



Blue sheep strongly affect snow leopard relative abundance but not livestock depredation in the Annapurna Conservation Area, Nepal

Marc Filla ^{a,1,*}, Rinzin Phunjok Lama ^{b,2}, Tashi Rapte Ghale ^{b,3}, Tim Filla ^{c,4}, Marco Heurich ^{d,e,f,5}, Matthias Waltert ^{a,6,*}, Igor Khorozyan ^{a,7}

^a Department of Conservation Biology, University of Goettingen, Bürgerstraße 50, 37073 Goettingen, Germany

^b Third Pole Conservancy, GPO Box 26288, Kathmandu, Nepal

^c Institute of Rheumatology, Medical Faculty, Heinrich Heine University Düsseldorf, Moorenstraße 5, 40227 Dusseldorf, Germany

^d Chair of Wildlife Ecology and Management, Faculty of Environment and Natural Resources, University of Freiburg, Tennenbacher Straße 4, 79106 Freiburg, Germany

^e Department of Visitor Management and National Park Monitoring, Bavarian Forest National Park, Freyunger Straße 2, 94481 Grafenau, Germany

^f Department of Forestry and Wildlife Management, Campus Evenstad, Inland Norway University of Applied Sciences, 2480 Koppang, Norway

ARTICLE INFO

Keywords:

Co-existence
Himalayan marmot
Human-wildlife conflict
Intervention strategy
Panthera uncia
Pseudois nayaur

ABSTRACT

Large carnivores play key roles in their ecosystems, but their protection is a major challenge in biodiversity conservation due to conflicts with human interests. The snow leopard (*Panthera uncia*) is the top predator of Asian high-altitude landscapes and faces various threats including wild prey depletion and illegal killings as a consequence of livestock depredation. As the interactions between snow leopards, wild prey, and livestock are still insufficiently understood, we studied the effects of 1) wild prey (blue sheep *Pseudois nayaur* and Himalayan marmots *Marmota himalayana*) and domestic prey on snow leopard relative abundance, and of 2) these ecological parameters and intervention applications on livestock depredation by snow leopards. In the Annapurna Conservation Area, Nepal, we monitored wildlife populations and livestock along transects (490.8 km) in 82 grid cells (4 × 4 km) in 2019 and 2021 and conducted questionnaire surveys to determine livestock depredation between 2018 and 2021 (n = 479 households). We applied generalized linear models (GLMs) and sample comparison testing to examine the effects of prey densities and other environmental and anthropogenic predictors on snow leopard relative abundance and livestock depredation. Blue sheep density strongly positively affected snow leopard relative abundance, which also increased with terrain ruggedness and decreased with increasing densities of livestock and the human population. The size of livestock holdings shaped depredation events of large livestock (yak, cattle and horse), whereas depredation events of sheep

* Corresponding authors.

E-mail addresses: marc.filla@biologie.uni-goettingen.de (M. Filla), matthiaswaltert@gmx.net (M. Waltert).

¹ ORCID ID: 0000-0001-7872-9449.

² ORCID ID: 0000-0002-7605-2443.

³ ORCID ID: 0000-0002-6661-6241.

⁴ ORCID ID: 0000-0001-5628-8398.

⁵ ORCID ID: 0000-0003-0051-2930.

⁶ ORCID ID: 0000-0001-7053-0291.

⁷ ORCID ID: 0000-0002-0657-7500.

<https://doi.org/10.1016/j.gecco.2022.e02153>

Received 24 February 2022; Received in revised form 9 May 2022; Accepted 10 May 2022

Available online 13 May 2022

2351-9894/© 2022 The Author(s). Published by Elsevier B.V. This is an open access article under the CC BY-NC-ND license (<http://creativecommons.org/licenses/by-nc-nd/4.0/>).

and goats, which accounted for most (68.6%) depredated animals, decreased with increasing human population density and marmot presence. The strong impact of blue sheep on snow leopard relative abundance supports demands for integrating this ungulate into conservation and management plans, including wild prey recovery and translocation. The rather weak evidence for effects of blue sheep on depredation events suggests that conflicts over livestock depredation by snow leopards would neither be inflicted nor solved by increasing wild prey abundance. This demonstrates the need to improve intervention strategies in the Annapurna region, such as predator-proofing corrals and optimizing daytime herding practices. We suggest further exploring the effects of marmots and other secondary prey on livestock depredation rates, and testing the suitability of additional interventions, e.g., dogs and deterrents, as conflict mitigation tools. Our results will support wildlife managers in setting conservation priorities to promote the long-term co-existence of local people and snow leopards.

1. Introduction

The Earth's current biodiversity loss is considered a human-induced mass extinction, with vertebrate extinction rates significantly exceeding natural background rates (Ceballos et al., 2015). Large carnivores are particularly prone to local extirpation due to their intrinsic biological traits, such as low reproductive rates, large energetic constraints, and wide-ranging behavior (Cardillo et al., 2005; Ripple et al., 2014). They suffered drastic population declines and massive range reductions during the past decades due to numerous anthropogenic threats, including habitat loss and degradation, utilization, wild prey depletion, and persecution (Ripple et al., 2014, 2015; Wolf and Ripple, 2017). This trend is alarming as large carnivores, besides their high socio-economic values, play key ecological roles at the top of natural food webs (Lindsey et al., 2007; Brashares et al., 2010; Ripple et al., 2014). Hence, their disappearance may negatively affect ecosystems through trophic cascades (Atkins et al., 2019; Hoeks et al., 2020), demanding a strong prioritization of carnivore conservation.

Human-carnivore conflicts are among the major drivers of carnivore declines globally (Woodroffe et al., 2005). Large carnivores are often killed in prevention or retaliation for livestock depredation (Treves and Karanth, 2003; Ripple et al., 2014), and this particularly applies to the world's wild felids, of which more than 75% have been found to be in conflict with human interests (Inskip and Zimmermann, 2009). Livestock depredation by large felids and other carnivores appears to be complex and influenced by a variety of human and ecological aspects, including predator-prey interactions (Wilkinson et al., 2020). While large carnivores exert direct predation effects and indirect behavior-mediated effects on their wild prey (Winnie Jr. and Creel, 2017), livestock may additionally affect wild prey positively (e.g., by enhancing wildlife habitats) and negatively (e.g., by displacement, competition, disease transmission; Schieltz and Rubenstein, 2016). Wild prey abundance, in turn, strongly shapes carnivore densities, as earlier studies showed (Fuller and Sievert, 2001; Carbone and Gittleman, 2002). High abundance of wild prey may reduce livestock depredation (Meriggi and Lovari, 1996; Odden et al., 2013; Khorozyan et al., 2015; Soofi et al., 2019), but can also fuel it by increasing incidental encounters of carnivores and livestock due to carnivore attraction or higher predator densities (Treves et al., 2004; Odden et al., 2008). Ultimately, conservation efforts targeting human-carnivore co-existence require a thorough understanding of these complex ecological relations to set priorities and implement locally specific measures (van Eeden et al., 2018).

The snow leopard (*Panthera uncia*) is the smallest representative of the big cats, which represents the top predator in high montane habitats of Asia, and is listed as 'Vulnerable' on the IUCN Red List of Threatened Species (Jackson and Hunter, 1996; Kitchener et al., 2016; McCarthy et al., 2017). Conflicts over livestock depredation pose a particular challenge for snow leopard conservation (McCarthy et al., 2017), as this felid inhabits remote landscapes, in which extensive livestock husbandry represents a major form of traditional land use and subsistence economy, and where the wild prey base is naturally limited (Mishra et al., 2003; Lyngdoh et al., 2014). Snow leopards are well-known for surplus killings (i.e., killing multiple individuals of livestock in a single attack), which may raise particular anger among local people (Thapa, 2021). At the same time, the snow leopard is also threatened by the decline of wild ungulates throughout its range resulting from habitat loss, competition with livestock, and poaching (Berger et al., 2013; Khan et al., 2013). All these threats to snow leopards are imminent and may accelerate in the future due to human population growth, habitat encroachment, and increasing competition for limited resources between people, livestock, snow leopards, and their wild prey (McCarthy and Chapron, 2003; Berger et al., 2013).

Interactions between snow leopards, wild prey, and livestock require more conservation-oriented research as the current knowledge remains insufficient and partially contradictory. For instance, wild ungulates can have positive effects on snow leopard habitat use and density (Sharma et al., 2015; Alexander et al., 2016a; Suryawanshi et al., 2017, 2021; Sharma et al., 2021; Yang et al., 2021), or exert weak or no effects hinting that factors other than prey density/occurrence can be important (Alexander et al., 2016b; Rovero et al., 2020). Likewise, some studies found that abundant wild prey populations lead to decreased livestock losses (Khorozyan et al., 2015; Bagchi et al., 2020), while others suggested an opposite scenario due to higher snow leopard densities (Suryawanshi et al., 2013, 2017), and yet others described these relationships to be more complex depending on livestock densities and study scales (Chetri et al., 2019a; Khanal et al., 2020). Furthermore, livestock depredation by snow leopards appears to be affected by livestock densities, topography, and locally used livestock protection interventions (hereafter interventions; Jackson et al., 2010; Johansson et al., 2015; Mishra et al., 2016; Mijiddorj et al., 2018). The relative importance of restoring wild prey compared to husbandry measures, especially interventions, is less well studied, but valuable given the need to prioritize conservation interventions. Also for the protection of snow leopards, a better understanding of snow leopard-prey-livestock interactions and identification of key conflict drivers are crucial

(Rashid et al., 2020).

The Annapurna region in central Nepal comprises excellent habitats for mountain wildlife and is considered to play a key role in snow leopard conservation due to partially high densities of this cat and as an important connecting area between its populations (McCarthy and Chapron, 2003; WWF, 2018; Chetri et al., 2019b). For the region, Chetri et al. (2019a) found the probability of livestock losses being lowest in areas with low livestock density and high wild prey density, while being highest in areas with abundant livestock and wild prey. That study did not consider intervention strategies and effects of wild prey on snow leopard relative abundance.

We studied interactions between snow leopards, wild prey, and livestock in the Annapurna Conservation Area (ACA), testing two hypotheses relevant to snow leopard conservation:

Hypothesis 1. Wild prey density positively affects snow leopard relative abundance.

Hypothesis 2. Livestock depredation by snow leopards decreases with increasing wild prey density, decreasing domestic prey density, and the application of interventions.

2. Material and methods

2.1. Study area

The Annapurna Conservation Area (ACA) was established in 1992 and covers 7629 km² in the Himalaya Biodiversity Hotspot (Mittermeier et al., 2004; Baral et al., 2019; Fig. 1). This protected area hosts about 100,000 people with traditional rights and access to natural resources, and diverse biotic assemblages including more than 1300 plant species and at least 128 mammal species (National Trust for Nature Conservation, 2015; Baral et al., 2019). Apart from livestock husbandry and crop farming, tourism is of increasing economic importance in the ACA with more than 100,000 visitors recorded annually (ACAP 2013 cited in Baral and Dhungana, 2014;

