Conservation ecology and mitigation of conflicts between livestock owners and snow leopards (*Panthera uncia*)

Dissertation

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Marc Filla

from Kempen, Germany

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Thesis Committee

Prof. Dr. Matthias Waltert
Department of Conservation Biology, Johann-Friedrich-Blumenbach Institute of Zoology and Anthropology

Prof. Dr. Niko Balkenhol
Department of Wildlife Sciences, Faculty of Forest Sciences and Forest Ecology

Dr. Igor Khorozyan
Department of Conservation Biology, Johann-Friedrich-Blumenbach Institute of Zoology and Anthropology

Members of the Examination Board

Reviewer: Prof. Dr. Matthias Waltert
Department of Conservation Biology, Johann-Friedrich-Blumenbach Institute of Zoology and Anthropology

Second Reviewer: Prof. Dr. Niko Balkenhol
Department of Wildlife Sciences, Faculty of Forest Sciences and Forest Ecology

Further members of the Examination Board:

Dr. Igor Khorozyan
Department of Conservation Biology, Johann-Friedrich-Blumenbach Institute of Zoology and Anthropology

Prof. Dr. Marco Heurich
Department of Forestry and Wildlife Management, Campus Evenstad, Inland Norway University of Applied Sciences; Chair of Wildlife Ecology and Management, Faculty of Environment and Natural Resources, University of Freiburg

Prof. Dr. Johannes Kamp
Department of Conservation Biology, Johann-Friedrich-Blumenbach Institute of Zoology and Anthropology

Prof. Dr. Andreas Schuldt
Department of Forest Nature Conservation, Faculty of Forest Sciences and Forest Ecology

Date of the oral examination: 5 May 2022

“Be the change you wish to see in the world”

Snow leopard (*Panthera uncia*) and blue sheep (*Pseudois nayaur*) observed in Manang, Annapurna Conservation Area, Nepal. Credits: snow leopard - Tashi R. Ghale, blue sheep - Marc Filla

Quotation: see Quote Investigator (2017)

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Summary

The world is currently facing an accelerated loss of biodiversity, which is considered a human-induced mass extinction. Large carnivores face a multitude of anthropogenic threats and are particularly prone to local extirpation due to their biological traits, including low reproductive rates and large spatial requirements. These animals play key ecological roles at the top of natural food webs and are of high socio-economic relevance, making their protection a priority in biodiversity conservation. This also applies to the snow leopard (*Panthera uncia*), which represents a top predator in high-altitude ecosystems of Asia, with only about 3,000 mature individuals remaining in the wild. The snow leopard faces various anthropogenic threats, including habitat loss and degradation, exploitation, wild prey depletion, and retaliatory killings as a consequence of livestock depredation. Addressing these threats requires intensive efforts at both international and local levels as snow leopards occupy vast spatial ranges in fragile and remote landscapes where livestock depredation poses a major obstacle to co-existence with local communities. Moreover, cryptic behaviour, low population densities, and hardly accessible terrain make population monitoring challenging, limiting the understanding of interactions between snow leopards, their wild prey, livestock, and humans, and, hence, impeding prioritisation of management actions.

The aims of this dissertation were to evaluate the performance of current conservation and management measures targeting the snow leopard and its high-altitude ecosystems and to generate more profound knowledge on relationships between snow leopards, wild prey populations, and livestock husbandry. By deducing relevant conservation implications, I intended to contribute to the preservation of the snow leopard and its natural habitats as well as to the long-term co-existence of this big cat and local communities in high-mountain landscapes of Asia.

Chapter 2 attends to the blue sheep (*Pseudois nayaur*), representing the main wild prey of snow leopards in the Annapurna region and elsewhere. This medium-sized ungulate is considered a common species but is increasingly threatened by anthropogenic activities. In spring and autumn 2019, my colleagues and I walked along transects (262.6 km) to monitor blue sheep in the Manang district of the Annapurna Conservation Area. We applied spatial and multivariate analyses to explore the population status and habitat choice of this ungulate. Total counts yielded minimum blue sheep density estimates of 6.0–7.8 individuals/km^2, which are quite high compared to other regions inside and outside the Nepalese Himalaya and roughly fit in the range of estimates in Manang before and after the establishment of this protected area in 1992. According to the applied generalised additive models (GAMs), habitat selection by blue sheep was mainly driven by elevation and vegetation characteristics, while the effects of anthropogenic variables were insignificant. These results suggest that the local blue sheep population has been largely maintained over the past 30 years, which can be interpreted as a

preliminary success of the integrated conservation and development approach in the Annapurna Conservation Area. In conclusion, our findings indicate the potential to protect mountain ungulates through integrated management approaches. We suggest establishing a long-term monitoring scheme for blue sheep to allow early detection of population trends as well as potentially time-lagged effects of ongoing tourism development in the Annapurna Conservation Area.

Chapter 3 examines the complex socio-ecological relationships between snow leopards, wild prey populations, livestock, and humans in the high-altitude landscape of the Annapurna region. The project team sampled a total of 82 study units (4 x 4 km cells) in the Annapurna Conservation Area, monitoring wildlife populations and livestock along transects (490.8 km) and conducting extensive questionnaire surveys (n = 479 households) to quantify livestock depredation between 2018 and 2021. The generalised linear models (GLMs) suggested 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. Marmot presence and increasing human population density were related to lower depredation rates of sheep and goats, which were attacked most frequently (38.5% of depredation events) and represented the majority of killed livestock (68.6%), whereas the size of livestock holdings seemingly shaped depredation rates of large livestock (yak, cattle, horse). The insights obtained from this study stress the crucial role of blue sheep for snow leopard populations and highlight the importance of integrating wild prey recovery into conservation and management plans. They also suggest that increasing wild prey abundance would neither solve nor inflict human-snow leopard conflicts over livestock depredation. Our findings call for an improvement of currently applied intervention strategies (e.g., predator-proofing corrals and optimising daytime herding practices) and further exploring the effects of secondary prey like marmots and additional interventions as mitigation tools. This work extends previous knowledge on the significance of wild ungulates for snow leopard populations and their effects on livestock depredation patterns, supporting wildlife managers in setting conservation priorities to promote the long-term co-existence of snow leopards and local communities.

Chapter 4 focuses on patterns of livestock depredation attributed to snow leopards and analyses the effects of husbandry practices and applied intervention strategies on reported depredation rates. In 2020, my colleagues conducted detailed interviews with 329 livestock owners living in the Manang and Mustang districts of the Annapurna Conservation Area. I applied Jacob's selectivity index, sample comparison tests, and multivariate models to investigate spatio-temporal variation in depredation, assess the vulnerability of different livestock species and groups, examine the potential effects of intervention strategies, and identify husbandry practices associated with depredation over the past two years.

The respondents reported snow leopard depredation to cause an estimated annual loss of 3.2–3.6% of livestock heads and to be a major cause of livestock mortality in both regions (25.4–39.8% of all deaths). Corralling during night-time and herding during daytime were the main but inconsistently applied intervention strategies, and these were not associated with decreases in reported livestock losses. However, some models indicated the potential of dogs, deterrents (light, dung burning, music playing, and flapping tape), and applications of multiple interventions to reduce night-time depredation of yaks. To validate our findings, we suggest conducting controlled randomised experiments to measure the effectiveness of these intervention strategies quantitatively. Finally, the application of the most effective and practical interventions has the potential to contribute to the long-term co-existence of snow leopards and humans in the Annapurna region and beyond.

In conclusion, this PhD project in the Nepalese Himalaya extended previous evidence on interactions between snow leopards, wild prey populations, livestock, and humans, providing relevant implications for the management and conservation of snow leopards and other mountain wildlife. First, it indicated a potential to preserve relatively high wild ungulate densities in mountain landscapes when integrating conservation and development agendas. Second, it confirmed a strong positive impact of blue sheep on snow leopard abundance, highlighting the importance of protecting this wild prey base, especially considering the limited effects observed on livestock depredation. Third, it showed an urgent need to improve the main intervention strategies and further explore additional ones to lay the foundation of human-snow leopard co-existence. Based on these findings, we recommend establishing regular monitoring schemes in the Annapurna Conservation Area, as well as elsewhere, to early detect population declines, assess the effects of conservation measures, and guide future management of snow leopards and other wildlife in high-mountain ecosystems.

Chapter 1

General introduction

Snow leopard (*Panthera uncia*) in Manang, Annapurna Conservation Area, Nepal. Credit: Tashi R. Ghale

1.1 The decline of large carnivores and their significance for biodiversity conservation

Nature is widely acknowledged for having an intrinsic value, and intact environmental systems also contribute to human well-being (Davidson 2013). In spite of that, anthropogenic activities increasingly threaten ecological processes and ecosystem services (Butchart et al. 2010; Cardinale et al. 2012). The current loss of biodiversity has reached devastating magnitudes up to the scale of a human-induced mass extinction, with vertebrate extinction rates being up to 100 times higher than background rates (Ceballos et al. 2015).

Large carnivores are particularly susceptible to local extirpation due to their intrinsic biological traits, such as vast spatial ranges, large energetic constraints, and low reproductive rates (Cardillo et al. 2005; Ripple et al. 2014). Today, these animals face a variety of anthropogenic threats (Ripple et al. 2014). High requirements for vast, secure, and food-rich areas bring along a high vulnerability to habitat loss, degradation, and fragmentation (Ripple et al. 2014). In addition, many species of large carnivores are directly exploited for meat, bones, fur, and other body parts (e.g., Lau et al. 2010). The depletion of the wild prey base is recognised as another major threat to large carnivores (Wolf and Ripple 2016), as their densities appear to be strongly correlated with wild prey abundance (Carbone and Gittleman 2002). Declines of wild prey may additionally trigger predator movements into areas with enhanced anthropogenic threats, such as road mortality (Jones 2000; Woodroffe 2000; Wolf and Ripple 2016). Active persecution to prevent or retaliate presumed or actual attacks on humans and their livestock represent another main threat to large carnivores (Woodroffe 2000; Ripple et al. 2014). As an immense proportion of the global land area is used for grazing domestic animals (Reid et al. 2008), the dispute about livestock depredation is of particular significance. The historic global extinctions of carnivore species, such as the Falkland wolf *Dusicyon australis* and the marsupial wolf *Thylacinus cynocephalus*, illustrate the possible magnitude of such human-carnivore conflicts (Woodroffe et al. 2005a). Nowadays, more than three quarters of the world's wild felids are in conflict with human interests (Inskip and Zimmermann 2009).

As a consequence of these serious threats, large carnivores have suffered drastic population declines and massive range reductions over the past centuries (Morrison et al. 2007; Ripple et al. 2014; Wolf and Ripple 2017). In fact, 61% of the world's 31 largest carnivores are categorised as threatened by the International Union for the Conservation of Nature (IUCN), and 77% of these species are in decline (Ripple et al. 2014). Today, large carnivores occupy only a small fraction of their former ranges, and intact carnivore guilds remain on only about one third of the world's land area compared to about 96% in historical times (Wolf and Ripple 2017).

These trends are alarming given the high ecological, economic, and social importance of large carnivores (Lindsey et al. 2007; Brashares et al. 2010; Ripple et al. 2014). Large carnivores form part of cultural heritage and identity, provide ecosystem services to local people, and generate benefits from wildlife tourism, marketing, and commercial activities (Brashares et al. 2010; Rode et al. 2021). These predators are commonly positioned at the top of natural food webs, in which they exert both direct predation effects and indirect behaviour-mediated effects on their prey as well as on other species like mesopredators (Prugh et al. 2009; Ripple et al. 2014; Suraci et al. 2016). Thus, the absence of large carnivores has detrimental effects on the ecosystems they inhabit (Berger et al. 2001; Atkins et al. 2019; Beschta and Ripple 2019; Hoeks et al. 2020).

In light of their key ecological role and high socio-economic importance on the one hand and their natural susceptibility to anthropogenic threats on the other hand, the protection of large carnivores and their habitats is given particular significance in biodiversity conservation. In that respect, many large carnivores have the potential to serve as so-called 'umbrella species', as they roam widely, and the protection of their habitats is, therefore, likely to also benefit other wildlife (Macdonald et al. 2012; Thornton et al. 2016). Moreover, large carnivores engage remarkable public attention and are thus considered 'flagship species', which can increase awareness of ecological problems and gain support for conservation initiatives (Sergio et al. 2006; Clucas et al. 2008). Finally, large carnivores may act as indicator species, as their presence or population status allows conclusions about the integrity of natural ecosystems (Ray et al. 2013).

1.2 The snow leopard: a threatened ambassador of high-altitude ecosystems

The snow leopard is the smallest representative of the so-called big cats and is considered a flagship, umbrella, and indicator species of high-mountain ecosystems in Asia (Snow Leopard Network 2014; Kitchener et al. 2016; United Nations Development Programme (UNDP) and Global Environment Facility (GEF) 2016; Figure 1.1). This big cat has evolutionarily adapted to living and hunting in cold climates and steep landscapes and is closely associated with alpine and subalpine zones above the treeline (Snow Leopard Network 2014; Kitchener et al. 2016). In the high mountain ranges of Asia, it plays a key ecological role at the top of the food chain (Lyngdoh et al. 2014). Snow leopards were found to prey on a broad number of species and to depend on livestock as well as on smaller mammals in parts of their range (Bagchi and Mishra 2006; Lyngdoh et al. 2014). Nevertheless, this big cat is considered to be close to a 'specialist' (Lovari and Mishra 2016), with medium-sized wild ungulates representing its staple diet (Lyngdoh et al. 2014). Snow leopards occupy large spatial ranges, with home range estimates varying considerably between about 12–13 km^2 (Jackson and Ahlborn 1989; McCarthy et al. 2005) and several hundred km^2 (> 600 km^2, Johansson et al. 2016).

In spite of its wide distribution across twelve range countries, the snow leopard is listed as 'Vulnerable' on the IUCN Red List of Threatened Species (McCarthy et al. 2017). Elusive and secretive behaviour, which contributed to the moniker 'the ghost of the mountains' (Snow Leopard Conservancy 2020), low population densities, and inaccessible habitats impede reliable and robust global population estimates (McCarthy et al. 2017). Conservative estimates assume that only about 3,000 mature individuals persist in the wild, and the snow leopard population trend is classified as 'Decreasing' (McCarthy et al. 2017). Similar to other large carnivores, a variety of anthropogenic threats are held responsible for the endangerment of this large felid.

First, wide-roaming solitary behaviour and resulting low population densities make this species susceptible to habitat loss, degradation, and fragmentation, which, in turn, can cause genetic impoverishment and threaten population viability (Riordan et al. 2016; Rashid et al. 2020). Ongoing and planned large infrastructure projects, mining activities, and land conversion are expected to further reduce habitat suitability (e.g., Farrington and Li 2016; Heiner et al. 2016; Zahler 2016; WWF Nepal 2018; Khan et al. 2021). Moreover, climate change and the presumed associated treeline shift are likely to negatively affect snow leopards by posing additional physiological challenges when forced to live at higher elevations, by increasing competition with sympatric predators, and by intensifying habitat fragmentation and population isolation (Forrest et al. 2012; Farrington and Li 2016; Li et al. 2021).

Second, declines in wild prey populations represent another major threat to snow leopards (McCarthy et al. 2017). The depletion of the snow leopard's wild prey base is a result of various processes, including habitat loss and fragmentation, interactions with livestock (e.g., competition, disease transmission), and poaching (e.g., Berger et al. 2013; Khan et al. 2013). As the wild prey base in the high mountain ranges is naturally limited, the protection of ungulates, especially blue sheep (*Pseudois nayaur*), Siberian ibex (*Capra sibrica*), and Himalayan tahr (*Hemitragus jemlahicus*), is considered a cornerstone of global snow leopard conservation, and further research on these prey populations is suggested (Lyngdoh et al. 2014). Ultimately, the survival of the snow leopard may be closely linked to success or failure in preserving and restoring its wild prey populations (Lovari and Mishra 2016).

Third, poaching for fur and other body parts (e.g., Li and Lu 2014) and killings to prevent or retaliate livestock depredation are other main threats to the snow leopard (Jackson et al. 2010; McCarthy et al. 2017). In fact, Nowell et al. (2016) estimated that about 55% of snow leopard poaching incidents in the past years resulted from conflicts over livestock depredation. Such cases are documented across the entire snow leopard range in spite of its full legal protection in all range countries (e.g., Hussain 2000; Mishra et al. 2003; Snow Leopard Network 2014; Mishra et al. 2016). Conflicts over livestock depredation are particularly relevant to the survival and protection of snow leopards living in rugged and remote landscapes where pastoralism

represents a traditional form of extensive land use and subsistence economy (Mishra et al. 2003, 2016) and in which the livelihoods of impoverished local communities may strongly depend on livestock (e.g., Chetri et al. 2017; Kusi et al. 2020). Snow leopards are capable of killing livestock of variable sizes, including small-bodied sheep and goats as well as large-bodied yaks and camels (Johansson et al. 2015). They are also known for surplus killings (i.e., killing multiple individuals in a single attack), which are likely to raise particular anger and cause negative attitudes among local people (Thapa 2021).

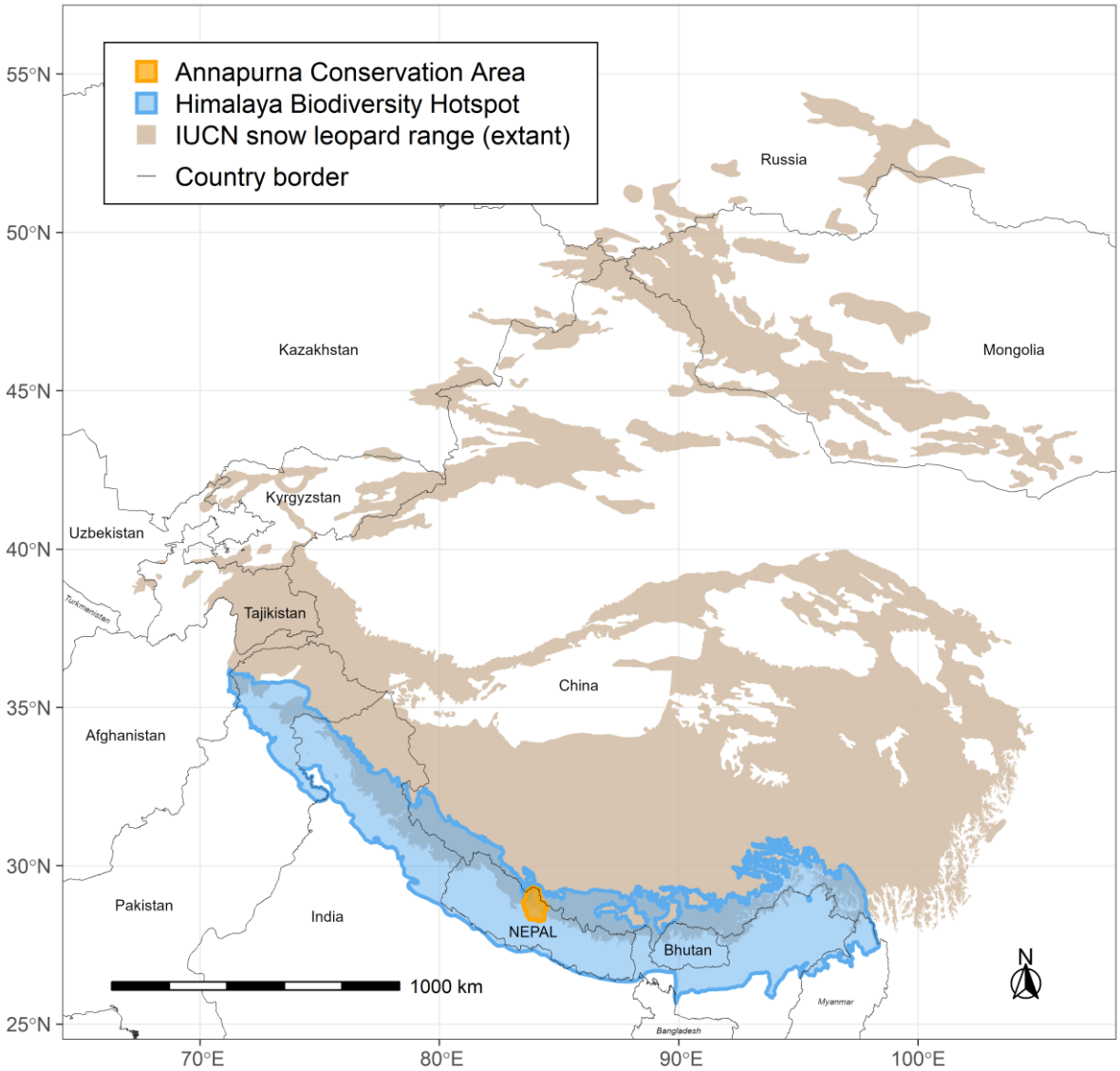

Figure 1.1. Distribution of the snow leopard (extant) and locations of the Himalaya Biodiversity Hotspot and Annapurna Conservation Area in Asia. The countries not belonging to the 12 snow leopard range countries are labelled in italics. Sources: DIVA-GIS 2015 - country borders; Panthera et al. 2017 - snow leopard range.

1.3 Protection of snow leopards and their habitats: key challenges and gaps in knowledge

In light of the snow leopard's socio-ecological relevance and its various merits in biodiversity conservation, the protection of this big cat is considered a crucial foundation of strategies directed towards the conservation of Asian mountain landscapes and biodiversity (Snow Leopard Network 2014). However, the protection of the snow leopard represents a great challenge to conservationists, wildlife managers, and other key stakeholders due to the multitude, complexity, and characteristics of threats faced by this predator and existing gaps in knowledge (Snow Leopard Network 2014).

First, the mentioned threats to snow leopard populations (see Chapter 1.2) require suitable management responses at various spatial scales. Habitat loss and deterioration are largely, though not exclusively, ascribed to global and transregional drivers, including global warming and large-scale infrastructure projects (e.g., Forrest et al. 2012; Sultan et al. 2022). Likewise, high mountain ranges inhabited by snow leopards and wild ungulates often form parts of international borders, exposing wildlife to (indirect) threats resulting from non-uniform conservation policies, military actions, and border fencing (e.g., Li et al. 2020; Sultan et al. 2022). Mitigation of such large-scale threats calls for transboundary planning and international cooperation (Rosen and Zahler 2016). Similarly, transnational factors like climate change and the developments of economic markets affect wild prey depletion (Berger et al. 2013; Aryal et al. 2014a), which may also be driven by local factors, such as competition with livestock, disease transmission by domestic animals, and poaching (e.g., Dagleish et al. 2007; Khan et al. 2013; Yang et al. 2021). Conflicts over livestock depredation, in turn, may emerge locally, especially in so-called 'hotspots' (Jackson and Wangchuk 2001). Nevertheless, in light of low population densities (Snow Leopard Network 2014; McCarthy et al. 2017) and large interbirth intervals with cubs spending almost two years with their mothers (Johansson et al. 2021), even the killing of just a few individuals may detrimentally affect entire snow leopard populations (e.g., Hussain 2000). In summary, it can therefore be said that the long-term well-being of snow leopard populations will depend on successful management strategies addressing these threats on various scales.

Second, the general scarcity of funding of biodiversity conservation (McCarthy et al. 2012) also poses an obstacle to snow leopard conservation in Asia (Jackson et al. 2010), requiring prioritisation of management actions. Unfortunately, the selection and implementation of suitable and most practical management actions are still impeded by remaining gaps in knowledge on interactions between snow leopards, humans, livestock, and wild prey, implying the need for more conservation-oriented research. In general, low population densities, rugged and remote habitats, and elusive behaviour make the monitoring of snow leopard populations

a challenge per se (Fox and Chundawat 2016; McCarthy et al. 2017). Moreover, the already limited knowledge on interactions between snow leopards, wild prey, and livestock husbandry is partially contradictory. For instance, some studies found a positive relationship between wild prey abundance and snow leopard density or habitat choice (Sharma et al. 2015; Alexander et al. 2016a; Suryawanshi et al. 2017; Sharma et al. 2021; Suryawanshi et al. 2021; Yang et al. 2021), while others reported no or only weak effects (Alexander et al. 2016b; Rovero et al. 2020). Similarly, abundant wild prey populations decreased livestock losses in some regions (Bagchi et al. 2020; see also Khorozyan et al. 2015), while just the opposite was observed elsewhere and ascribed to increased snow leopard densities (Suryawanshi et al. 2013; Suryawanshi et al. 2017), and yet other studies reported more complex relationships dependent on livestock densities and study scales (Chetri et al. 2019a; Khanal et al. 2020a). In addition, some studies found terrain characteristics and livestock protection interventions (hereafter interventions) to significantly affect livestock depredation by snow leopards (Jackson et al. 2010; Johansson et al. 2015; Mishra et al. 2016; Mijiddorj et al. 2018). To sum up, the knowledge on interactions between snow leopards, wild prey, livestock, and local people remains limited and partially contradictory, and especially the relative importance of various management actions, such as wild prey restoration and improved livestock husbandry, has rarely been studied. Ultimately, a thorough understanding of these complex relationships and the relative importance of management actions is needed to set conservation priorities and implement useful measures that secure the protection of the big cat and its natural habitats.

1.4 Research objectives and thesis structure

Based on the challenges and gaps in knowledge mentioned above, the present PhD project was designed to evaluate the performance of conservation and management actions targeting the snow leopard and its habitats and to generate more profound knowledge on the interactions between snow leopards, wild prey, livestock, and local people. More specifically, this study aimed at 1) assessing the performance of protected area management concepts in preserving biodiversity, indicated by the blue sheep as the main snow leopard prey, 2) analysing the effects of wild prey on snow leopard (relative) abundance and livestock depredation rates attributed to this predator, and 3) identifying suitable intervention strategies and husbandry practices reducing livestock depredation rates (Figure 1.2). By combining the findings from these analyses, the overall goal of this PhD project was to deduce relevant conservation implications that contribute to the long-term preservation of the snow leopard and high-altitude ecosystems in Asia.

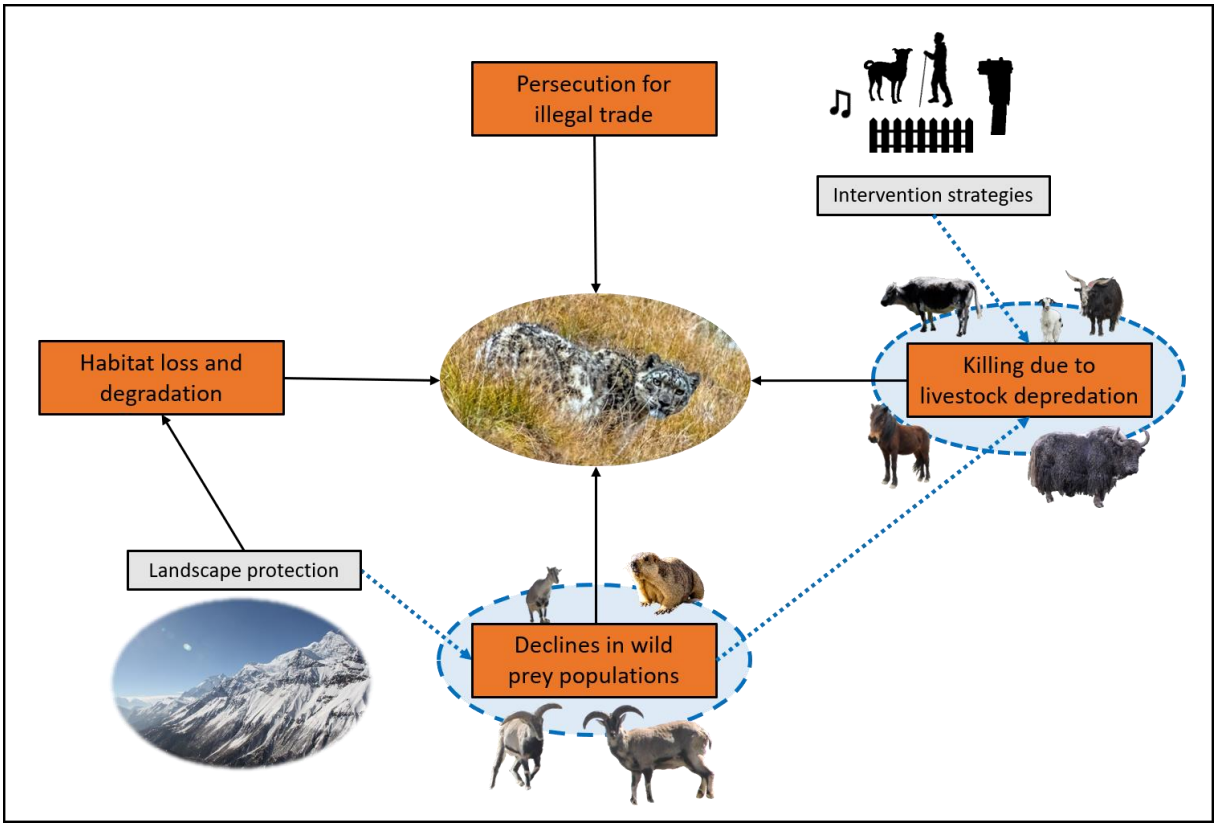

Figure 1.2. A simplified conceptual scheme of threats to the globally threatened snow leopard and research objectives of this PhD project. Orange boxes show the main current threats to snow leopards, blue dashed ovals highlight the threats mainly addressed in this PhD project, and blue dotted arrows show the effects and interactions examined in various research activities. Credits: snow leopard and Himalayan marmot - Tashi R. Ghale (Third Pole Conservancy); horse and Foxlights - Rinzin P. Lama; mountain landscape, blue sheep, yak, cattle, sheep and goat - Marc Filla.

The Annapurna Conservation Area (ACA) in central Nepal offered excellent conditions for this study (Figure 1.1). First, the ACA is considered a role model for the management of high-mountain landscapes in Asia (Bhuju et al. 2007), as it follows an integrated conservation and development concept, which aims at linking poverty reduction and biodiversity conservation (Sanderson and Redford 2003; Roe et al. 2013). In fact, this protected area, which was established in 1992, covers a large area of 7,629 km^2 in the Himalaya Biodiversity Hotspot and hosts both a diverse wildlife community including at least 1300 plant species, 514 bird species, and 128 mammal species (Mittermeier et al. 2005; Baral et al. 2019) and about 100,000 people with traditional rights and access to natural resources (National Trust for Nature Conservation 2015). While crop farming and livestock husbandry represent traditional (subsistence) economies in the ACA (Bhuju et al. 2007; Baral et al. 2019), tourism is of increasing importance, with more than 170,000 tourists visiting the Annapurna region annually and generating financial revenues for local households (Bhuju et al. 2007; National Trust for Nature Conservation 2018; Baral et al. 2019). Second, this protected area in central Nepal, which hosts about 10% of the global snow leopard population (McCarthy and Mallon 2016), plays a

significant role in snow leopard conservation. The ACA comprises excellent habitats for the big cat and other mountain wildlife (Aryal et al. 2016; WWF Nepal 2018), represents an important potential corridor for adjacent snow leopard populations (Ministry of Forests and Soil Conservation 2017), and is associated with partially high densities of snow leopards and wild ungulates (Wegge et al. 2012; Thapa et al. 2021a). Third, the vast landscape of the Annapurna region shows a considerable variation in environmental parameters like habitat types and topography (Bhuju et al. 2007; Baral et al. 2019), wildlife densities (e.g., Aryal et al. 2014a; Thapa et al. 2021), and livestock husbandry (e.g., Lama 2018), implying excellent conditions to study the effects of these parameters. Fourth, due to various human-wildlife conflicts, this protected area itself is in need of additional management actions benefiting the long-term co-existence of wildlife populations and local people (Baral et al. 2019).

