonal movements of each species. It would be interesting to investigate the movements of resident and dispersing snow leopard individuals to see whether any individuals are found at elevations < 2500 m all year round and whether they are seen to switch prey species more regularly as they share a niche area with multiple species.

The SDM has highlighted highly suitable areas of the landscape within Kazakhstan for both predator and prey species and where these species share a niche. These populations are important to snow leopard conservation as they form part of a corridor between the north and south snow leopard world wide range. Mountain habitats are vulnerable to environmental change and anthropogenic influences, and climate change poses a range of serious threats, including melting glaciers, changing rainfall patterns, unpredictable weather conditions, and increasing temperatures. For mountain species like snow leopards, climate change has immediate impacts with temperature, competition from other predators, precipitation changes and increasing human activity fragmenting suitable habitat (Riordan et al., 2015). A widespread upward encroachment of subalpine forests would displace regionally unique alpine tundra habitats and possibly cause the loss of alpine species. Therefore, the warmer and wetter conditions consistent with climate change predictions in this region may result in vegetation communities at higher altitudes, with forests ascending into alpine areas, the snow leopards’ preferred habitat (Forrest et al., 2012). Similar to Forrest et al. (2012), we assume that the impacts of climate change on snow leopards will be primarily through changes in habitat, rather than through direct physiological impacts of temperature and precipitation. With additional pressure from farming practices and the threat of species shifts in relation to habitat shifts related to climate change, there is still information about current population dynamics that need to be understood before mitigation strategies can be developed for the future. Within Kazakhstan there may be resident and transient snow leopard individuals. However, these individuals are seen to follow prey to lower forested elevations. This leads to questions about the degree of adaptability the snow leopard has regarding prey species and habitat usage which need further investigation.

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