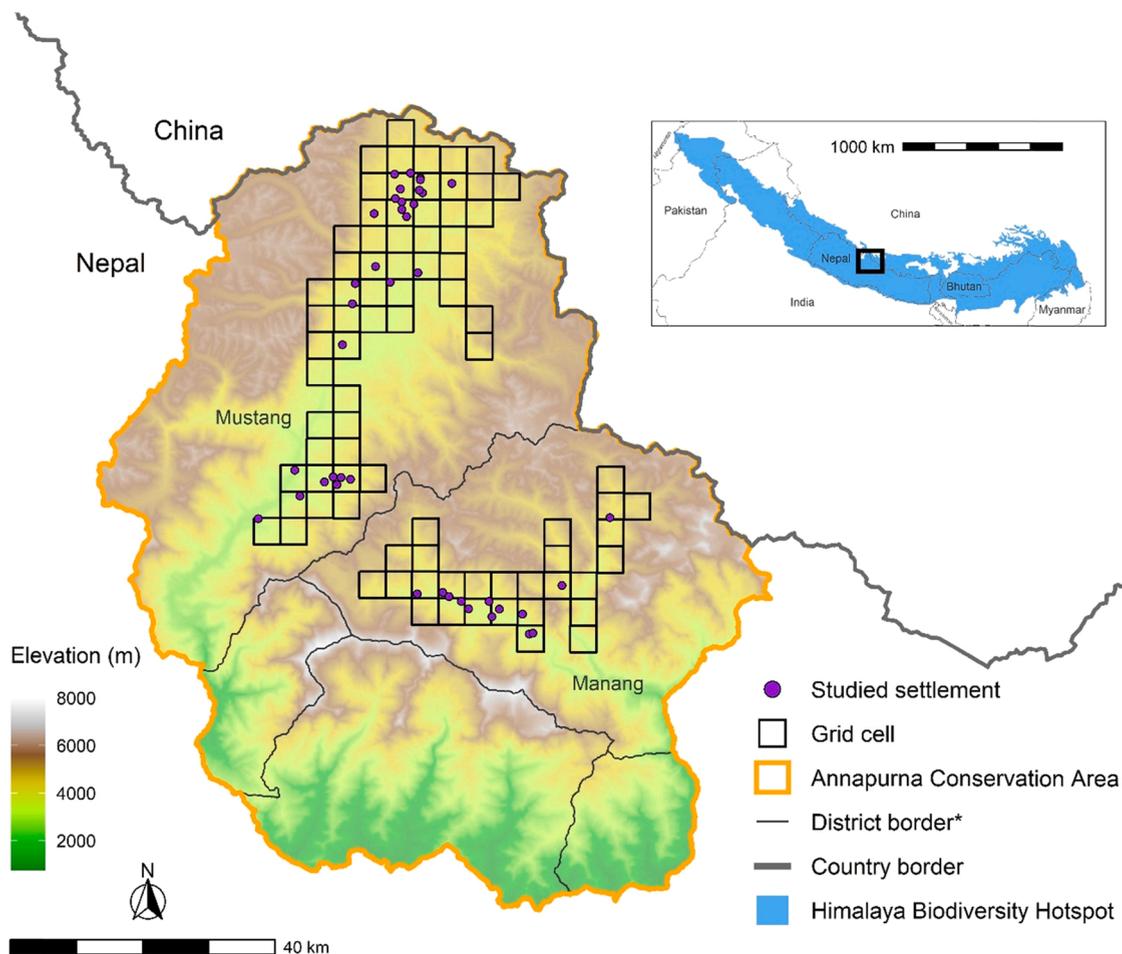


Fig. 1. Study area covered by 82 grid cells in the Annapurna Conservation Area (Nepal) within the Himalaya Biodiversity Hotspot. Sources: NASA/METI/AIST/Japan Spacesystems and U.S./Japan ASTER Science Team 2009 (elevation); Conservation International (2011) (Hotspot location); DIVA-GIS (2015) (country borders); Humanitarian Data Exchange (2021) (district borders).

Baral et al., 2019).

This study was conducted in the bordering districts Mustang and Manang of the ACA (approximately 28.57971–29.31300°N, 83.70784 – 84.33805°E; Fig. 1). Elevations in the studied area range from about 2680 to 5690 m above sea level (a.s.l.), and the dominant climates are arid steppe cold in Upper Mustang and cold and polar in Manang (Karki et al., 2015). Seasonal daily air temperatures are strongly related to elevations and range from about – 10 °C in winter to about 10 °C during the monsoon (Karki et al., 2015; Department of Hydrology and Meteorology, 2017). Location in the rain shadow of the Annapurna Range results in very low precipitation, with only about 150 mm of mean annual precipitation recorded in parts of Upper Mustang and about 600 mm in Manang (Karki et al., 2015; Department of Hydrology and Meteorology, 2017). Forested areas are scarce in the deserts and steppes of Upper Mustang (Paudel and Andersen, 2013). In Manang, forests reach up to elevations of 4400 m a.s.l. and are dominated by the East Himalayan fir (*Abies spectabilis*) on the southern slopes and by the Himalayan birch (*Betula utilis*) on the northern slopes (Chhetri et al., 2017). Shrublands, alpine grasslands, and alpine meadows adjoin the treeline, above which the highest elevations are shaped by barren lands and permanent snow fields (Shrestha and Wegge, 2008).

Apart from the snow leopard, the study area hosts other large carnivores including the Himalayan wolf (*Canis lupus chanco*), Eurasian lynx (*Lynx lynx*), and brown bear (*Ursus arctos*; Baral et al., 2019). The wild ungulate community is diverse and dominated by the blue sheep (*Pseudois nayaur*), which represents the main wild prey species of snow leopards and occurs at the highest densities in Manang (e.g., Oli, 1994; Aryal et al., 2014a; Chetri et al., 2017), as well as the Himalayan tahr (*Hemitragus jemlahicus*), Tibetan argali (*Ovis ammon hodgsoni*), Tibetan gazelle (*Procapra picticaudata*), kiang (*Equus kiang*), and musk deer (*Moschus* spp.; Oli, 1994; Chetri et al., 2017; Baral et al., 2019; Singh et al., 2019). Smaller mammals are the Himalayan marmot (*Marmota himalayana*), woolly hare (*Lepus oiostolus*), and pikas (*Ochotona* spp.; Chetri et al., 2017). Livestock owners keep large species including yaks (*Bos grunniens*), cattle (*B. taurus*), dzos (*B. grunniens* × *B. taurus*), horses (*E. caballus*), and mules (*E. asinus* × *E. caballus*), and smaller species including sheep (*Ovis aries*) and goats (*Capra hircus*; Chetri et al., 2017).

2.2. Data collection

This study was based on wildlife monitoring efforts and questionnaire surveys in the ACA between March 2019 and May 2021. To account for the vast landscape, remoteness of scattered settlements, local dialects (Chetri et al., 2019a), and official rules during the COVID-19 pandemic, surveys were supported and/or conducted by wildlife biologists and trained local field assistants.

2.2.1. Wildlife monitoring

To ensure representative sampling of the ACA, we created a grid of 4 × 4 km cells (Alexander et al., 2016a; Soofi et al., 2019), which compromised the large spatial ranges of snow leopards (e.g., Aryal et al., 2014b; Johansson et al., 2016), and smaller movement and grazing patterns of wild ungulates and livestock (Wegge 1976, cited in Jackson, 1996). We selected sampling grids based on geographic and ecological requirements of snow leopards (mean elevation 3000 - 5000 m: Aryal et al., 2014b; <50% forest cover: McCarthy and Chapron, 2003; Lovari et al., 2013), and the proximity to settlements (<10 km), which was determined by herding practices (Aryal et al., 2014c) and logistic constraints (Alexander et al., 2016a). We monitored snow leopards, blue sheep, marmots, and livestock during three field visits in spring (March - May; 32 days in 2019 and 63 days in 2021) and autumn (September - October; 28 days in 2019). We covered as many grid cells as possible considering personnel, logistic, and environmental constraints (i.e., availability of skilled field assistants and accessibility of the respective areas during the survey periods). In each grid cell, we established transects along the ridgelines, cliff bases, river and stream gorges, mountain passes, and trails following discussions with knowledgeable local people, analyses of satellite images, and verification of terrain accessibility. These features are used by snow leopards for traveling and marking (Jackson and Hunter, 1996; Fox and Chundawat, 2016) and/or provide a good view of the surrounding landscape.

To monitor the relative abundance of snow leopards, we applied sign surveys following the Snow Leopard Information Management System (SLIMS) technique (Jackson and Hunter, 1996). This methodology is a standardized and frequently used measure of snow leopard relative abundance and may produce reliable results comparable with those of camera trapping and genetic analyses when accounting for potential sources of observer bias and environmental variation (McCarthy et al., 2008). As recommended, we applied this method along predefined and relatively short transect sections (hereafter SLIMS sections) associated with high sign detectability, mainly ridgelines and cliff bases, where we recorded snow leopard scrapes, putative scats, pugmarks and spraying/rubbing sites (Jackson and Hunter, 1996; Sharma et al., 2006). To minimize effects of environmental variation, we applied the SLIMS technique only in spring, which offers high sign detectability due to intense snow leopard marking activity, favorable weather conditions, and relatively little anthropogenic disturbance (Jackson and Hunter, 1996; Fox and Chundawat, 2016). To minimize the observer bias (McCarthy et al., 2008), either of two experienced wildlife biologists (RPL, TRG) led the SLIMS surveys in each grid cell.

To monitor prey populations, we conducted total counts of blue sheep, which are the main wild prey of snow leopards in the study area (e.g., Aryal et al., 2014b; Chetri et al., 2017), and livestock in spring and autumn. These counts were conducted by teams of 2–3 trained observers who were equipped with 10 × 32 binoculars (Kowa SV) and scanned the surrounding habitats while slowly walking along the transects and from suitable vantage points (Leki et al., 2018). Total counts were conducted predominantly during the morning (6:00–10:00 a.m.) and afternoon hours (2:00–6:00 p.m.) coinciding with the peaks of blue sheep feeding activities (Liu et al., 2005). Upon encounters of the target species, we marked the observer location and denoted the compass direction (degree), distance (m), and angle (degree) to the detected individual or to the center of detected groups by using a compass, GPS device (Garmin GPSMAP 64 s), and rangefinder (Leica Rangemaster CRF 1000-R). To avoid double counts, especially of blue sheep, we aimed at sampling adjacent grid cells in the shortest possible intervals and took notes of group composition (sex and age classes) and unique

characteristics like coloration patterns and broken horns (Leki et al., 2018). We also denoted observations of Himalayan marmots, a secondary prey species (Aryal et al., 2014b; Lyngdoh et al., 2014; Chetri et al., 2017), and their burrows.

One team member participating in the prey surveys verified correct locations of blue sheep, livestock, and marmots in ArcGIS 10.3.1 (Esri, USA) and QGIS 3.4.8 (QGIS Development Team). In addition, we used the Visibility tool in ArcGIS to map the actual survey area, i.e. the visible surface (viewshed) along the transects. Based on field experience, we either used the maximum sighting distance of 1000 m or adjusted it if landscape characteristics and weather conditions reduced visibility (Thapa et al., 2021). If necessary, we manually edited the obtained viewsheds.

2.2.2. Questionnaire surveys

Between July 2020 and May 2021, we conducted questionnaire surveys in all major permanent settlements located in the studied grid cells (Fig. 1). To ensure study feasibility and data quality (i.e., to include all settlements and to sample a representative number of households per settlement), we aimed at sampling one third to one fourth of all households with livestock in each settlement (Hanson et al., 2019). The households were initially selected based on snowball sampling (i.e., we identified households after consultations with key informants, usually conservation officers and knowledgeable local people; Goodman, 1961; Alexander et al., 2015; Hacker et al., 2021), and we additionally interviewed randomly selected household respondents, for instance at public gatherings (Young et al., 2018), when the number of livestock owners met during the snowball sampling was not sufficient.

Before starting the interviews, respondents were informed about project goals, independence of this study on compensation schemes, and security and anonymity of their information. As suggested by Young et al. (2018), we implemented a pilot study in spring 2019 and modified our questionnaire form thereafter. The respondents were asked about their current livestock holdings including the number of adult (≥ 2 years) and juvenile (< 2 years) individuals, which served as a measure of livestock availability (Khorozyan et al., 2018). Moreover, we recorded the locations of the main summer and winter grazing areas, interventions used, livestock losses in the past two years, details of depredation events (e.g., age class, date, daytime) and wildlife observations near livestock grazing areas. The mapping of livestock grazing areas was supported by local people who were able to interpret maps of the study area and familiar with local pasture names. To prevent species misidentification and to optimize the credibility of the gathered information, we 1) showed printed photographs of wildlife and livestock species, 2) asked for specific evidence/indications that livestock was killed by snow leopards and not by other predators (e.g., direct observations, signs), 3) cross-checked relevant information with local conservation officers and neighboring herders whenever possible, and 4) back-checked about 10% of the households by telephone interviews (Hanson et al., 2019). We omitted data from households with considerable changes in livestock husbandry over the survey period.

Table 1

List of predictor variables included in the models addressing snow leopard relative abundance (Hypothesis 1) and livestock depredation by snow leopards (Hypothesis 2) based on monitoring and questionnaire data collected in the Annapurna Conservation Area (Nepal) between 2019 and 2021.

Predictor variable	Unit	Model Hypothesis 1	Models Hypothesis 2	Source
Elevation	m	+		NASA/METI/AIST/Japan Spacesystems and U.S./Japan ASTER Science Team (2009)
Terrain ruggedness	m	+	+	computed from Elevation
Human population density	number of people/pixel	+	+	WorldPop (2020)
Snow leopard relative abundance	scrapes/km	+ ^a	+	own monitoring data
Livestock density	individuals/km ²	+	+ ^b	own monitoring data
Blue sheep density	individuals/km ²	+	+	own monitoring data
Marmot occurrence	categorical: presence, absence	+	+	own monitoring data
Longitude	degree	+		own monitoring data
Latitude	degree	+		own monitoring data
Proportion in prey community ^c	%		+ ^b	
Livestock holding size	individuals/owner		+ ^b	own questionnaire data
Proportion of juveniles	%		+ ^b	own questionnaire data
Guarding by shepherds ^d	categorical: daily, not daily		+ ^b	own questionnaire data
Use of corrals ^d	categorical: daily, not daily		+ ^b	own questionnaire data
Use of other interventions ^e	categorical: use, no use		+ ^b	own questionnaire data

^a as the response variable (transect length considered as an offset).

^b considering the respective livestock species.

^c based on blue sheep and livestock observations.

^d categorized as 'not daily' if livestock was only partially guarded by shepherds or in night-time corrals.

^e during night-time; including dogs, acoustic and light deterrents.