To address the research questions outlined above, various research activities, including wildlife monitoring and questionnaire surveys, were carried out in the Annapurna region between March 2019 and July 2021. Fieldwork in the Annapurna Conservation Area was conducted in close cooperation with the Nepalese NGO *Third Pole Conservancy* (formerly *Global Primate Network Nepal*) and was partially affected by and delayed due to consequences and restrictions arising from the COVID-19 pandemic. Eventually, the surveys yielded three scientific publications, which deal with different socio-ecological aspects of human-wildlife co-existence in the Nepalese Himalaya and represent the backbone of my dissertation.

Chapter 2 focuses on the blue sheep, a common but increasingly threatened wild ungulate that represents the main prey of snow leopards in the Annapurna Conservation Area (Chetri et al. 2017) and elsewhere (Lyngdoh et al. 2014). We analysed wildlife monitoring data collected along transects covering a total length of 262.6 km in the Manang district and used multivariate models to examine the population status and habitat choice of this medium-sized ungulate. The analysis of data collected almost 30 years after the establishment of the Annapurna Conservation Area and its comparison with earlier data from the same study area allow conclusions about the long-term effectiveness of the applied integrated conservation and development approach and, thus, has important implications for the future protection and management of high mountain ranges in Asia.

Chapter 3 addresses the complex relationships between snow leopards, wild prey, livestock, and humans. This part of the dissertation is based on extensive monitoring efforts and questionnaire surveys in a total of 82 study units (4 x 4 km cells) in the Annapurna Conservation Area, which were sampled between 2019 and 2021. I conducted multivariate analyses to illuminate the effects of wild and domestic prey densities on snow leopard relative abundance and identify ecological and husbandry factors associated with livestock depredation by snow leopards. The work lays an important foundation for a better understanding of interactions

between snow leopards and prey populations. It further evaluates the relative importance of wild prey populations for snow leopard abundance and conflicts over livestock depredation. The results of this study will support wildlife managers in setting priorities for the protection of the globally threatened cat and its natural habitats.

Chapter 4 examines the patterns of livestock depredation attributed to snow leopards in the Annapurna region as well as the effects of intervention strategies applied by local livestock owners. This work was based on questionnaire data from 329 households and designed to examine the spatio-temporal variation in depredation, reveal vulnerable livestock species and groups, analyse the potential effectiveness of intervention strategies, and identify husbandry parameters associated with depredation. This study suggests a number of suitable and practical intervention strategies to mitigate human-snow leopard conflicts and, thereby, benefit human-snow leopard co-existence in the Annapurna region and beyond.

During the dissertation period, I was also involved in related projects and scientific studies addressing large carnivore ecology and human-carnivore co-existence, which resulted in the following scientific publications:

- Soofi, M., Qashqaei, A. T., Mousavi, M., Hadipour, E., Filla, M., Kiabi, B. H., Bleyhl, B., Ghoddousi, A., Balkenhol, N., Royle, A., Pavey, C. R., Khorozyan, I., Waltert, M. (2022). Quantifying the relationship between prey density, livestock and illegal killing of leopards. *Journal of Applied Ecology*, Accepted Author Manuscript. https://doi.org/10.1111/1365-2664.14163
- Melovski, D., Ivanov, G., Stojanov, A., Avukatov, V., Gonev, A., Pavlov, A., Breitenmoser, U., von Arx, M., Filla, M., Krofel, I., Signer, J., Balkenhol, N. (2020). First insight into the spatial and foraging ecology of the critically endangered Balkan lynx (*Lynx lynx balcanicus*, Buresh 1941). *Hystrix, the Italian Journal of Mammalogy* **31**, 26-34. https://doi.org/10.4404/hystrix-00254-2019
- Signer, J., Filla, M., Schoneberg, S., Kneib, T., Bufka, L., Belotti, E., Heurich, M. (2019). Rocks rock: the importance of rock formations as resting sites of the Eurasian lynx *Lynx lynx*. *Wildlife Biology* **1**, 1-5. https://doi.org/10.2981/wlb.00489
- 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. *Journal of Applied Ecology* **56**, 365-374. https://doi.org/10.1111/1365-2664.13266

Chapter 2

Population density and habitat selection of blue sheep in Annapurna Conservation Area

Blue sheep (*Pseudois nayaur*) in the Phu Valley, Annapurna Conservation Area, Nepal. Credit: Marc Filla

Publication: In the shadows of snow leopards and the Himalayas: density and habitat selection of blue sheep in Manang, Nepal

Marc Filla, Rinzin P. Lama, Tashi R. Ghale, Johannes Signer, Tim Filla, Raja R. Aryal, Marco Heurich, Matthias Waltert, Niko Balkenhol, Igor Khorozyan

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Abstract

There is a growing agreement that conservation needs to be proactive and pay increased attention to common species and to the threats they face. The blue sheep (*Pseudois nayaur*) plays a key ecological role in sensitive high-altitude ecosystems of Central Asia and is among the main prey species for the globally vulnerable snow leopard (*Panthera uncia*). As the blue sheep has been increasingly exposed to human pressures, it is vital to estimate its population dynamics, protect the key populations, identify important habitats, and secure a balance between conservation and local livelihoods. We conducted a study in Manang, Annapurna Conservation Area (Nepal), to survey blue sheep on 60 transects in spring (127.9 km) and 61 transects in autumn (134.7 km) of 2019, estimate their minimum densities from total counts, compare these densities with previous estimates, and assess blue sheep habitat selection by the application of generalised additive models (GAMs). Total counts yielded minimum density estimates of 6.0–7.7 and 6.9–7.8 individuals/km^2 in spring and autumn, respectively, which are relatively high compared to other areas. Elevation and, to a lesser extent, land cover indicated by the normalized difference vegetation index (NDVI) strongly affected habitat selection by blue sheep, whereas the effects of anthropogenic variables were insignificant. Animals were found mainly in habitats associated with grasslands and shrublands at elevations between 4,200 and 4,700 m. We show that the blue sheep population size in Manang has been largely maintained over the past three decades, indicating the success of the integrated conservation and development efforts in this area. Considering a strong dependence of snow leopards on blue sheep, these findings give hope for the long-term conservation of this big cat in Manang. We suggest that long-term population monitoring and a better understanding of blue sheep-livestock interactions are crucial to maintain healthy populations of blue sheep and, as a consequence, of snow leopards.

2.1 Introduction

Conservation initiatives have long been focused on rare and threatened species that face an imminent risk of extinction (Lindenmayer et al. 2011). However, common species are essential to secure functioning of species assemblages and ecosystems, and rare species may additionally rely on specific interactions with them. Therefore, even small declines in populations of common species may significantly disrupt natural processes (Gaston and Fuller 2008). In addressing this issue, there is a growing agreement that conservation needs to be proactive and pay increased attention to common species and to the threats they face (Gaston and Fuller 2008; Lindenmayer et al. 2011). Moreover, monitoring these populations is key for the early detection of population declines and for the evaluation and selection of conservation and management strategies (Gaston and Fuller 2008; Waltert et al. 2008; Frimpong 2018).

The blue sheep (*Pseudois nayaur*) is distributed from the Qilian Mountains in the north to the Himalayas in the south and is an example of a common species with a key ecological role in the mountain ecosystems of Central Asia (Harris 2014). Due to its wide distribution, a presumably large global population, and a lack of documented severe population declines, the blue sheep is listed as a species of 'Least Concern' on the IUCN Red List of Endangered Species (Harris 2014). However, blue sheep and other mountain ungulates have been increasingly threatened by human pressures (Berger et al. 2013). Climate change, expansion of the human population, and infrastructure development are rapidly reducing blue sheep habitats (Cui and Graf 2009; Aryal et al. 2016). Suitable habitats are not only being reduced but also degraded by co-existing and competing livestock (Mishra et al. 2004; Suryawanshi et al. 2010; Bhattacharya et al. 2020) which also poses a risk for disease transmission (Dagleish et al. 2007; Gibb et al. 2020). In addition, illegal killing and legal hunting for subsistence or trophies (Aryal et al. 2010, 2015a; Næss and Bårdsen 2016) have a potential to harm local blue sheep populations.

The effects of these threats are alarming, especially considering the pivotal ecological role of blue sheep in low-productivity high-altitude ecosystems. Here, ungulates may affect plant species diversity and distribution through seed dispersal (Aryal et al. 2015b; Shrestha and Moe 2015), and blue sheep represent the main wild prey for sympatric large carnivores, such as the globally vulnerable snow leopard (*Panthera uncia*; Lyngdoh et al. 2014). The snow leopard, which is a Himalayan flagship species, may heavily depend on blue sheep and selectively hunts these ungulates throughout their range (Aryal et al. 2014b; Lyngdoh et al. 2014; Shrestha et al. 2018). Therefore, protection of blue sheep populations is crucial to fulfil larger conservation goals such as maintaining ecosystem integrity and ecological functions, strengthening wildlife capacities to withstand increasingly difficult environmental conditions

created by climate change, and fostering co-existence between wildlife and local rural communities.

Although blue sheep persist in unprotected lands at reasonable densities, protected areas are likely to harbour population strongholds in several range countries (Harris 2014). For instance, most suitable blue sheep habitats in Nepal are located within protected areas (Aryal et al. 2016), which accommodate relatively high densities of these ungulates (e.g., Shrestha and Wegge 2008a). It is still a debate whether such abundance of wild prey would potentially reduce human-carnivore conflicts over livestock depredation (Khorozyan et al. 2015; Chetri et al. 2017) or increase them (Suryawanshi et al. 2017). Either way, detailed knowledge of habitat requirements by blue sheep is essential to identify and protect their key habitats and to support large and viable populations (Loehle and Li 1996). Moreover, understanding blue sheep habitat preferences is also important to boost potential translocation programs. Recent calls for translocation programs to recover local blue sheep populations and mitigate human-snow leopard conflicts (Aryal et al. 2013, 2014c; Ferretti et al. 2014; Hanson et al. 2020) demand for the assessment of habitat quality in release sites (Wolf et al. 1998). Previous investigations of blue sheep were focused on species distribution (Aryal et al. 2016), habitat use and preferences (Wegge 1979; Wilson 1981; Khatiwada et al. 2007; Bhardwaj et al. 2010; Aryal et al. 2014c), resource partitioning and overlap with sympatric wild ungulates or livestock (Namgail et al. 2004; Shrestha and Wegge 2008a; Namgail et al. 2009; Suryawanshi et al. 2010; Bhattacharya et al. 2020), and foraging/bedding site selection (Liu et al. 2005a, 2007). Despite this, fine-scale habitat requirements of blue sheep are still insufficiently studied. There is also limited knowledge about the main factors that shape blue sheep habitat selection. Based on this, it remains obscure whether blue sheep are more strongly affected by ecological or anthropogenic factors, which is relevant for conservation planning and management.

In this study, we aimed to estimate minimum blue sheep densities from total counts, determine population changes over time, and assess habitat selection for the Manang area of Annapurna Conservation Area, Nepal. Compared to other regions, this protected area harboured high blue sheep densities before and shortly after its official establishment (e.g., Sherpa and Oli 1988 cited in Oli 1991; Oli 1994; Shrestha and Wegge 2008a). The management strategy of the Annapurna Conservation Area follows an integrated conservation and development program aiming to achieve conservation goals and socio-economic improvement, mainly through the implementation of ecotourism (Adams et al. 2004; Shrestha et al. 2010; Baral 2013; Baral et al. 2019). This approach has been widely used throughout the blue sheep range (Nepal 2002). As in other conservation programs, we consider blue sheep population trends in the study area as an important indicator of the effectiveness of such management strategies in regard to wildlife conservation (Waltert et al. 2008; Ghoddousi et al. 2019). We anticipate that a combination of our results with earlier studies (Oli 1994; Shrestha and Wegge 2008a;

Bhattacharya et al. 2020, to name a few) will provide useful recommendations for the management and conservation of blue sheep also beyond the Annapurna region.

2.2 Material and methods

2.2.1 Study area

The Annapurna Conservation Area (ACA; IUCN management category VI) is located in the Himalaya Biodiversity Hotspot, covers an area of 7,629 km^2, and forms the largest protected area in Nepal (Mittermeier et al. 2005; Bhuju et al. 2007; Figure 2.1). It provides habitats to at least 128 mammal, 514 bird, and more than 1,300 plant species, and hosts over 100,000 inhabitants (Baral et al. 2019). First tested in a single village development committee and in close cooperation with local people, the ACA was initiated in 1986 and officially gazetted in 1992 (Baral et al. 2019). This protected area has been managed through a long-term participatory integrated conservation and development program by a non-governmental organisation, the National Trust for Nature Conservation. Local people are still allowed to live within the ACA boundaries, maintain traditional rights, and have access to natural resources. Financial resources generated from ecotourism and other sources have been invested in social capacity building, community development, and environmental education rather than in armed military guards (Baral et al. 2019).

The present study was carried out in the Manang area (28°35′3″–28°50′11″N, 83°52′43″–84°20′16″E; Figure 2.1). Elevations of the effective study area (~450 km^2) range from 2,870 m to 6,150 m above sea level (a.s.l.). Located in the rain shadow of the Annapurna Range, it is one of the driest areas in the Nepalese Himalaya, with the mean annual precipitation of ~400 mm and most precipitation falling as snow during winter (ICIMOD/MENRIS 1995 cited in Aase and Vetaas 2007; Karki et al. 2015; Chetri et al. 2017). Mean daily air temperatures range from less than -20°C in winter to slightly above 20°C in summer (Oli 1991; Department of Hydrology and Meteorology 1999 cited in Aase and Vetaas 2007). Vegetation structure is determined by elevation and slope (Shrestha and Wegge 2008a). Forests at lower elevations comprise the Himalayan white pine (*Pinus wallichiana*), East Himalayan fir (*Abies spectabilis*), Himalayan birch (*Betula utilis*), and black juniper (*Juniperus indica*; Ghimire and Lekhak 2007). Above the timberline, vegetation is grouped into shrublands, alpine meadows, and alpine grasslands (Shrestha and Wegge 2008a). The highest elevations are dominated by barren lands and permanent snowfields (Shrestha and Wegge 2008a).

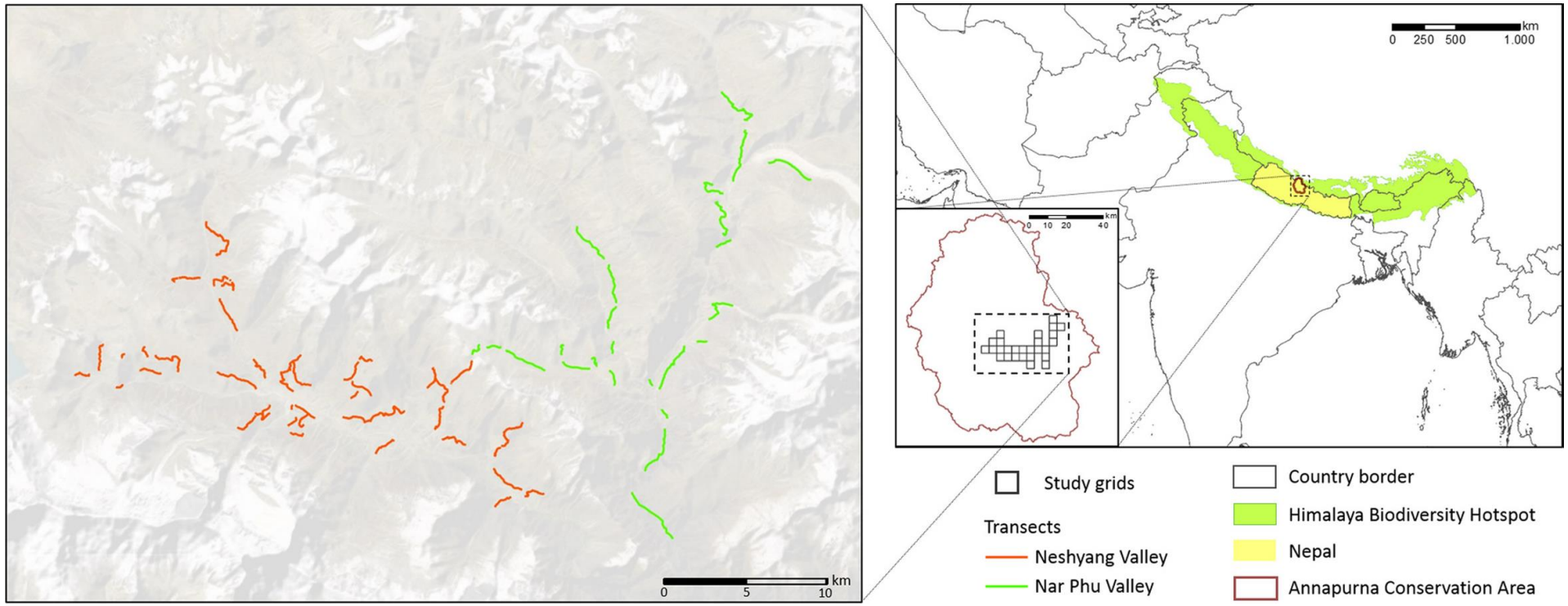

Figure 2.1. Location of Manang study area in the Annapurna Conservation Area within the Himalaya Biodiversity Hotspot (Created in ArcGIS® 10.3.1). Sources: Esri, Digital Globe, GeoEye, Earthstar Geographics, CNES/Airbus DS, USDA, USGS, Aero Grid, IGN, and the GIS User Community; Conservation International 2011 (Hotspot location); DIVA-GIS 2015 (country borders).

In spite of its harsh environmental conditions, the Manang area is relatively rich in mammalian species. Apart from the blue sheep, the Himalayan musk deer (*Moschus leucogaster*) and Himalayan tahr (*Hemitragus jemlahicus*) add to the ungulate community at lower elevations (Chetri et al. 2017). Several large and medium carnivores occur in the area, including the snow leopard, Himalayan wolf (*Canis lupus chanco*), golden jackal (*Canis aureus*), and red fox (*Vulpes vulpes*; Chetri et al. 2017). The small mammal community is composed of such species as the Pallas's cat (*Otocolobus manul*), small mustelids (*Mustela* spp. and *Martes* spp.), and several species of voles (*Alticola* spp.) and pikas (*Ochotona* spp.; Oli 1994; Chetri et al. 2017).

The livestock community includes sheep (*Ovis aries*), goats (*Capra hircus*), yaks (*Bos grunniens*), cattle (*B. taurus*), dzo (*B. grunniens* × *B. taurus*), mules (*Equus asinus* × *E. caballus*), and horses (*E. caballus*; Chetri et al. 2017). Livestock husbandry and crop farming are among the main subsistence economies in the area, with tourism being of increasing importance (Bhuju et al. 2007; Chetri et al. 2017; Baral et al. 2019).

2.2.2 Data collection

This study was based on two field surveys in late winter/spring (March–May 2019; hereafter referred to as spring) and in late summer/autumn (September–October 2019, hereafter referred to as autumn). To identify potential study units, we placed a grid of 4 x 4 km cells over the study area. This cell size compromised daily movements and home ranges of blue sheep (Schaller 1967 cited in Garland Jr. 1983; Wegge 1976 cited in Jackson 1996) and snow leopards (Jackson 1996; Johansson et al. 2016). We further selected study units based on geographical and ecological living conditions of blue sheep (mean elevation 3,000–5,000 m and forest cover < 50%; Aryal et al. 2014b; Harris 2014) and also considered logistic challenges and accessibility (distance to settlements < 10 km; Alexander et al. 2016a). In selected grid cells, we placed transects along the features that are commonly used by blue sheep, snow leopards, and other wildlife and that typically provide good visibility over the surrounding area. These included riverbeds and ridgelines (Jackson 1996; Suryawanshi et al. 2013), as well as other paths and potential connecting habitats. Such features were selected after consultation with local people and verification of terrain accessibility, and they were assumed to be unbiased to habitat preferences by blue sheep. Seasonal differences in transect lengths were predominantly due to terrain inaccessibility caused by unexpected snowfall.

We counted blue sheep mainly during the morning (6:00–10:00 a.m.) and afternoon hours (2:00–6:00 p.m.) when blue sheep activity is high (Liu et al. 2005b), by teams of 2–3 skilled observers, including wildlife biologists and experienced local field assistants. We scanned adjacent ridgelines, slopes, gullies, and valleys by 10 x 32 binoculars (Kowa SV) and stopped

regularly at suitable vantage points (Leki et al. 2018). Upon spotting blue sheep, we marked the observer position and measured the distance (m), angle (degree), and compass direction to the centre of the detected animal cluster or individual (degree) using a handheld GPS (Garmin GPSMAP 64s), range finder (Leica Rangemaster CRF 1000-R), and compass. Whenever possible, we classified blue sheep as adult males, adult females, and subadults (< 2 years; Aryal et al. 2010). To avoid double-counting, we noted unique features of individuals, such as broken horns and colouration patterns, and aimed at sampling adjacent grid cells on consecutive days (Leki et al. 2018). Blue sheep locations were plotted, verified, and modified in ArcGIS 10.3.1 (Esri, USA) and QGIS 3.4.8 (QGIS Development Team).

We used ten environmental predictor variables to analyse habitat use and selection by blue sheep: elevation, slope, terrain ruggedness, aspect, normalized difference vegetation index (NDVI), livestock presence, distance to cliff, distance to stream, distance to settlement, and distance to trail. Elevation was obtained from a digital elevation model of 30-m resolution (DEM; ASTER Digital Elevation Model; NASA/METI/AIST/Japan Spacesystems and U.S./ Japan ASTER Science Team 2009). The DEM also served as a basis for the calculations of slope (degree; Horn 1981), terrain ruggedness (m; Riley et al. 1999), and aspect (degree; Horn 1981). For the analysis of habitat selection, we converted the aspect to the deviation of the surface orientation from the south. Thereby, we accounted for the ecological relevance of this variable (i.e., south-facing slopes receiving most solar radiation) and prevented problems from fitting smoothing terms to a continuous variable with a circular orientation (i.e., 0°N is equal to 360°N).

In the absence of a fine-scale land-cover map, we used NDVI (Rouse et al. 1974), which quantifies vegetation greenness based on remote sensing data, as an indicator of land cover and a proxy for food availability. We applied the Annual Composite function in Google Earth Engine (Gorelick et al. 2017) to calculate the median annual NDVI from satellite images with adequate cloud cover. To link NDVI with actual land cover, we first classified land-cover types at 203 predefined locations by satellite imagery and ground-truthing. These included the grassland, shrubland, agricultural land, forest, settlement, barren land, water body, and permanent snowfield. We then extracted NDVI values at corresponding locations, assigned NDVI ranges to each land-cover type, and applied the Wilcoxon rank-sum test to check for differences in NDVI among land-cover types (Figure S2.1; Table S2.1).

In addition, we assessed livestock presence (1)/absence (0), including large (yak, cattle, dzo, and horse) and small species (sheep and goat). We monitored and mapped livestock from transects using the same methodology as for blue sheep. We created 500-m buffers around livestock locations to derive areas with livestock presence and absence during the survey. As blue sheep and livestock can graze together (R. P. Lama and M. Filla, personal observations), we considered this quite short buffer distance as reasonable to affect blue sheep-livestock

interactions (see Table S2.2 for model outputs with different buffer widths). As various geographic features and human presence potentially influence blue sheep, we additionally calculated the distances to cliff (m), stream (m), settlement (m), and trail (m). Cliffs represent a potential escape cover, and we defined them as slopes exceeding 45° and larger than 90 m^2 (Namgail et al. 2004; Bhattacharya et al. 2020). Streams were identified from DEM using the Fill, Flow Direction, and Flow Accumulation tools in ArcGIS. The actual stream network was adjusted and finalised through the comparison with rivers mapped in OpenStreetMap (https://download.geofabrik.de), ground-truthing, and interpretation of satellite images. Locations of settlements were provided by governmental authorities (Survey Department, Government of Nepal 2019), and we amended this layer by adding long-term herder camps and by removing abandoned settlements and individual huts. Trails commonly used by tourists and/or local people were derived from OpenStreetMap (https://download.geofabrik.de). These trail locations were checked and modified by ground-truthing and based on expert judgment.

2.2.3 Data analysis

In order to yield comparable estimates of blue sheep population size to previous studies in the study area, we extrapolated the minimum blue sheep density from total counts along the transects. Due to good visibility and often sparse vegetation at high elevations, we considered this approach as suitable to provide conservative estimates. We estimated this minimum density as the number of animals counted per area surveyed, irrespective of sex/age classes involved (Oli 1994; Aryal et al. 2014c). Therefore, we summed up all blue sheep individuals observed within the buffers around transects. To obtain the actual survey area, we used the Visibility tool in ArcGIS and calculated the visible surface (viewshed) within the buffers of 1,000–1,500 m around the transects. The thresholds of 1,000 and 1,500 m were the maximum sighting distances considered in our surveys, that is, they outlined the areas that were scanned with the most reasonable effort. In fact, the 1,000-m buffer included 93.5% and the 1,500-m buffer included 99.0% of all blue sheep groups spotted along the transects. We manually corrected total surfaces by adding individual pixels (i.e., areas surveyed but categorised as ‘not visible’) and subtracting areas not sampled due to low visibility. We received the upper and lower limits of minimum density estimates by considering the adjusted 1,000- and 1,500-m viewsheds, respectively.

We analysed habitat use by blue sheep from all sightings in the study area, including incidental encounters. To analyse habitat selection, we compared actual blue sheep presence sites along the transects with available sites. In order to sample available sites, we first created a large number of random pseudo-absence points (n = 50,000) in the 1,500-m viewshed around the transects. We then sampled from these points with the probabilities obtained from a density function of an exponential distribution parameterised with the observed distances of blue

sheep to the transects ($rate_{spring}$ = 0.0035; $rate_{autumn}$ = 0.0024). As recommended by Barbet-Massin et al. (2012), we drew 100 times as many points as we had field observations for each survey to gain a good model performance based on approximately 10,000 pseudo-absence points per season.

We randomly attributed observed group sizes to pseudo-absence points in spring as we did not find a significant correlation between the group size and the distance to the transect in this season (Pearson's $r = -0.090$, $p = 0.389$). In contrast, these parameters were positively correlated in autumn (Pearson's $r = 0.242$, $p = 0.012$). Therefore, we fitted a linear model where we explained the group size as a function of the intercept and the distance to the transect. The coefficients were 8.498 ± 1.893 ($p < 0.001$) for the intercept and 0.009 ± 0.003 ($p = 0.012$) for the distance to the transect.

We investigated the effects of the above-mentioned environmental predictor variables on habitat selection by blue sheep using generalised additive models (GAMs). GAMs have been increasingly used in habitat selection analyses (e.g., Rayment et al. 2015; Dupke et al. 2017; Liang et al. 2017, to name a few), they are rather flexible and capable of modelling nonlinear relationships, which is appropriate for ecological datasets (Guisan et al. 2002), and we expected them to optimally fit various predictor variables. Blue sheep presence (1)/pseudo-absence (0) served as the binary response variable in models separated for spring and autumn. Due to seasonal fluctuations and regular fission-fusion changes in group composition and size (Wang and Hoffmann 1987; Oli 1996; Schaller 1973 cited in Harris 2014), we treated each observation of single animals or groups as independent and adjusted for the number of adults by weighting. In the weighting process, we did not change the total number of observations in order not to erroneously increase the sample size. Each observation was assigned the weight as the number of adults divided by the total number of adults and multiplied by the total number of observations. The number of adult blue sheep was defined as the number of identified adults added by the number of unidentified individuals multiplied by the ratio of adults among all classified individuals. As recommended by Barbet-Massin et al. (2012), we attributed the same total weight to pseudo-absence points as to presence locations. We examined multicollinearity between predictor variables before modelling. Either of two variables was excluded if the absolute value of Pearson's correlation coefficient was equal to or greater than 0.7 (Dormann et al. 2013). Thus, we excluded terrain ruggedness which was highly correlated with slope (r_{spring} = 0.948, r_{autumn} = 0.945). We decided to retain the slope due to its better comparability across the studies (e.g., Aryal et al. 2014c). We further excluded livestock presence from spring models due to its high correlation with the distance to settlement (r_{spring} = -0.721). We retained the distance to settlement since most livestock is gathered around settlements in late winter/early spring and the locations of settlements were complete, yet some livestock could go undetected. Blue sheep observations in forested areas

were omitted from GAMs as we assumed a significantly lower detection probability in this land-cover type (see Figure S2.2 and Table S2.3 for model outputs with forested areas included).

We analysed the relative importance of variables through a random permutation procedure. We randomised one variable and then calculated the correlation between the predictions made by the randomised and original models (Thuiller et al. 2009). For each variable, we repeated this procedure 100 times to account for random effects. Then, we calculated a raw importance value for each variable as one minus mean correlation between the predictions made by the original and randomised models (Thuiller et al. 2009). Eventually, we standardised the relative importance values to the sum of one.

We performed sensitivity analyses by repeatedly modifying various assumptions and parameters, such as the location of random pseudo-absence points and inclusion/exclusion of forested areas. Modification of these parameters did not change the main model outputs (Figures S2.2-S2.5; Table S2.3). We conducted data processing and statistical analyses in R (R version 3.6.0; R Core Team 2019) unless otherwise indicated. The following R packages were used: Distance (Miller et al. 2019), dplyr (Wickham et al. 2019), ggplot2 (Wickham 2016), gratia (Simpson 2020), MASS (Venables and Ripley 2002), mgcv (Wood 2011), polycor (Fox 2019), raster (Hijmans 2019a), readxl (Wickham and Bryan 2019), rgdal (Bivand et al. 2019), rgeos (Bivand and Rundel 2019), sf (Pebesma 2018), and sp (Pebesma and Bivand 2005). We used standard error (SE) as a measure of variation.

2.3 Results

2.3.1 Population density

We covered 60 transects of a total length of 127.9 km in spring (mean: 2.1 ± 0.2 km/transect) and 61 transects of a total length of 134.7 km in autumn (mean: 2.2 ± 0.2 km/transect). Altogether, we spotted 1,905 blue sheep (143 observations) during the fieldwork in spring and 2,058 blue sheep (146 observations) during the fieldwork in autumn. Thereof, 1,408 individuals (94 observations) were spotted along the transects in spring and 1,648 individuals (108 observations) in autumn. Blue sheep group size ranged from single animals to 86 individuals in spring and to 113 individuals in autumn. Mean group size was 14.4 ± 1.3 individuals in spring and 14.4 ± 1.5 individuals in autumn.

A total of 1,387/1,408 and 1,419/1,606 blue sheep were spotted within 1,000/1,500 m from the transects in spring and autumn, respectively. The conservative extrapolation of minimum blue sheep densities yielded 6.0–7.7 individuals/km^2 and 6.9–7.8 individuals/km^2 over the surveyed area (180–234 km^2) in spring and autumn, respectively (see Table S2.4 for density estimates based on alternative maximum sighting distances). These estimates were higher in Nar Phu

Valley (7.6–10.0 individuals/km^2 in spring and 7.9–9.4 individuals/km^2 in autumn) than in Neshyang Valley (4.6–5.9 individuals/km^2 in spring and 6.0–6.6 individuals/km^2 in autumn; Figure 2.1; see Table S2.5 for fine-scale density estimates).

2.3.2 Habitat use and selection

Blue sheep were sighted between 3,440 m and 4,958 m a.s.l., though pellets indicated their presence also at higher elevations around 5,100 m (R. P. Lama and M. Filla, unpublished data). The majority of individuals was observed at 4,200–4,600 m a.s.l. in spring (mean: 4,276 ± 6 m a.s.l.) and 4,300–4,700 m a.s.l. in autumn (mean: 4,443 ± 6 m a.s.l.; Figure 2.2). This seasonal difference in altitudinal use by blue sheep was significant (Wilcoxon rank-sum test: W = 1,150,206, $p < 0.001$). In both seasons, blue sheep used a gradient of slope declivity ranging from flat terrain to steep cliffs (> 50°), but most animals were spotted in moderately rugged terrain to rather strong slopes (Figure 2.2). Blue sheep used mainly southern slopes in spring, whereas this pattern was less distinct in autumn (Figure 2.2).

We spotted blue sheep in various land-cover types, including grasslands, shrublands, agricultural lands, barren lands, snowfields, and open forests. In spring, the majority (77.5%) of animals used habitats having NDVI values between 0.25 and 0.5 and associated mainly with grasslands, shrublands, and agricultural lands (see Figure S2.1). The same applied to autumn (55.0%), though the use of less vegetated habitats increased in this season. Overall, the NDVI values of habitats used by blue sheep did not differ between spring and autumn (Wilcoxon rank-sum test: W = 1,921,320, $p = 0.684$).

Blue sheep observed from the transects were rarely encountered close to villages: 2.8% of adults were < 200 m away from settlements, and 7.9% were < 500 m away, in comparison with 5.2% and 16.9% of randomly chosen adults. In contrast, we regularly spotted blue sheep close to hiking trails and streams: 25.7% and 18.1% of adult blue sheep observed from the transects were < 200 m away from hiking trails and streams, respectively (Figure S2.6). In addition, 27.8% of adult blue sheep observed from the transects were spotted close (< 500 m) to livestock in spring, while this applied to only 17.3% of individuals in autumn.

The GAMs fitted to model habitat selection by blue sheep were capable of explaining 19.0% and 27.0% of the deviance in spring (n = 8,927, adjusted $R^2 = 0.159$) and autumn (n = 10,283, adjusted $R^2 = 0.200$), respectively. Elevation and land cover were the only significant variables ($p < 0.05$) for habitat selection by blue sheep in both seasons (Table 2.1).

In spring, blue sheep preferred elevations between 4,250 m and 4,550 m a.s.l. (Figure 2.3). Moreover, they selected land-cover types having NDVI values associated mainly with grasslands, shrublands, and agricultural lands (NDVI = 0.40–0.49) and avoided land-cover

types with NDVI values associated with less vegetated habitats (i.e., barren lands, glaciers, and water bodies; NDVI < 0.14; Figures 2.3 and S2.1; Table S2.1).

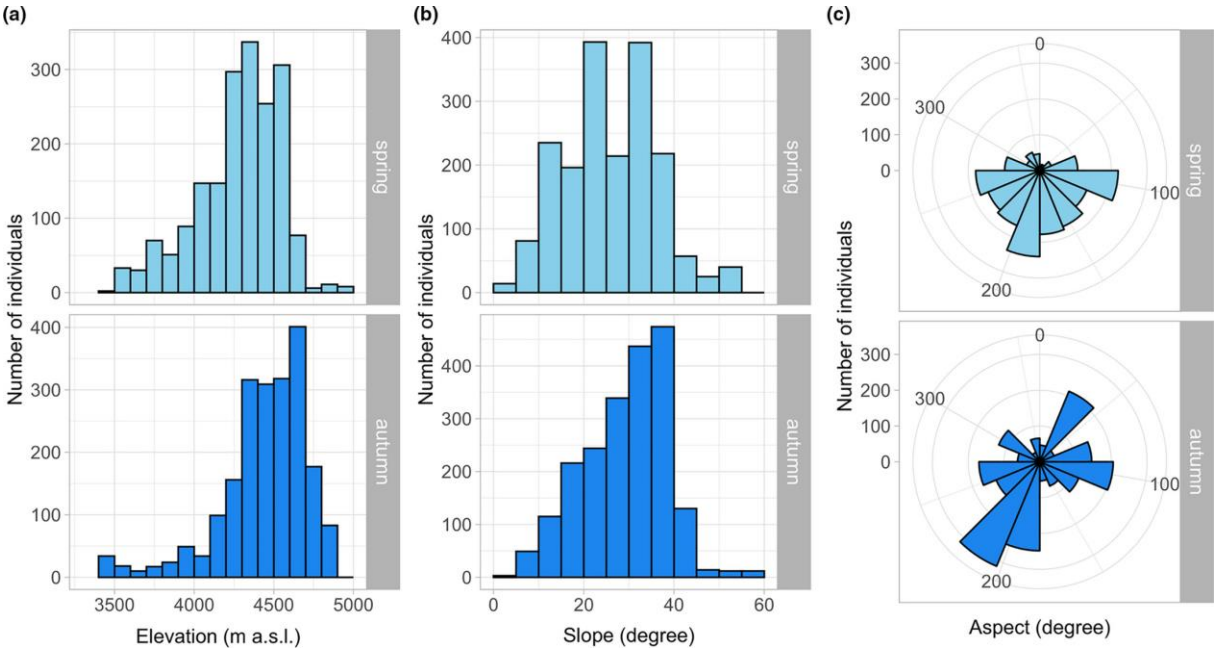

Figure 2.2. Habitat use by blue sheep in Manang. Shown are the frequencies of elevations (a), slopes (b), and aspects (c) used by blue sheep based on direct observations in spring and autumn.

In autumn, blue sheep selected elevations between 4,300 m and 4,800 m a.s.l. (Figure 2.4). Besides, animals avoided areas with little vegetation (barren lands, permanent snowfields, and water bodies; NDVI < 0.14) and preferred land-cover types having NDVI values associated mainly with grasslands and agricultural lands (NDVI > 0.47; Figures 2.4 and S2.1; Table S2.1).

The importance of variables varied among seasons. Elevation and, to a lesser extent, land cover shaped blue sheep habitat selection (Figure 2.5). Elevation had the strongest explanatory power in both seasons (spring: 47.6%; autumn: 62.3%), whereas land cover was important in spring (39.1%) but much less so in autumn (17.9%).

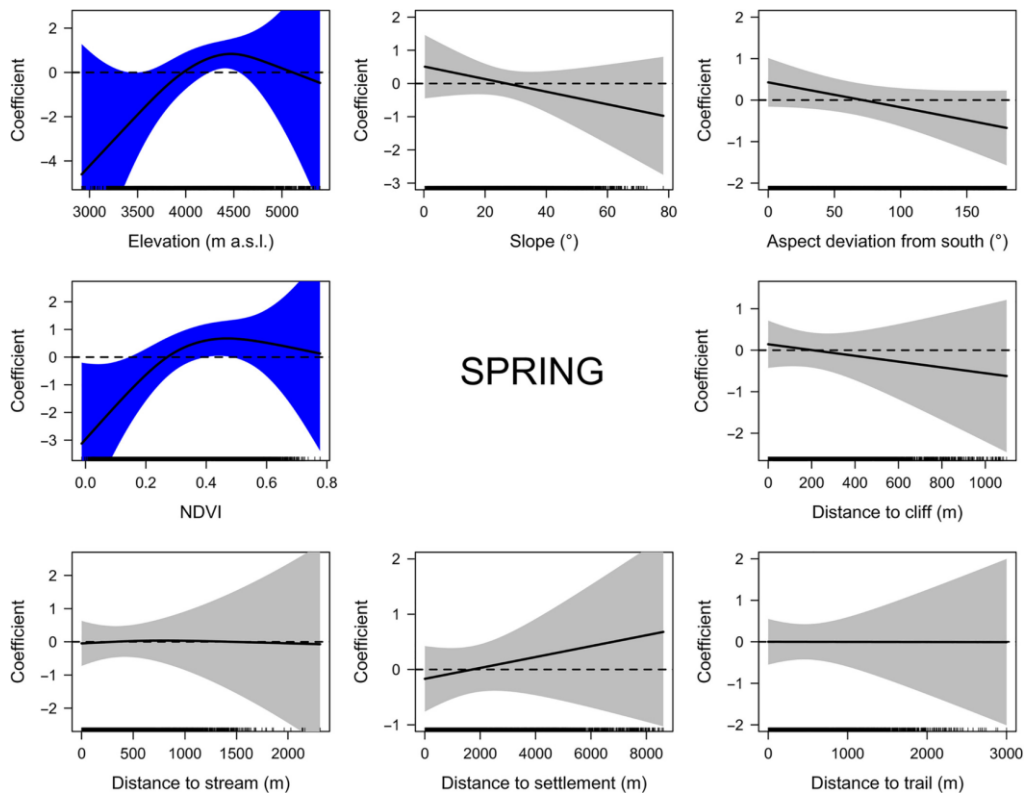

Figure 2.3. Plots of generalised additive models (GAMs) describing habitat selection by blue sheep in Manang based on direct observations in spring. The confidence intervals of significant variables are blue.

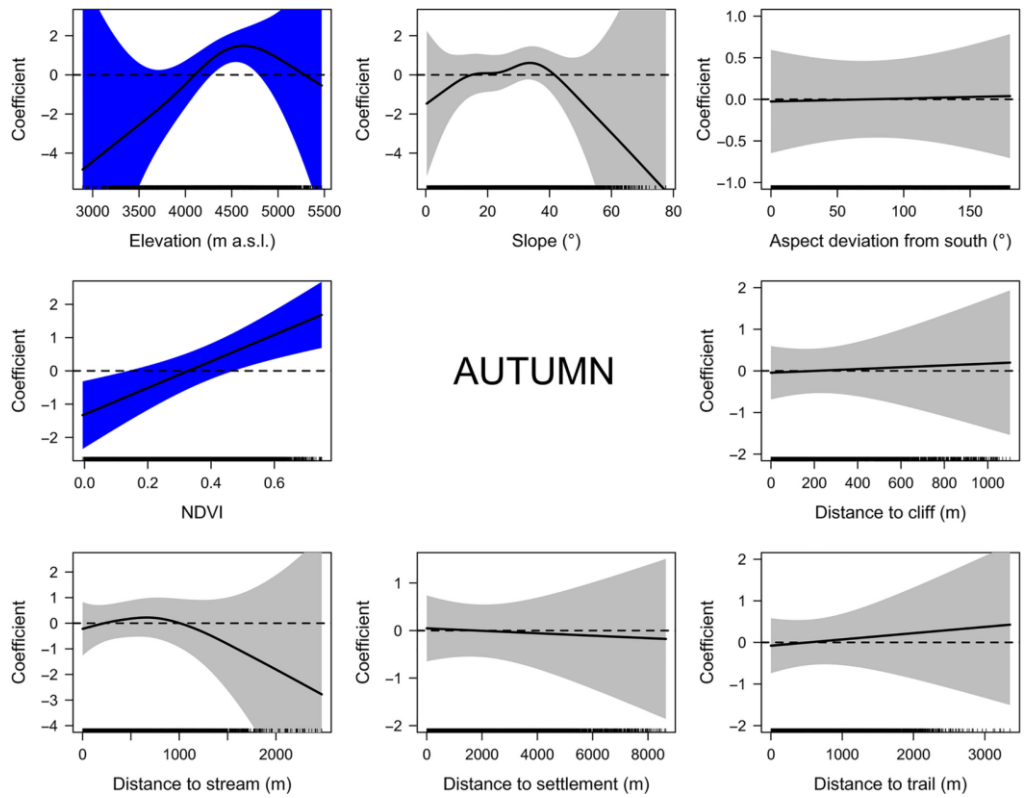

Figure 2.4. Plots of generalised additive models (GAMs) describing habitat selection by blue sheep in Manang based on direct observations in autumn. The confidence intervals of significant variables are blue.

Table 2.1. Summary of generalised additive models (GAMs) describing habitat selection by blue sheep in Manang based on direct observations in spring and autumn. The estimates of the coefficient, standard error (SE), z-values (z), and p-values (p) are shown for categorical variables (not given for spring due to multicollinearity). The estimated degrees of freedom (edf), residual degrees of freedom (Ref.df), chi-square test statistics (χ^2) and p-values (p) are given for continuous variables.

Variables	**Spring**				**Autumn**			
Categorical variables								
	Coefficient	SE	z	p	Coefficient	SE	z	p
(Intercept)	-0.662	0.222	-2.985	0.003	-1.003	0.303	-3.316	0.001
Livestock	-	-	-	-	-0.444	0.436	-1.019	0.308
Continuous variables								
	edf	Ref.df	χ^2	p	edf	Ref.df	χ^2	p
Elevation	2.250	2.888	12.832	0.006	2.740	3.499	21.939	<0.001
Slope	1.000	1.001	1.141	0.286	3.580	4.491	6.323	0.199
Aspect	1.017	1.034	2.428	0.127	1.000	1.001	0.011	0.918
NDVI	2.181	2.775	11.475	0.008	1.000	1.000	10.773	0.001
Cliff	1.000	1.000	0.452	0.502	1.000	1.000	0.049	0.825
Stream	1.087	1.169	0.012	0.903	1.927	2.457	2.071	0.403
Settlement	1.000	1.000	0.611	0.435	1.000	1.000	0.044	0.835
Trail	1.001	1.002	0.000	0.995	1.001	1.001	0.182	0.670

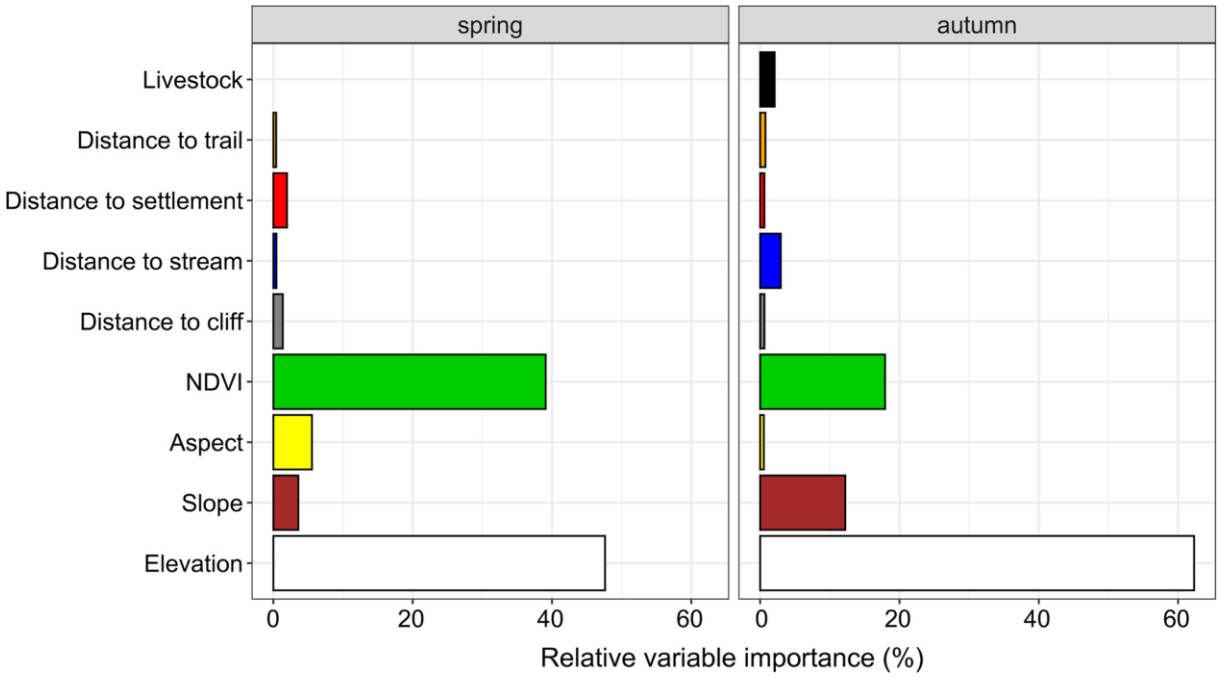

Figure 2.5. Relative variable importance (%) in generalised additive models (GAMs) describing habitat selection by blue sheep in Manang based on direct observations in spring and autumn.

2.4 Discussion

This study shows that now, almost thirty years after the official establishment of the Annapurna Conservation Area, blue sheep densities in Manang are still rather high. Habitat selection by this ungulate is primarily driven by elevation and, to a lesser extent, by land cover indicated by NDVI, whereas the considered anthropogenic variables apparently have limited effects. Blue sheep tend to occur at higher elevations in autumn than in spring and select habitats associated with green vegetation, including grasslands and shrublands.

The main purpose of this study was to estimate the minimum blue sheep density in Manang, which would be comparable with minimum densities of this species in other areas and time periods. We applied total counts, which, apart from producing such minimum density estimates, are also cost-effective and reliable for the analysis of population trends in mountain ungulates (Loison et al. 2006; Largo et al. 2008). Our result (6.0–7.7 individuals/km^2 in spring and 6.9–7.8 individuals/km^2 in autumn) is similar to previously reported densities in the Manang area both before and after the official establishment of the Annapurna Conservation Area (before: 6.6–10.2 individuals/km^2; Sherpa and Oli 1988 cited in Oli 1991; Wegge and Oli 1988 cited in Oli 1991; Oli 1994; after: 6.3–9.4 individuals/km^2; Thapa 2005; Shrestha and Wegge 2008a; Wegge et al. 2012) and might compromise the alarming result of Aryal et al. (2014c; 2.1 individuals/km^2).

When compared with similar studies in other parts of the species range, the minimum blue sheep densities in Manang can be considered as being relatively high. For instance, in other parts of the Nepalese Himalaya the minimum densities were estimated as 0.5–4.2 individuals/km^2 in Upper Mustang in the Annapurna Conservation Area (WWF Nepal 2013; Aryal et al. 2014c; R. P. Lama and M. Filla, unpublished data), Dhorpatan Hunting Reserve (Wilson 1981; Aryal et al. 2010), Manaslu Conservation Area (Devkota et al. 2017), Api Nampa Conservation Area (Khanal et al. 2020b), Kangchenjunga Conservation Area (Thapa 2006 cited in Khanal et al. 2020b), and Shey Phoksundo National Park (Thapa 2006 cited in Khanal et al. 2020b). The studies outside of Nepal reported 0.7–7.1 individuals/km^2 in Bhutan (Wangchuck Centennial National Park, Shrestha et al. 2012 cited in Leki et al. 2018), India (Ladakh region, Fox et al. 1991; Spiti region, Mishra et al. 2004), and China (Qinghai and Gansu Provinces, Schaller et al. 1988; Helan Mountains, Wang et al. 1998).

We consider our minimum density estimates as encouraging for conservation efforts implemented in the Annapurna Conservation Area. In this protected area, wildlife conservation has been pursued through the implementation of an integrated conservation and development program that accounts for local needs in balance with conservation agenda (Baral et al. 2019). Such programs are reported to vary in their effectiveness to protect biodiversity (Wells et al. 1999; Newmark and Hough 2000), but our study shows that the maintenance of relatively high

densities of wildlife, at least blue sheep, appears possible despite ongoing socio-economic development (Baral et al. 2019). We assume that various favourable conditions, including the absence of strong hunting pressure by humans (R. P. Lama and T. R. Ghale, personal communication) and the availability of high-quality foraging areas (Harris 2014), are the main causes of high blue sheep density in Manang. Moreover, local people generally have positive attitudes towards blue sheep (Oli et al. 1994). In these conditions, blue sheep may habituate to humans, as shown in areas with a large number of pilgrims and tourists (Bhardwaj et al. 2010; Zhang et al. 2013), but may still remain vigilant at the expense of their foraging and resting time budgets (Jiang et al. 2013).

However, this apparent conservation success should not lead to overly optimistic conclusions and complacency since current developments may threaten the ecosystem and affect blue sheep in the future. There are new projects for infrastructure development in the area, such as construction of roads to remote villages and tourist facilities for ever-increasing visitor numbers (Baral et al. 2019; R. P. Lama and M. Filla, personal observations). This will further increase the pressure on wildlife populations and habitats, with lag effects to be noticed only after some time (Bürgi et al. 2017). In addition, international tourism as a key component of the integrated conservation and development program implemented in the Annapurna region may not be an ideal long-term solution as it contributes to climate change through increased carbon emissions (Hall et al. 2013), which threatens mountain wildlife and landscapes (Tse-ring et al. 2010).

Extrapolation of wildlife densities from total counts does not account for undetected individuals, thus leading to density underestimation (Gaillard et al. 2003; Corlatti et al. 2015). Since previous studies illustrated that detection probability of mountain ungulates may be low even by experienced scientists (Wingard et al. 2011; Tumursukh et al. 2016), our estimates from total counts should be taken as conservative. We expect that the application of double-observer counts (Nichols et al. 2000), which are commonly applied when monitoring mountain ungulates (e.g., Suryawanshi et al. 2012; Ghoddousi et al. 2016), would produce more accurate density estimates. Distance sampling is a common technique of wildlife counting (Buckland et al. 1993), but its applicability to mountain landscapes is debated (Wingard et al. 2011; Suryawanshi et al. 2012; Corlatti et al. 2015). A preliminary re-analysis of our study results using a distance sampling approach indicated that the underestimation by minimum densities from total counts could be substantial (M. Filla and R. P. Lama, unpublished data).

Keeping healthy populations of blue sheep is key for the maintenance of ecological balance and conservation of other species in the fragile high-altitude ecosystem of the Annapurna Conservation Area. The blue sheep is the only medium-sized herbivore commonly present at high elevations throughout the region and represents the main prey for the snow leopard, thus shaping a high relative density of this threatened predator (Gaston and Fuller 2008; Wegge et

al. 2012; Chetri et al. 2017; McCarthy et al. 2017). The significance of blue sheep as a vital prey resource is likely to increase if local people make more efforts to protect their livestock from depredation. Local absence or low abundance of alternative prey, such as the Himalayan marmot (*Marmota himalayana*) and woolly hare (*Lepus oiostolus*), in Manang, adds to an increased dependence of snow leopards on blue sheep abundance (Wegge et al. 2012). Likewise, wolves recently recolonised Manang, and they also use this food resource, though not selectively (Chetri et al. 2017; Lama et al. 2017). Therefore, we recommend establishing a regular long-term monitoring scheme for blue sheep in Manang. Such monitoring programs have been implemented in protected landscapes elsewhere (Zhang et al. 2012), and they can be realised by trained staff to provide reliable information to wildlife managers of the Annapurna Conservation Area. We suggest a monitoring system to be based either on total counts along the systematically placed transects and from vantage points or on double-observer counts as a standardised method accounting for detection probability (Nichols et al. 2000). Total counts allow for the detection of population changes (Loison et al. 2006; Largo et al. 2008), whereas double-observer counts yield more reliable abundance and density estimates and enable managers to derive additional conservation parameters, such as the carrying capacity and hotspots for snow leopards (e.g., Suryawanshi et al. 2012; Aryal et al. 2014c; Khanal et al. 2020b).

Apart from predation risk, foraging availability and thermal conditions shape the distribution and habitat use of wild ungulates (e.g., Hebblewhite and Merrill 2009; van Beest et al. 2012), and these parameters seemed to also affect habitat selection by blue sheep in Manang. Our study shows that blue sheep selected habitats mainly on a basis of elevation and land cover indicated by NDVI, both in spring and in autumn. This is in line with other blue sheep studies in Phu Valley in Manang, Nepal (Shrestha and Wegge 2008b), and in Ladakh, India (Namgail et al. 2009). In our study, blue sheep selected elevations of 4,250–4,550 m a.s.l. in spring and significantly higher elevations in autumn. As elevation is a surrogate of air temperature in the Nepalese Himalaya (Mokhov and Akperov 2006; Aryal et al. 2016), it affects species distribution by determining snowfall, vegetation phenology, and food availability (Aryal et al. 2014c). Particularly, in Manang, blue sheep distribution is limited by forests at lower elevations and by sparsely vegetated barren lands with considerable snow cover at higher elevations (Shrestha and Wegge 2008a; Shrestha and Vetaas 2009).

Land cover, which is a proxy for food availability, was the second most important variable determining blue sheep distribution. In our study, the species was closely associated with grasslands and shrublands, which is in line with previous studies (Shrestha and Wegge 2008a; Bhardwaj et al. 2010; Harris 2014). This pattern reflects the dietary preference of graminoids and forbs by blue sheep (Liu et al. 2007; Shrestha and Wegge 2008a; Aryal et al. 2015b). Agricultural land also displayed the NDVI range of habitats selected by blue sheep. However,

agricultural fields in the surroundings of settlements were rather infrequently used by blue sheep and did not alter the main model output (Figure S2.5). Nevertheless, occasional crop-raiding is possible, mainly of barley (*Hordeum* spp.) and buckwheat (*Fagopyrum* spp.; Baral et al. 2019; R. P. Lama and T. R. Ghale, personal communication), which requires increased attention due to concerns expressed in light of translocation programs (Hanson et al. 2020). Moreover, our study suggests the avoidance of barren lands by blue sheep in both seasons. These lands could be used more frequently during the periods of lower activities, like bedding and resting (Wilson 1981; Liu et al. 2005a, b) spent in secluded places, but we did not cover these periods during our surveys. Interestingly, occasional spotting of blue sheep in open forests disagrees with the general opinion that, except for the Helan Mountain Range, blue sheep avoid entering forested areas (Harris 2014).

Contrary to our expectations, we did not find strong evidence of a negative impact of livestock presence/absence on blue sheep distribution in Manang at a fine scale. This is in line with our occasional observations of livestock and blue sheep grazing together (R. P. Lama and M. Filla, personal observations). Theoretically, this result could be affected by non-detection of livestock if they grazed in secluded places or were released from their night sheds late. But we think that such events were rare and did not influence our main conclusions. Moreover, we assume that livestock densities had a stronger effect on blue sheep than livestock presence/absence. The consideration of livestock densities might have increased model performance, but we could not estimate this parameter from our current data. However, blue sheep-livestock interactions were negative in autumn at larger scales more than 1 km apart (Table S2.2), thus indicating that livestock can be a serious threat to blue sheep due to habitat loss and fragmentation, disease transmission, and dietary competition (Dagleish et al. 2007; Shrestha and Wegge 2008a; Suryawanshi et al. 2010; Bhattacharya et al. 2020). Therefore, more knowledge is needed about the relationships between livestock and blue sheep.

Conclusion

This study in the Nepalese Himalaya demonstrated that quite high densities of blue sheep, a key prey species for the threatened snow leopard, have been maintained in an area in which conservation and development agendas have been combined. Moreover, we describe how elevation and land cover shape habitat selection by blue sheep in the absence of strong hunting pressure by humans, which is relevant for blue sheep management, habitat protection, and potential translocation programs. In light of the importance of blue sheep in high-altitude ecosystems, we suggest to conduct more research on blue sheep-livestock interactions and to establish a standardised blue sheep monitoring program based on total counts and/or double-observer counts for the benefit of blue sheep and snow leopards.

2.5 Acknowledgments

We thank the Department of National Parks and Wildlife Conservation, Government of Nepal, and the National Trust for Nature Conservation (NTNC)/Annapurna Conservation Area Project (ACAP) for granting permission (Ref: 439/075/076) to conduct this research. We are thankful to Third Pole Conservancy for assistance in fieldwork coordination and to T. R. Gurung and K. Magar for their help in the field. Moreover, we thank M. Soofi, P. Roig Boixeda, M. Püttmanns, and A. Laux for general advice and suggestions on earlier drafts of this manuscript. We appreciate constructive comments made by three anonymous reviewers on an earlier version of this manuscript. M. Filla received a PhD scholarship by Heinrich Böll Foundation. Fieldwork was additionally funded by the National Geographic Society, Breuckmann Foundation, Academy for the Protection of Zoo Animals and Wildlife e.V., Heinrich Böll Foundation, Tatzmania Löffingen, and The Alongside Wildlife Foundation. Open access funding enabled and organised by Projekt DEAL.

2.6 Supplementary material

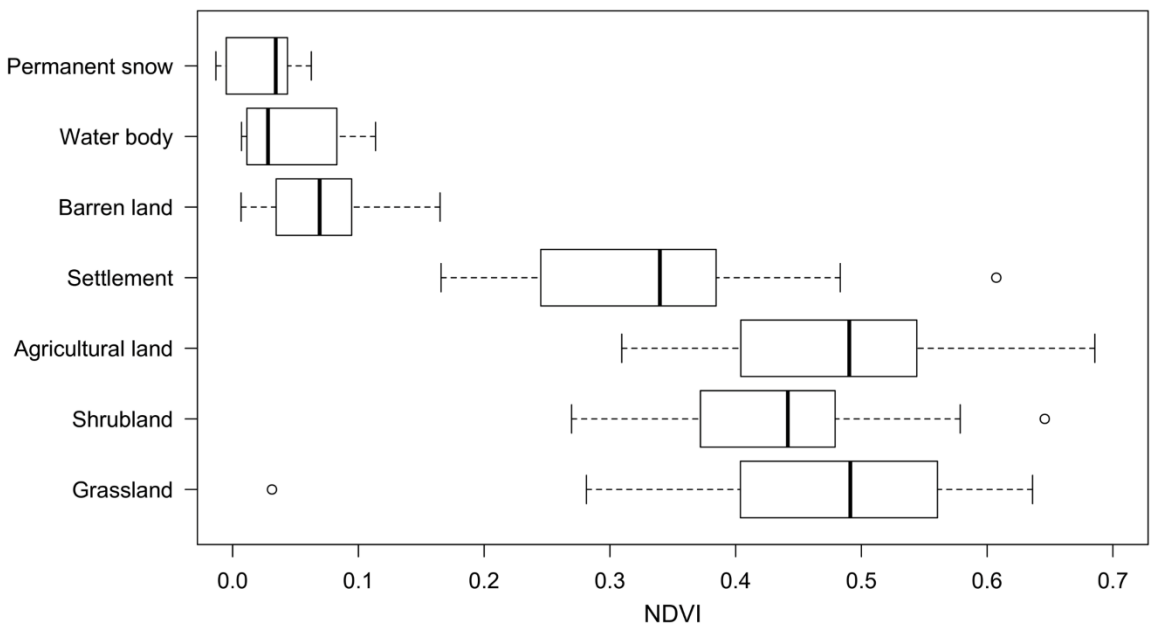

Figure S2.1. Normalized difference vegetation index (NDVI) of various land-cover types in Manang based on 203 predefined validation points. The land-cover types in these locations were distributed throughout the study area and verified by ground-truthing or analysis of satellite imagery ($n_{permanent\ snow}$ = 11; $n_{water\ body}$ = 9; $n_{barren\ land}$ = 34; $n_{settlement}$ = 19; $n_{agricultural\ land}$ = 20; $n_{shrubland}$ = 40; $n_{grassland}$ = 43; not shown: n_{forest} = 27).