2.2.3. Environmental predictor variables

We prepared the spatial data layers of predictor variables relevant to snow leopard abundance and human-snow leopard interactions. Elevation (m) was received from a digital elevation model of 30-m resolution (DEM; NASA/METI/AIST/Japan Space-systems and U.S./Japan ASTER Science Team, 2009), and this layer was also used to calculate terrain ruggedness (m; Riley et al., 1999). In addition, we investigated anthropogenic influence by including the estimated human population density (number of people per pixel (~1 km² at the equator); WorldPop, 2020).

2.3. Data analysis

2.3.1. Effects of blue sheep and livestock density on snow leopard relative abundance

Addressing Hypothesis 1, we conducted a multivariate analysis to examine the effects of wild and domestic prey availability on snow leopard relative abundance in the study area (Guisan et al., 2002).

We assessed the relative abundance of snow leopards (response variable) by counting the number of scrapes, the most frequently encountered sign type (84.4% of all signs; Table A1), per SLIMS section. We disregarded other signs, such as putative snow leopard scats, to reduce the observer bias and prevent species misidentification (Janečka et al., 2008; see Table A2 for sensitivity analysis based on all sign types). To account for the variable lengths of SLIMS sections, this parameter was incorporated in the model as an offset (Soofi et al., 2019). We assigned a weight to each SLIMS section based on its location in the grid net (i.e., each grid cell contributed equally) and length (i.e., if multiple SLIMS sections occurred in the same grid, they were additionally weighted proportionally to their lengths).

We considered various potential ecological, geographic, and anthropogenic confounding factors as predictor variables (Table 1). These were the minimum densities (hereafter densities) of blue sheep and livestock (yak, cattle, dzo, horse, sheep, and goat; the number of individuals per survey area), marmot occurrence (presence/absence), elevation (m), terrain ruggedness (m), human population density (number of people per pixel), and the location (longitude, latitude and their interaction).

The blue sheep and livestock densities were calculated by dividing the number of animals spotted during the prey counts by the respective survey areas (e.g., Aryal et al., 2014a). Blue sheep numbers and survey areas were computed within the 2000-m wide buffers around the SLIMS sections. This buffer width accounted for the reported minimum home ranges of female snow leopards (~12 km², Jackson and Ahlborn, 1989; ~13 km², McCarthy et al., 2005; see Table A2 for sensitivity analysis based on alternative buffer widths). Wherever applicable, we calculated mean densities based on prey counts in spring and autumn. This accounted for the longevity and repeated use of snow leopard scrape sites (Ahlborn and Jackson, 1988), imperfect detection of blue sheep and livestock (Suryawanshi et al., 2012), anticipated small home ranges of blue sheep (Cui 2007 cited in Zhang et al., 2013), and overlap of habitats and elevation ranges used by blue sheep and livestock in both seasons (Shrestha and Wege, 2008; Filla et al., 2021; see Table A2 for sensitivity analysis based on grids covered in both seasons). We recorded the presence/absence of Himalayan marmots based on direct sightings and observations of active burrows.

Elevation and terrain ruggedness were both gathered on the SLIMS sections. Elevation was included as a quadratic term as we expected snow leopards and blue sheep to avoid extremely low and high elevations (Aryal et al., 2014b; Filla et al., 2021; see Table A2 for sensitivity analysis including elevation as a linear term). Human population density was extracted from the means of 100 points regularly distributed across the survey area.

Moreover, we considered the locations of SLIMS section centroids (longitude, latitude, and their interaction; Chetri et al., 2017). These variables accounted for spatial differences within the vast study area, such as climatic conditions and vegetation characteristics (e.g., Karki et al., 2015), that might not be adequately represented by other predictor variables and potentially affected the density and detectability of snow leopard signs. More importantly, this procedure suggested an improved model performance based on residual plots and Moran's I statistics (Moran, 1950) by accounting for spatial autocorrelation, i.e., variables at nearby locations not being independent from each other (Legendre, 1993; see Table A2 for sensitivity analysis ignoring spatial autocorrelation).

To ease model convergence, all continuous predictor variables were standardized by subtracting the mean and dividing by the standard deviation (SD). We applied a negative binomial model to account for overdispersion (variance ≠ mean; Gelman and Hill, 2007). As we were primarily interested in the impacts of prey variables and needed to account for confounding effects of other predictor variables, we did not perform model selection. We tested for multicollinearity of predictor variables based on the variance inflation factor (VIF) and excluded variables if VIF > 3 (Soofi et al., 2019).

We assessed the relative importance of each predictor variable in a random permutation procedure (Thuiller et al., 2009). Therefore, we randomized one variable 100 times and calculated a raw importance value for the respective variable as one minus the mean correlation of predictions made by the original model and the randomized models. We obtained relative importance values by standardizing them to the sum of one (Thuiller et al., 2009). We conducted various sensitivity analyses to verify the validity of model outputs by alternating model parameters (e.g., buffer width) and model set-up (e.g., model terms; Table A2).

2.3.2. Effects of snow leopard relative abundance, blue sheep and livestock density, and intervention strategies on livestock depredation by snow leopards

Addressing Hypothesis 2, we applied generalized linear models (GLMs; Guisan et al., 2002; Bolker et al., 2009; O'Hara and Kotze, 2010), which are frequently used in human-wildlife conflicts (Alexander et al., 2015; Khorozyan et al., 2017; Soofi et al., 2019), to assess the effects of various parameters on livestock depredation attributed to snow leopards.

We ran separate models for the most frequent livestock species including small livestock (sheep and goats; n = 130 holdings) and large livestock (yaks (n = 62), cattle (n = 390), and horses (n = 294)). Sheep and goats were pooled for the analyses as these animals

are usually kept in mixed herds. The number of depredation events in the 2-year survey period, which was significantly correlated with the number of depredated animals ($r = 0.613$, $p < 0.001$, 95% CI = 0.570–0.653), served as the response variable.

We applied Poisson regression to examine the effects of ecological factors, topographic conditions, and anthropogenic parameters on livestock depredation events attributed to snow leopards. The predictor variables were the relative abundance of snow leopards (number of scrapes per km of SLIMS transect), densities of blue sheep and the respective livestock species (number of animals per km² of survey area), proportion of the respective livestock species in the observed prey community (i.e., blue sheep and livestock combined), marmot occurrence (presence/absence), terrain ruggedness (m), human population density (number of people per pixel), livestock holding size (number of animals of the respective livestock species kept in a household), proportion of juveniles (%), daytime guarding by shepherds (daily/not daily), use of night-time corrals (daily/not daily), and the application of additional night-time interventions including dogs, acoustic and light deterrents (use/no use). Husbandry parameters were categorized as ‘not daily’ if livestock was only partially guarded by shepherds or in night-time corrals (i.e., intervention strategies were restricted to specific age/sex groups or seasons; Table 1).

All predictor variables were prepared based on 1500-m buffers around summer and winter grazing areas of livestock. This buffer width was selected after visual examination of the dimensions of unfenced grazing areas (based on field experience and satellite imagery) and accounted for movement patterns and scattering of livestock (Aryal et al., 2014c; see Table A3 for sensitivity analysis based on an alternative buffer width). In contrast to the analysis addressing Hypothesis 1, we were unable to adequately assign prey densities/presence directly to each studied household, as sampling intensities differed around grazing areas (i.e., the immediate surroundings of some grazing areas were hardly covered or sampled irregularly). Therefore, we used a 2-step approach to assign these predictor values to the respective households. First, we assessed prey densities/presence for each grid cell. Second, we computed these parameters for grazing areas by considering all grid cells in their 1500-m buffers and proportional to their relative overlap. We used the means of 100 regularly-distributed points in the buffered grazing areas to compile terrain ruggedness and human population density.

We weighted summer and winter grazing areas equally and excluded households with grazing areas remote (> 1500 m) from the grid cells ($n = 21$). For horses, which were more frequently depredated during summer ($\chi^2 = 12.86$, $p = 0.005$), we additionally ran models based on summer data only (see Table A4). We used the same procedure to examine multicollinearity of predictor variables as in the model addressing Hypothesis 1. The candidate models were ranked based on the Akaike Information Criterion corrected for small sample size (AIC_c; Akaike, 1973; Grueber et al., 2011), and the best models were defined as those with $\Delta\text{AIC}_c < 2$ (Burnham and Anderson, 2002; Khorozyan et al., 2017). If multiple models performed best ($\Delta\text{AIC}_c < 2$), we produced multi-model averaged results (Grueber et al., 2011). Additionally, we conducted χ^2 and Mann-Whitney U tests to compare samples and provide support to model outputs.

All analyses were conducted in R v. 4.1.1 (R Core Team, 2021). We used the standard error of the mean (SE) as a measure of variation for estimated parameters (i.e., model outputs) and the standard deviation as a measure of variation for observed variables (e.g., grid-wise survey efforts and prey densities), unless otherwise indicated. The packages *DHARMA* (Hartig, 2021), *geosphere* (Hijmans, 2019), *MASS* (Venables and Ripley, 2002), *MuMin* (Barton, 2020), *performance* (Lüdtke et al., 2021), and *pscl* (Zeileis et al., 2008) were used for data analyses, and the packages *cowplot* (Wilke, 2020), *ggplot2* (Wickham, 2016), and *ggspatial* (Dunnington, 2021) were applied for data visualization.

3. Results

3.1. General

Overall, we covered 82 grid cells (Manang: $n = 27$, Mustang: $n = 55$) of which 50 (Manang: $n = 26$, Mustang: $n = 24$) were sampled in both spring and autumn (Table A1). We walked along a total transect length of 285.2 km in spring (3.5 ± 1.2 km/grid cell) and 205.6 km in autumn (4.0 ± 1.1 km/grid cell). The SLIMS sections monitored during spring surveys were located in 78 grid cells and had a total length of 54.8 km (0.7 ± 0.2 km/grid cell). We interviewed a total of 479 livestock owners (Manang: $n = 163$, Mustang: $n = 316$) who kept 15,130 individuals of livestock, mainly sheep and goats (69.6%), yaks (13.5%), and cattle (11.6%). Full information about the sampling effort is provided in Table A1.

3.2. Wildlife and livestock monitoring

We detected snow leopard signs in most grid cells ($n = 71$, 86.6%; Manang: 25, 92.6%; Mustang: 46, 83.6%). A total of 1242 snow leopard signs were encountered along SLIMS sections, which were mainly scrapes (84.4%), followed by putative scats (14.5%) and pugmarks (1.0%; Table A1). The scrape encounter rate varied considerably among the SLIMS sections ranging from 0.0 to 166.3 scrapes/km, and it was higher in grid cells in Manang (31.5 ± 32.8 scrapes/km) than in Mustang (9.9 ± 11.5 scrapes/km; $U = 1071$, $p < 0.001$).

We observed blue sheep along the transects in 44 (53.7%) grid cells (Manang: $n = 26$, 96.3%, Mustang: $n = 18$, 32.7%), and their densities were higher in grid cells in Manang (8.5 ± 8.1 individuals/km²) than in Mustang (1.2 ± 2.7 individuals/km²; $U = 1305.5$, $p < 0.001$). Livestock was observed along the transects in 63 (76.8%) grid cells (Manang: $n = 25$, 92.6%, Mustang: $n = 38$, 69.1%). The observed densities of livestock in grid cells were higher, though not significantly, in Mustang (40.7 ± 55.0 individuals/km²) than in Manang (8.8 ± 9.0 individuals/km²; $U = 622$, $p = 0.234$). Overall, the grid-wise densities of blue sheep (3.6 ± 6.2 individuals/km²) were much lower than those of livestock (30.2 ± 47.6 individuals/km²; $U = 1898.5$, $p < 0.001$). This also applied to grid cells in Mustang ($U = 699$, $p < 0.001$) but not in Manang ($U = 370$, $p = 0.931$). Marmots and their burrows were observed in 10 (12.2%) grid

cells, all of which were located in Mustang.

3.3. Effects of blue sheep and livestock density on snow leopard relative abundance

The relative abundance of snow leopards increased with blue sheep density ($\beta = 0.293 \pm 0.145$, $p = 0.043$) and terrain ruggedness ($\beta = 0.264 \pm 0.122$, $p = 0.031$) and decreased with increasing densities of livestock ($\beta = -0.249 \pm 0.126$, $p = 0.048$) and the human population ($\beta = -0.382 \pm 0.150$, $p = 0.011$; Fig. 2; Table A5). The model also showed statistically significant effects of latitude (more in the south, i.e. in Manang) and its interaction with longitude (i.e., more in the Phu valley in the north-east of Manang) on snow leopard relative abundance (Fig. 2; Table A5). According to relative variable importance, the density of blue sheep was the most important parameter affecting snow leopard relative abundance (32.1%), followed by latitude (22.3%), terrain ruggedness (12.8%), and human population density (11.5%; Fig. 2; Table A5).