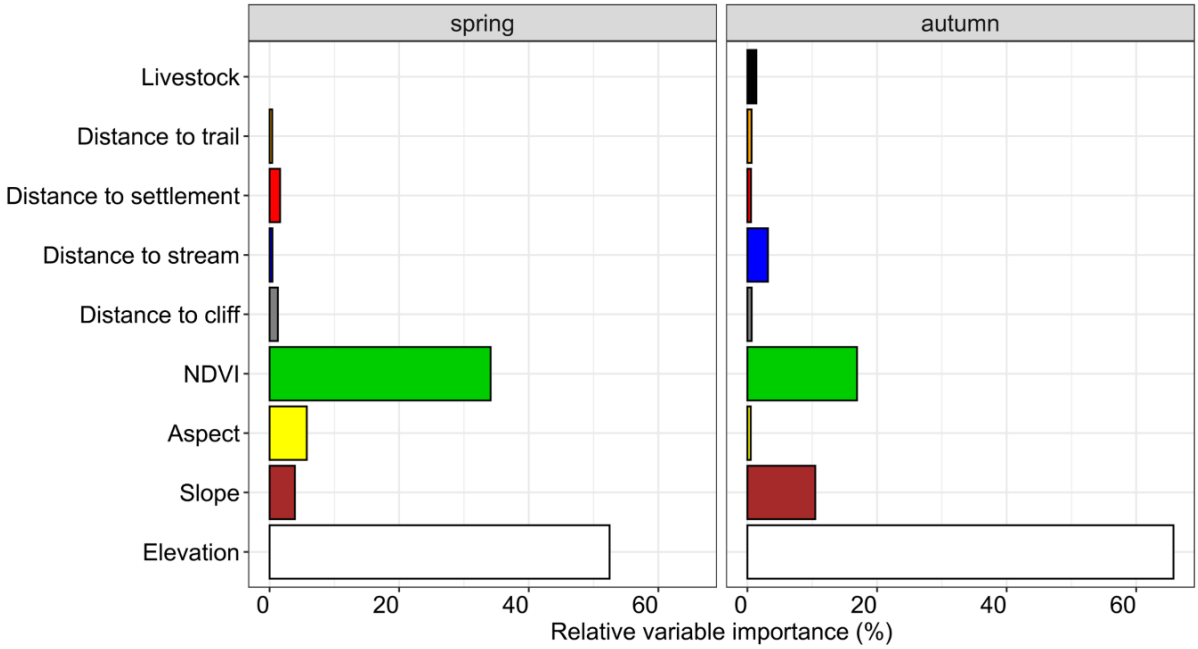

Figure S2.2. Sensitivity analysis with the inclusion of forested areas. Relative variable importance (%) in generalised additive models (GAMs) describing habitat selection by blue sheep in Manang based on direct observations in spring and autumn.

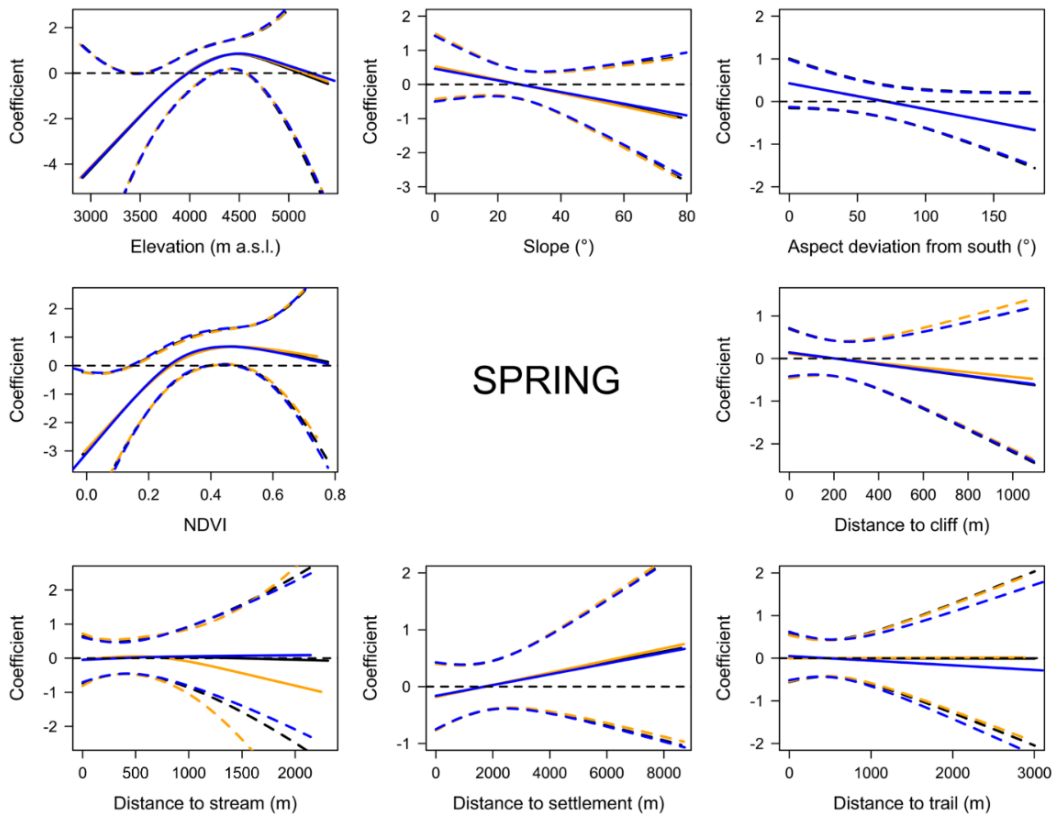

Figure S2.3. Sensitivity analysis with different sets of random points. Plots of generalised additive models (GAMs) describing habitat selection by blue sheep in Manang based on direct observations in spring. Shown are the smooth terms based on the model presented in the paper (black) in comparison with the models using two different sets of random points (orange, blue).

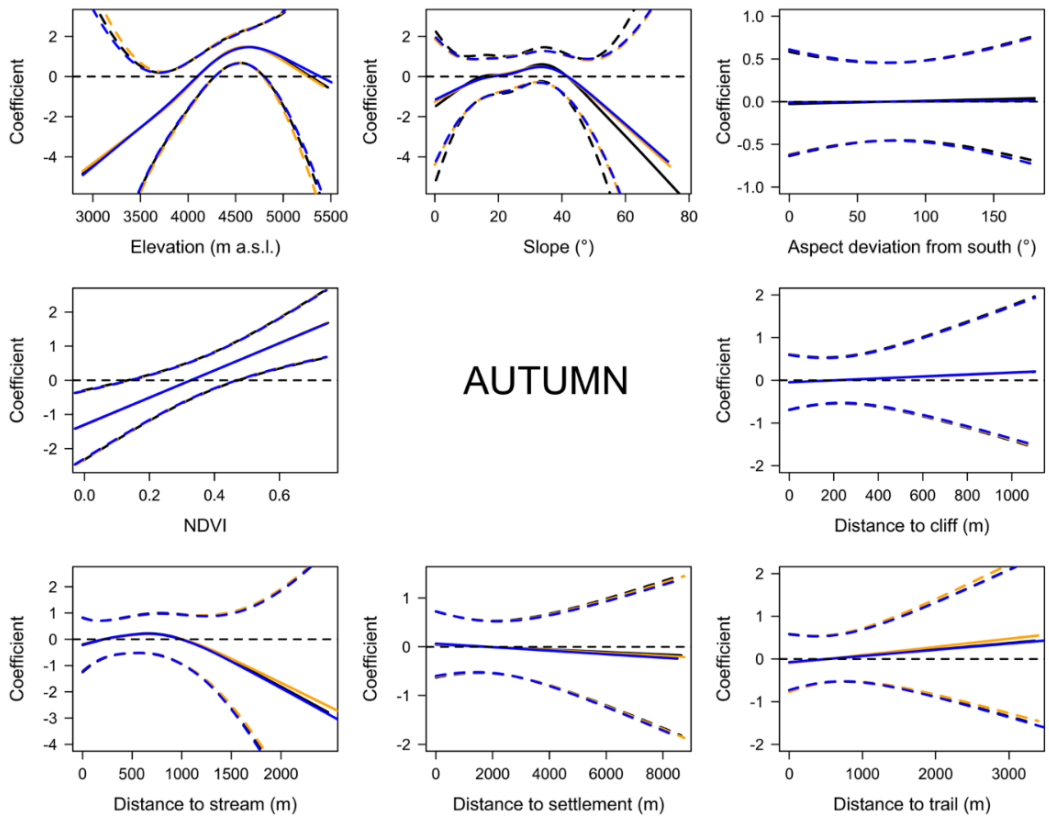

Figure S2.4. Sensitivity analysis with different sets of random points. Plots of generalised additive models (GAMs) describing habitat selection by blue sheep in Manang based on direct observations in autumn. Shown are the smooth terms based on the model presented in the paper (black) in comparison with the models using two different sets of random points (orange, blue).

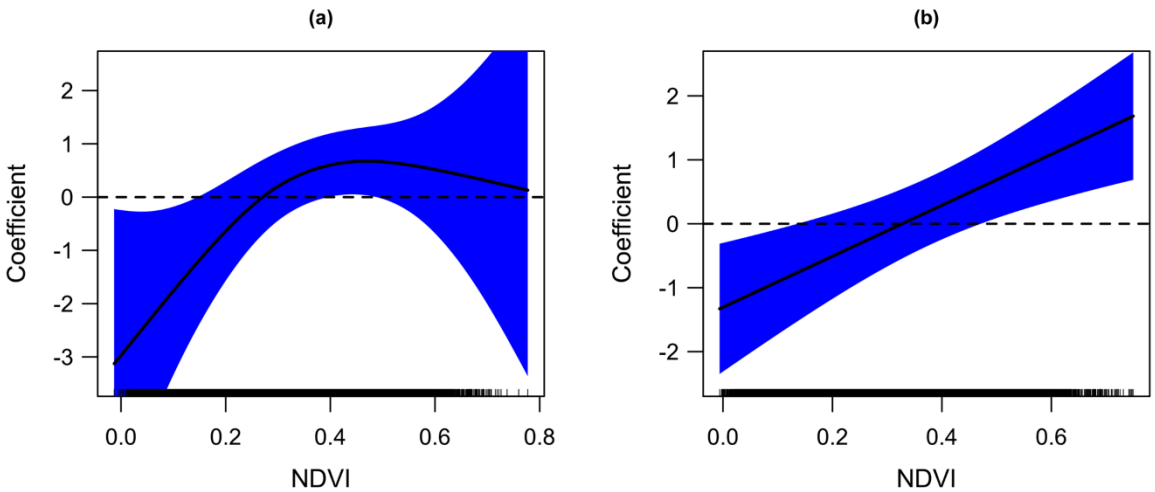

Figure S2.5. Sensitivity analysis with the exclusion of locations near settlements (< 500 m). Plots of generalised additive models (GAMs) describing habitat selection by blue sheep in Manang based on direct observations in spring (a) and autumn (b). Shown are the smooth terms for the normalized difference vegetation index (NDVI).

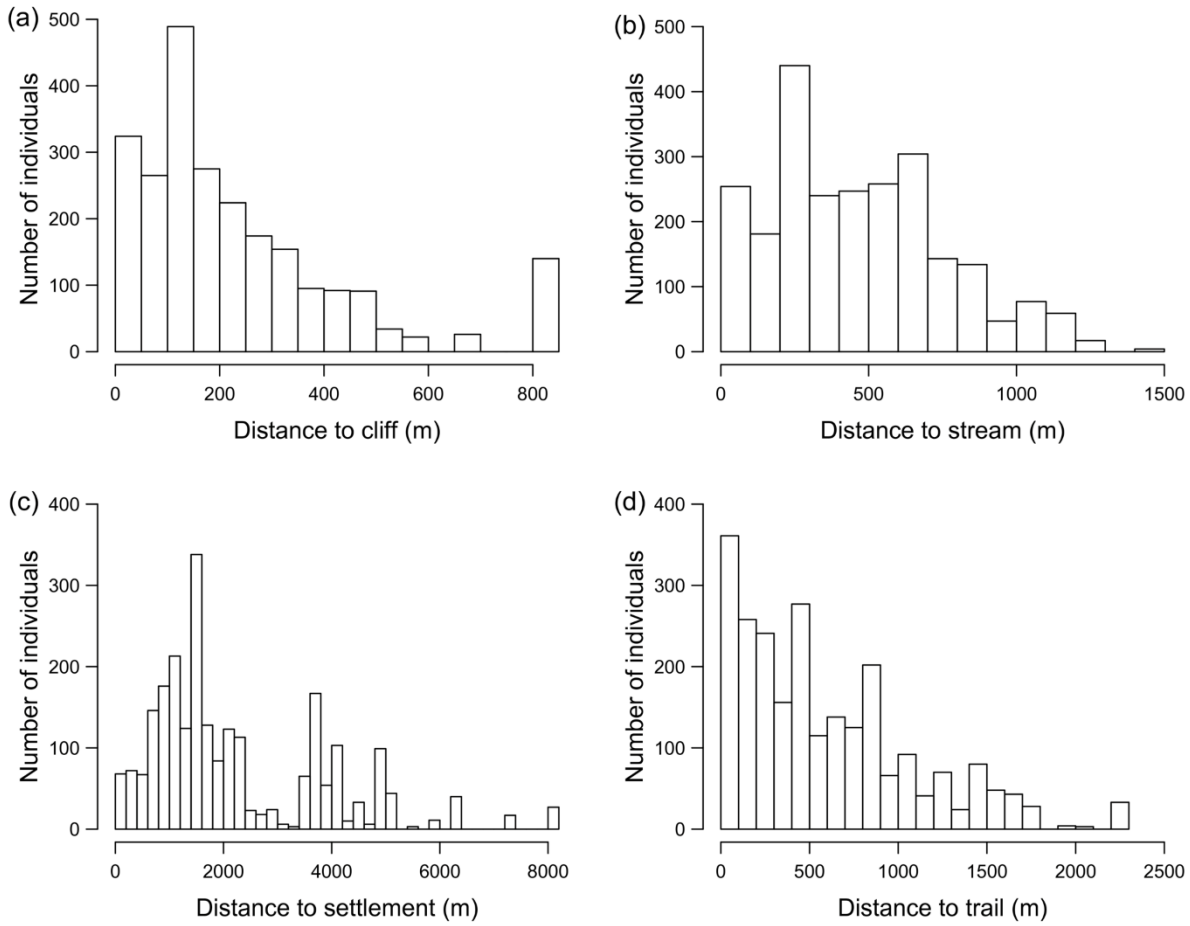

Figure S2.6. Habitat use by blue sheep in Manang. Shown are the frequencies of distances of adult blue sheep to cliff (a), stream (b), settlement (c) and trail (d) based on direct observations in spring and autumn.

Table S2.1. P-values of pairwise Wilcoxon rank-sum test of the normalized difference vegetation index (NDVI) of various land-cover types in Manang based on 203 predefined validation points. The land-cover types in these locations were distributed throughout the study area and verified by ground-truthing or analysis of satellite imagery ($n_{permanent\ snow}$ = 11; $n_{water\ body}$ = 9; $n_{barren\ land}$ = 34; $n_{settlement}$ = 19; $n_{agricultural\ land}$ = 20; $n_{shrubland}$ = 40; $n_{grassland}$ = 43; *not used in the analysis: n_{forest} = 27)

	Forest*	**Grassland**	**Shrubland**	**Agricultural land**	**Settlement**	**Barren land**	**Water body**
Grassland	0.022	-	-	-	-	-	-
Shrubland	<0.001	0.109	-	-	-	-	-
Agricultural land	0.098	1.000	0.225	-	-	-	-
Settlement	<0.001	<0.001	0.003	<0.001	-	-	-
Barren land	<0.001	<0.001	<0.001	<0.001	<0.001	-	-
Water body	<0.001	<0.001	<0.001	<0.001	<0.001	0.276	-
Permanent snow	<0.001	<0.001	<0.001	<0.001	<0.001	0.017	1.000

Table S2.2. Sensitivity analysis with alternative buffer widths around livestock locations. Summary of generalised additive models (GAMs) describing habitat selection by blue sheep in Manang based on direct observations in spring and autumn. The estimates of the coefficient, standard error (SE), z-values (z) and p-values (p) are shown for the effects of livestock presence. The asterisk (*) indicates that distance to settlement was excluded from spring models due to high correlation with livestock presence (|r| > 0.7).

Buffer width (m)	**Spring**				**Autumn**			
	Coefficient	SE	z	p	Coefficient	SE	z	p
100	0.232	1.211	0.192	0.848	1.009	1.376	0.733	0.464
250	0.770	0.515	1.495	0.135	-0.252	0.702	-0.359	0.720
500*	0.165	0.413	0.400	0.689	-0.444	0.436	-1.019	0.308
750*	0.558	0.401	1.392	0.164	-0.588	0.393	-1.497	0.135
1000	0.250	0.437	0.571	0.568	-0.830	0.397	-2.090	0.037
1500*	-0.034	0.467	-0.073	0.942	-1.071	0.400	-2.698	0.007

Table S2.3. Sensitivity analysis with the inclusion of forested areas. Summary of generalised additive models (GAMs) describing habitat selection by blue sheep in Manang based on direct observations in spring and autumn. The estimates of the coefficient, standard error (SE), z-values (z), and p-values (p) are shown for categorical variables (not given for spring due to multicollinearity). The estimated degrees of freedom (edf), residual degrees of freedom (Ref.df), chi-square test statistics (χ^2) and p-values (p) are given for continuous variables.

Variables	**Spring**				**Autumn**			
Categorical variables								
	Coefficient	SE	z	p	Coefficient	SE	z	p
(Intercept)	-0.774	0.241	-3.218	0.001	-1.044	0.301	-3.464	<0.001
Livestock	-	-	-	-	-0.339	0.433	-0.783	0.434
Continuous variables								
	edf	Ref.df	χ^2	p	edf	Ref.df	χ^2	p
Elevation	2.282	2.931	13.435	0.003	2.746	3.511	24.355	<0.001
Slope	1.001	1.002	1.349	0.246	2.905	3.689	5.893	0.182
Aspect	1.071	1.137	2.878	0.119	1.000	1.001	0.006	0.939
NDVI	2.199	2.798	11.227	0.010	1.000	1.001	10.766	0.001
Cliff	1.001	1.002	0.470	0.494	1.001	1.002	0.078	0.781

Stream	1.061	1.120	0.011	0.903	1.962	2.502	2.423	0.355
Settlement	1.000	1.001	0.540	0.463	1.000	1.000	0.025	0.875
Trail	1.001	1.002	0.000	0.999	1.001	1.001	0.108	0.743

Table S2.4. Estimated blue sheep density in Neshyang Valley and Nar Phu Valley in Manang. Minimum density estimates are extrapolated from total counts and consider various maximum sighting distances for viewshed calculations along the transects.

Maximum sighting distance (m)	Area	Season	Visible area (km^2)	Blue sheep counted (N)	Blue sheep density (N/km^2)
500	Neshyang Valley	spring	56.0	543	9.7
		autumn	59.8	384	6.4
	Nar Phu Valley	spring	43.9	704	16.0
		autumn	43.1	609	14.1
1000	Neshyang Valley	spring	98.6	578	5.9
		autumn	102.3	679	6.6
	Nar Phu Valley	spring	81.2	809	10.0
		autumn	78.8	740	9.4
1500	Neshyang Valley	spring	124.3	578	4.6
		autumn	127.0	766	6.0
	Nar Phu Valley	spring	108.7	830	7.6
		autumn	106.6	840	7.9
2000	Neshyang Valley	spring	135.6	578	4.3
		autumn	139.2	766	5.5
	Nar Phu Valley	spring	116.1	830	7.1
		autumn	119.1	882	7.4

Table S2.5. Summary of efforts to monitor blue sheep in Manang based on the maximum sighting distance of 1500 m.

Grid cell ID	Valley	Spring 2019				Autumn 2019			
		Transect length (km; [number])	View-shed (km^2)	Blue sheep counted (N)	Blue sheep density (N/km^2)	Transect length (km; [number])	View-shed (km^2)	Blue sheep counted (N)	Blue sheep density (N/km^2)
595	Nar Phu	3.6 [1]	6.9	199	29.0	4.0 [1]	7.2	152	21.0
619	Nar Phu	5.3 [2]	10.8	203	18.9	6.4 [2]	11.9	194	16.3
620	Nar Phu	3.3 [1]	9.0	10	1.1	4.0 [1]	9.0	185	20.6
635	Neshyang	5.5 [1]	7.6	29	3.8	5.4 [1]	7.6	144	19.0
640	Nar Phu	3.2 [1]	6.8	78	11.5	3.2 [1]	6.7	35	5.2
642	Nar Phu	4.4 [2]	7.5	89	11.8	4.1 [2]	7.0	108	15.3
658	Neshyang	2.5 [1]	6.7	80	11.9	-	-	-	-
659	Neshyang	7.3 [4]	9.3	170	18.3	6.2 [3]	10.7	159	14.9
664	Nar Phu	4.0 [2]	10.2	111	10.9	4.7 [2]	10.4	24	2.3
666	Nar Phu	3.6 [2]	8.5	37	4.4	4.1 [2]	7.1	17	2.4
682	Neshyang	4.7 [3]	8.8	35	4.0	5.3 [4]	9.6	58	6.0
683	Neshyang	6.3 [3]	8.4	30	3.6	6.6 [3]	8.9	84	9.5
684	Neshyang	4.8 [2]	9.9	71	7.2	5.2 [2]	10.8	36	3.3
685	Neshyang	6.8 [1]	10.0	46	4.6	8.0 [2]	11.1	61	5.5
686	Neshyang	5.0 [3]	8.4	30	3.6	5.8 [3]	8.3	83	10.0
687	Neshyang, Nar Phu	6.7 [4]	8.2	30	3.7	8.0 [4]	9.8	79	8.1
688	Nar Phu	3.5 [2]	10.4	0	0.0	3.7 [2]	10.9	30	2.8

689	Nar Phu	4.9 [5]	11.4	103	9.1	5.9 [5]	11.1	69	6.2
690	Nar Phu	4.2 [2]	10.0	0	0.0	4.0 [2]	11.0	10	0.9
709	Neshyang	2.7 [2]	2.8	0	0.0	4.4 [3]	4.9	5	1.0
710	Neshyang	3.2 [3]	7.7	3	0.4	4.7 [4]	9.6	20	2.1
711	Neshyang	7.9 [2]	11.1	0	0.0	7.5 [2]	11.2	2	0.2
712	Neshyang	4.4 [2]	7.9	28	3.5	4.6 [2]	8.3	24	2.9
713	Neshyang	6.2 [2]	9.0	6	0.7	5.6 [2]	7.8	11	1.4
715	Nar Phu	4.1 [2]	7.5	0	0.0	4.1 [2]	7.5	16	2.1
736	Neshyang	5.0 [3]	9.1	20	2.2	5.4 [3]	9.1	0	0.0
738	Nar Phu	3.8 [1]	6.3	0	0.0	3.8 [1]	6.2	0	0.0
1001	Nar Phu	1.0 [1]	3.2	0	0.0	-	-	-	-

Chapter 3

Effects of wild prey and livestock husbandry on snow leopard relative abundance and livestock depredation

Blue sheep (*Pseudois nayaur*) in Manang, Annapurna Conservation Area, Nepal. Credit: Tashi R. Ghale

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

Marc Filla, Rinzin P. Lama, Tashi R. Ghale, Tim Filla, Marco Heurich, Matthias Waltert, Igor Khorozyan

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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 x 4 km) and conducted questionnaire surveys to determine livestock depredation between 2018 and 2021 (n = 479 households). We applied generalised 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 human population. The size of livestock holdings shaped depredation events of large livestock (yak, cattle, and horse), whereas depredation events of sheep 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 optimising 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.

3.1 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 behaviour (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, utilisation, wild prey depletion, and persecution (Ripple et al. 2014; Ripple et al. 2015; Wolf and Ripple 2016). 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 prioritisation of carnivore conservation.

Human-carnivore conflicts are among the major drivers of carnivore declines globally (Woodroffe et al. 2005b). Large carnivores are often killed in prevention or retaliation of 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 behaviour-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). A 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. 2018a).

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 between people, livestock, snow leopards, and their wild prey for limited resources (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 cause positive effects on snow leopard habitat use and density (Sharma et al. 2015; Alexander et al. 2016a; Suryawanshi et al. 2017; Sharma et al. 2021; Suryawanshi 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; Suryawanshi et al. 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. 2020a). 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 prioritise conservation interventions. Also for the protection of snow leopards in Asia, 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 Nepal 2018; Chetri et al. 2019b). For the region, Chetri et al. (2019a) found the probability of livestock losses to be lowest in areas with low livestock density and high wild prey density while being highest in areas with abundant livestock and wild prey. This 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: 1) wild prey density positively affects snow leopard relative abundance (Hypothesis 1), and 2) livestock depredation by snow leopards increases with decreasing wild prey density, increasing domestic prey density, and a lack of interventions (Hypothesis 2).

3.2 Material and methods

3.2.1 Study area

The Annapurna Conservation Area (ACA) was established in 1992 and covers 7,629 km^2 in the Himalaya Biodiversity Hotspot (Mittermeier et al. 2005; Baral et al. 2019; Figure 3.1). This protected area hosts about 100,000 people with traditional rights and access to natural resources and diverse biotic assemblages, including more than 1,300 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; 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; Figure 3.1). Elevations in the studied area range from about 2,680 to 5,690 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 4,400 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 2008a).

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. 2014c; 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).

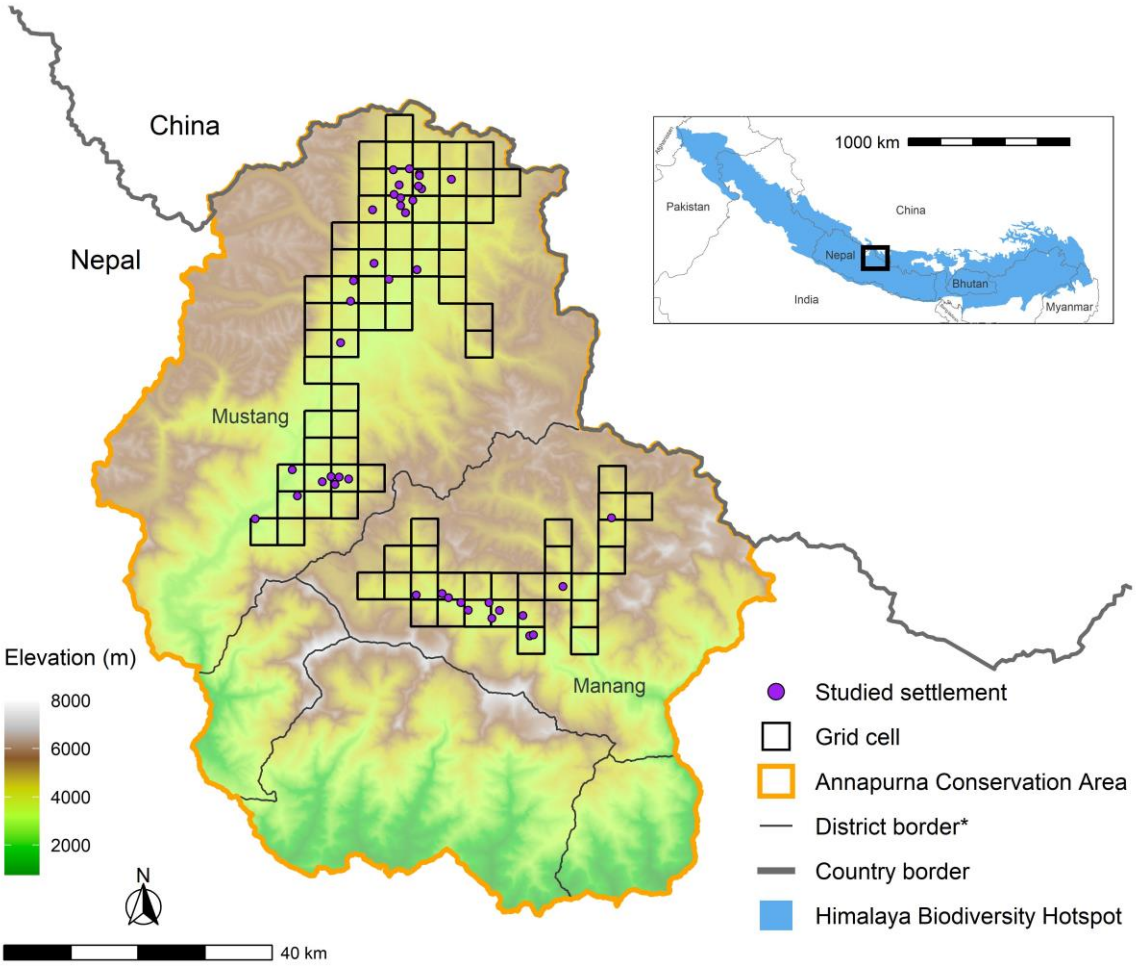

Figure 3.1. Study area covered by 82 grid cells in the Annapurna Conservation Area (Nepal) within the Himalaya Biodiversity Hotspot. Sources: NASA/METI/AIST/Japan Spacesystems and U.S./Japan ASTER Science Team 2009 (elevation); Conservation International 2011 (Hotspot location); DIVA-GIS 2015 (country borders); Humanitarian Data Exchange 2021 (district borders). *inside the Annapurna Conservation Area.

3.2.2 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.

Wildlife monitoring

To ensure representative sampling of the ACA, we created a grid of 4 x 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 3,000–5,000 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. 2014d) and logistic constraints (Alexander et al. 2016a). We monitored snow leopards, blue sheep, marmots, and livestock during three field visits in spring (March–May) and autumn (September–October) 2019 and 2021. 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 travelling 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 standardised 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). To minimise the effects of environmental variation, we applied the SLIMS technique only in spring, which offers high sign detectability due to intense snow leopard marking activity, favourable weather conditions, and relatively little anthropogenic disturbance (Jackson and Hunter 1996;

Fox and Chundawat 2016). To minimise 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 x 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. 2005b). Upon encounters of the target species, we denoted the observer location, compass direction (degree), distance (m), and angle (degree) to the detected individual or to the centre of detected groups by using a compass, GPS device (Garmin GPSMAP 64s), 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 colouration 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.

We verified the 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 1,000 m or adjusted it if landscape characteristics and weather conditions reduced visibility (Thapa et al. 2021). If necessary, we manually edited the obtained viewsheds.

Questionnaire surveys

Between July 2020 and May 2021, we conducted questionnaire surveys in all major permanent settlements located in the studied grid cells (Figure 3.1). 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, the independence of this study on compensation schemes, and the 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 optimise 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 neighbouring 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.

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 Spacesystems 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 km^2 at the equator); WorldPop 2020).

3.2.3 Data analysis

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 S3.1), 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 S3.2 for sensitivity analysis based on all sign types). To account for the variable lengths of SLIMS sections, this parameter was incorporated into 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 3.1). 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. 2014c). Blue sheep numbers and survey areas were computed within the 2,000-m wide buffers around SLIMS sections, which accounted for reported minimum home ranges of female snow leopards (~12 km^2, Jackson and Ahlborn 1989; ~13 km^2, McCarthy et al. 2005; see Table S3.2 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 Wegge 2008a; Filla et al. 2021; see Table S3.2 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 S3.2 for sensitivity analysis with elevation as a linear term). The 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 of each other (Legendre 1993; see Table S3.2 for sensitivity analysis ignoring spatial autocorrelation).

To ease model convergence, all continuous predictor variables were standardised 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 randomised 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 randomised models. We obtained relative importance values by standardising 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 S3.2).

Table 3.1. 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]categorised 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

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 generalised 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 km^2 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 categorised 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 3.1).

All predictor variables were prepared based on 1500-m buffers around summer and winter grazing areas of livestock. This buffer width was selected after a 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. 2014d; see Table S3.3 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 (χ^2 = 12.86, p = 0.005), we additionally ran models based on summer data only (see Table S3.4). We used the same procedure to examine the 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 $\Delta AIC_c < 2$ (Burnham and Anderson 2002; Khorozyan et al. 2017). If multiple models performed best ($\Delta AIC_c < 2$), 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 version 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 2019b), *MASS* (Venables and Ripley 2002), *MuMIn* (Barton 2020), *performance* (Lüdecke 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 visualisation.

3.3 Results

3.3.1 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 S3.1). 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 S3.1.

3.3.2 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 1,242 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 S3.1). 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/km^2) than in Mustang (1.2 ± 2.7 individuals/km^2; 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/km^2) than in Manang (8.8 ± 9.0 individuals/km^2; U = 622, p = 0.234). Overall, the grid-wise densities of blue sheep (3.6 ± 6.2 individuals/km^2) were much lower than those of livestock (30.2 ± 47.6 individuals/km^2; 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.

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

The relative abundance of snow leopards increased with blue sheep density (β = 0.293 ± 0.145, p = 0.043) and terrain ruggedness (β = 0.264 ± 0.122, p = 0.031) and decreased with increasing densities of livestock (β = -0.249 ± 0.126, p = 0.048) and human population (β = -0.382 ± 0.150, p = 0.011; Figure 3.2; Table S3.5). 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 (Figure 3.2; Table S3.5). 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%; Figure 3.2; Table S3.5).

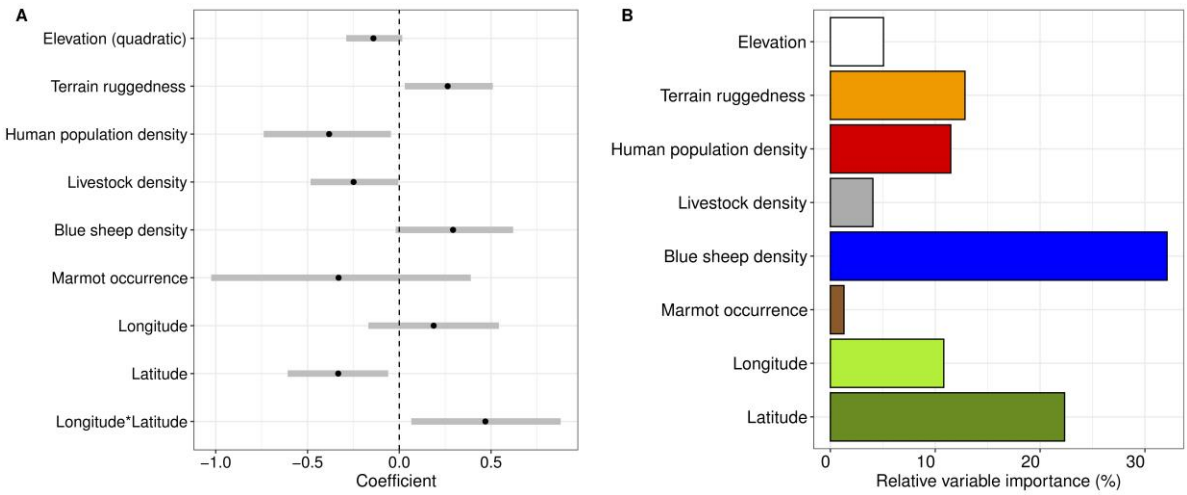

Figure 3.2. Effects (A) of various predictor variables on snow leopard relative abundance in the Annapurna Conservation Area and their relative importance (B) based on the full negative binomial model. In A, black dots show the estimates of the coefficients, and grey horizontal bars indicate the 95% confidence intervals.

3.3.4 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 3.2). 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).

Table 3.2. 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												
	Yak		Cattle		Dzo		Horse		Goat		Sheep		Total
	ad.	juv.	ad.	juv.	ad.	juv.	ad.	juv.	ad.	juv.	ad.	juv.	
Manang	1,158	403	386	82	0	0	197	15	921	331	52	22	3,567
Mustang	370	105	930	359	121	2	421	34	7,526	1,471	187	24	11,550
Total	1,528	508	1,316	441	121	2	618	49	8,447	1,802	239	46	15,117
	Livestock losses attributed to snow leopards												
	Yak		Cattle		Dzo		Horse		Goat		Sheep		Total
	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

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 3.3). 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 3.3). 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 3.3).

Table 3.3. Summary of model-averaged results of the best generalised linear models (GLMs, ΔAICc < 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	Esti-mate	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 – -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 – -0.928**	**<0.001**
	Snow leopard relative abundance	**-0.037**	**0.016**	**-0.068 – -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 – -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 – -0.012**	**0.010**
	Marmot occurrence	**-0.996**	**0.404**	**-1.795 – -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

3.4 Discussion

This study revealed a strong positive effect of blue sheep density on snow leopard relative abundance in the Annapurna Conservation Area (ACA), which was also influenced by study areas, increased with terrain ruggedness and decreased with increasing densities of livestock and 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 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; Sharma et al. 2021; Suryawanshi 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 2008a; Wegge 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 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 affected the occurrence, activity, and habitat selection 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, which 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), on snow leopard relative abundance. 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. 2005b) 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 a main mortality factor (33.2%) in the ACA 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 behaviour (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). Consequently, the construction of predator-proof corrals, which require relatively high acquisition costs and cannot be used year-round in case of seasonal shifts of grazing areas but are successfully implemented elsewhere (Jackson and Wangchuk 2004; Samelius et al. 2021), may significantly reduce livestock depredation in non-transhumant areas of the Annapurna region.

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 standardised designs and the application of the most suitable interventions could further reduce livestock losses.

In order to optimise 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 to 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 Figure S3.1), and 4) our findings could also be affected by other parameters related to marmot habitats affecting snow leopard hunting behaviour 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 (Figure S3.2), and the presence of marmots as an alternative prey may indeed discourage predator attacks and/or specialisation 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 behavioural adaptations at the expense of foraging activities (Aryal et al. 2015c; 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 is considered a suitable index of relative abundance when accounting for potential sources of bias (McCarthy et al. 2008; Valentová 2017). Accordingly, 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 a 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 Figure S3.3), and the effects of rather high prey densities require further investigation.

Conclusions

This study demonstrated a pivotal ecological role of blue sheep in 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 optimising 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.

3.5 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 Department of National Parks and Wildlife Conservation (DNPWC), Government of Nepal (research permit 2075/76/1667), 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 personally 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 support in statistical analyses, and C. Frank, A. Laux, and M. Püttmanns for general advice.

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3.6 Supplementary material

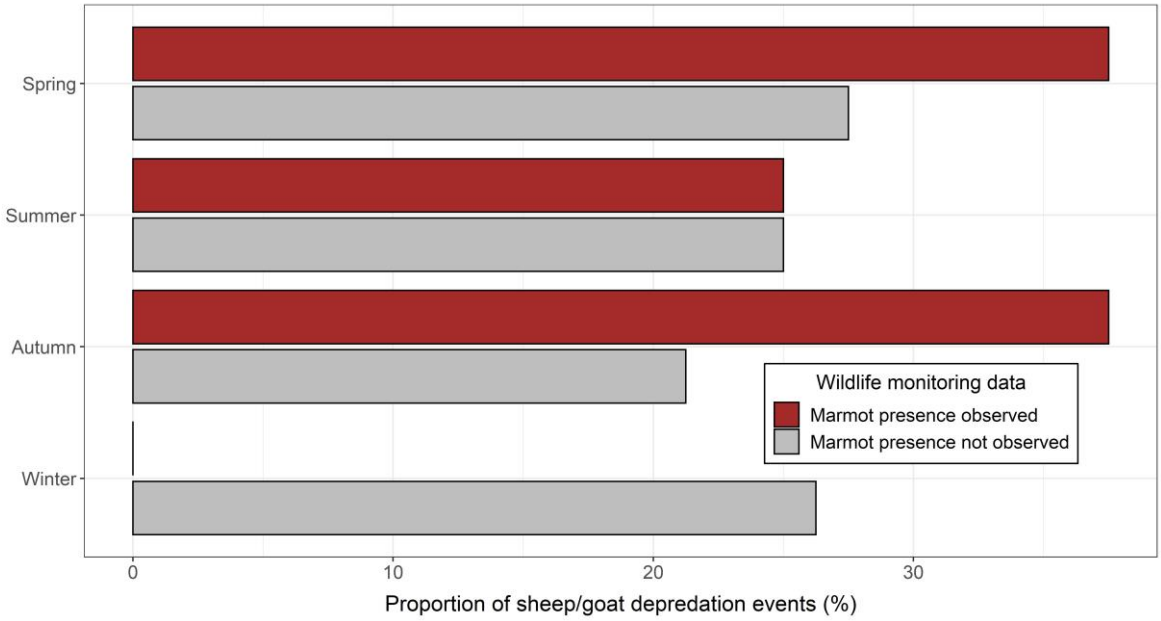

Figure S3.1. Seasonal distribution of snow leopard depredation events on sheep and goats in the Annapurna Conservation Area between 2018 and 2021 dependent on the presence (n = 8) and absence (n = 80) of Himalayan marmots around livestock grazing areas. The presence/absence of marmots was classified based on grid cells in 1500-m buffers around grazing areas.

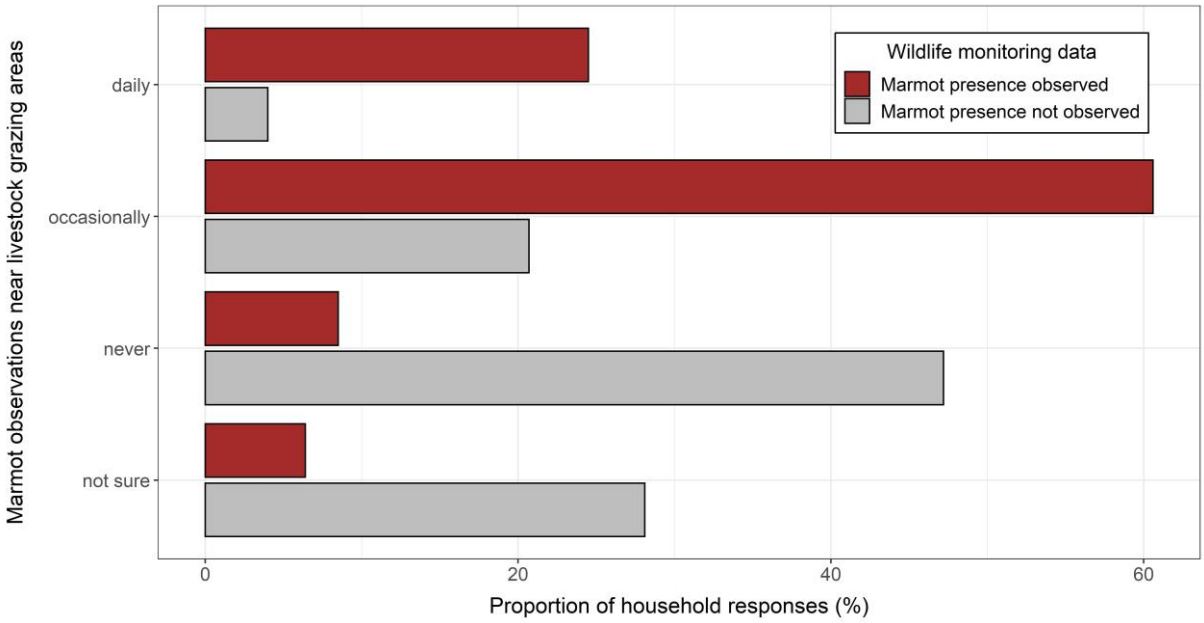

Figure S3.2. Comparison of information obtained from questionnaires (n = 479) and monitoring efforts regarding the occurrence/observation of Himalayan marmots near livestock grazing areas in the Annapurna Conservation Area between 2018 and 2021.

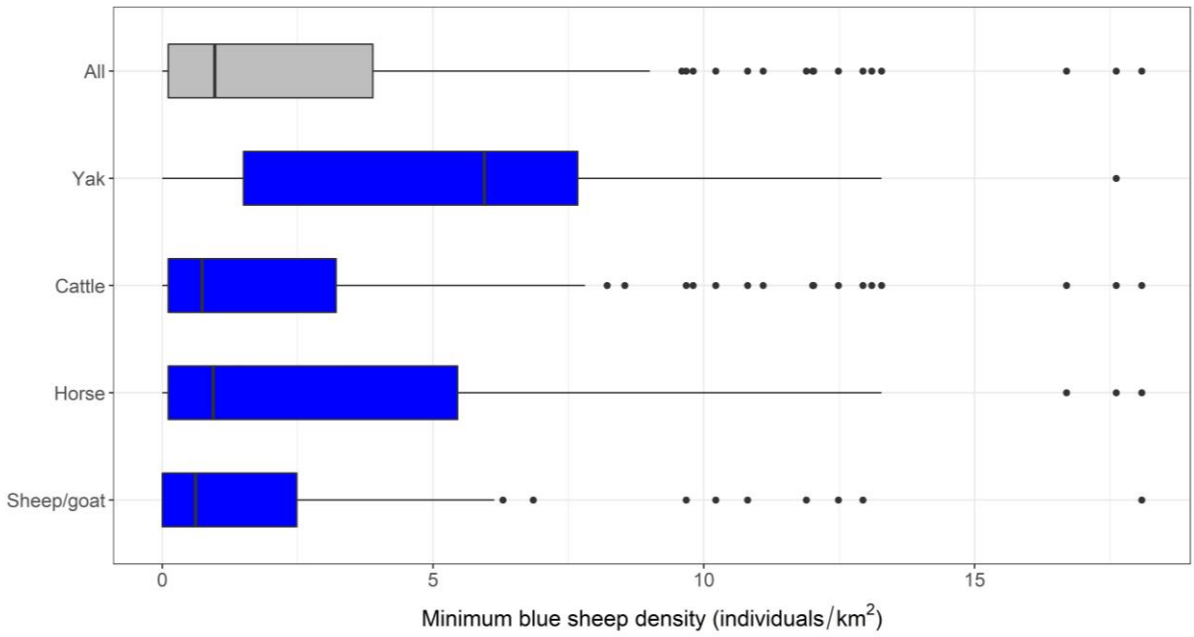

Figure S3.3. The minimum blue sheep densities around livestock grazing areas in the Annapurna Conservation Area. The minimum densities were calculated for each household based on total counts conducted between 2019 and 2021 in grid cells in 1,500m-buffers around grazing areas. Only households included in livestock depredation models were considered.

Table S3.1: Summary of wildlife monitoring efforts in the Annapurna Conservation Area between 2019 and 2021.

Area	**Grid cells**		**Transects**				**SLIMS sections**				
	Total (n)	Sampled twice (n)	Length (km; spring)		Length (km; autumn)		Length (km)		Scrapes		
			Total	Per grid cell (mean ± SD)	Total	Per grid cell (mean ± SD)	Total	Per grid cell (mean ± SD)	Total	Proportion among all signs (%)	Rate (n/km)
Manang	27	26	105.6	3.9 ± 1.1	115.3	4.4 ± 1.1	17.0	0.7 ± 0.3	664	86.1	39.1
Mustang	55	24	179.6	3.3 ± 1.2	90.3	3.6 ± 0.9	37.8	0.7 ± 0.3	384	81.5	10.2
Total	82	50	285.2	3.5 ± 1.2	205.6	4.0 ± 1.1	54.8	0.7 ± 0.2	1,048	84.4	19.1

Table S3.2. Sensitivity analysis: Summary of full negative binomial models describing the effects of predictor variables on snow leopard relative abundance in the Annapurna Conservation Area. The estimates of the coefficients, standard errors (SE), p-values (p), 95% confidence intervals (95% CI), and relative variable importance (RVI) are shown for all predictor variables.

Predictor variable	Estimate	SE	p	95% CI	RVI (%)
Alternative model type: zero-inflated model (count results shown)					
Livestock density	-0.142	0.122	0.247	-0.381 – 0.982	3.4
Blue sheep density	0.307	0.142	0.031	0.028 – 0.586	43.4
Marmot occurrence	0.148	0.372	0.690	-0.580 – 0.877	0.5
Alternative response variable: all snow leopard signs					
Livestock density	-0.233	0.124	0.059	-0.461 – 0.006	4.2
Blue sheep density	0.312	0.147	0.034	-0.006 – 0.645	43.1
Marmot occurrence	-0.292	0.365	0.424	-0.970 – 0.418	1.2
Alternative predictor set: elevation included as a quadratic and linear term					
Livestock density	-0.237	0.126	0.060	-0.471 – 0.005	3.2
Blue sheep density	0.325	0.147	0.027	0.006 – 0.658	35.5
Marmot occurrence	-0.197	0.395	0.618	-0.935 – 0.556	0.4
Alternative predictor set: small and large livestock grouped separately					
Small livestock density	-0.252	0.134	0.060	-0.551 – 0.052	4.8
Large livestock density	-0.016	0.140	0.910	-0.284 – 0.256	0.0
Blue sheep density	0.290	0.145	0.046	-0.023 – 0.617	31.7
Marmot occurrence	-0.358	0.390	0.358	-1.071 – 0.378	1.2
Alternative predictor set: longitude and latitude excluded (spatial autocorrelation present)					
Livestock density	-0.309	0.132	0.019	-0.543 – -0.069	5.7
Blue sheep density	0.431	0.134	0.001	0.160 – 0.734	72.4
Marmot occurrence	-0.683	0.346	0.048	-1.370 – 0.046	4.5
Exclusion of SLIMS sections in grid cells not adequately monitored in either spring or autumn					
Livestock density	-0.175	0.291	0.547	-0.831 – 0.490	2.7
Blue sheep density	0.307	0.191	0.107	-0.116 – 0.747	42.6
Marmot occurrence	-0.940	0.685	0.170	-2.369 – 0.443	7.9
Exclusion of one SLIMS section located slightly outside the grid cells					
Livestock density	-0.250	0.127	0.048	-0.486 – -0.005	4.3
Blue sheep density	0.284	0.148	0.055	-0.040 – 0.621	31.0
Marmot occurrence	-0.331	0.374	0.376	-1.030 – 0.395	1.3
Alternative buffer width: 1000 m					
Livestock density	-0.109	0.123	0.375	-0.357 – 0.150	1.2
Blue sheep density	0.142	0.135	0.294	-0.164 – 0.495	9.7
Marmot occurrence	-0.221	0.389	0.569	-0.957 – 0.553	0.7
Alternative buffer width: 3000 m					
Livestock density	-0.251	0.146	0.085	-0.534 – 0.033	6.2
Blue sheep density	0.266	0.154	0.085	-0.073 – 0.626	34.5
Marmot occurrence	-0.260	0.356	0.466	-0.985 – 0.477	1.3

Alternative buffer width: 5000 m					
Livestock density	-0.384	0.163	0.018	-0.712 – -0.064	12.5
Blue sheep density	0.314	0.161	0.051	-0.009 – 0.656	31.7
Marmot occurrence	-0.838	0.327	0.010	-1.488 – -0.198	9.9

Table S3.3. Sensitivity analysis: Summary of model-averaged results of the best generalised linear models (GLMs, ΔAICc < 2) describing the effects of predictor variables on the number of livestock depredation events in the Annapurna Conservation Area between 2018 and 2021 based on an alternative buffer width of 2000 m. 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. [B] considering yak, cattle, dzo, horse, sheep, goat, and blue sheep.

Species	Predictor variable	Esti-mate	SE	95% CI	p
Yak	**Intercept**	**-2.478**	**0.838**	**-4.151 – -0.805**	**0.004**
	Human population density	0.032	0.045	-0.016 – 0.154	0.482
	Terrain ruggedness	**0.138**	**0.054**	**0.031 – 0.245**	**0.011**
	Proportion of juveniles	**0.017**	**0.008**	**0.001 – 0.033**	**0.036**
	Livestock holding size	**0.016**	**0.003**	**0.009 – 0.023**	**<0.001**
	Use of other interventions[A]	0.058	0.159	-0.211 – 0.766	0.717
	Blue sheep density	0.005	0.017	-0.031 – 0.092	0.761
	Yak density	-0.005	0.016	-0.082 – 0.029	0.760
	Guarding by shepherds	0.016	0.099	-0.365 – 0.816	0.870
Cattle	**Intercept**	**-3.236**	**1.206**	**-5.605 – -0.867**	**0.007**
	Blue sheep density	**0.118**	**0.041**	**0.037 – 0.199**	**0.004**
	Livestock holding size	**0.139**	**0.046**	**0.049 – 0.229**	**0.002**
	Use of corrals	**-1.926**	**0.497**	**-2.903 – -0.949**	**<0.001**
	Snow leopard relative abundance	**-0.039**	**0.017**	**-0.072 – -0.005**	**0.025**
	Terrain ruggedness	0.119	0.106	-0.026 – 0.342	0.263
	Proportion of juveniles	0.001	0.005	-0.011 – 0.025	0.805
	Contribution to prey community[B]	-0.069	0.492	-3.020 – 1.965	0.889
	Guarding by shepherds	0.003	0.025	-0.109 – 0.155	0.908
Horse	**Intercept**	**-2.084**	**0.403**	**-2.877 – -1.291**	**<0.001**
	Use of corrals	-0.537	0.523	-1.678 – 0.148	0.305
	Proportion of juveniles	0.008	0.009	-0.003 – 0.030	0.407
	Livestock holding size	**0.240**	**0.097**	**0.050 – 0.430**	**0.013**
	Snow leopard relative abundance	-0.005	0.010	-0.039 – 0.007	0.600
	Human population density	-0.016	0.028	-0.102 – 0.022	0.568
	Marmot occurrence	0.071	0.190	-0.222 – 0.901	0.708

	Terrain ruggedness	0.004	0.022	-0.050 – 0.183	0.850
	Horse density	-0.001	0.011	-0.137 – 0.050	0.908
	Blue sheep density	-0.002	0.015	-0.116 – 0.052	0.866
	Guarding by shepherds	0.007	0.090	-0.628 – 0.925	0.940
Sheep and goat	Intercept	-0.004	0.274	-0.545 – 0.537	0.989
	Human population density	**-0.049**	**0.020**	**-0.088 – -0.011**	**0.013**
	Marmot occurrence	**-0.811**	**0.369**	**-1.541 – -0.081**	**0.029**
	Livestock holding size	0.001	0.001	-0.001 – 0.005	0.547
	Blue sheep density	-0.023	0.039	-0.138 – 0.030	0.547
	Snow leopard relative abundance	0.005	0.009	-0.010 – 0.034	0.611
	Proportion of juveniles	0.000	0.002	-0.008 – 0.013	0.899

Table S3.4. Sensitivity analysis: Summary of model-averaged results of the best generalised linear models (GLMs, ΔAICc < 2) describing horse depredation attributed to snow leopards in the Annapurna Conservation Area between 2018 and 2021 based on summer data. The estimates of the coefficient, standard errors (SE), 95% confidence intervals (95% CI), and p-values (p) are shown. Predictor variables with $p < 0.05$ are highlighted in bold.

Species	Predictor variable	Esti-mate	SE	95% CI	p
Horse	**Intercept**	**-3.116**	**0.441**	**-3.984 – -2.249**	**<0.001**
	Livestock holding size	**0.358**	**0.112**	**0.137 – 0.579**	**0.002**
	Marmot occurrence	0.133	0.292	-0.274 – 1.214	0.650
	Use of corrals	-0.296	0.503	-1.806 – 0.407	0.557
	Proportion of juveniles	0.006	0.010	-0.006 – 0.035	0.553
	Snow leopard relative abundance	-0.004	0.009	-0.038 – 0.009	0.643
	Guarding by shepherds	0.010	0.106	-0.681 – 1.114	0.928
	Blue sheep density	0.002	0.012	-0.046 – 0.088	0.878
	Terrain ruggedness	0.003	0.020	-0.061 – 0.208	0.880

Table S3.5. Summary of the full negative binomial model describing the effects of predictor variables on snow leopard relative abundance in the Annapurna Conservation Area. The estimates of the coefficients, standard errors (SE), 95% confidence intervals (95% CI), p-values (p), and relative variable importance (RVI) are shown for all predictor variables.

Variable	**Estimate**	**SE**	**95% CI**	**p**	**RVI (%)**
Intercept	-3.988	0.148	-4.276 – -3.683	<0.001	
Elevation (quadratic)	-0.141	0.074	-0.289 – 0.016	0.057	5.1
Terrain ruggedness	0.264	0.122	0.030 – 0.510	0.031	12.8
Human population density	-0.382	0.150	-0.739 – -0.045	0.011	11.5
Livestock density	-0.249	0.126	-0.484 – -0.005	0.048	4.1
Blue sheep density	0.293	0.145	-0.020 – 0.621	0.043	32.1
Marmot occurrence	-0.331	0.371	-1.025 – 0.390	0.373	1.3
Longitude	0.187	0.173	-0.169 – 0.543	0.277	10.8
Latitude	-0.333	0.140	-0.608 – -0.061	0.017	22.3
Longitude*Latitude	0.469	0.201	0.065 – 0.879	0.019	

Chapter 4

Patterns of livestock depredation by snow leopards and effects of intervention strategies

A livestock herd composed of domestic sheep (*Ovis aries*) and goats (*Capra hircus*) in Manang, Annapurna Conservation Area, Nepal. Credit: Marc Filla

Manuscript: Patterns of livestock depredation by snow leopards and effects of intervention strategies: lessons from the Nepalese Himalaya

Marc Filla, Rinzin P. Lama, Tim Filla, Marco Heurich, Niko Balkenhol, Matthias Waltert, Igor Khorozyan

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Abstract

Context: Large carnivores are increasingly threatened by anthropogenic activities, and their protection is among the main goals of biodiversity conservation. The snow leopard (*Panthera uncia*) inhabits high-mountain landscapes where livestock depredation drives this species into conflicts with local people and poses an obstacle to its conservation.

Aims: Therefore, it is crucial to identify the livestock groups most vulnerable to depredation, target them in the implementation of practical interventions, and assess the effectiveness of intervention strategies for conflict mitigation. We present a novel attempt to evaluate intervention strategies for particularly vulnerable species, age groups, times, and seasons.

Methods: In 2020, we conducted questionnaire surveys in two regions of the Annapurna Conservation Area, Nepal (Manang, n = 146 respondents and Upper Mustang, n = 183). We applied sample comparison testing, Jacobs' selectivity index, and generalised linear models (GLMs) to assess rates and spatio-temporal heterogeneity of depredation, reveal vulnerable livestock groups, analyse potential effects of applied intervention strategies, and identify husbandry factors relevant to depredation.

Key results: Snow leopard predation was a major cause of livestock mortality in both regions (25.4–39.8%), resulting in an estimated annual loss of 3.2–3.6% of all livestock. The main intervention strategies (e.g., corrals during night-time and herding during daytime) were applied inconsistently and not associated with decreases in reported livestock losses. In contrast, we found some evidence that dogs, deterrents (light, music playing, flapping tape, and dung burning), and the use of multiple interventions were associated with a reduction in reported night-time depredation of yaks.

Conclusions and implications: We suggest conducting controlled randomised experiments for quantitative assessment of the effectiveness of mentioned dogs, deterrents, and the use of multiple interventions, and widely applying the most effective ones in local communities. This would contribute to the long-term co-existence of snow leopards and humans in the Annapurna region and beyond.

4.1 Introduction

Today, the world faces an accelerated loss of biodiversity that is referred to as a human-induced mass extinction (Ceballos et al. 2015). Large carnivores are particularly prone to extirpation and have suffered massive range contractions and population declines over the last decades (Ripple et al. 2014). These animals play key ecological roles at the top of natural food webs and hold considerable social significance and economic importance (Lindsey et al. 2007; Brashares et al. 2010; Ripple et al. 2014; Hoeks et al. 2020). Therefore, the protection of large carnivores and their habitats is vital to preserve biodiversity (Ripple et al. 2014).

Habitat loss and degradation, direct persecution, utilisation, and wild prey depletion are among the main threats to large carnivores (Ripple et al. 2014). Moreover, vast spatial ranges and obligatory meat-eating cause livestock depredation, which, in turn, drives large carnivores into direct competition and conflicts with humans (Treves and Karanth 2003; Ripple et al. 2014; van Eeden et al. 2018b). Whether actually occurring or merely perceived, livestock depredation commonly causes the preventive and retaliatory killing of carnivores (van Eeden et al. 2018b) and may deteriorate their populations, especially near protected areas where conflicts are most intense (Ugarte et al. 2019). Therefore, conflicts with humans over livestock depredation are of high relevance to the conservation of various large carnivores, such as big cats (Inskip and Zimmermann 2009; Khorozyan and Waltert 2021) and the snow leopard (*Panthera uncia*) in particular (WWF 2015; McCarthy et al. 2017).

The snow leopard inhabits the mountain ranges of Asia and is classified as 'Vulnerable' according to the IUCN Red List of Threatened Species (McCarthy et al. 2017). Wild ungulates represent the main prey of snow leopards globally (Lyngdoh et al. 2014; McCarthy et al. 2017), but livestock may dominate this predator's diet in parts of its range (e.g., Anwar et al. 2011; Bocci et al. 2017). Snow leopard depredation on livestock appears to be affected by environmental conditions (e.g., wild prey abundance, stalking cover) and livestock availability, which arises from livestock density, grazing area characteristics, and applications of livestock protection interventions (hereafter interventions; Jackson 2012). The patterns of livestock depredation by snow leopards are complex and variable (Jackson et al. 2010; Chetri et al. 2019a), requiring solid research on the efficacy of existing mitigation strategies (Rashid et al. 2020). It is widely agreed that mitigation of human-snow leopard conflicts is key to the conservation of this big cat and its long-term co-existence with local people across its range (Jackson et al. 2010; Snow Leopard Network 2014; Jackson and Lama 2016).