3.4. Effects of snow leopard relative abundance, blue sheep and livestock density, and intervention strategies on livestock depredation by snow leopards

The respondents attributed the loss of 773 individuals of livestock to snow leopards in the past two years, which implies an annual depredation rate of 2.6% (Table 2). Snow leopards accounted for 33.2% of all livestock losses in the given period. Diseases, weather extremes, and accidents (57.0%) were the main livestock mortality factors, while other predators (wolf, red fox (*Vulpes vulpes*), golden jackal (*Canis aureus*), feral dog (*Canis lupus familiaris*)) were responsible for 9.3% of losses, and 0.5% of losses were due to other/unknown causes. According to the respondents, most depredation events ($n = 316$) were targeted on sheep and goats (38.5%) and yaks (33.2%), with sheep and goats contributing to the majority of depredated animals (68.6%; 18.1% for yaks).

Events of sheep and goat depredation occurred equally frequently during daytime (50.0% of depredation events with known depredation time, $n = 56$) and night-time (50.0%, $n = 56$), which also applied to yaks (daytime: 50.5%, $n = 52$; night-time: 49.5%, $n = 51$). A majority of cattle and horse depredation events with known depredation time took place during night-time (65.7%, $n = 23$ for cattle and 78.4%, $n = 29$ for horses).

The number of sheep and goat depredation events decreased with increasing human population density ($\beta = -0.051 \pm 0.019$, $p = 0.010$) and marmot presence ($\beta = -0.996 \pm 0.404$, $p = 0.014$; Table 3). For all species of large livestock, the number of depredation events was positively associated with the total number of the respective livestock species kept by the owner (yak: $\beta = 0.015 \pm 0.004$, $p < 0.001$; cattle: $\beta = 0.136 \pm 0.046$, $p = 0.003$; horse: $\beta = 0.236 \pm 0.097$; $p = 0.015$; Table 3). Moreover, cattle depredation increased with blue sheep density ($\beta = 0.107 \pm 0.038$, $p = 0.005$), while it decreased with the relative abundance of snow leopards ($\beta = -0.037 \pm 0.016$, $p = 0.020$) and the daily use of night-time corrals ($\beta = -1.879 \pm 0.484$; $p < 0.001$; Table 3).

4. Discussion

This study in the Annapurna Conservation Area (ACA) revealed a strong positive effect of blue sheep density on snow leopard relative abundance, which also increased with terrain ruggedness and decreased with increasing densities of livestock and the human population. In contrast, blue sheep had limited effects on livestock depredation patterns. The size of livestock holdings was the main determinant of depredation losses for large species of livestock (yak, cattle, and horses), while depredation of sheep and goats

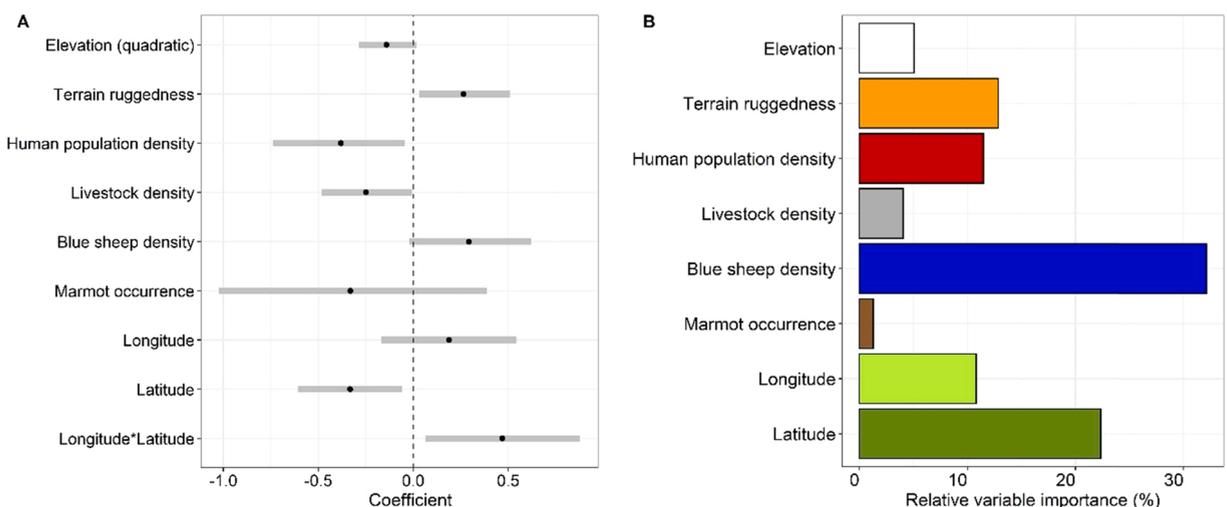


Fig. 2. Effects (A) of various predictor variables on snow leopard relative abundance in the Annapurna Conservation Area and their relative importance (B) based on the full negative binomial model. In A, black dots show the estimates of the coefficients and gray horizontal bars indicate the 95% confidence intervals.

Table 2

Livestock holdings and losses attributed to snow leopards in sampled households of Manang (n = 163) and Mustang (n = 316) between 2018 and 2021. Abbreviations: ad. = adults, juv. = juveniles.

	Livestock holding size												Total
	Yak		Cattle		Dzo		Horse		Goat		Sheep		
	ad.	juv.	ad.	juv.	ad.	juv.	ad.	juv.	ad.	juv.	ad.	juv.	
Manang	1158	403	386	82	0	0	197	15	921	331	52	22	3567
Mustang	370	105	930	359	121	2	421	34	7526	1471	187	24	11,550
Total	1528	508	1316	441	121	2	618	49	8447	1802	239	46	15,117
	Livestock losses attributed to snow leopards												Total
	Yak		Cattle		Dzo		Horse		Goat		Sheep		
	ad.	juv.	ad.	juv.	ad.	juv.	ad.	juv.	ad.	juv.	ad.	juv.	
Manang	35	83	23	13	0	0	16	8	80	10	9	0	277
Mustang	11	11	5	1	1	0	16	20	391	28	12	0	496
Total	46	94	28	14	1	0	32	28	471	38	21	0	773

Table 3

Summary of model-averaged results of the best generalized linear models (GLMs, $\Delta\text{AICc} < 2$) describing the effects of predictor variables on the number of livestock depredation events in the Annapurna Conservation Area between 2018 and 2021. The estimates of the coefficients, standard errors (SE), 95% confidence intervals (95% CI), and p-values (p) are shown for all models. Predictor variables with $p < 0.05$ are highlighted in bold. ^A during night-time.

Species	Predictor variable	Estimate	SE	95% CI	p
Yak	Intercept	-1.591	1.020	-3.606–0.425	0.122
	Terrain ruggedness	0.080	0.072	0.013–0.228	0.266
	Proportion of juveniles	0.013	0.009	0.000–0.032	0.158
	Livestock holding size	0.015	0.004	0.008–0.022	< 0.001
	Use of other interventions ^A	0.212	0.261	-0.093–0.864	0.421
	Human population density	0.010	0.026	-0.028–0.130	0.717
	Yak density	-0.020	0.029	-0.102–0.010	0.493
	Blue sheep density	0.009	0.021	-0.021–0.092	0.679
	Guarding by shepherds	0.080	0.214	-0.208–1.041	0.710
Cattle	Intercept	-3.260	1.176	-5.570 to –0.951	0.006
	Blue sheep density	0.107	0.038	0.033–0.181	0.005
	Livestock holding size	0.136	0.046	0.045–0.228	0.003
	Use of corrals	-1.879	0.484	-2.830 to –0.928	< 0.001
	Snow leopard relative abundance	-0.037	0.016	-0.068 to –0.006	0.020
	Terrain ruggedness	0.122	0.102	-0.002–0.330	0.233
	Proportion of juveniles	0.001	0.005	-0.013–0.024	0.799
Horse	Intercept	-2.111	0.458	-3.012 to –1.210	< 0.001
	Use of corrals	-0.559	0.526	-1.690–0.157	0.289
	Proportion of juveniles	0.009	0.010	-0.002–0.031	0.364
	Livestock holding size	0.236	0.097	0.045–0.428	0.015
	Snow leopard relative abundance	-0.007	0.012	-0.042–0.007	0.539
	Terrain ruggedness	0.009	0.034	-0.051–0.206	0.784
	Human population density	-0.011	0.023	-0.090–0.024	0.622
	Marmot occurrence	0.085	0.209	-0.223–0.941	0.687
	Horse density	-0.004	0.020	-0.127–0.053	0.825
	Blue sheep density	-0.002	0.013	-0.113–0.049	0.877
Guarding by shepherds	0.002	0.057	-0.655–0.896	0.968	
Sheep and goat	Intercept	-0.067	0.459	-0.972–0.839	0.885
	Human population density	-0.051	0.019	-0.089 to –0.012	0.010
	Marmot occurrence	-0.996	0.404	-1.795 to –0.198	0.014
	Blue sheep density	-0.040	0.047	-0.152–0.021	0.399
	Livestock holding size	0.001	0.001	-0.001–0.005	0.578
	Terrain ruggedness	0.016	0.037	-0.049–0.156	0.673
	Snow leopard relative abundance	0.003	0.007	-0.010–0.031	0.691
	Proportion of juveniles	0.000	0.002	-0.007–0.014	0.849
	Sheep and goat density	0.000	0.001	-0.011–0.006	0.922

decreased with increasing human population density and marmot presence. These findings have clear implications for the management and conservation of the snow leopard and its wild prey base.

In line with **Hypothesis 1**, snow leopard relative abundance was positively affected and strongly shaped by blue sheep density. Blue sheep are currently listed as a species of ‘Least Concern’ (Harris, 2014), but like other wild ungulates they are increasingly threatened by various human activities, including poaching and habitat degradation due to competition with livestock (Mishra et al., 2003, 2004; Cui and Graf, 2009; Berger et al., 2013; Shrestha and Moe, 2015; Yakha and Chalise, 2021; Yang et al., 2021). Our results confirm earlier studies demonstrating positive effects of blue sheep and other wild ungulates on habitat use and density of snow leopards (Sharma et al., 2015; Alexander et al., 2016a; Suryawanshi et al., 2017, 2021; Sharma et al., 2021; Yang et al., 2021). Moreover, they

support the general pattern of a positive relationship between large carnivore density and wild prey biomass (Fuller and Sievert, 2001). We assume that significant effects of latitude and its interaction with longitude also result, at least partially, from spatial differences in prey availability. In fact, snow leopard relative abundance increased in southern grid cells (i.e., in Manang), especially in the north-eastern part of this district, the Phu valley. This area, where we observed the highest blue sheep densities and snow leopard relative abundance, is indeed known to host quite high densities of both species (Shrestha and Wegge, 2008; Wegge et al., 2012; McCarthy et al., 2017; Filla et al., 2021; Thapa et al., 2021).

Apart from blue sheep density, snow leopard relative abundance was positively affected by terrain ruggedness. This is likely to be caused by natural preferences of these cats for rugged terrain with cliffs and moderate to steep slopes, which are used for hunting and resting (Jackson, 1996; McCarthy et al., 2005; Fox and Chundawat, 2016; McCarthy et al., 2017). The positive effect of terrain ruggedness, which is assumed to be inversely linked with human activity and disturbance (Cristescu et al., 2019), and the negative effect of increasing human population density may also reflect a risk-avoidance strategy (e.g., Wolf and Ale, 2009), as humans pose a major mortality factor for snow leopards (Nowell et al., 2016). In line with that, these parameters affect the occurrence, activity, and habitat selection also of other large carnivores (e.g., Rauset et al., 2013; Dorresteijn et al., 2014; O'Neill et al., 2020; Ripari et al., 2022, to name a few). Human disturbance may also explain a negative impact of livestock on snow leopard relative abundance: livestock represents potential prey but is often accompanied by shepherds and may additionally suppress or displace wild prey (Salvatori et al., 2021; Yang et al., 2021). We acknowledge that this finding could be affected by methodological constraints, as large herds of livestock may trample down and reduce the number of snow leopard signs (Jackson and Hunter, 1996), and as we counted prey populations at times of high blue sheep activity (Liu et al., 2005) when some livestock remained in corrals (RPL, personal observation).

In contrast to our expectations (Hypothesis 2), blue sheep density and use of interventions showed only limited effects on livestock depredation by snow leopards, which was the main mortality factor (33.2%) in the study area and affected 2.6% of livestock annually. In the present study, we did not find significant effects of blue sheep density on depredation rates of sheep and goats as well as yaks, which accounted for the majority of killed animals (86.7%) and depredation events (71.7%). On the one hand, previous studies of large carnivores from various taxa reported an inverse relationship between wild prey abundance and livestock depredation (Meriggi and Lovari, 1996; Odden et al., 2013; Soofi et al., 2019, to name a few), and Khorozyan et al. (2015) even identified critical thresholds of wild prey abundance for predicting human-felid conflicts. On the other hand, abundant wild prey and its overlap with livestock may also increase depredation (e.g., Treves et al., 2004; Odden et al., 2008). Such contrasting results are also reported for the snow leopard (e.g., Suryawanshi et al., 2013; Bagchi et al., 2020). Though we are unable to explain these discrepancies, they prompt that livestock depredation by snow leopards might actually be affected by a variety of factors, such as individual predator behavior (e.g., Linnell et al., 1999; Johansson et al., 2015) and husbandry practices (e.g., Mijiddorj et al., 2018). Either way, our results suggest that conflicts over livestock depredation by snow leopards would neither be inflicted nor solved by increasing wild prey abundance, reinforcing the need to implement suitable intervention strategies (Jackson et al., 2010).