Compensation schemes to collectively offset livestock losses have been successfully implemented in various parts of the snow leopard range (e.g., Hussain 2000; Mishra et al. 2003; Gurung et al. 2011). In parallel, improved husbandry and interventions are at the heart of the initiatives addressing human-snow leopard conflicts (e.g., Jackson et al. 2010; Snow

Leopard Network 2014; Jackson 2015). Numerous intervention strategies have been implemented across the globe to protect livestock from predators like snow leopards (Krafte Holland et al. 2018; Khorozyan and Waltert 2021), and positive effects have been observed following the improvement of livestock pens (e.g., Jamwal et al. 2019; Samelius et al. 2021). Feasibility and effectiveness of intervention strategies are potentially reduced by financial constraints (e.g., Gehring et al. 2010; Lance et al. 2010), landscape characteristics (e.g., Faccioni et al. 2015), predator habituation (Khorozyan and Waltert 2019), and individual behaviour patterns (Linnell et al. 1999). Therefore, interventions require local context-specific applications that are feasible, practical, and account for cultural values and environmental conditions (van Eeden et al. 2018a). Despite their high relevance, the effects of intervention strategies often remain insufficiently evaluated, and a sound evidence base is urgently needed to boost conservation projects benefiting snow leopards and other carnivores (Krafte Holland et al. 2018; van Eeden et al. 2018b; Rashid et al. 2020; Khorozyan and Waltert 2021).

Interventions are essential to protect snow leopards from human retaliation and to secure local rural livelihoods from socio-economic hardship inflicted by livestock losses to depredation (e.g., Jackson et al. 2010; Mijiddorj et al. 2018). One of the areas in need of interventions is the Annapurna Conservation Area (ACA) which represents a vast massif of suitable habitats for this predator, its prey, and other wildlife (Baral et al. 2019). As in many regions across the snow leopard range, local people are often poor and may heavily depend on livestock for subsistence and economic purposes (Spiteri and Nepal 2008; Chetri et al. 2017). Therefore, it is not surprising that livestock losses attributed to snow leopards may provoke negative attitudes of local pastoralists in the Annapurna region (Oli et al. 1994; Hanson et al. 2019; Tiwari et al. 2020) as observed elsewhere (e.g., Mishra et al. 2003). This is also likely to trigger retaliatory actions despite the intrinsic value and outstanding roles of snow leopards in local culture and ecotourism (Oli et al. 1994; Aryal et al. 2014d; Vannelli et al. 2019; Hacker et al. 2021). Hence, mitigation of such conflicts is crucial to lay the ground for the long-term co-existence of humans and snow leopards and maintaining viable snow leopard populations also in the Annapurna region. For this, it becomes fundamental to identify key targets for interventions, which requires information on when and where snow leopards attack livestock, what species and sex/age groups of livestock are primarily affected, what intervention strategies are most effective and practical, and what factors shape depredation occurrence and rates.

In this study, we attempted to fill this gap in knowledge by investigating snow leopard-livestock interactions in two regions of the ACA, which differ considerably in landscape conditions, prey availability, and livestock husbandry (Pokharel and Chetri 2006; Aryal et al. 2014b; Tiwari et al. 2020). Here, we aimed to (1) assess the general patterns and rates of livestock depredation by snow leopards, (2) examine livestock selectivity, (3) reveal seasonal and daytime variation

in depredation, (4) analyse the realised effectiveness of applied intervention strategies, and (5) identify the main husbandry factors associated with livestock depredation by snow leopards.

4.2 Material and methods

4.2.1 Study area

The ACA, which was established in 1992, forms part of the Himalaya Biodiversity Hotspot and covers 7,629 km^2 in central Nepal (Mittermeier et al. 2005; Baral et al. 2019; Figure 4.1). This protected area hosts a diverse wildlife community, including at least 128 mammal and 514 bird species, as well as more than 1,300 plant species (Baral et al. 2019). About 100,000 people live within the boundaries of the protected area and maintain traditional rights and access to natural resources (National Trust for Nature Conservation 2015). Livestock husbandry and crop farming rank among the main (subsistence) economies in the ACA, with tourism playing an increasingly important role (Bhuju et al. 2007; Baral et al. 2019).

The present study was conducted in the adjoining districts Manang (Neshyang valley, western parts of Manang) and Mustang (northern parts of Upper Mustang) in the ACA (28°36′53″–29°14′28″N, 83°52′40″–84°9′11″E; Figure 4.1), where livestock is abundant and grazes in (partially) excellent snow leopard habitats (Aryal et al. 2014b, 2014d, 2016). Studied settlements were located at elevations ranging from approximately 3,100 m to 4,200 m above sea level (a.s.l.), with elevations of the surrounding grazing areas exceeding 4,500 m a.s.l. Seasonal daily air temperatures range from a minimum of about -10°C in winter to a maximum of about 10°C during the monsoon (Department of Hydrology and Meteorology 2017). Located in the rain shadow of the Annapurna Range, this area receives less than 300 mm of annual precipitation in Upper Mustang and about 600 mm in Manang (Department of Hydrology and Meteorology 2017). The Upper Mustang region is covered mainly by cold deserts deprived of forest (Chetri et al. 2017; Ghezzi et al. 2017) and is characterised by an arid cold steppe climate with strong winds (Karki et al. 2015). In contrast, the Manang region has polar and cold climates (Aryal et al. 2014b; Karki et al. 2015) and is covered by forests comprised of the Himalayan white pine (*Pinus wallichiana*), East Himalayan fir (*Abies spectabilis*), Himalayan birch (*Betula utilis*), and black juniper (*Juniperus indica*; Ghimire and Lekhak 2007). Vegetation above the timberline in Manang is composed of shrublands, alpine meadows and alpine grasslands, with barren land and permanent snow fields dominating the highest elevations (Shrestha and Wegge 2008a).

Large carnivores in the ACA include the snow leopard, brown bear (*Ursus arctos*), Himalayan wolf (*Canis lupus chanco*), and Eurasian lynx (*Lynx lynx*; Baral et al. 2019). The wild ungulate community is more diverse in Upper Mustang (Chetri et al. 2017), but the blue sheep (*Pseudois*

nayaur), which represents the main snow leopard prey (Chetri et al. 2017), occurs at higher densities in Manang (e.g., Oli 1994; Aryal et al. 2014b). The other wild ungulates are the Tibetan argali (*Ovis ammon hodgsoni*), kiang (*Equus kiang*), Tibetan gazelle (*Procapra picticaudata*), Himalayan musk deer (*Moschus leucogaster*), Kashmir musk deer (*Moschus cupreus*), and Himalayan tahr (*Hemitragus jemlahicus*; Oli 1994; Chetri et al. 2017; Baral et al. 2019; Singh et al. 2019). The livestock community includes mainly yaks (*Bos grunniens*), cattle (*B. taurus*), dzos (*B. grunniens* × *B. taurus*), sheep (*Ovis aries*), goats (*Capra hircus*), horses (*E. caballus*), and mules (*E. asinus* × *E. caballus*; Chetri et al. 2017).

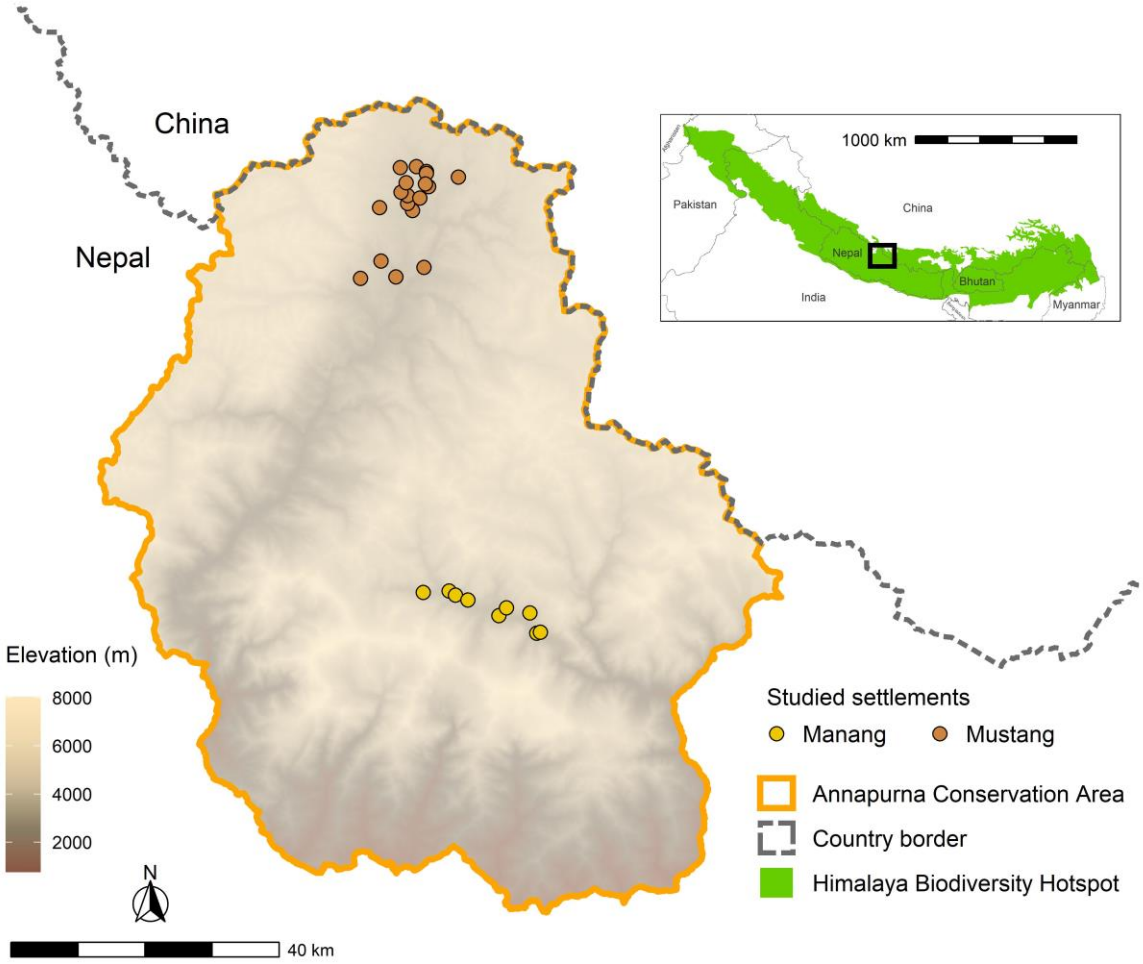

Figure 4.1. Location of 27 studied settlements in the study area (black rectangle) in Manang and Upper Mustang, Annapurna Conservation Area. Sources: Conservation International 2011 (Hotspot location); DIVA-GIS 2015 (country borders); NASA/METI/AIST/Japan Spacesystems and U.S./Japan ASTER Science Team 2009 (elevation).

4.2.2 Questionnaire survey

We conducted a semi-structured questionnaire survey in 27 major settlements located in our study regions between July and October 2020 (Figure 4.1). The interviews were conducted by

trained local community members to account for local dialects, vast landscape, remote and scattered settlements (Chetri et al. 2019a), and to meet official regulations during the COVID-19 pandemic. The training was conducted distantly by video calls by one of us (RPL) using the same questionnaire forms and procedures. To balance competing needs (i.e., sampling intensively enough to represent each village but also extensively enough to include each village), we aimed to survey approximately 25–35% of the households with livestock in each village (Hanson et al. 2019). We selected households by a mixture of snowball sampling (i.e., respondents were identified following the recommendations of initial informants - mainly conservation officers and local people, who were aware of livestock owners in the settlement; Goodman 1961) and interviewing randomly selected household respondents at public meetings when not enough livestock owners were available during visits (Young et al. 2018).

All respondents (one per household) were informed beforehand about the aim of this study, anonymity and security of their information, and that the survey was unrelated to any compensation and compliance schemes. The questionnaire survey was initiated only after participants had given their verbal consent. The questionnaire form used during the survey was modified following a pilot study in spring 2019, as recommended elsewhere (Young et al. 2018). We asked the respondents about their current livestock holdings, including the number of adult (≥ 2 years) and juvenile (< 2 years) individuals, which was a measure of livestock availability (Khorozyan et al. 2018). Additionally, for each household, we recorded livestock losses within the past two years (July 2018 – June 2020), applied intervention strategies (Figure 4.2) and details of depredation events (date, time, interventions used).

We took various steps to increase the reliability of the reported but unverified depredation data. Printed photographs of wild and domestic animals were shown to the respondents to secure the correct classification of species. We validated the credibility of the respondents' information by (1) recording the reasons why they believed that livestock was killed by snow leopards and not by other predators (e.g., direct observation, signs), (2) cross-checking with village heads, independent herders, and local conservation officers, and (3) back-checking about 10% of the households (Hanson et al. 2019). We omitted cases with considerable changes in livestock husbandry, such as livestock holdings or intervention applications, over the past 24 months.

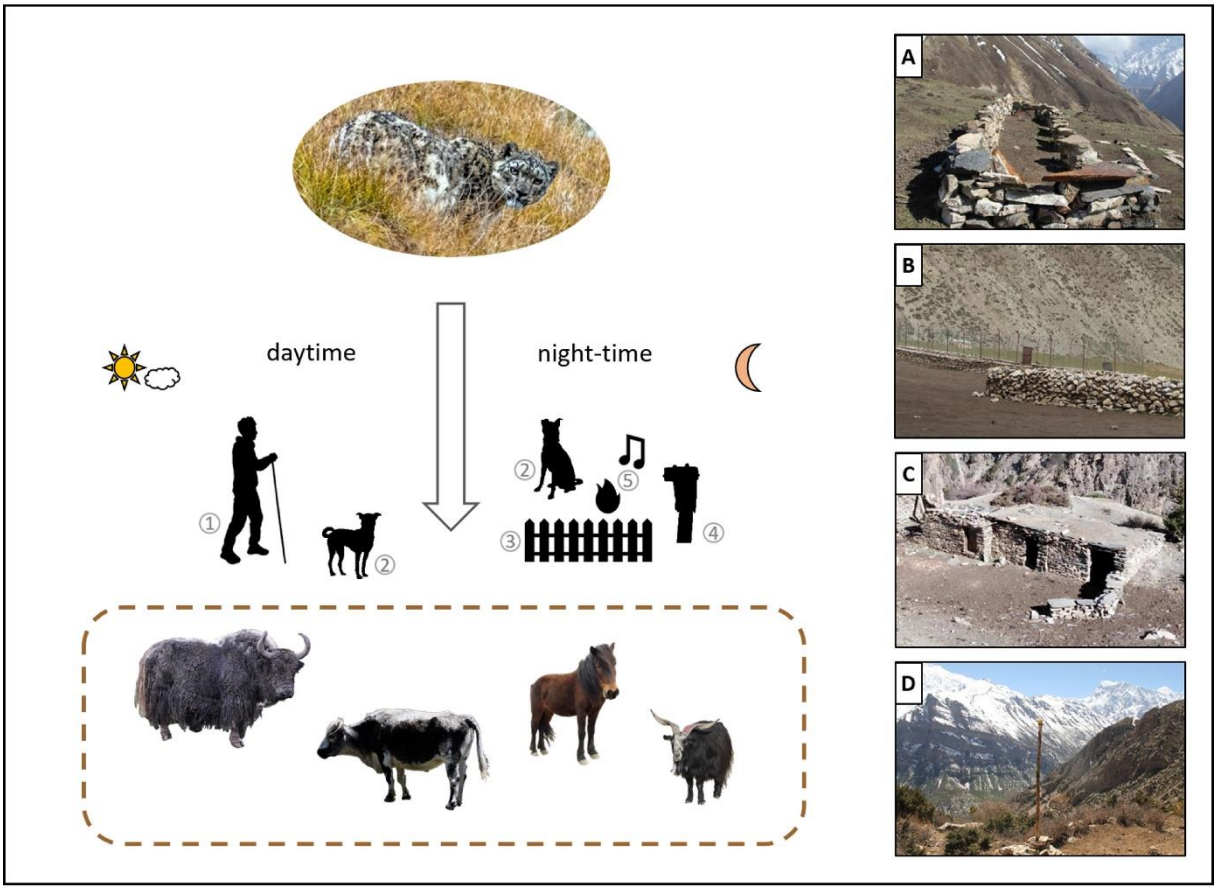

Figure 4.2. Conceptual scheme of intervention strategies used to reduce livestock depredation by snow leopards in Manang and Upper Mustang during daytime and night-time. Symbols: 1 - herding, 2 - guarding dogs, 3 - corrals, 4 - Foxlights, 5 - other interventions (music playing, other light deterrents, flapping tapes, and dung burning); Photographs: A - simple stone wall corral, B - wire-fenced corral, C - stone wall hut/house, D - Foxlights; Credits: snow leopard - Tashi R. Ghale (Third Pole Conservancy), A and C - Marc Filla, B and D - Rinzin P. Lama.

4.2.3 Data analysis

We analysed depredation data only for livestock losses attributed to snow leopards. We pooled sheep and goats for the analyses as these animals are kept in mixed herds and protected by the same interventions. We classified daytime herding practices as daily herding, variable herding (restricted to specific age groups or seasons), occasional checking (for livestock survival and health condition), or no herding. Likewise, we classified the use of night-time corrals as daily, variable (restricted to specific age groups or seasons), or no use. Based on corral building material and structure, we distinguished between simple stone wall corrals (including simple mud-brick corrals), wire-fenced corrals, and traditional stone wall huts/houses (with roofs and air inlets; Figure 4.2). We further recorded the use of guarding dogs, solar-powered light deterrents (Foxlights®, Bexley North, Australia), and other interventions wherever applicable.

We checked for differences and similarities in livestock holding patterns between Manang and Upper Mustang by comparing the composition of the overall livestock community (χ^2 test) and the abundance of each livestock species per household (Mann-Whitney U test).

We applied Jacobs' selectivity index (J_i) to measure the preference or avoidance of livestock species by snow leopards (J_i; Jacobs 1974; e.g., Lyngdoh et al. 2014):

$J_i = (r_i - p_i) / (r_i + p_i - 2*r_i*p_i)$

where r_i is the proportion of the i-th livestock species among the killed individuals and p_i is the proportion of the respective species in the livestock community. This index ranges from +1 (strong preference) to -1 (strong avoidance), with values of 0 indicating no selectivity (i.e., livestock is killed proportionally to its availability; Khorozyan et al. 2018). We also assessed the selection of age groups by calculating J_i for adult and juvenile individuals of each livestock species. We calculated confidence intervals by bootstrapping (1,000 iterations) and considered selectivity indices as significant if 95% confidence intervals (95% CI) did not overlap with 0 (Soofi et al. 2019).

Moreover, we assessed seasonal and daytime differences in livestock depredation by snow leopards. Taking into account regional climatic conditions, we differentiated between depredation events in spring (March–May), summer (June–August), autumn (September–November), and winter (December–February; Department of Hydrology and Meteorology 2017; Rai et al. 2020). We also differentiated between depredation events during daytime and night-time when the time of the attack was known and did not fall into transition times (i.e., dusk/dawn). We examined seasonal and daytime differences in depredation patterns within Manang and Upper Mustang and between these regions by using the χ^2 test (frequency of depredation events) and the Mann-Whitney U test (number of animals killed per depredation event).

In addition, we applied generalised linear models (GLMs; O'Hara and Kotze 2010) to evaluate the realised effectiveness of intervention strategies (model set 1) and to identify the main husbandry variables influencing livestock depredation attributed to snow leopards in the study area (model set 2).

In the first set of GLMs, we assessed the realised effectiveness of intervention strategies by running separate models for each livestock species, region, depredation time (daytime and night-time), and intervention as long as there was variation in the use of interventions. Depredation losses, which are closely linked with predator conservation, can be described not only by the mere presence/absence of losses but also by numbers of predator attacks and numbers of killed animals. Therefore, we set up three models with the response variables of depredation occurrence (yes/no; logistic regression), the number of depredation events during the 2-year survey period, and the number of depredated livestock individuals during the 2-year

survey period. For the last two response variables, we used (zero-inflated) Poisson GLMs if the assumption of Poisson distribution was met (mean = variance) and (zero-inflated) negative binomial GLMs in case of overdispersion (variance > mean; Gelman and Hill 2007). The application of intervention strategies (daytime - herding: daily/not daily; night-time - corrals: daily/not daily, guarding dogs: yes/no, Foxlights: yes/no, other interventions: yes/no; for yaks in Manang also the number of night-time interventions and the use of multiple interventions during night-time: yes/no) served as a predictor variable. In this set of GLMs, we adjusted for the total number of livestock owned and the proportion of juveniles by using these parameters as additional predictor variables. We standardised these two continuous variables by subtraction of the mean and division of this difference by the standard deviation. We did not perform model selection in order not to drop the target variables or confounding variables. In this set of models, we did not include the region as an additional predictor variable, as the mentioned geographic and ecological differences between Manang and Mustang could have obscured the effects of intervention strategies. Likewise, we were unable to include this predictor as part of interaction terms due to insufficient intervention application ($n \leq 5$ cases) in either region. We applied the Mann-Whitney U test to compare the numbers of individuals killed during attacks with and without specific interventions being active.

In the second set of GLMs, we examined the main husbandry variables influencing livestock depredation by snow leopards in the Annapurna region. We ran separate models for each species and depredation time (daytime and night-time) and used the same response and predictor variables as in the first set of models but allowed more than one intervention strategy at a time. Moreover, we included the region (Manang or Upper Mustang) as an additional predictor variable to account for differences in geographic and ecological factors, such as landscape characteristics, snow leopard abundance, and wild prey density, though our data did not allow us to derive individual conclusions about these parameters. We checked for multicollinearity of predictor variables by using the variance inflation factor (VIF) and excluded either of the variables if VIF > 3 (Soofi et al. 2019). As this model set was intended to reveal the main husbandry factors relevant to depredation, we performed model selection analyses with the use of all remaining predictor variables in the candidate models. We ranked models according to the Akaike Information Criterion corrected for small sample size (AIC_c; Akaike 1973; Grueber et al. 2011), selected the best models based on $\Delta AIC_c < 2$ (Burnham and Anderson 2002) and produced multi-model averaged results (Grueber et al. 2011).

We excluded small samples ($n \leq 5$, e.g., cattle killed in Upper Mustang or horses attacked during daytime) from the analyses. We calculated the standard error of the mean (SE) as a measure of variation unless otherwise indicated. Data processing and statistical analyses were conducted in R version 3.6.0 (R Core Team 2019). We used the R packages *MASS* (Venables and Ripley 2002), *MuMIn* (Barton 2020), *performance* (Lüdecke et al. 2021), and *pscl* (Zeileis

et al. 2008) for data analyses, and *cowplot* (Wilke 2020), *ggplot2* (Wickham 2016), and *ggspatial* (Dunnington 2021) for data visualisation.

4.3 Results

4.3.1 Livestock holdings, mortality, and depredation

We interviewed a total of 146 livestock owners with 2,947 animals in Manang and 183 livestock owners with 5,635 animals in Upper Mustang (Table 4.1). Livestock owners in Upper Mustang kept significantly more animals (mean ± standard deviation (SD) 30.8 ± 62.6) than livestock owners in Manang (20.2 ± 34.9; U = 10,482, $p = 0.001$; Tables 4.1 and S4.1). The composition of the livestock community differed between the two regions ($\chi^2 = 1478.7$, $p < 0.001$; Table S4.2). Sheep/goats dominated the livestock community in Upper Mustang (72.3% of the total livestock), while yaks (40.5%) and sheep/goats (37.9%) were most abundant in Manang (Table 4.1).

The respondents attributed the loss of 357 animals in Upper Mustang (mean ± SD 2.0 ± 6.6 animals per household) and 210 animals in Manang (1.4 ± 2.3 animals per household) to snow leopards over the 2-year survey period (Table 4.2). This implies annual depredation rates of 3.2% in Upper Mustang and 3.6% in Manang (Table 4.2). Snow leopards killed mainly yaks (42.4% of total livestock depredation losses) and sheep/goats (31.4%) in Manang, whereas they killed mainly sheep/goats (83.8%) in Upper Mustang (Table 4.2). Over the 2-year survey period, snow leopards were the main mortality factor for horses in both Manang (82.6% of total horse mortality cases) and Upper Mustang (72.7%) and had much lower impacts on cattle and yak, especially in Upper Mustang (Table 4.2). Overall, snow leopards were the main livestock mortality factor in Manang (39.8%), followed by diseases/accidents (38.2%) and other predators (21.4%), and they accounted for 25.4% of livestock mortality in Upper Mustang, where the majority of livestock mortality was ascribed to diseases/accidents (69.0%) and only a small proportion to other predators (5.6%; Table 4.2).

Table 4.1. Livestock holdings of sampled households in Manang (n = 146) and Upper Mustang (n = 183).

Region	Species	Number			Proportion of livestock (%)	Present in % of livestock holdings	Mean number per household	Mean number per household keeping a given livestock species
		Total	Adults	Juveniles				
Manang	yak	1,192	881	311	40.5	22.6	8.2	36.1
	cattle	464	382	82	15.7	87.0	3.2	3.7
	dzo	0	0	0	0.0	0.0	0.0	
	horse	175	160	15	5.9	64.4	1.2	1.9
	sheep/goat	1,116	810	306	37.9	17.8	7.6	42.9
	all	2,947	2,233	714	100.0		20.2	
Upper Mustang	yak	440	336	104	7.8	7.1	2.4	33.8
	cattle	808	546	262	14.3	94.5	4.4	4.7
	dzo	22	22	0	0.4	6.0	0.1	2.0
	horse	293	273	20	5.2	67.2	1.6	2.4
	sheep/goat	4,072	3,057	1,015	72.3	29.0	22.3	76.8
	all	5,635	4,234	1,401	100.0		30.8	

Table 4.2. Livestock losses attributed to snow leopards and other mortality causes in sampled households of Manang (n = 146) and Upper Mustang (n = 183) during 2018–2020.

Region	Species	Livestock depredation by snow leopards								Livestock mortality			
		Number killed			Proportion of depredated livestock (%)	Proportion of households keeping a given livestock species with depredation (%)	Mean number killed per household	Mean number killed per household keeping a given livestock species	Depredation rate (%/year)	Number lost to other causes	Total number lost	Mortality rate (%/year)	Contribution of snow leopards to mortality (%)
		Total	Adults	Juveniles									
Manang	yak	89	26	63	42.4	72.7	0.6	2.7	3.7	147	236	9.9	37.7
	cattle	36	23	13	17.1	20.5	0.2	0.3	3.9	50	86	9.3	41.9
	dzo												
	horse	19	13	6	9.0	17.0	0.1	0.2	5.4	4	23	6.6	82.6
	sheep/goat	66	61	5	31.4	50.0	0.5	2.5	3.0	117	183	8.2	36.1
	all	210	123	87	100.0	47.3	1.4	1.4	3.6	318	528	9.0	39.8
Upper Mustang	yak	21	10	11	5.9	53.8	0.1	1.6	2.4	234	255	29.0	8.2
	cattle	4	4	0	1.1	2.3	0.0	0.0	0.2	104	108	6.7	3.7
	dzo	1	1	0	0.3	9.1	0.0	0.1	2.3	0	1	2.3	100.0
	horse	32	13	19	9.0	22.8	0.2	0.3	5.5	12	44	7.5	72.7
	sheep/goat	299	287	12	83.8	60.4	1.6	5.4	3.7	700	999	12.3	29.9
	all	357	315	42	100.0	36.6	2.0	2.0	3.2	1,050	1,407	12.5	25.4

4.3.2 Livestock selection

The Jacobs' selectivity index (J_i) indicated a slight preference of snow leopards for horses in Upper Mustang (J_i = 0.28) and a similar though not statistically significant pattern in Manang (J_i = 0.22; Figure 4.3). Cattle were avoided in Upper Mustang (J_i = -0.87) but taken proportionally to their availability in Manang (J_i = 0.05). Yaks were killed proportionally to their availability in both Manang (J_i = 0.04) and Upper Mustang (J_i = -0.15; Figure 4.3). Sheep/goats were significantly preferred by snow leopards in Upper Mustang (J_i = 0.33) but not in Manang (J_i = -0.14; Figure 4.3). In regard to livestock age groups, snow leopards significantly avoided adult individuals of yaks (Manang: J_i = -0.75; Upper Mustang (not significant): J_i = -0.56), horses (Manang: J_i = -0.66; Upper Mustang: J_i = -0.90), and cattle (Manang: J_i = -0.45) in comparison with their juveniles, but selected adult individuals of sheep/goats (Manang: J_i = 0.64; Upper Mustang: J_i = 0.78).

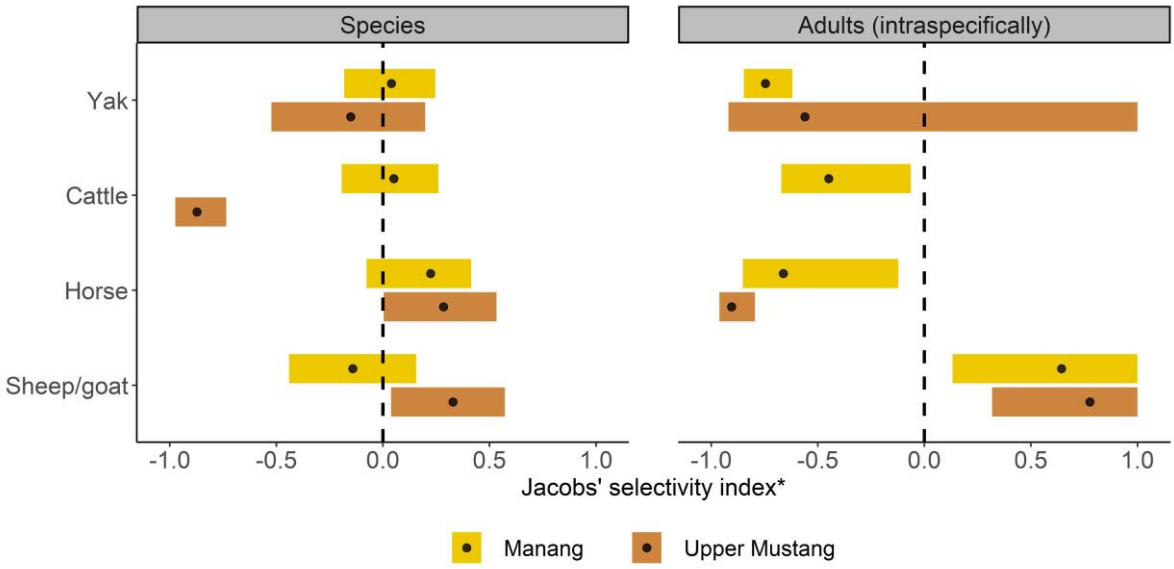

Figure 4.3. Jacobs' selectivity index* for livestock species and adult individuals (intraspecifically) based on depredation losses attributed to snow leopards in Manang and Upper Mustang during 2018–2020. The black points show the plain indices, and the horizontal bars indicate the 95% confidence intervals. *Not shown for small samples (n ≤ 5).