In that respect, daily guarding by shepherds did not significantly affect depredation rates of large livestock and many attacks on sheep and goats occurred in the presence of shepherds during daylight hours. Such losses could possibly be reduced by avoiding rugged pastures and keeping an eye over straggling individuals (Johansson et al., 2015; Mijiddorj et al., 2018), though we acknowledge that these recommendations might be hard to implement if shepherds supervise several hundred individuals and have to trade off the depredation risk against the quality of foraging areas.

Likewise, although the daily use of night-time corrals reduced cattle depredation rates and showed a similar trend for horses, snow leopards often attacked yaks, sheep, and goats in simple corrals and stone wall huts/houses during night-time, which frequently resulted in surplus killings (i.e., killing of multiple individuals in a single attack; Jackson and Wangchuk, 2001). Snow leopards are agile predators that can easily jump over simple stone wall corrals and also enter stone wall huts/houses through small openings and air inlets (Samelius et al., 2021; Thapa, 2021). Predator-proof corrals have been successfully implemented elsewhere (Jackson and Wangchuk, 2004; Samelius et al., 2021) and may significantly reduce livestock depredation in non-transhumant areas of the Annapurna region. These, however, may require relatively high acquisition costs and may not be used year-round in case of seasonal shifts of grazing areas (see Jackson and Wangchuk, 2004; Samelius et al., 2021).

Additional interventions like guarding dogs and deterrents might further reduce night-time losses. In the present study, we were unable to analyse individual effects of such intervention strategies, and the application of additional night-time interventions (merged as one category) did not significantly affect yak depredation. However, previous studies showed the potential of guarding dogs and non-lethal deterrents to mitigate human-carnivore conflicts (e.g., Augugliaro et al., 2020; Naha et al., 2020). Hence, more knowledge on the effectiveness of such interventions based on controlled experiments with standardized designs and the application of the most suitable interventions could further reduce livestock losses.

In order to optimize intervention applications, wildlife managers need to identify the households most vulnerable to depredation. In agreement with earlier studies in the ACA (Chetri et al., 2019a; Tiwari et al., 2020), we found the total number of animals to be the main determinant of depredation on large livestock (yaks, cattle, and horses). Hence, intervention improvements in large livestock holdings might be most efficient. Nevertheless, we suggest not to disregard owners keeping fewer animals because such owners may be more dependent on their livestock and respond to losses more negatively (Ikeda, 2004). Other factors may also be relevant for the tolerance of depredation, such as education level and religious attitudes (Li et al., 2014; Tiwari et al., 2020; Hacker et al., 2021).

Interestingly, our results suggest that the presence of Himalayan marmots around grazing areas reduced sheep/goat depredation. This finding needs to be considered cautiously as 1) marmots were mapped rather broadly, 2) they occurred in areas with relatively low snow leopard relative abundance, 3) we found no seasonal differences in depredation patterns between areas with and without marmots (see Fig. A1), and 4) our findings could also be affected by other parameters related to marmot habitats affecting snow leopard hunting behavior and shepherd effectiveness, such as terrain-dependent visibility and vegetation characteristics (our

information). Nevertheless, our marmot monitoring data closely matched the responses of livestock owners (Fig. A2), and the presence of marmots as an alternative prey may indeed discourage predator attacks and/or specialization on livestock (e.g., Linnell et al., 1999; see also Lowrey et al., 2016), especially in areas devoid of blue sheep. In fact, marmots represent an important, but seasonally available, secondary prey for snow leopards (Oli et al., 1993; Lyngdoh et al., 2014), and the availability of marmots and other small mammals is generally supposed to affect the seasonal dependence of snow leopards on livestock (Lhagvasuren and Munkhtsog, 2002; Bagchi and Mishra, 2006; Aryal et al., 2014b; Lham et al., 2021). Hence, we consider the protection of marmots and their habitats to be another essential component of conservation actions in high-altitude ecosystems like the Annapurna region where livestock competes for limited resources and can cause behavioral adaptations at the expense of foraging activities (Aryal et al., 2015; Poudel et al., 2016; own unpublished information). Their role and potential benefits in mitigating human-snow leopard conflicts deserve further investigation.

In the present study, we were unable to consider absolute snow leopard densities, as obtainable from camera trapping and genetic analyses, and assessed the relative abundance of snow leopards across the vast study area based on the SLIMS methodology developed by Jackson and Hunter (1996). However, this approach is commonly used in snow leopard surveys and considered a suitable index of relative abundance when placing transects in areas with high sign probability and accounting for potential sources of bias (Sharma et al., 2006; McCarthy et al., 2008; Valentová, 2017). Accordingly, we located SLIMS sections mainly along ridgelines and cliff bases and we accounted for bias arising from both the observer (all SLIMS surveys were led by one of two trained wildlife biologists) and environmental variation (all surveys were conducted in spring). Besides, we could not verify all depredation records attributed to snow leopards. However, we aimed to retain the most reliable self-reported records through data cross- and back-checking. Consequently, the mentioned potential limitations are unlikely to have affected our main results. Moreover, our models addressing livestock depredation considered only few households from areas with rather high blue sheep density, such as the Nar Phu valley, because we had to exclude some households due to significant recent changes in livestock numbers or as livestock grazed outside the studied grid cells. Hence, our conclusions about the main determinants of livestock depredation mainly apply to areas with low to moderate prey densities (see Fig. A3), and the effects of rather high prey densities require further investigation.

5. Conclusions

This study demonstrated a pivotal ecological role of blue sheep for snow leopard persistence in the Nepalese Himalaya. Our results reinforce a demand for integrating this ungulate into the management and conservation plans (Alexander et al., 2016a), and support the claims to foster snow leopard populations by wild prey recovery and translocation (Mishra et al., 2003; Aryal et al., 2013; Ferretti et al., 2014). Such programs should carefully consider the concerns of local people (Hanson et al., 2020) and can ideally be combined with other long-term initiatives including environmental education and livelihood diversification (Vannelli et al., 2019; Murali et al., 2020). We call for more in-depth examinations of the effects of marmots and other secondary prey on livestock depredation by snow leopards. To mitigate depredation, we suggest improving current intervention strategies, including predator-proofing corrals and optimizing daytime herding practices, and testing the suitability of additional interventions, such as guarding dogs and non-lethal deterrents. These actions will contribute to the conservation of snow leopards and benefit their co-existence with local people in the Annapurna region and beyond.

Funding

This work was supported by the Heinrich Böll Foundation (Ph.D. scholarship P136047), the National Geographic Society (Grant number EC-58331R-19), Breuckmann Foundation, Academy for the Protection of Zoo Animals and Wildlife e.V., Tatzmania Löffingen, and The Alongside Wildlife Foundation. We also acknowledge support by the Open Access Publication Fund of Göttingen University.

Declaration of Competing Interest

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

Data Availability

Upon acceptance of this manuscript, we will upload various datasets, including the anonymized questionnaire data and the processed modeling data, to the Dryad data repository.

Acknowledgments

This study was conducted within the framework of a PhD project on human-snow leopard co-existence. Permits for fieldwork were granted by the Government of Nepal (research permit 2075/76/1667), Department of National Parks and Wildlife Conservation (DNPWC), and the National Trust for Nature Conservation (NTNC)/Annapurna Conservation Area Project (ACAP; research permit 439/075/076). We appreciate the great support of Third Pole Conservancy in project coordination and implementation, and of B. Gurung, N. Gurung, D. Sangmo, D. Tsering, P. Yangdon, K. Gurung, and T. Gurung in planning and conducting the questionnaire surveys. Moreover, we thank R. R. Aryal for support in geographic data compilation, J. Signer for help in statistical analyses, and C.

Frank, A. Laux and M. Püttmanns for general advice.

Appendix A. Supplementary material

Supplementary data associated with this article can be found in the online version at [doi:10.1016/j.gecco.2022.e02153](https://doi.org/10.1016/j.gecco.2022.e02153).

References

- Ahlborn, G., Jackson, R.M., 1988. Marking in free-ranging snow leopards in west Nepal: a preliminary assessment. In: Proceedings of the Fifth International Snow Leopard Symposium. International Snow Leopard Trust: Bellevue, USA.
- Akaike, H., 1973. Information theory and an extension of the maximum likelihood principle. In: Petrov, B.N. and Csaki, F. (Eds.), Proceedings of the Second International Symposium on Information Theory, Akadémiai Kiadó: Budapest, Hungary, pp. 267–281.
- Alexander, J., Chen, P., Damerell, P., Youkui, W., Hughes, J., Shi, K., Riordan, P., 2015. Human wildlife conflict involving large carnivores in Qilianshan, China and the minimal paw-print of snow leopards. *Biol. Conserv.* 187, 1–9. <https://doi.org/10.1016/j.biocon.2015.04.002>.
- Alexander, J.S., Shi, K., Tallents, L.A., Riordan, P., 2016a. On the high trail: examining determinants of site use by the Endangered snow leopard *Panthera uncia* in Qilianshan, China. *Oryx* 50, 231–238. <https://doi.org/10.1017/S0030605315001027>.
- Alexander, J.S., Gopalaswamy, A.M., Shi, K., Hughes, J., Riordan, P., 2016b. Patterns of snow leopard site use in an increasingly human-dominated landscape. *PLoS One* 11, e0155309. <https://doi.org/10.1371/journal.pone.0155309>.
- Aryal, A., Brunton, D., Raubenheimer, D., 2013. Habitat assessment for the translocation of blue sheep to maintain a viable snow leopard population in the Mt Everest Region, Nepal. *Zool. Ecol.* 23, 66–82. <https://doi.org/10.1080/21658005.2013.765634>.
- Aryal, A., Brunton, D., Ji, W., Raubenheimer, D., 2014a. Blue sheep in the Annapurna Conservation Area, Nepal: habitat use, population biomass and their contribution to the carrying capacity of snow leopards. *Integr. Zool.* 34–45.
- Aryal, A., Brunton, D., Ji, W., Karmacharya, D., McCarthy, T., Bencini, R., Raubenheimer, D., 2014b. Multipronged strategy including genetic analysis for assessing conservation options for the snow leopard in the central Himalaya. *J. Mammal.* 95, 871–881. <https://doi.org/10.1644/13-MAMM-A-243>.
- Aryal, A., Brunton, D., Ji, W., Barraclough, R.K., Raubenheimer, D., 2014c. Human–carnivore conflict: ecological and economical sustainability of predation on livestock by snow leopard and other carnivores in the Himalaya. *Sustain. Sci.* 9, 321–329. <https://doi.org/10.1007/s11625-014-0246-8>.
- Aryal, A., Brunton, D., Ji, W., Rothman, J., Coogan, S.C.P., Adhikari, B., Su, J., Raubenheimer, D., 2015. Habitat, diet, macronutrient, and fiber balance of Himalayan marmot (*Marmota himalayana*) in the Central Himalaya, Nepal. *J. Mammal.* 96, 308–316. <https://doi.org/10.1093/jmammal/gyv032>.
- Atkins, J.L., Long, R.A., Pansu, J., Daskin, J.H., Potter, A.B., Stalmans, M.E., Tarnita, C.E., Pringle, R.M., 2019. Cascading impacts of large-carnivore extirpation in an African ecosystem. *Science* 364, 173–177. <https://doi.org/10.1126/science.aau3561>.
- Augugliaro, C., Christe, P., Janchivlamdan, C., Baymanday, H., Zimmermann, F., 2020. Patterns of human interaction with snow leopard and co-predators in the Mongolian western Altai: current issues and perspectives. *Glob. Ecol. Conserv.* 24, e01378. <https://doi.org/10.1016/j.gecco.2020.e01378>.
- Bagchi, S., Mishra, C., 2006. Living with large carnivores: predation on livestock by the snow leopard (*Uncia uncia*). *J. Zool.* 268, 217–224. <https://doi.org/10.1111/j.1469-7998.2005.00030.x>.
- Bagchi, S., Sharma, R.K., Bhatnagar, Y.V., 2020. Change in snow leopard predation on livestock after revival of wild prey in the Trans-Himalaya. *Wildl. Biol.* 2020. <https://doi.org/10.2981/wlb.00583>.
- Baral, N., Dhungana, A., 2014. Diversifying finance mechanisms for protected areas capitalizing on untapped revenues. *For. Policy Econ.* 41, 60–67. <https://doi.org/10.1016/j.forpol.2014.01.002>.
- Baral, R., Subedi, A., Yadav, S.K., (Eds.), 2019. Wild Mammals of the Annapurna Conservation Area. National Trust for Nature Conservation, Annapurna Conservation Area Project: Pokhara, Nepal.
- Barton, K., 2020. MuMIn: Multi-Model Inference. R Package Version 1.43.17. Available at: (<https://CRAN.R-project.org/package=MuMIn>). (Accessed May 2021).
- Berger, J., Buuveibaatar, B., Mishra, C., 2013. Globalization of the cashmere market and the decline of large mammals in Central Asia. *Conserv. Biol.* 27, 679–689. <https://doi.org/10.1111/cobi.12100>.
- Bolker, B.M., Brooks, M.E., Clark, C.J., Geange, S.W., Poulsen, J.R., Stevens, M.H.H., White, J.S.S., 2009. Generalized linear mixed models: a practical guide for ecology and evolution. *Trends Ecol. Evol.* 24, 127–135. <https://doi.org/10.1016/j.tree.2008.10.008>.
- Brashares, J.S., Prugh, L.R., Stoner, C.J., Epps, C.W., 2010. Ecological and conservation implications of mesopredator release. In: Terborgh, J., Estes, J.A. (Eds.), *Trophic Cascades: Predators, Prey, and the Changing Dynamics of Nature*, Island Press: Washington DC, USA, pp. 221–240.
- Burnham, K.P., Anderson, D.R. (Eds.), 2002. *Model Selection and Multimodel Inference: A Practical Information-theoretic Approach*. Springer: New York, USA.
- Carbone, C., Gittleman, J.L., 2002. A common rule for the scaling of carnivore density. *Science* 295, 2273–2276. <https://doi.org/10.1126/science.1067994>.
- Cardillo, M., Mace, G.M., Jones, K.E., Bielby, J., Bininda-Emonds, O.R., Sechrest, W., Orme, C.D.L., Purvis, A., 2005. Multiple causes of high extinction risk in large mammal species. *Science* 309, 1239–1241. <https://doi.org/10.1126/science.1116030>.
- Ceballos, G., Ehrlich, P.R., Barnosky, A.D., Garcia, A., Pringle, R.M., Palmer, T.M., 2015. Accelerated modern human-induced species losses: entering the sixth mass extinction. *Sci. Adv.* 1, e1400253. <https://doi.org/10.1126/sciadv.1400253>.
- Chetri, M., Odden, M., Wegge, P., 2017. Snow leopard and Himalayan wolf: food habits and prey selection in the Central Himalayas, Nepal. *PLoS One* 12, e0170549. <https://doi.org/10.1371/journal.pone.0170549>.
- Chetri, M., Odden, M., Devineau, O., Wegge, P., 2019a. Patterns of livestock depredation by snow leopards and other large carnivores in the Central Himalayas, Nepal. *Glob. Ecol. Conserv.* 17, e00536. <https://doi.org/10.1016/j.gecco.2019.e00536>.
- Chetri, M., Odden, M., Sharma, K., Flagstad, Ø., Wegge, P., 2019b. Estimating snow leopard density using fecal DNA in a large landscape in north-central Nepal. *Glob. Ecol. Conserv.* 17, e00548. <https://doi.org/10.1016/j.gecco.2019.e00548>.
- Chhetri, P.K., Shrestha, K.B., Cairns, D.M., 2017. Topography and human disturbances are major controlling factors in treeline pattern at Barun and Manang area in the Nepal Himalaya. *J. Mt. Sci.* 14, 119–127. <https://doi.org/10.1007/s11629-016-4198-6>.
- Conservation International, 2011. *Biodiversity Hotspots Revisited*. Available at: (<https://databasin.org/datasets>). (Accessed March 2020).
- Cristescu, B., Domokos, C., Teichman, K.J., Nielsen, S.E., 2019. Large carnivore habitat suitability modelling for Romania and associated predictions for protected areas. *PeerJ* 7, e6549. <https://doi.org/10.7717/peerj.6549>.
- Cui, X., Graf, H.F., 2009. Recent land cover changes on the Tibetan Plateau: a review. *Clim. Chang.* 94, 47–61. <https://doi.org/10.1007/s10584-009-9556-8>.
- Department of Hydrology and Meteorology (Ed.), 2017. *Observed Climate Trend Analysis of Nepal (1971–2014)*. Department of Hydrology and Meteorology: Kathmandu, Nepal.
- DIVA-GIS, 2015. *DIVA-GIS: Free, Simple & Effective*. Available at: (<http://www.diva-gis.org/Data>). (Accessed March 2020).
- Dorresteijn, I., Hanspach, J., Kecskés, A., Latková, H., Mezey, Z., Sugár, S., von Wehrden, H., Fischer, J., 2014. Human-carnivore coexistence in a traditional rural landscape. *Landsc. Ecol.* 29, 1145–1155. <https://doi.org/10.1007/s10980-014-0048-5>.
- Dunntington, D., 2021. *ggspatial: Spatial Data Framework for ggplot2*. R Package Version 1.1.5. Available at: (<https://CRAN.R-project.org/package=ggspatial>). (Accessed May 2021).
- Ferretti, F., Lovari, S., Minder, I., Pellizzi, B., 2014. Recovery of the snow leopard in Sagarmatha (Mt. Everest) National Park: effects on main prey. *Eur. J. Wildl. Res.* 60, 559–562. <https://doi.org/10.1007/s10344-014-0810-7>.

- Filla, M., Lama, R.P., Ghale, T.R., Signer, J., Filla, T., Aryal, R.R., Heurich, M., Waltert, M., Balkenhol, N., Khorozyan, I., 2021. In the shadows of snow leopards and the Himalayas: density and habitat selection of blue sheep in Manang, Nepal. *Ecol. Evol.* 11, 108–122. <https://doi.org/10.1002/ece3.6959>.
- Fox, J.L., Chundawat, R.S., 2016. What is a snow leopard? *Behavior and ecology*. In: McCarthy, T., Mallon, D. (Eds.), *Snow Leopards*. Academic Press, Amsterdam, Netherlands, pp. 13–21.
- Fuller, T.K., Sievert, P.R., 2001. Carnivore demography and the consequences of changes in prey availability. In: Gittleman, J.L., Funk, S.M., Macdonald, D.W., Wayne, R.K. (Eds.), *Carnivore Conservation*. Cambridge University Press, Cambridge, UK, pp. 163–178.
- Gelman, A., Hill, J., 2007. *Data Analysis Using Regression and Multilevel/hierarchical Models*. Cambridge University Press, New York, USA.
- Goodman, L.A., 1961. Snowball sampling. *Ann. Math. Stat.* 32, 148–170. <https://doi.org/10.1214/aoms/1177705148>.
- Grueber, C.E., Nakagawa, S., Laws, R.J., Jamieson, I.G., 2011. Multimodel inference in ecology and evolution: challenges and solutions. *J. Evolut. Biol.* 24, 699–711. <https://doi.org/10.1111/j.1420-9101.2010.02210.x>.
- Guisan, A., Edwards Jr., T.C., Hastie, T., 2002. Generalized linear and generalized additive models in studies of species distributions: setting the scene. *Ecol. Model.* 157, 89–100. [https://doi.org/10.1016/S0304-3800\(02\)00204-1](https://doi.org/10.1016/S0304-3800(02)00204-1).
- Hacker, C.E., Dai, Y., Cheng, Y., Zhang, Y., Zhang, Y., Miller, L.J., Janecka, J.E., 2021. Determinants of herder attitudes towards the Vulnerable snow leopard *Panthera uncia* in Yushu Prefecture, China. *Oryx* 55, 783–790. <https://doi.org/10.1017/S0030605319001315>.
- Hanson, J.H., Schutgens, M., Leader-Williams, N., 2019. What factors best explain attitudes to snow leopards in the Nepal Himalayas? *PLoS One* 14, e0223565. <https://doi.org/10.1371/journal.pone.0223565>.
- Hanson, J.H., Schutgens, M., Lama, R.P., Aryal, A., Dhakal, M., 2020. Local attitudes to the proposed translocation of blue sheep *Pseudois nayaur* to Sagarmatha National Park, Nepal. *Oryx* 54, 344–350. <https://doi.org/10.1017/S0030605318000157>.
- Harris, R.B., 2014. *Pseudois nayaur*. The IUCN Red List of Threatened Species 2014, e.T61513537A64313015. (<https://www.iucnredlist.org/ja/species/61513537/64313015>). (Accessed November 2021).
- Hartig, F., 2021. DHARMA: Residual Diagnostics for Hierarchical (Multi-Level / Mixed) Regression Models. R Package Version 0.4.4. Available at: (<https://CRAN.R-project.org/package=DHARMA>). (Accessed October 2021).
- Hijmans, R.J., 2019. geosphere: Spherical Trigonometry. R Package Version 1.5–10. Available at: (<https://CRAN.R-project.org/package=geosphere>). (Accessed January 2020).
- Hoeks, S., Huijbregts, M.A.J., Busana, M., Harfoot, M.B.J., Svenning, J.-C., Santini, L., 2020. Mechanistic insights into the role of large carnivores for ecosystem structure and functioning. *Ecography* 43, 1752–1763. <https://doi.org/10.1111/ecog.05191>.
- Humanitarian Data Exchange, 2021. Nepal – Subnational Administrative Boundaries. Available at: (<https://data.humdata.org/dataset/administrative-boundaries-of-nepal>). (Accessed 07 October 2021).
- Ikeda, N., 2004. Economic impacts of livestock depredation by snow leopard *Uncia uncia* in the Kanchenjunga Conservation Area, Nepal Himalaya. *Environ. Conserv.* 31, 322–330. <https://doi.org/10.1017/S0376892904001778>.
- Inskip, C., Zimmermann, A., 2009. Human-felid conflict: a review of patterns and priorities worldwide. *Oryx* 43, 18–34. <https://doi.org/10.1017/S003060530899030X>.
- Jackson, R., Ahlborn, G., 1989. Snow leopards (*Panthera uncia*) in Nepal: home range and movements. *Natl. Geogr. Res.* 5, 161–175.
- Jackson, R., Wangchuk, R., 2001. Linking snow leopard conservation and people-wildlife conflict resolution: grassroots measures to protect the endangered snow leopard from herder retribution. *Endanger. Species Update* 18, 138–141.
- Jackson, R.M., Wangchuk, R., 2004. A community-based approach to mitigating livestock depredation by snow leopards. *Hum. Dimens. Wildl.* 9, 307–315. <https://doi.org/10.1080/10871200490505756>.
- Jackson, R.M., 1996. Home Range, Movements and Habitat Use of Snow Leopard (*Uncia uncia*) in Nepal (Ph.D. thesis). University of London, London, p. 233.
- Jackson, R.M., Hunter, D.O., 1996. *Snow Leopard Survey and Conservation Handbook*. 2nd ed., International Snow Leopard Trust: Seattle, Washington, USA.
- Jackson, R.M., Mishra, C., McCarthy, T.M., Ale, S.B., 2010. Snow leopards: conflict and conservation. In: MacDonald, D.W., Loveridge, A.J. (Eds.), *Biology and Conservation of Wild Felids*, Oxford University Press: New York, USA, pp. 417–430.
- Janečka, J.E., Jackson, R., Yuquang, Z., Diqiang, L., Munkhtsog, B., Buckley-Beason, V., Murphy, W.J., 2008. Population monitoring of snow leopards using noninvasive collection of scat samples: a pilot study. *Anim. Conserv.* 11, 401–411. <https://doi.org/10.1111/j.1469-1795.2008.00195.x>.
- Johansson, O., McCarthy, T., Samelius, G., André, H., Tumursukh, L., Mishra, C., 2015. Snow leopard predation in a livestock dominated landscape in Mongolia. *Biol. Conserv.* 184, 251–258. <https://doi.org/10.1016/j.biocon.2015.02.003>.
- Johansson, O., Rauset, G.R., Samelius, G., McCarthy, T., André, H., Tumursukh, L., Mishra, C., 2016. Land sharing is essential for snow leopard conservation. *Biol. Conserv.* 203, 1–7. <https://doi.org/10.1016/j.biocon.2016.08.034>.
- Karki, R., Talchabhadel, R., Aalto, J., Baidya, S.K., 2015. New climatic classification of Nepal. *Theor. Appl. Climatol.* 125, 799–808.
- Khan, M.Z., Khan, B., Awan, S., Khan, G., Ali, R., 2013. High-altitude rangelands and their interfaces in Gilgit-Baltistan, Pakistan: current status and management strategies. In: Ning, W., Rawat, G.S., Joshi, S., Ismail, M., Sharma, E. (Eds.), *High-Altitude Rangelands and their Interfaces in the Hindu Kush Himalayas*, pp. 68–77.
- Khanal, G., Mishra, C., Suryawanshi, K.R., 2020. Relative influence of wild prey and livestock abundance on carnivore-caused livestock predation. *Ecol. Evol.* 10, 11787–11797. <https://doi.org/10.1002/ece3.6815>.
- Khorozyan, I., Ghoddousi, A., Soofi, M., Waltert, M., 2015. Big cats kill more livestock when wild prey reaches a minimum threshold. *Biol. Conserv.* 192, 268–275. <https://doi.org/10.1016/j.biocon.2015.09.031>.
- Khorozyan, I., Soofi, M., Soufi, M., Hamidi, A.K., Ghoddousi, A., Waltert, M., 2017. Effects of shepherds and dogs on livestock depredation by leopards (*Panthera pardus*) in north-eastern Iran. *PeerJ* 5, e3049. <https://doi.org/10.7717/peerj.3049>.
- Khorozyan, I., Ghoddousi, S., Soufi, M., Soofi, M., Waltert, M., 2018. Cattle selectivity by leopards suggests ways to mitigate human-leopard conflict. *Ecol. Evol.* 8, 8011–8018. <https://doi.org/10.1002/ece3.4351>.
- Kitchener, A.C., Driscoll, C.A., Yamaguchi, N., 2016. What is a snow leopard? Taxonomy, morphology, and phylogeny. In: McCarthy, T., Mallon, D. (Eds.), *Snow Leopards*. Academic Press, Amsterdam, Netherlands, pp. 3–11.
- Legendre, P., 1993. Spatial autocorrelation: trouble or new paradigm? *Ecology* 74, 1659–1673. <https://doi.org/10.2307/1939924>.
- Leki, Thinley, Rajaratnam, P.R., Shrestha, R., 2018. Establishing baseline estimates of blue sheep (*Pseudois nayaur*) abundance and density to sustain populations of the endangered snow leopard (*Panthera uncia*) in Western Bhutan. *Wildl. Res.* 45, 38–46. <https://doi.org/10.1071/WR16218>.
- Lhagavasuren, B., Munkhtsog, B., 2002. The yak population in Mongolia and its relation with snow leopards as a prey species. In: Jianlin, H., Richard, C., Hanotte, O., McVeigh, C., Rege, J.E.O. (Eds.), *Proceedings of the Third International Congress on Yak Held in Lhasa, PR China, 4–9 September 2000*. ILRI Proceedings: Nairobi, Kenya, pp. 69–75.
- Lham, D., Cozzi, G., Sommer, S., Wangchuk, S., Lham, K., Ozgul, A., 2021. Ecological determinants of livestock depredation by the snow leopard *Panthera uncia* in Bhutan. *J. Zool.* 314, 275–284. <https://doi.org/10.1111/jzo.12883>.
- Li, J., Wang, D., Yin, H., Zhaxi, D., Jiagong, Z., Schaller, G.B., Mishra, C., McCarthy, T.M., Wang, H., Wu, L., Xiao, L., Basang, L., Zhang, Y., Zhou, Y., Lu, Z., 2014. Role of Tibetan Buddhist monasteries in snow leopard conservation. *Conserv. Biol.* 28, 87–94. <https://doi.org/10.1111/cobi.12135>.
- Lindsey, P.A., Alexander, R., Mills, M.G.L., Romanach, S., Woodroffe, R., 2007. Wildlife viewing preferences of visitors to protected areas in South Africa: implications for the role of ecotourism in conservation. *J. Ecotour.* 6, 19–33. <https://doi.org/10.2167/joe133.0>.
- Linnell, J.D.C., Odden, J., Smith, M.E., Aanes, R., Swenson, J.E., 1999. Large carnivores that kill livestock: do “problem individuals” really exist? *Wildl. Soc. Bull.* 27, 698–705.
- Liu, Z., Wang, X., Li, Z., Cui, D., Li, X., 2005. Seasonal variation of diurnal activity budgets by blue sheep (*Pseudois nayaur*) with different age-sex classes in Helan Mountain. *Zool. Res.* 26, 350–357.
- Lovari, S., Minder, I., Ferretti, F., Mucci, N., Randi, E., Pellizzi, B., 2013. Common and snow leopards share prey, but not habitats: competition avoidance by large predators? *J. Zool.* 291, 127–135. <https://doi.org/10.1111/jzo.12053>.