4.3.3 Seasonal and daytime depredation patterns

In Manang, most attacks of snow leopards on livestock occurred in spring (28.3%) and summer (32.9%), while most attacks in Upper Mustang occurred in summer (37.0%) and autumn (28.4%; Figure 4.4; Table S4.3). However, these seasonal differences were not significant for any livestock species (χ^2 tests; Table S4.2).

Snow leopards attacked livestock more frequently during night-time than during daytime in Upper Mustang ($\chi^2 = 10.64$, $p = 0.001$) but not in Manang ($\chi^2 = 0.09$, $p = 0.767$; Figure 4.4; Tables S4.2 and S4.4). The daytime depredation patterns of yak ($\chi^2 = 5.24$, $p = 0.022$) and sheep/goat ($\chi^2 = 12.10$, $p = 0.001$) were significantly different between Manang (more attacks during daytime) and Upper Mustang (more attacks during night-time; Figure 4.4; Table S4.2). Horses in Manang ($\chi^2 = 4.97$, $p = 0.026$) and sheep/goats in Upper Mustang ($\chi^2 = 7.56$, $p = 0.006$) were more frequently attacked by snow leopards during night-time (Figure 4.4; Table S4.2). Snow leopards killed significantly more individuals of sheep/goats during night-time attacks (mean ± SD 8.0 ± 11.7 individuals/attack) compared to daytime attacks (1.5 ± 0.7 individuals/attack; $U = 66.5$, $p < 0.001$), and the same applied also to yaks (daytime: 1.0 ± 0.2 individuals/attack, night-time: 1.7 ± 1.3 individuals/attack; $U = 496$, $p < 0.001$), while these numbers did not differ between daytimes for cattle and horses (Table S4.1).

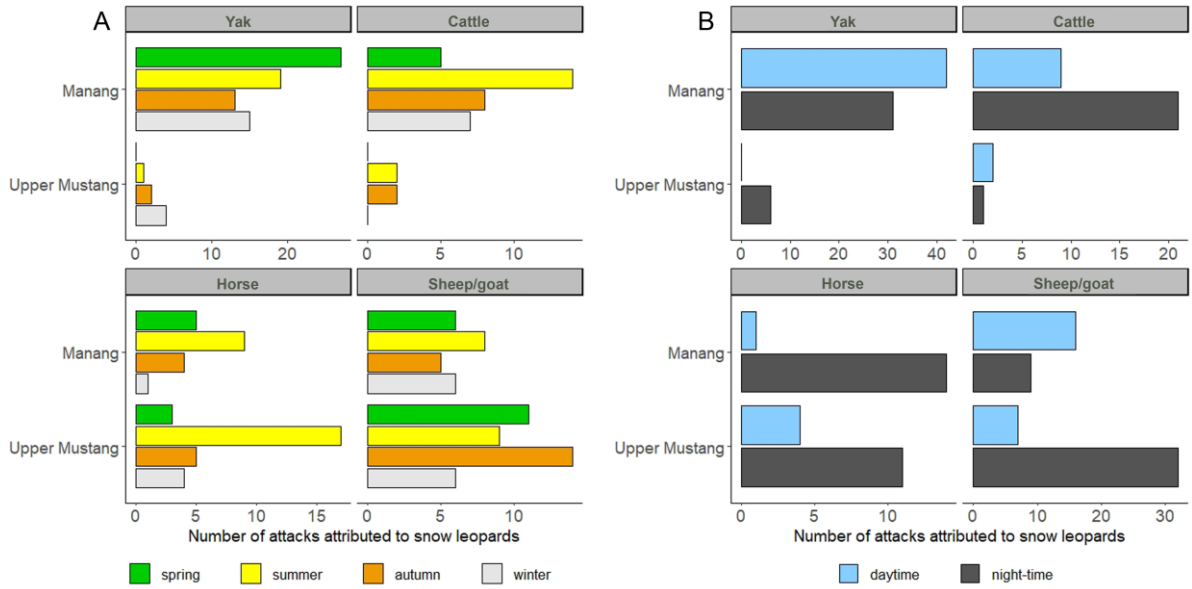

Figure 4.4. Seasonal (A) and daytime* (B) patterns of livestock depredation attributed to snow leopards in Manang and Upper Mustang during 2018–2020. *Few cases of attacks that occurred at unknown times and during transition times (dusk and dawn) are disregarded.

4.3.4 Use, effects, and impact of interventions

Daily herding of grazing animals during daylight hours was practised by all sheep/goat owners and the majority of yak owners in both study regions and by most cattle owners and some horse owners in Upper Mustang (Figures S4.1 and S4.2; Table S4.5). Sheep/goats were kept in night-time corrals daily, which also applied to most cattle in Upper Mustang, but the use of corrals was more flexible for other livestock species (Figures S4.1 and S4.2; Table S4.5). Simple stone wall corrals were used for most juvenile yaks in both regions as well as for the majority of sheep/goats and dzos in Upper Mustang, while traditional stone wall huts/houses

provided shelter to cattle and horses in both regions and to sheep/goats in Manang (Table S4.5). Dogs were used infrequently, mainly for guarding shepherd huts near night-time corrals for yaks in Manang (Figures S4.1 and S4.2; Table S4.5). The use of Foxlights and other night-time interventions (other light deterrents, music playing, flapping tapes, and dung burning) was reported exclusively by yak owners in Manang (Figures S4.1 and S4.2; Table S4.5).

Daily herding was not associated with a significant reduction in reported daytime depredation of cattle but was associated with increases in the reported number of snow leopard attacks on yaks ($\beta = 2.273 \pm 1.109$, $p = 0.040$) and yak losses ($\beta = 2.346 \pm 1.103$, $p = 0.034$) during daytime in Manang (Table 4.3). The daily use of night-time corrals was not associated with significant changes in reported horse depredation in Upper Mustang (Table 4.3). Noteworthy, shepherds of daily herded livestock in Manang were practically absent during one third (33.3%) of daytime attacks on yaks and a half (50.0%) of daytime attacks on cattle. Similarly, all horses killed at night-time were attacked outdoors even though they were supposed to be in corrals ($n_{attacks} = 9$). Foxlights were not associated with significant changes in reported yak depredation occurrence ($\beta = -0.327 \pm 1.049$, $p = 0.755$), which also applied to the number of depredation events ($\beta = -0.495 \pm 0.505$, $p = 0.327$) and depredated animals ($\beta = -0.295 \pm 0.471$, $p = 0.531$). For various reasons, these devices were inactive during 41.7% of night-time depredation events claimed by their owners. The presence of dogs near yak corrals during night-time was not associated with strong reductions in the reported depredation occurrence ($\beta = -1.463 \pm 0.936$, $p = 0.118$) and frequency ($\beta = -0.695 \pm 0.436$, $p = 0.111$) but tended to be so for the number of depredated individuals ($\beta = -0.764 \pm 0.394$, $p = 0.053$), which also applied to the use of other interventions (music playing, other light deterrents, flapping tapes, and dung burning; $\beta = -0.748 \pm 0.384$, $p = 0.052$). The use of multiple interventions was associated with a decrease in the reported frequency of yak depredation events ($\beta = -0.929 \pm 0.406$, $p = 0.022$) and the reported number of yaks depredated during night-time ($\beta = -0.947 \pm 0.364$, $p = 0.009$). Snow leopards killed similar numbers of sheep/goats per attack in simple stone wall corrals ($U = 93.5$, $p = 0.381$) and wire-fenced corrals ($U = 8$, $p = 0.346$) in Upper Mustang as in traditional stone wall huts/houses in Manang (Table S4.1). The presence of shepherds ($U = 182$, $p = 0.329$) during daytime and active Foxlights ($U = 144$, $p = 0.233$) and dog presence ($U = 49$, $p = 0.745$) during night-time were not associated with significant changes in the reported number of yaks killed per attack in Manang (Table S4.1).

According to the model-averaged results of the top-ranked models in the second set of GLMs, the region (Manang or Upper Mustang) was the only predictor with a significant effect on cattle depredation during daytime and night-time and on sheep/goat depredation during daytime, which were both higher in Manang (Tables 4.4 and S4.6). Moreover, according to the top-ranked models, keeping more individuals of yaks, horses, and sheep/goats was associated

with increases in the reported depredation occurrence and frequency as well as the reported number of depredated animals during night-time (Tables 4.4 and S4.6). The application of multiple interventions was the only intervention-related strategy associated with a significant decrease in reported depredation rates in the top-ranked models, and it applied to the number of yaks lost during night-time ($\beta = -0.843 \pm 0.313$, $p = 0.007$; Tables 4.4 and S4.6).

Table 4.3. Summary of generalised linear models (GLMs) describing the effects of interventions on livestock depredation attributed to snow leopards in Manang and Upper Mustang during 2018–2020. The models are adjusted for the total number of animals kept and the proportion of juveniles in holdings.

Intervention	Species	Time	Region	Model type	Response variable	Estimate	SE	95% CI	p
daily herding[A]	cattle	daytime	Manang	binomial	depredation yes/no	0.576	1.033	-1.441 – 2.683	0.577
				Poisson	number of depredation events	0.495	0.940	-1.382 – 2.368	0.599
				Poisson	number of livestock depredated	0.495	0.940	-1.382 – 2.368	0.599
	yak	daytime	Manang	binomial	depredation yes/no	2.338	1.605	-0.569 – 6.136	0.145
				Poisson	number of depredation events	2.273	1.109	0.449 – 5.243	0.040
				Poisson	number of livestock depredated	2.346	1.103	0.539 – 5.310	0.034
daily use of corrals	horse	night-time	Upper Mustang	binomial	depredation yes/no	0.408	0.873	-1.598 – 1.985	0.640
				Poisson	number of depredation events	0.271	0.803	-1.637 – 1.679	0.736
				Poisson	number of livestock depredated	0.619	0.680	-0.907 – 1.856	0.363
dogs near corral	yak	night-time	Manang	binomial	depredation yes/no	-1.463	0.936	-3.493 – 0.278	0.118
				Poisson	number of depredation events	-0.695	0.436	-1.627 – 0.110	0.111
				Poisson (zero-inflated)	number of livestock depredated	-0.764	0.394	-1.537 – 0.009	0.053
Foxlights	yak	night-time	Manang	binomial	depredation yes/no	-0.327	1.049	-2.553 – 1.714	0.755
				Poisson	number of depredation events	-0.495	0.505	-1.436 – 0.575	0.327
				Poisson (zero-inflated)	number of livestock depredated	-0.295	0.471	-1.217 – 0.627	0.531
other interventions	yak	night-time	Manang	binomial	depredation yes/no	-0.077	0.989	-2.169 – 1.826	0.938
				Poisson	number of depredation events	-0.646	0.460	-1.563 – 0.252	0.160

				Poisson (zero-inflated)	number of livestock depredated	-0.748	0.384	-1.500 – 0.005	0.052
number of interventions[B]	yak	night-time	Manang	binomial	depredation yes/no	-0.233	0.451	-1.172 – 0.647	0.606
				Poisson	number of depredation events	-0.257	0.213	-0.688 – 0.154	0.229
				Poisson (zero-inflated)	number of livestock depredated	-0.294	0.184	-0.654 – 0.066	0.110
multiple interventions[C]	yak	night-time	Manang	binomial	depredation yes/no	-1.003	0.904	-2.948 – 0.686	0.267
				Poisson	number of depredation events	-0.929	0.406	-1.750 – -0.145	0.022
				Poisson (zero-inflated)	number of livestock depredated	-0.947	0.364	-1.662 – -0.233	0.009

[A]compared to herds with occasional checks

[B]including dogs, Foxlights, and other interventions (music playing, other light deterrents, flapping tapes, and dung burning)

[C]use (yes/no) of multiple (> 1) interventions, including dogs, Foxlights, and other interventions (music playing, other light deterrents, flapping tapes, and dung burning)

Table 4.4. Summary of model-averaged results of the top-ranked generalised linear models (GLMs, ΔAICc < 2) describing livestock depredation attributed to snow leopards in Manang and Upper Mustang during 2018–2020. Only intercepts and predictors with p < 0.05 in model-averaged results are shown.

Species	Day-time	Model type	Response variable	Predictor variable	Esti-mate	SE	95% CI	p
yak	daytime	total_number + proportion_juveniles + shepherds_daily + region						
		binomial	depredation yes/no	Intercept	-0.230	1.434	-3.080 – 2.619	0.874
		Poisson	number of depredation events	Intercept	-1.793	1.053	-3.914 – 0.328	0.098
		Poisson	number of animals depredated	Intercept	-1.813	1.050	-3.929 – 0.302	0.093
				shepherds_daily_yes	2.266	1.093	0.065 – 4.467	0.044
	night-time	total_number + proportion_juveniles + dogs_use + foxlights_use + other_interventions_use + region						
		binomial	depredation yes/no	Intercept	0.257	0.398	-0.542 – 1.057	0.528
				total_number	1.220	0.437	0.340 – 2.100	0.007
		binomial[A]	depredation yes/no	Intercept	0.152	0.345	-0.544 – 0.848	0.668
				total_number	1.194	0.423	0.342 – 2.045	0.006
		binomial[B]	depredation yes/no	Intercept	0.196	0.379	-0.566 – 0.958	0.615
				total_number	1.212	0.427	0.352 – 2.073	0.006
		Poisson	number of depredation events	Intercept	-0.324	0.271	-0.867 – 0.219	0.243
				proportion_juveniles	0.472	0.206	0.056 – 0.888	0.026
				total_number	0.477	0.172	0.130 – 0.823	0.007
		Poisson[A]	number of depredation events	Intercept	-0.431	0.223	-0.881 – 0.019	0.060
				proportion_juveniles	0.475	0.206	0.058 – 0.891	0.025
				total_number	0.467	0.162	0.140 – 0.795	0.005
		Poisson[B]	number of depredation events	Intercept	-0.180	0.380	-0.932 – 0.572	0.639
				total_number	0.511	0.171	0.168 – 0.855	0.004
				count_Intercept	0.455	0.230	0.004 – 0.906	0.048

		zero-inflated negative binomial	number of animals depredated	count_total_number	0.709	0.159	0.397 – 1.021	<0.001
				zero_Intercept	-1.292	0.716	-2.696 – 0.111	0.071
		zero-inflated negative binomial[A]	number of animals depredated	count_Intercept	0.274	0.218	-0.153 – 0.702	0.209
				count_total_number	0.661	0.170	0.328 – 0.993	<0.001
				zero_Intercept	-1.336	0.783	-2.871 – 0.199	0.088
		zero-inflated negative binomial[B]	number of animals depredated	count_Intercept	0.546	0.196	0.163 – 0.930	0.005
				count_multiple_interventions_use_yes	-0.843	0.313	-1.457 – -0.229	0.007
				count_total_number	0.722	0.141	0.445 – 0.998	<0.001
				zero_Intercept	-1.368	0.675	-2.690 – -0.046	0.043
cattle	daytime	total_number + proportion_juveniles + shepherds_daily + region						
		binomial	depredation yes/no	Intercept	-2.793	0.439	-3.657 – -1.929	0.000
				region_UpperMustang	-1.851	0.857	-3.537 – -0.165	0.031
		Poisson	number of depredation events	Intercept	-2.731	0.397	-3.512 – -1.949	<0.001
				region_UpperMustang	-1.899	0.838	-3.549 – -0.250	0.024
		Poisson	number of animals depredated	Intercept	-2.731	0.397	-3.512 – -1.949	<0.001
				region_UpperMustang	-1.899	0.838	-3.549 – -0.250	0.024
	night-time	total_number + proportion_juveniles + corral_use_daily + region						
		binomial	depredation yes/no	Intercept	-1.800	0.293	-2.377 – -1.223	<0.001
				region_UpperMustang	-4.032	1.352	-6.691 – -1.373	0.003
		negative binomial	number of depredation events	Intercept	-1.767	0.263	-2.284 – -1.251	<0.001
				region_UpperMustang	-3.704	1.197	-6.059 – -1.348	0.002
		negative binomial	number of animals depredated	Intercept	-1.652	0.273	-2.190 – -1.115	<0.001
				region_UpperMustang	-3.781	1.192	-6.127 – -1.436	0.002
horse	night-time	total_number + proportion_juveniles + corral_use_daily + region						
		binomial	depredation yes/no	Intercept	-2.161	0.347	-2.844 – -1.478	<0.001
				total_number	0.551	0.217	0.124 – 0.977	0.011

		Poisson	number of depredation events	Intercept	-2.117	0.321	-2.748 – -1.485	<0.001
				total_number	0.506	0.191	0.131 – 0.881	0.008
		Poisson	number of animals depredated	Intercept	-2.143	0.297	-2.727 – -1.559	<0.001
				total_number	0.464	0.188	0.094 – 0.834	0.014
sheep/ goat	daytime	total_number + proportion_juveniles + region						
		binomial	depredation yes/no	Intercept	-0.660	0.421	-1.497 – 0.178	0.123
				region_UpperMustang	-1.617	0.631	-2.874 – -0.360	0.012
		negative binomial	number of depredation events	Intercept	-0.507	0.342	-1.188 – 0.174	0.145
				region_UpperMustang	-1.675	0.554	-2.779 – -0.572	0.003
		negative binomial	number of animals depredated	Intercept	-0.061	0.428	-0.914 – 0.792	0.888
				region_UpperMustang	-1.964	0.626	-3.210 – -0.718	0.002
	night-time	total_number + proportion_juveniles + region						
		binomial	depredation yes/no	Intercept	-0.388	0.368	-1.118 – 0.341	0.297
		Poisson	number of depredation events	Intercept	-0.851	0.278	-1.403 – -0.299	0.003
		zero-inflated negative binomial	number of animals depredated	count_Intercept	1.684	0.351	0.997 – 2.371	<0.001
				count_total_number	0.407	0.140	0.133 – 0.681	0.004
				zero_Intercept	0.102	0.269	-0.425 – 0.630	0.703

[A]total_number + proportion_juveniles + number_interventions + region
[B]total_number + proportion_juveniles + multiple_interventions_use + region

4.4 Discussion

This study reveals important insights into the pattern and spatial heterogeneity of livestock depredation by snow leopards and provides targets for management and mitigation measures in the Annapurna region, where livestock depredation by snow leopards remains a serious issue of conservation concern. Annual livestock depredation rates attributed to these predators in our study area (3.2–3.6% of livestock holdings) were similar to the estimates previously reported from the same region (1.0%–5.6%; Oli et al. 1994; Wegge et al. 2012; Aryal et al. 2014d; Lama 2018; Tiwari et al. 2020). They are at moderate levels compared to other areas with lower (0.2–0.3%; e.g., Alexander et al. 2015; Devkota et al. 2017; Augugliaro et al. 2020) and higher (up to 10.4%; e.g., Devkota et al. 2013; Khanal et al. 2020a) levels of depredation by snow leopards. Snow leopards were among the main mortality factors for livestock during the survey period, being responsible for up to 40% of livestock losses. Consequently, snow leopard depredation is one of the top threats to rural livelihoods in the Annapurna region and of relatively high relevance, particularly compared to other areas where harsh environmental conditions, sympatric predators, and diseases account for a greater proportion of livestock mortality (e.g., Li et al. 2013; Suryawanshi et al. 2013; Din et al. 2017). Therefore, we reiterate that reducing livestock depredation by enhanced livestock protection is a top priority for snow leopard conservation and local livelihoods in the Annapurna region.

Generally, we found substantial differences in livestock selection and depredation patterns between Manang and Upper Mustang. These may be related to differences in intervention applications but may also be caused by other parameters like small-scale landscape characteristics, snow leopard and wild prey abundance, and individual prey selection, which we were unable to account for due to the lack of appropriate information. Although it still remains obscure how strongly these variables influence livestock depredation by snow leopards (e.g., Khorozyan et al. 2015; Suryawanshi et al. 2017; Khanal et al. 2020a), this information is also essential for wildlife managers to consider to mitigate human-snow leopard conflicts. Either way, the heterogeneity of livestock depredation in two adjacent districts of the same protected area observed in this study confirms demands for site-specific and locally-adapted conservation measures (Chetri et al. 2019a).

In Upper Mustang, most snow leopard attacks on livestock were targeted on sheep/goats, occurred during night-time, and frequently included surplus killings, i.e. depredation of multiple individuals in a single attack (Jackson and Wangchuk 2001; with a maximum of 74 individuals in our study). Hence, better protection of sheep/goats during night-time, when these animals were in corrals and when the majority of depredation events were reported, is urgently needed to mitigate conflicts in Upper Mustang, and corral improvement might appear to be the most promising solution. Simple stone wall corrals, which are used in Upper Mustang, are designed

to keep flocks together, but they do not prevent intrusions of agile and jumping predators like snow leopards (Samelius et al. 2021; see Figure 4.2). Improvement of night-time corrals successfully reduced and even eliminated night-time attacks of snow leopards in other parts of their range (e.g., Jackson and Wangchuk 2004; Jamwal et al. 2019; Samelius et al. 2021). Although construction of predator-proof corrals requires comparatively high acquisition costs, time, and workforce (Jackson and Wangchuk 2004), it is meaningful in areas like Upper Mustang, where minor repairs of simple stone wall corrals are not enough. In addition, night-time depredation of sheep/goats in Manang, where these animals are kept in stone wall huts/houses, could be reduced by minor corral improvements, for example, covering openings with wire mesh or similar material (Kuksin and Kuksina 2009). A disadvantage of corrals is that they are stationary and cannot be used year-round if local pastoralism is based on seasonal shifts of grazing grounds, which is at least partially practised by transhumant families in Upper Mustang (Aryal et al. 2014d).

To offset costs and immobility of night-time corrals, it appears reasonable to combine them with additional, more flexible interventions. Our findings from Manang suggest that the presence of dogs and the use of other interventions, including light deterrents, flapping tapes, music playing, and dung burning, may have helped to reduce the number of yaks depredated during night-time. However, our data is not sufficient to disentangle the individual effectiveness of each of these interventions. Guarding dogs can promote human-carnivore co-existence when they are properly bred, bonding to livestock groups, and trained for attentiveness, watchfulness, and trustworthiness, but they can be ineffective otherwise (e.g., Rust et al. 2013; Eklund et al. 2017; Khorozyan et al. 2017; Kinka and Young 2019; Khorozyan and Waltert 2021). A recent study in Mongolia confirmed that dogs might also be an effective intervention strategy against snow leopards (Augugliaro et al. 2020). However, when implementing projects to mitigate human-carnivore conflicts, one should bear in mind that dogs may also impede conservation efforts by disease transmission, wildlife displacement, and predation (Namgail 2004; Hughes and Macdonald 2013; Baral et al. 2019). Light deterrents and acoustic devices should theoretically be effective against snow leopards, which are known to avoid centres of anthropogenic activity (e.g., Wolf and Ale 2009), though not in all parts of their range (e.g., Alexander et al. 2016b). Promisingly, Foxlights discouraged wild felids from killing livestock elsewhere (Ohrens et al. 2019; Naha et al. 2020). We did not find significant positive effects of Foxlights, which were inactive during many depredation events claimed by the owners, and we do not know whether this was so due to malfunctioning or non-use. However, our results suggest that the use of other interventions, which were mainly light/acoustic deterrents and dung burning, tended to reduce the number of yaks depredated during night-time, though we are unable to ascribe this observation to specific types of interventions. Interestingly, our findings also hint that the use and possibly rotation of multiple interventions

may be a valuable strategy to reduce livestock losses to snow leopards. Although more research is needed to disentangle the effects of individual intervention strategies, the use of multiple interventions may prevent predator habituation, which can rapidly reduce the effectiveness of deterrents and guarding animals (Khorozyan and Waltert 2019).

During the nights, livestock owners holding more individuals of yaks, horses and sheep/goats suffered higher depredation losses, making these large holdings potential targets for conservation efforts. However, we argue that interventions should be focused not only on such hotspot large holdings, but also on small households where losses are proportionally much higher and owners can suffer and respond more negatively (Ikeda 2004).

Apart from night-time losses, daytime depredation added up to livestock mortality, especially in Manang. Daytime attacks were reported on closely herded sheep/goats and on more scattered herds of yaks and cattle. Although herders were absent during many attacks on yaks, depredation also frequently occurred in the presence of herders who supervised this species and small livestock. The numbers of yaks killed per daytime attacks were similar in the presence and absence of herders. Daily herding was even associated with increased numbers of snow leopard attacks on yaks and increased yak losses during daytime, while we did not find a relationship between the daily application of herding and cattle depredation during daytime. Presumably, the former result might occur as shepherds witnessing attacks might be more likely to assign depredation to snow leopards than owners finding carcasses only. In general, the effectiveness of shepherds as a traditional intervention strategy (Linnell et al. 2012) is affected by the number, age, and experience of shepherds (e.g., Ogada et al. 2003; Tumenta et al. 2013). A recent study from the adjoining Nar Phu valley linked the ineffectiveness of herding with the high age of herders and the rare use of guarding dogs (Tiwari et al. 2020). Although our data does not allow us to make conclusions about the effects of shepherd age and experience, insights from other areas suggest that daytime losses to snow leopards could be reduced by careful control of straggling individuals and avoidance of rugged pastures (Johansson et al. 2015; Mijiddorj et al. 2018). More knowledge on livestock kill sites (e.g., Krofel et al. 2021) obtained from questionnaire surveys or telemetry studies would yield valuable information for the prevention of depredation during daylight hours. Nevertheless, it is important to bear in mind that snow leopards are not the only factor to be considered by livestock owners who need to trade off various threats and benefits to livestock, such as depredation risk and foraging access, when selecting suitable pasture areas for their animals.

Conclusion

The results of our study in the Nepalese Himalaya affirmed the need to implement, improve, and test suitable mitigation measures that benefit human-snow leopard co-existence. We demonstrate spatial differences in livestock depredation patterns by snow leopards in the Annapurna region. Our findings suggest that improved night-time protection of sheep/goats, particularly in Upper Mustang, and of yaks in combination with changes in daytime herding practices and the use of deterrents might be key to reducing livestock depredation. We call for more controlled randomised experimental research on the long-term effectiveness of dogs and other non-invasive intervention strategies, such as light and acoustic deterrents, in isolation, combination, and rotation. The suggested interventions should address site-specific local conditions, consider ethical issues of proper sampling, and be carried out in parallel with other conservation measures to enhance positive effects on snow leopards and local livelihoods. These measures may include investments in livestock health to reduce non-predator mortality, improved grazing management to benefit wild prey populations and limit disease transmission, and promotion of alternative sources of income, such as tourism-related activities and sales of handicrafts (e.g., Mishra et al. 2003; Jackson 2012; Vannelli et al. 2019). The incorporation of interventions to local livelihoods will safeguard co-existence for the benefit of humans and snow leopards.

4.5 Acknowledgments

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4.6 Supplementary material

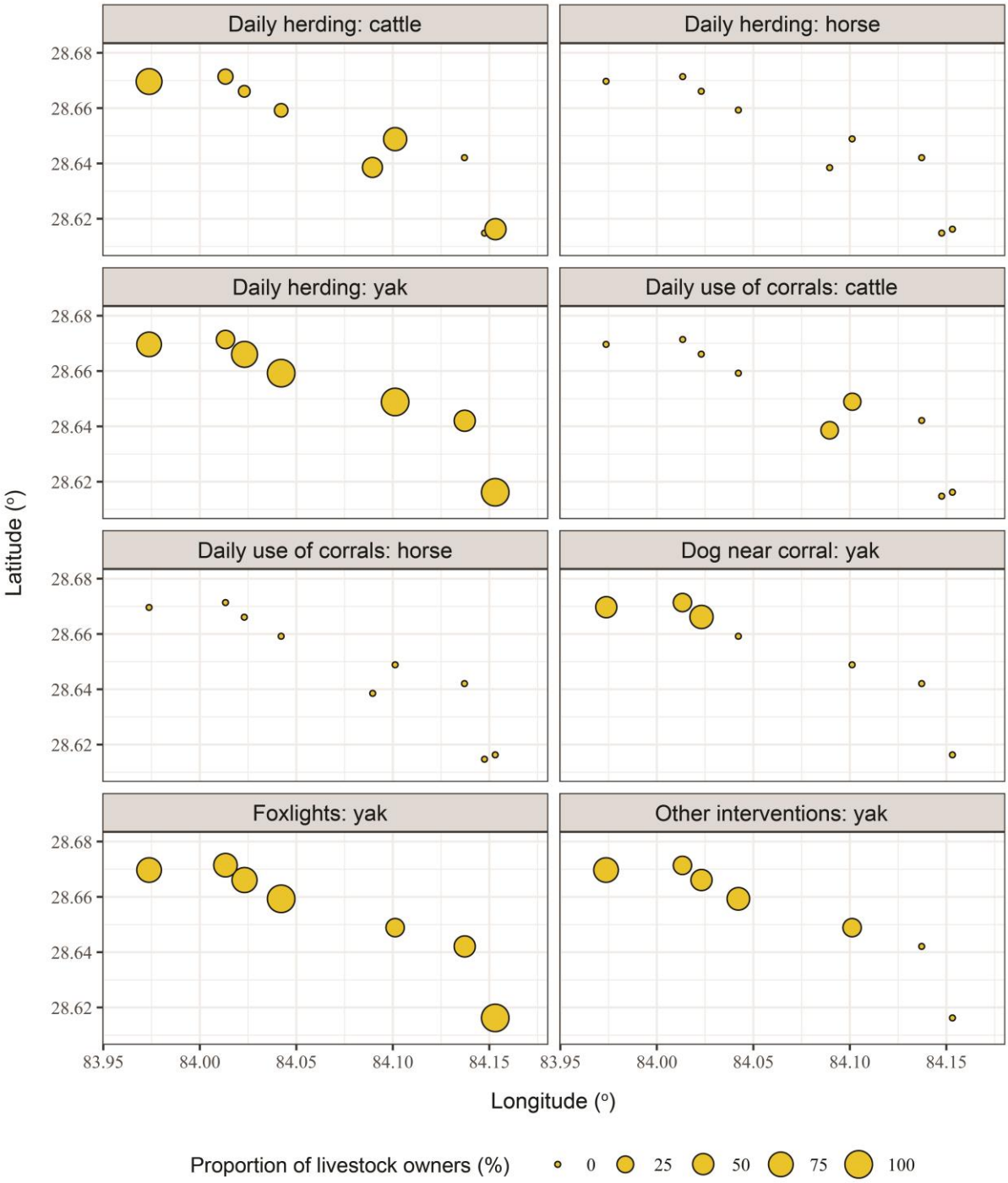

Figure S4.1. The proportion of interviewed livestock owners applying given intervention strategies to protect various livestock species in studied settlements (circles) in Manang in the Annapurna Conservation Area during 2018–2020.