- Lowrey, B., Elbroch, L.M., Broberg, L., 2016. Is individual prey selection driven by chance or choice? A case study in cougars (*Puma concolor*). *Mammal Res.* 61, 353–359. <https://doi.org/10.1007/s13364-016-0292-y>.
- Lüdecke, D., Ben-Shachar, M.S., Patil, I., Waggoner, P., Makowski, D., 2021. Performance: an R package for assessment, comparison and testing of statistical models. *J. Open Source Softw.* 6, 3139. <https://doi.org/10.21105/joss.03139>.
- Lyngdoh, S., Shrottriya, S., Goyal, S.P., Clements, H., Hayward, M.W., Habib, B., 2014. Prey preferences of the snow leopard (*Panthera uncia*): regional diet specificity holds global significance for conservation. *PLoS One* 9, e100071. <https://doi.org/10.1371/journal.pone.0088349>.
- McCarthy, K.P., Fuller, T.K., Ming, M., McCarthy, T.M., Waits, L., Jumabaev, K., 2008. Assessing estimators of snow leopard abundance. *J. Wildl. Manag.* 72, 1826–1833. <https://doi.org/10.2193/2008-040>.
- McCarthy, T.M., Fuller, T.K., Munkhtsog, B., 2005. Movements and activities of snow leopards in Southwestern Mongolia. *Biol. Conserv.* 124, 527–537. <https://doi.org/10.1016/j.biocon.2005.03.003>.
- McCarthy, T., Mallon, D., Jackson, R., Zahler, P., McCarthy, K., 2017. *Panthera uncia*. The IUCN Red List of Threatened Species 2017: e.T22732A50664030. Available at: (<https://dx.doi.org/10.2305/IUCN.UK.2017-2.RLTS.T22732A50664030.en>). (Accessed August 2020).
- McCarthy, T.M., Chapron, G. (Eds.), 2003. *Snow Leopard Survival Strategy*. International Snow Leopard Trust and Snow Leopard Network: Seattle, USA.
- Meriggi, A., Lovari, S., 1996. A review of wolf predation in southern Europe: does the wolf prefer wild prey to livestock? *J. Appl. Ecol.* 33, 1561–1571. (<https://www.jstor.org/stable/2404794>).
- Mijidodorj, T.N., Alexander, J.S., Samelius, G., Badola, R., Rawat, G.S., Dutta, S., 2018. Livestock depredation by large carnivores in the South Gobi, Mongolia. *Wildl. Res.* 45, 237–246. <https://doi.org/10.1071/WR18009>.
- Mishra, C., Allen, P., McCarthy, T., Madhusudan, M.D., Bayarjargal, A., Prins, H.H.T., 2003. The role of incentive programs in conserving the snow leopard. *Conserv. Biol.* 17, 1512–1520. <https://doi.org/10.1111/j.1523-1739.2003.00092.x>.
- Mishra, C., van Wieren, S.E., Ketner, P., Heitkönig, I.M.A., Prins, H.H.T., 2004. Competition between domestic livestock and wild bharal *Pseudois nayaur* in the Indian Trans-Himalaya. *J. Appl. Ecol.* 41, 344–354. <https://doi.org/10.1111/j.0021-8901.2004.00885.x>.
- Mishra, C., Redpath, S.R., Suryawanshi, K.R., 2016. Livestock predation by snow leopards: conflicts and the search for solutions. In: McCarthy, T., Mallon, D. (Eds.), *Snow Leopards*. Academic Press, Amsterdam, Netherlands, pp. 59–67.
- Mittermeier, R.A., Gil, P.R., Hoffmann, M., Pilgrim, J., Brooks, T., Mittermeier, C.G., Lamoreux, J., Fonseca, G.A.B., 2004. Hotspots Revisited: Earth's Biologically Richest and Most Endangered Ecoregions. CEMEX: Mexico City, Mexico.
- Moran, P.A.P., 1950. Notes on continuous stochastic phenomena. *Biometrika* 37, 17–23. (<https://www.jstor.org/stable/2332142>).
- Murali, R., Alexander, J.S., Sharma, K., Mijidodorj, N., Agvaansteren, B., Nawaz, M.A., Bijoer, A., Dutta, A., Suryawanshi, K., Jumabay Uulu, K., Mishra, C., 2020. Awareness and Education Strategy for Snow Leopard and Ecosystem Conservation. Background papers for policy recommendations. Global Snow Leopard and Ecosystem Protection Program: Bishkek, Kyrgyz Republic.
- Naha, D., Chaudhary, P., Sonker, G., Sathyakumar, S., 2020. Effectiveness of non-lethal predator deterrents to reduce livestock losses to leopard attacks within a multiple-use landscape of the Himalayan region. *PeerJ* 8, e9544. <https://doi.org/10.7717/peerj.9544>.
- NASA/METI/AIST/Japan Space Systems and U.S./Japan ASTER Science Team, 2009. ASTER Global Digital Elevation Model [ASTGMTv002]. NASA EOSDIS Land Processes DAAC. Available at: (<https://doi.org/10.5067/ASTER/ASTGMT.002>). (Accessed January 2019).
- National Trust for Nature Conservation, 2015. Annual Report 2015. National Trust for Nature Conservation (NTNC): Khumaltar, Nepal.
- Nowell, K., Li, J., Paltsyn, M., Sharma, R.K., 2016. An Ounce of Prevention: Snow Leopard Crime Revisited. TRAFFIC Report. TRAFFIC: Cambridge, UK.
- O'Hara, R.B., Kotze, D.J., 2010. Do not log-transform count data. *Methods Ecol. Evol.* 1, 118–122. <https://doi.org/10.1111/j.2041-210X.2010.00021.x>.
- O'Neill, H.M.K., Durant, S.M., Woodroffe, R., 2020. What wild dogs want: habitat selection differs across life stages and orders of selection in a wide-ranging carnivore. *BMC Zool.* 5, 1. <https://doi.org/10.1186/s40850-019-0050-0>.
- Odden, J., Herfindal, I., Linnell, J.D., Andersen, R., 2008. Vulnerability of domestic sheep to lynx depredation in relation to roe deer density. *J. Wildl. Manag.* 72, 276–282. <https://doi.org/10.2193/2005-537>.
- Odden, J., Nilsen, E.B., Linnell, J.D.C., 2013. Density of wild prey modulates lynx kill rates on free-ranging domestic sheep. *PLoS ONE* 8, e79261. <https://doi.org/10.1371/journal.pone.0079261>.
- Oli, M.K., 1994. Snow leopards and blue sheep in Nepal: densities and predator: prey ratio. *J. Mammal.* 75, 998–1004. <https://doi.org/10.2307/1382482>.
- Oli, M.K., Taylor, I.R., Rogers, D.M., 1993. Diet of the snow leopard (*Panthera uncia*) in the Annapurna Conservation Area, Nepal. *J. Zool.* 231, 365–370. <https://doi.org/10.1111/j.1469-7998.1993.tb01924.x>.
- Paudel, K.P., Andersen, P., 2013. Response of rangeland vegetation to snow cover dynamics in Nepal Trans Himalaya. *Clim. Chang.* 117, 149–162. <https://doi.org/10.1007/s10584-012-0562-x>.
- Poudel, B.S., Spooner, P.G., Matthews, A., 2016. Behavioural changes in marmots in relation to livestock grazing disturbance: an experimental test. *Eur. J. Wildl. Res.* 62, 491–495. <https://doi.org/10.1007/s10344-016-1014-0>.
- R Core Team, 2021. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing: Vienna, Austria.
- Rashid, W., Shi, J., ur Rahim, I., Sultan, H., Dong, S., Ahmad, L., 2020. Research trends and management options in human-snow leopard conflict. *Biol. Conserv.* 242, 108413. <https://doi.org/10.1016/j.biocon.2020.108413>.
- Rauset, G.R., Mattisson, J., André, H., Chapron, G., Persson, J., 2013. When species' ranges meet: assessing differences in habitat selection between sympatric large carnivores. *Oecologia* 172, 701–711. <https://doi.org/10.1007/s00442-012-2546-y>.
- Riley, S.J., DeGloria, S.D., Elliot, R., 1999. A terrain ruggedness index that quantifies topographic heterogeneity. *Interm. J. Sci.* 5, 23–27.
- Ripari, L., Premier, J., Belotti, E., Bluhm, H., Breitenmoser-Würsten, C., Bufka, L., Červený, J., Drouet-Hoguet, N., Fuxjäger, C., Jędrzejewski, W., Kont, R., Koubek, P., Kowalczyk, R., Krofel, M., Krojerová-Prokešová, J., Molinari-Jobin, A., Okarma, H., Oliveira, T., Remm, J., Schmidt, K., Zimmermann, F., Kramer-Schadt, S., Heurich, M., 2022. Human disturbance is the most limiting factor driving habitat selection of a large carnivore throughout Continental Europe. *Biol. Conserv.* 266, 109446. <https://doi.org/10.1016/j.biocon.2021.109446>.
- Ripple, W.J., Estes, J.A., Beschta, R.L., Wilmers, C.C., Ritchie, E.G., Hebblewhite, M., Berger, J., Elmhagen, B., Letnic, M., Nelson, M.P., Schmitz, O.J., Smith, D.W., Wallach, A.D., Wirsing, A.J., 2014. Status and ecological effects of the world's largest carnivores. *Science* 343, 1241484. <https://doi.org/10.1126/science.1241484>.
- Ripple, W.J., Newsome, T.M., Wolf, C., Dirzo, R., Everatt, K.T., Galetti, M., Hayward, M.W., Kerley, G.I.H., Levi, T., Lindsey, P.A., Macdonald, D.W., Malhi, Y., Painter, L.E., Sandom, C.J., Terborgh, J., van Valkenburgh, B., 2015. Collapse of the world's largest herbivores. *Sci. Adv.* 1, e1400103. <https://doi.org/10.1126/sciadv.1400103>.
- Rovero, F., Augugliaro, C., Havmøller, R., Groff, C., Zimmermann, F., Oberosler, V., Tenan, S., 2020. Co-occurrence of snow leopard *Panthera uncia*, Siberian ibex *Capra sibirica* and livestock: potential relationships and effects. *Oryx* 54, 118–124. <https://doi.org/10.1017/S0030605317001685>.
- Salvatori, M., Tenan, S., Oberosler, V., Augugliaro, C., Christe, P., Groff, C., Krofel, M., Zimmermann, F., Rovero, F., 2021. Co-occurrence of snow leopard, wolf and Siberian ibex under livestock encroachment into protected areas across the Mongolian Altai. *Biol. Conserv.* 261, 109294. <https://doi.org/10.1016/j.biocon.2021.109294>.
- Samelius, G., Suryawanshi, K., Frank, J., Agvaansteren, B., Baasandamba, E., Mijidodorj, T., Johansson, Ö., Tumursukh, L., Mishra, C., 2021. Keeping predators out: testing fences to reduce livestock depredation at night-time corrals. *Oryx* 55, 466–472. <https://doi.org/10.1017/S0030605319000565>.
- Schieltz, J.M., Rubenstein, D.I., 2016. Evidence based review: positive versus negative effects of livestock grazing on wildlife. What do we really know? *Environ. Res. Lett.* 11, 113003. <https://doi.org/10.1088/1748-9326/11/11/113003>.
- Sharma, R.K., Bhatnagar, Y.V., Mishra, C., 2015. Does livestock benefit or harm snow leopards? *Biol. Conserv.* 190, 8–13. <https://doi.org/10.1016/j.biocon.2015.04.026>.
- Sharma, R.K., Sharma, K., Borchers, D., Bhatnagar, Y.V., Suryawanshi, K.R., Mishra, C., 2021. Spatial variation in population-density of snow leopards in a multiple use landscape in Spiti Valley, Trans-Himalaya. *PLoS ONE* 16, e0250900. <https://doi.org/10.1371/journal.pone.0250900>.

- Sharma, S., Dutta, T., Bhatnagar, Y.V., 2006. Marking site selection by free ranging Snow leopard (*Uncia uncia*). In: McNeely, J.A., McCarthy, T.M., Smith, A., Olsivg-Whittaker, L., Wilkramanayake, E. (Eds.), *Conservation Biology in Asia*. Society for Conservation Biology Asia Section and Resources Himalaya: Kathmandu, Nepal, pp. 197–213.
- Shrestha, B.B., Moe, S.R., 2015. Plant diversity and composition associated with Himalayan musk deer latrine sites. *Zool. Ecol.* 25, 295–304. <https://doi.org/10.1080/21658005.2015.1069498>.
- Shrestha, R., Wegge, P., 2008. Wild sheep and livestock in Nepal Trans-Himalaya: coexistence or competition? *Environ. Conserv.* 35, 125–136. <https://doi.org/10.1017/S0376892908004724>.
- Singh, P.B., Khatiwada, J.R., Saud, P., Jiang, Z., 2019. mtDNA analysis confirms the endangered Kashmir musk deer extends its range to Nepal. *Sci. Rep.* 9, 4895. <https://doi.org/10.1038/s41598-019-41167-4>.
- Soofi, M., Ghoddousi, A., Zeppenfeld, T., Shokri, S., Soufi, M., Egli, L., Jafari, A., Ahmadpour, M., Qashqaei, A., Ghadirian, T., Filla, M., Kiabi, B., Balkenhol, N., Waltert, M., Khorozyan, I., 2019. Assessing the relationship between illegal hunting of ungulates, wild prey occurrence and livestock depredation rate by large carnivores. *J. Appl. Ecol.* 56, 365–374. <https://doi.org/10.1111/1365-2664.13266>.
- Suryawanshi, K., Reddy, A., Sharma, M., Khanyari, M., Bijoor, A., Rathore, D., Jaggi, H., Khara, A., Malgaonkar, A., Ghoshal, A., Patel, J., Mishra, C., 2021. Estimating snow leopard and prey populations at large spatial scales. *Ecol. Solut. Evid.* 2, e12115 <https://doi.org/10.1002/2688-8319.12115>.
- Suryawanshi, K.R., Bhatnagar, Y.V., Mishra, C., 2012. Standardizing the double-observer survey method for estimating mountain ungulate prey of the endangered snow leopard. *Oecologia* 169, 581–590. <https://doi.org/10.1007/s00442-011-2237-0>.
- Suryawanshi, K.R., Bhatnagar, Y.V., Redpath, S., Mishra, C., 2013. People, predators and perceptions: patterns of livestock depredation by snow leopards and wolves. *J. Appl. Ecol.* 50, 550–560. <https://doi.org/10.1111/1365-2664.12061>.
- Suryawanshi, K.R., Redpath, S.M., Bhatnagar, Y.V., Ramakrishnan, U., Chaturvedi, V., Smout, S.C., Mishra, C., 2017. Impact of wild prey availability on livestock predation by snow leopards. *R. Soc. Open Sci.* 4, 170026 <https://doi.org/10.1098/rsos.170026>.
- Thapa, K., 2021. An experience of surplus killing of livestock by a snow leopard in Nepal. *CATnews* 74, 18–21.
- Thapa, K., Jackson, R., Gurung, L., Acharya, H.B., Gurung, R.K., 2021. Applying the double observer methodology for assessing blue sheep population size in Nar Phu valley, Annapurna Conservation Area, Nepal. *Wildl. Biol.* 2021 <https://doi.org/10.2981/wlb.00877>.
- Thuiller, W., Lafourcade, B., Engler, R., Araújo, M.B., 2009. BIOMOD - a platform for ensemble forecasting of species distributions. *Ecography* 32, 369–373. <https://doi.org/10.1111/j.1600-0587.2008.05742.x>.
- Tiwari, M.P., Devkota, B.P., Jackson, R.M., Chhetri, B.B.K., Bagale, S., 2020. What factors predispose households in trans-Himalaya (central Nepal) to livestock predation by snow leopards? *Animals* 10, 2187. <https://doi.org/10.3390/ani10112187>.
- Treves, A., Karanth, K.U., 2003. Human-carnivore conflict and perspectives on carnivore management worldwide. *Conserv. Biol.* 17, 1491–1499. <https://doi.org/10.1111/j.1523-1739.2003.00059.x>.
- Treves, A., Naughton-Treves, L., Harper, E.K., Mladenoff, D.J., Rose, R.A., Sickley, T.A., Wydeven, A.P., 2004. Predicting human-carnivore conflict: a spatial model derived from 25 years of data on wolf predation on livestock. *Conserv. Biol.* 18, 114–125. <https://doi.org/10.1111/j.1523-1739.2004.00189.x>.
- Valentová, K.A., 2017. Abundance and threats to the survival of the snow leopard - a review. *Eur. J. Environ. Sci.* 7, 73–93. <https://doi.org/10.14712/23361964.2017.7>.
- van Eeden, L.M., Crowther, M.S., Dickman, C.R., Macdonald, D.W., Ripple, W.J., Ritchie, E.G., Newsome, T.M., 2018. Managing conflict between large carnivores and livestock. *Conserv. Biol.* 32, 26–34. <https://doi.org/10.1111/cobi.12959>.
- Vannelli, K., Hampton, M.P., Namgail, T., Black, S.A., 2019. Community participation in ecotourism and its effect on local perceptions of snow leopard (*Panthera uncia*) conservation. *Hum. Dimens. Wildl.* 24, 180–193. <https://doi.org/10.1080/10871209.2019.1563929>.
- Venables, W.N., Ripley, B.D., 2002. *Modern Applied Statistics with S*, 4th ed. Springer, New York, USA.
- Wegge, P., Shrestha, R., Flagstad, Ø., 2012. Snow leopard *Panthera uncia* predation on livestock and wild prey in a mountain valley in northern Nepal: implications for conservation management. *Wildl. Biol.* 18, 131–141. <https://doi.org/10.2981/11-049>.
- Wickham, H., 2016. *ggplot2: Elegant Graphics for Data Analysis*. Springer: New York, USA.
- Wilke, C.O., 2020. *cowplot: Streamlined Plot Theme and Plot Annotations for 'ggplot2'*. R package version 1.1.1. Available at: (<https://CRAN.R-project.org/package=cowplot>). (Accessed May 2021).
- Wilkinson, C.E., McInturff, A., Miller, J.R.B., Yovovich, V., Gaynor, K.M., Calhoun, K., Karandikar, H., Martin, J.V., Parker-Shames, P., Shawler, A., van Scoyoc, A., Brashares, J.S., 2020. An ecological framework for contextualizing carnivore-livestock conflict. *Conserv. Biol.* 34, 854–867. <https://doi.org/10.1111/cobi.13469>.
- Winnie Jr., J., Creel, S., 2017. The many effects of carnivores on their prey and their implications for trophic cascades, and ecosystem structure and function. *Food Webs* 12, 88–94. <https://doi.org/10.1016/j.fooweb.2016.09.002>.
- Wolf, C., Ripple, W.J., 2017. Range contractions of the world's large carnivores. *R. Soc. Open Sci.* 4, 170052 <https://doi.org/10.1098/rsos.170052>.
- Wolf, M., Ale, S., 2009. Signs at the top: habitat features influencing snow leopard *Uncia uncia* activity in Sagarmatha National Park, Nepal. *J. Mammal.* 90, 604–611. <https://doi.org/10.1644/08-MAMM-A-002R1.1>.
- Woodroffe, R., Thirgood, S., Rabinowitz, A. (Eds.), 2005. *People and Wildlife: Conflict or Co-existence?* Conservation Biology. Cambridge University Press: Cambridge, UK (<https://doi.org/10.1017/CBO9780511614774>).
- WorldPop, 2020. Open Spatial Demographic Data and Research. Available at: (<https://www.worldpop.org/doi/10.5258/SOTON/WP00674>). (Accessed November 2021).
- WWF Nepal, 2018. *Infrastructure Assessment in Snow Leopard Habitat of Nepal*. WWF Nepal: Kathmandu, Nepal.
- Yakha, T.B., Chalise, M.K., 2021. A glimpse of blue sheep (*Pseudois nayaur*) hunting in Api Nampa Conservation Area (ANCA) Nepal. *J. Inst. Sci. Technol.* 26, 9–12. <https://doi.org/10.3126/jist.v26i2.41269>.
- Yang, C., Zhang, P., Wu, Y., Dai, Q., Luo, G., Zhou, H., Zhao, D., Ran, J., 2021. Livestock limits snow leopard's space use by suppressing its prey, blue sheep, at Gongga Mountain, China. *Glob. Ecol. Conserv.* 29, e01728 <https://doi.org/10.1016/j.gecco.2021.e01728>.
- Young, J.C., Rose, D.C., Mumby, H.S., Benitez-Capistros, F., Derrick, C.J., Finch, T., Garcia, C., Home, C., Marwaha, E., Morgans, C., Parkinson, S., Shah, J., Wilson, K.A., Mukherjee, N., 2018. A methodological guide to using and reporting on interviews in conservation science research. *Methods Ecol. Evol.* 9, 10–19. <https://doi.org/10.1111/2041-210X.12828>.
- Zeileis, A., Kleiber, C., Jackman, S., 2008. Regression models for count data in R. *J. Stat. Softw.* 27, 1–25. <https://doi.org/10.18637/jss.v027.i08>.
- Zhang, M., Wang, X., Ding, Y., 2013. Flight responses of blue sheep in Ningxia Helan Mountain National Nature Reserve. *J. Vertebr. Biol.* 62, 185–192. <https://doi.org/10.25225/fozo.v62.i3.a3.2013>.