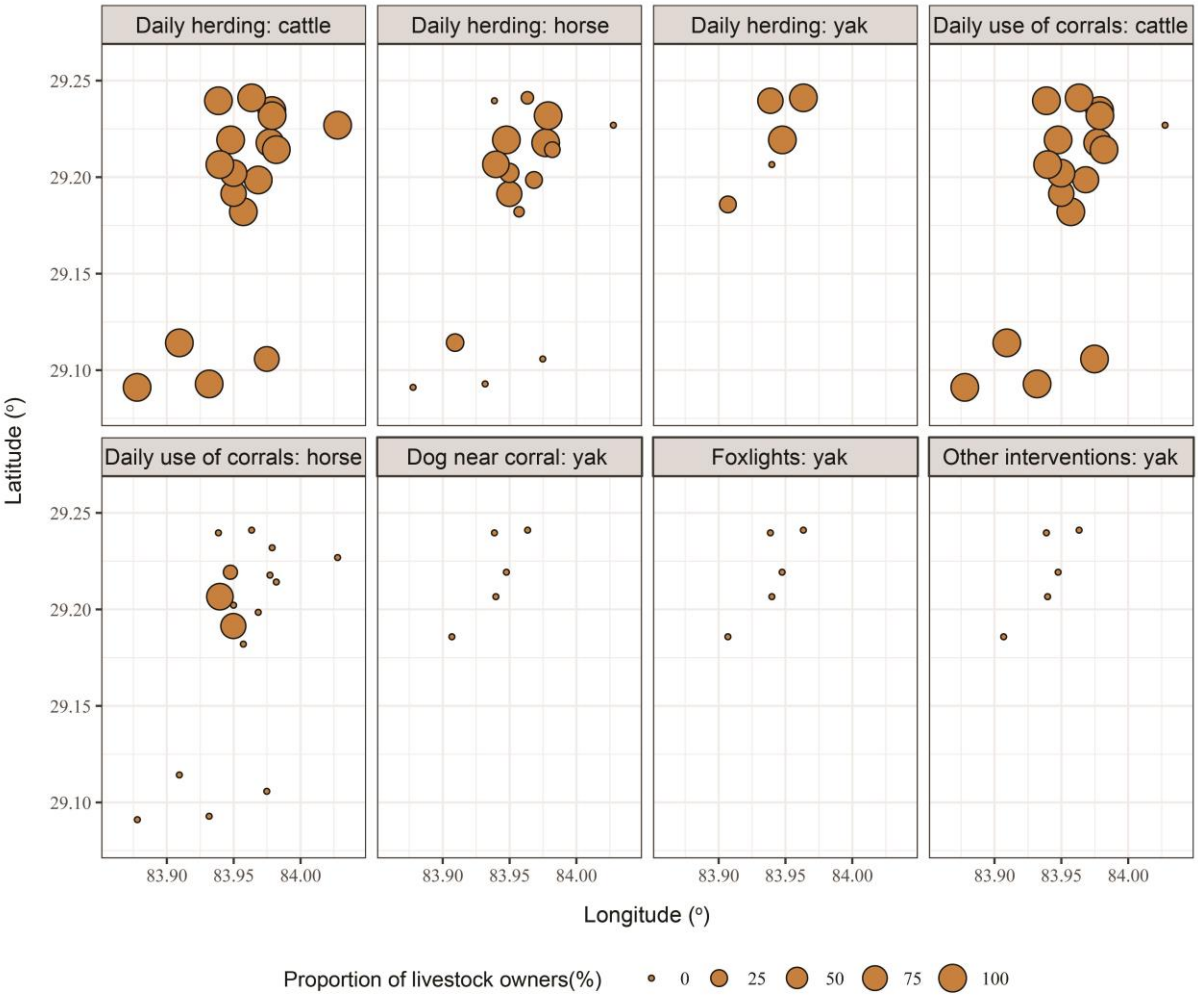

Figure S4.2. The proportion of interviewed livestock owners applying given intervention strategies to protect various livestock species in studied settlements (circles) in Upper Mustang in the Annapurna Conservation Area during 2018–2020.

Table S4.1. Results of Mann-Whitney U tests to analyse livestock depredation attributed to snow leopards in Manang and Upper Mustang during 2018–2020.

Parameter/Comparison	Group 1			Group 2			Test statistics	
	Definition	Sample size	Mean	Definition	Sample size	Mean	U	p
Size of the livestock holding: yak	Manang	146	8.2	Upper Mustang	183	2.4	15,434	<0.001
Size of the livestock holding: cattle	Manang	146	3.2	Upper Mustang	183	4.4	8,547.5	<0.001
Size of the livestock holding: dzo	Manang	146	0.0	Upper Mustang	183	0.1	12,556	0.003
Size of the livestock holding: horse	Manang	146	1.2	Upper Mustang	183	1.6	11,462	0.022
Size of the livestock holding: sheep/goat	Manang	146	7.6	Upper Mustang	183	22.3	11,682	0.009
Size of the livestock holding: all	Manang	146	20.2	Upper Mustang	183	30.8	10,482	0.001
Number of animals killed per attack: yak	daytime	42	1.0	night-time	37	1.7	496	<0.001
Number of animals killed per attack: cattle	daytime	11	1.0	night-time	22	1.1	110	0.332
Number of animals killed per attack: horse	daytime	5	1.0	night-time	25	1.1	57.5	0.562
Number of animals killed per attack: sheep/goat	daytime	23	1.5	night-time	41	8.0	66.5	<0.001
Number of animals killed per attack: all	daytime	81	1.2	night-time	125	3.5	3,239	<0.001
Number of sheep/goats killed per attack in corral	stone wall hut/house	9	4.6	simple stone wall corral	26	9.4	93.5	0.381
Number of sheep/goats killed per attack in corral	stone wall hut/house	9	4.6	wire-fenced corral	3	10.0	8	0.346
Number of sheep/goats killed per attack in corral	simple stone wall corral	26	9.4	wire-fenced corral	3	10.0	31.5	0.614
Number of yaks killed per attack during daytime	shepherds present	28	1.0	shepherds absent	14	1.0	182	0.329
Number of yaks killed per attack during night-time	Foxlights active	14	1.6	Foxlights inactive	17	1.2	144	0.233
Number of yaks killed per attack during night-time	dogs present	4	1.3	dogs absent	27	1.4	49	0.745

Table S4.2. Results of χ2 tests to analyse livestock depredation attributed to snow leopards in Manang and Upper Mustang during 2018–2020.

Parameter/Comparison	Species	Sample size		Test statistics	
		Manang	Upper Mustang	χ^2	p
Differences in the composition of the livestock community between Manang and Upper Mustang	all			1478.7	<0.001
Seasonal differences in depredation patterns in Manang	yak	74		2.92	0.404
Seasonal differences in depredation patterns in Manang	cattle	34		2.41	0.491
Seasonal differences in depredation patterns in Manang	horse	19		3.83	0.280
Seasonal differences in depredation patterns in Manang	sheep/goat	25		0.36	0.948
Seasonal differences in depredation patterns in Manang	all	152		4.10	0.251
Seasonal differences in depredation patterns in Upper Mustang	yak		7	2.85	0.415
Seasonal differences in depredation patterns in Upper Mustang	cattle		4	2.67	0.446
Seasonal differences in depredation patterns in Upper Mustang	horse		29	7.03	0.071
Seasonal differences in depredation patterns in Upper Mustang	sheep/goat		40	1.77	0.622
Seasonal differences in depredation patterns in Upper Mustang	all		80	4.35	0.226
Seasonal differences in depredation patterns between Manang and Upper Mustang	yak	74	7	7.01	0.071
Seasonal differences in depredation patterns between Manang and Upper Mustang	cattle	34	4	2.43	0.488
Seasonal differences in depredation patterns between Manang and Upper Mustang	horse	19	29	2.92	0.405
Seasonal differences in depredation patterns between Manang and Upper Mustang	sheep/goat	25	40	2.46	0.482
Seasonal differences in depredation patterns between Manang and Upper Mustang	all	152	80	4.71	0.194
Daytime differences in depredation patterns in Manang	yak	73		0.56	0.455
Daytime differences in depredation patterns in Manang	cattle	30		1.74	0.188
Daytime differences in depredation patterns in Manang	horse	15		4.97	0.026
Daytime differences in depredation patterns in Manang	sheep/goat	25		0.51	0.475
Daytime differences in depredation patterns in Manang	all	143		0.09	0.767
Daytime differences in depredation patterns in Upper Mustang	yak		6	1.78	0.182
Daytime differences in depredation patterns in Upper Mustang	cattle		3	0.00	1.000

Daytime differences in depredation patterns in Upper Mustang	horse		15	0.88	0.348
Daytime differences in depredation patterns in Upper Mustang	sheep/goat		39	7.56	0.006
Daytime differences in depredation patterns in Upper Mustang	all		63	10.64	0.001
Daytime differences in depredation patterns between Manang and Upper Mustang	yak	73	6	5.24	0.022
Daytime differences in depredation patterns between Manang and Upper Mustang	cattle	30	3	0.42	0.521
Daytime differences in depredation patterns between Manang and Upper Mustang	horse	15	15	0.96	0.327
Daytime differences in depredation patterns between Manang and Upper Mustang	sheep/goat	25	39	12.10	0.001
Daytime differences in depredation patterns between Manang and Upper Mustang	all	143	63	12.18	<0.001

Table S4.3. Seasonal patterns of livestock depredation attributed to snow leopards in Manang and Upper Mustang during 2018–2020.

Season	**Species**	**Attacks by snow leopards**				**Individuals depredated by snow leopards**			
		Manang		Upper Mustang		Manang		Upper Mustang	
		Number	Proportion (%)	Number	Proportion (%)	Number	Proportion (%)	Number	Proportion (%)
spring	yak	27	36.5	0	0.0	34	38.2	0	0.0
	cattle	5	14.7	0	0.0	5	13.9	0	0.0
	horse	5	26.3	3	10.3	5	26.3	3	9.4
	sheep/goat	6	24.0	11	27.5	21	31.8	100	33.4
	all	43	28.3	14	17.3	65	31.0	103	28.9
summer	yak	19	25.7	1	14.3	23	25.8	2	9.5
	cattle	14	41.2	2	50.0	16	44.4	2	50.0
	horse	9	47.4	17	58.6	9	47.4	20	62.5
	sheep/goat	8	32.0	9	22.5	18	27.3	34	11.4
	all	50	32.9	30	37.0	66	31.4	59	16.5
autumn	yak	13	17.6	2	28.6	15	16.9	4	19.0
	cattle	8	23.5	2	50.0	8	22.2	2	50.0
	horse	4	21.1	5	17.2	4	21.1	5	15.6
	sheep/goat	5	20.0	14	35.0	8	12.1	80	26.8
	all	30	19.7	23	28.4	35	16.7	91	25.5

winter	yak	15	20.3	4	57.1	17	19.1	15	71.4
	cattle	7	20.6	0	0.0	7	19.4	0	0.0
	horse	1	5.3	4	13.8	1	5.3	4	12.5
	sheep/goat	6	24.0	6	15.0	19	28.8	85	28.4
	all	29	19.1	14	17.3	44	21.0	104	29.1

Table S4.4. Daytime patterns of livestock depredation attributed to snow leopards in Manang and Upper Mustang during 2018–2020. Depredation events at unknown times of attack and during transition times (dusk and dawn) are disregarded.

Time	**Species**	**Attacks by snow leopards**				**Number of individuals killed by snow leopards**				**Number of individuals killed per attack**		
		Manang		Upper Mustang		Manang		Upper Mustang		Manang	Upper Mustang	combined
		Number	%	Number	%	Number	%	Number	%			
daytime	yak	42	57.5	0	0.0	44	50.0	0	0.0	1.0		1.0
	cattle	9	30.0	2	66.7	9	28.1	2	66.7	1.0	1.0	1.0
	horse	1	6.7	4	26.7	1	6.7	4	23.5	1.0	1.0	1.0
	sheep/goat	16	64.0	7	17.9	25	37.9	10	3.4	1.6	1.4	1.5
	all	68	47.6	13	20.6	79	39.3	16	4.8	1.2	1.2	1.2
night-time	yak	31	42.5	6	100.0	44	50.0	18	100.0	1.4	3.0	1.7
	cattle	21	70.0	1	33.3	23	71.9	1	33.3	1.1	1.0	1.1
	horse	14	93.3	11	73.3	14	93.3	13	76.5	1.0	1.2	1.1
	sheep/goat	9	36.0	32	82.1	41	62.1	286	96.6	4.6	8.9	8.0
	all	75	52.4	50	79.4	122	60.7	318	95.2	1.6	6.4	3.5

Table S4.5. List of interventions applied by livestock owners in Manang and Upper Mustang during 2018–2020.

Region	Species	House-holds (n)	Shepherd herding during daytime grazing			Corral use during night-time			Corral type during night-time			Dogs		Fox-lights	Other inter-ventions[A]
			daily	vari-able	occa-sional	daily	vari-able	never	simple stone wall corral	iron/ wire-fenced corral	stone wall hut/ house	Day-time	Night-time		Night-time
Manang	yak	33	27	2	4	0	33	0	33	1	0	0	12	25	15
	cattle	127	36	7	84	5	122	0	0	0	127	0	0	1	0
	dzo	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	horse	94	0	0	94	0	94	0	0	0	94	0	0	0	0
	sheep/ goat	26	26	0	0	26	0	0	0	0	26	1	1	0	0
Upper Mustang	yak	13	8	4	1	0	12	1	11	1	0	0	0	0	0
	cattle	172	168	0	4	160	12	0	0	0	172	0	0	0	0
	dzo	11	1	0	10	0	11	0	11	0	0	0	0	0	0
	horse	123	38	0	85	17	106	0	1	0	122	0	0	0	0
	sheep/ goat	53	53	0	0	53	0	0	50	3	0	1	1	0	0

[A]including other light deterrents, music playing, flapping tapes, and dung burning

Table S4.6. Summary of model-averaged results of the top-ranked generalised linear models (GLMs, ΔAICc < 2) describing livestock depredation attributed to snow leopards in Manang and Upper Mustang during 2018–2020.

Species	Daytime	Model type	Response variable	Predictor variable	Estimate	SE	95% CI	p
yak	daytime	total_number + proportion_juveniles + shepherds_daily + region						
		binomial	depredation yes/no	Intercept	-0.230	1.434	-3.080 – 2.619	0.874
				region_UpperMustang	-20.682	2,649.5	-5,365.4 – 5,324.0	0.994
				shepherds_daily_yes	1.407	1.511	-1.593 – 4.407	0.358
				total_number	0.963	0.762	-0.552 – 2.478	0.213
		Poisson	number of depredation events	Intercept	-1.793	1.053	-3.914 – 0.328	0.098
				region_UpperMustang	-19.127	2,334.6	-4,730.5 – 4,692.3	0.994
				shepherds_daily_yes	2.189	1.099	-0.024 – 4.402	0.053
				total_number	0.146	0.168	-0.188 – 0.481	0.391
				proportion_juveniles	-0.116	0.197	-0.509 – 0.276	0.561
			number of animals depredated	Intercept	-1.813	1.050	-3.929 – 0.302	0.093
				region_UpperMustang	-19.168	2,320.9	-4,702.7 – 4,664.4	0.994
				shepherds_daily_yes	2.266	1.093	0.065 – 4.467	0.044
				total_number	0.129	0.159	-0.188 – 0.445	0.425
				proportion_juveniles	-0.119	0.195	-0.507 – 0.269	0.548
	night-time	total_number + proportion_juveniles + dogs_use + foxlights_use + other_interventions_use + region						
		binomial	depredation yes/no	Intercept	0.257	0.398	-0.542 – 1.057	0.528
				total_number	1.220	0.437	0.340 – 2.100	0.007
				proportion_juveniles	0.188	0.330	-0.469 – 0.845	0.575
				dogs_use_yes	-0.386	0.699	-1.777 – 1.005	0.586
		binomial[A]	depredation yes/no	Intercept	0.152	0.345	-0.544 – 0.848	0.668
				total_number	1.194	0.423	0.342 – 2.045	0.006
				proportion_juveniles	0.157	0.298	-0.437 – 0.751	0.605

		binomial[B]	depredation yes/no	Intercept	0.196	0.379	-0.566 – 0.958	0.615
				total_number	1.212	0.427	0.352 – 2.073	0.006
				proportion_juveniles	0.126	0.274	-0.420 – 0.671	0.652
				multiple_interventions_use_yes	-0.099	0.377	-0.853 – 0.655	0.798
		Poisson	number of depredation events	Intercept	-0.324	0.271	-0.867 – 0.219	0.243
				proportion_juveniles	0.472	0.206	0.056 – 0.888	0.026
				total_number	0.477	0.172	0.130 – 0.823	0.007
				dogs_use_yes	-0.215	0.390	-0.990 – 0.560	0.586
				region_UpperMustang	-0.271	0.446	-1.157 – 0.615	0.549
				other_interventions_use_yes	-0.097	0.284	-0.663 – 0.468	0.736
		Poisson[A]	number of depredation events	Intercept	-0.431	0.223	-0.881 – 0.019	0.060
				proportion_juveniles	0.475	0.206	0.058 – 0.891	0.025
				total_number	0.467	0.162	0.140 – 0.795	0.005
				region_UpperMustang	-0.162	0.348	-0.856 – 0.531	0.646
		Poisson[B]	number of depredation events	Intercept	-0.180	0.380	-0.932 – 0.572	0.639
				multiple_interventions_use_yes	-0.441	0.516	-1.461 – 0.579	0.397
				region_UpperMustang	-0.415	0.589	-1.579 – 0.748	0.484
				total_number	0.511	0.171	0.168 – 0.855	0.004
				proportion_juveniles	0.330	0.279	-0.222 – 0.883	0.241
		zero-inflated negative binomial	number of animals depredated	count_Intercept	0.455	0.230	0.004 – 0.906	0.048
				count_other_interventions_use_yes	-0.578	0.411	-1.383 – 0.228	0.160
				count_total_number	0.709	0.159	0.397 – 1.021	<0.001
				zero_Intercept	-1.292	0.716	-2.696 – 0.111	0.071
				count_proportion_juveniles	0.052	0.128	-0.200 – 0.303	0.686
				count_Intercept	0.274	0.218	-0.153 – 0.702	0.209
				count_total_number	0.661	0.170	0.328 – 0.993	<0.001

		zero-inflated negative binomial[A]	number of animals depredated	zero_Intercept	-1.336	0.783	-2.871 – 0.199	0.088
				count_number_of_interventions	-0.146	0.179	-0.498 – 0.206	0.415
				count_proportion_juveniles	0.085	0.164	-0.236 – 0.406	0.606
		zero-inflated negative binomial[B]	number of animals depredated	count_Intercept	0.546	0.196	0.163 – 0.930	0.005
				count_multiple_interventions_use	-0.843	0.313	-1.457 – -0.229	0.007
				count_total_number	0.722	0.141	0.445 – 0.998	<0.001
				zero_Intercept	-1.368	0.675	-2.690 – -0.046	0.043
				count_proportion_juveniles	0.084	0.156	-0.222 – 0.389	0.592
cattle	daytime	total_number + proportion_juveniles + shepherds_daily + region						
		binomial	depredation yes/no	Intercept	-2.793	0.439	-3.657 – -1.929	<0.001
				region_UpperMustang	-1.851	0.857	-3.537 – -0.165	0.031
				total_number	0.439	0.224	-0.002 – 0.880	0.051
				proportion_juveniles	-0.042	0.218	-0.471 – 0.388	0.849
				shepherds_daily_yes	0.079	0.430	-0.767 – 0.925	0.854
		Poisson	number of depredation events	Intercept	-2.731	0.397	-3.512 – -1.949	<0.001
				region_UpperMustang	-1.899	0.838	-3.549 – -0.250	0.024
				total_number	0.181	0.195	-0.202 – 0.563	0.354
				shepherds_daily_yes	0.140	0.460	-0.764 – 1.045	0.761
				proportion_juveniles	-0.031	0.171	-0.367 – 0.304	0.856
		Poisson	number of animals depredated	Intercept	-2.731	0.397	-3.512 – -1.949	<0.001
				region_UpperMustang	-1.899	0.838	-3.549 – -0.250	0.024
				total_number	0.181	0.195	-0.202 – 0.563	0.354
				shepherds_daily_yes	0.140	0.460	-0.764 – 1.045	0.761
				proportion_juveniles	-0.031	0.171	-0.367 – 0.304	0.856
	night-time	total_number + proportion_juveniles + corral_use_daily + region						
		binomial	depredation yes/no	Intercept	-1.800	0.293	-2.377 – -1.223	<0.001
				region_UpperMustang	-4.032	1.352	-6.691 – -1.373	0.003
				total_number	0.128	0.197	-0.259 – 0.515	0.517

				proportion_juveniles	0.222	0.289	-0.346 – 0.791	0.443
				corral_use_daily_yes	0.553	0.937	-1.288 – 2.394	0.556
		negative binomial	number of depredation events	Intercept	-1.767	0.263	-2.284 – -1.251	<0.001
				region_UpperMustang	-3.704	1.197	-6.059 – -1.348	0.002
				proportion_juveniles	0.115	0.213	-0.302 – 0.533	0.588
				corral_use_daily_yes	0.270	0.648	-1.004 – 1.544	0.678
				total_number	0.028	0.094	-0.156 – 0.212	0.764
		negative binomial	number of animals depredated	Intercept	-1.652	0.273	-2.190 – -1.115	<0.001
				region_UpperMustang	-3.781	1.192	-6.127 – -1.436	0.002
				proportion_juveniles	0.173	0.254	-0.326 – 0.672	0.497
				corral_use_daily_yes	0.199	0.613	-1.006 – 1.403	0.747
				total_number	0.028	0.106	-0.181 – 0.237	0.792
horse	night-time	total_number + proportion_juveniles + corral_use_daily + region						
		binomial	depredation yes/no	Intercept	-2.161	0.347	-2.844 – -1.478	<0.001
				region_UpperMustang	-0.393	0.509	-1.393 – 0.608	0.441
				total_number	0.551	0.217	0.124 – 0.977	0.011
				proportion_juveniles	0.033	0.121	-0.206 – 0.271	0.788
				corral_use_daily_yes	0.036	0.314	-0.582 – 0.654	0.908
		Poisson	number of depredation events	Intercept	-2.117	0.321	-2.748 – -1.485	<0.001
				region_UpperMustang	-0.480	0.490	-1.444 – 0.483	0.328
				total_number	0.506	0.191	0.131 – 0.881	0.008
				proportion_juveniles	0.125	0.167	-0.205 – 0.454	0.458
		Poisson	number of animals depredated	Intercept	-2.143	0.297	-2.727 – -1.559	<0.001
				proportion_juveniles	0.172	0.177	-0.176 – 0.520	0.333
				total_number	0.464	0.188	0.094 – 0.834	0.014
				region_UpperMustang	-0.283	0.404	-1.078 – 0.512	0.485
				corral_use_daily_yes	0.088	0.344	-0.589 – 0.764	0.800
sheep/ goat	daytime	total_number + proportion_juveniles + region						
		binomial		Intercept	-0.660	0.421	-1.497 – 0.178	0.123

			depredation yes/no	region_UpperMustang	-1.617	0.631	-2.874 – -0.360	0.012
				proportion_juveniles	0.101	0.226	-0.346 – 0.548	0.658
				total_number	-0.060	0.259	-0.573 – 0.454	0.820
		negative binomial	number of depredation events	Intercept	-0.507	0.342	-1.188 – 0.174	0.145
				region_UpperMustang	-1.675	0.554	-2.779 – -0.572	0.003
				proportion_juveniles	0.053	0.162	-0.267 – 0.373	0.745
				total_number	-0.045	0.215	-0.471 – 0.381	0.836
		negative binomial	number of animals depredated	Intercept	-0.061	0.428	-0.914 – 0.792	0.888
				region_UpperMustang	-1.964	0.626	-3.210 – -0.718	0.002
				total_number	-0.086	0.297	-0.675 – 0.503	0.775
	night-time	total_number + proportion_juveniles + region						
		binomial	depredation yes/no	Intercept	-0.388	0.368	-1.118 – 0.341	0.297
				total_number	0.639	0.348	-0.053 – 1.332	0.070
				region_UpperMustang	0.189	0.403	-0.608 – 0.986	0.642
				proportion_juveniles	-0.027	0.121	-0.267 – 0.214	0.827
		Poisson	number of depredation events	Intercept	-0.851	0.278	-1.403 – -0.299	0.003
				total_number	0.095	0.122	-0.146 – 0.337	0.438
				region_UpperMustang	0.150	0.306	-0.456 – 0.756	0.628
				proportion_juveniles	-0.009	0.063	-0.135 – 0.116	0.886
		zero-inflated negative binomial	number of animals depredated	count_Intercept	1.684	0.351	0.997 – 2.371	<0.001
				count_total_number	0.407	0.140	0.133 – 0.681	0.004
				zero_Intercept	0.102	0.269	-0.425 – 0.630	0.703
				count_region_UpperMustang	0.268	0.393	-0.501 – 1.038	0.494
				count_proportion_juveniles	0.035	0.088	-0.136 – 0.207	0.688

[A]total_number + proportion_juveniles + number_interventions + region

[B]total_number + proportion_juveniles + multiple_interventions_use + region

Chapter 5

Synopsis

Sunset view onto Manaslu from Manang, Annapurna Conservation Area, Nepal. Credit: Marc Filla

5.1 Conclusions

This PhD thesis sheds light on the interactions between snow leopards, their wild prey, livestock, and humans in the Nepalese Himalayas. It has relevant implications for the management and conservation of snow leopards and other wildlife in high mountain ranges. Specifically, it 1) indicates the principal feasibility of maintaining relatively high densities of mountain ungulates when integrating conservation and development agendas, 2) suggests a strong impact of blue sheep on snow leopard abundance but not on livestock depredation rates, highlighting the significance of protecting this wild prey base, and 3) illustrates the urgent need of improving current intervention strategies and further exploring additional ones to lay the ground for human-snow leopard co-existence.

A landscape perspective on snow leopard management: integrated conservation and development as a glimmer of hope?

Protection of snow leopards and their natural habitats depends on the successful interaction of both land sparing (i.e., separating biodiversity conservation and commodity production) and land sharing (i.e., integrating biodiversity conservation and commodity production) approaches (Fischer et al. 2014; Butsic and Kümmerle 2015; Johansson et al. 2016). In fact, 40% of protected areas in the range of the snow leopard are smaller than an average home range of one male snow leopard, and only 3–13% are large enough to host 15 females (Johansson et al. 2016). In mountain ranges occupied by snow leopards, the promotion of (eco)tourism as an alternative livelihood represents a central component of integrated conservation and development programs (Nepal 2002; Roe et al. 2013). This approach also applies to the Annapurna Conservation Area, where tourism has been established as a major component of the local economy, with more than 1,000 businesses estimated to benefit from now more than 170,000 tourists visiting the Annapurna region annually (National Trust for Nature Conservation 2018, 2020). While positive financial and non-monetary effects on local livelihoods come as no surprise (Spiteri and Nepal 2008; Anup K.C. et al. 2015) and increased interest in conservation among local communities has been noted (Baral et al. 2007), the actual impact on biodiversity is less well studied.

In that respect, this PhD thesis yields important knowledge regarding the potential to maintain relatively high blue sheep densities in the Manang district of Annapurna Conservation Area. In fact, our density estimates, which broadly matched a contemporaneous study (Thapa et al. 2021) and, hence, appear reliable, fit in the range of most estimates before and after establishing this protected area in 1992 (see Chapter 2). Likewise, habitat selection of blue sheep was primarily driven by non-human factors, suggesting potential habituation to anthropogenic activities (Bhardwaj et al. 2010; Zhang et al. 2013). These findings may be

linked to a number of favourable conditions, including the absence of strong hunting pressure, availability of high-quality foraging areas, and principally positive attitudes by local people (Oli et al. 1994; Harris 2014; R. P. Lama and T. R. Ghale, personal communication). Taking into consideration also the reported positive developments of forest parameters and trends in some other wildlife populations (Bajracharya et al. 2005), we interpret our findings as a preliminary indicator of the success of the integrated management approach and, hence, as an indication of how alternative livelihood generation and biodiversity conservation goals can be combined in mountain landscapes inhabited by snow leopards.

However, I do not want to draw overly optimistic conclusions from the apparent conservation success and express some concerns about the long-term sustainability of this approach in the Annapurna region. Specifically, the large number of visitors to the region brings not only financial revenues but also carries ecological burdens, as tourists use above-average amounts of natural resources and produce an immense amount of litter (National Trust for Nature Conservation 2020). During our fieldwork, we observed various developments, such as the construction of new visitor facilities and roads to remote villages, which demonstrate the ongoing growth of the tourism sector and its increasing pressure on the fragile ecosystem (Baral et al. 2019, R. P. Lama and M. Filla, personal observations). The effects of tourism development on populations of blue sheep and other wildlife may not yet be detectable and may only become apparent after some time (Bürgi et al. 2017). Apart from that, I doubt that boosting international tourism represents an ideal long-term solution for high mountain ranges, as this considerably increases carbon emissions (Lenzen et al. 2018) and, thereby, threatens mountain ecosystems and their constituent biodiversity (e.g., Tse-ring et al. 2010). Eventually, mass tourism and its corresponding negative consequences (Butler 1980) could ruin the natural and cultural charm that attracts tourists to mountain landscapes like the Annapurna region (Baral et al. 2019). The issues and consequences covered here should be considered carefully by the key stakeholders in the Annapurna Conservation Area to secure successful biodiversity conservation in balance with economic perspectives into the future.

Protection of wild ungulates as a key element of snow leopard conservation

Adding to a growing body of literature (e.g., Alexander et al. 2016a; Sharma et al. 2021; Suryawanshi et al. 2021; Yang et al. 2021, to name a few), this PhD study highlights the significance of wild ungulates, namely blue sheep, for snow leopards in the Annapurna Conservation Area. Wild mountain ungulates lay the foundation for viable predator populations and also affect plant communities and ecosystem integrity within the snow leopard's range (e.g., Shrestha and Moe 2015; Baltzinger et al. 2019). Globally, the wild ungulate species which form the staple diet of snow leopards are classified as either 'Least Concern' or 'Near Threatened' by the IUCN Red List of Threatened Species (Harris 2014; Lyngdoh et al. 2014;

Ale et al. 2020; Reading et al. 2020a, b). However, this should not cause complacency as conservation needs to be proactive and pay increasing attention also to common species, which may greatly affect ecosystem functioning and services (Gaston 2010; Lindenmayer et al. 2011; Winfree et al. 2015; Frimpong 2018). Hence, the multitude of threats faced by mountain ungulates, including poaching and hunting, habitat loss and degradation, and competition with livestock (Harris 2014; Ale et al. 2020; Reading et al. 2020a, b), and the current rates of population declines (Ale et al. 2020; Reading et al. 2020a, b) are of conservation concern. In conclusion, addressing the aforementioned anthropogenic threats, strengthening mountain ungulate protection and recovery, and increasing awareness of their ecological significance should be key components of snow leopard conservation (Lyngdoh et al. 2014).

Effective intervention strategies as milestones towards human-snow leopard co-existence

While intact wild prey populations form the basis for thriving snow leopard populations, maintaining high predator densities requires safeguarding snow leopards from retaliatory killings, and the application of effective interventions appears to be a crucial approach to reduce livestock depredation (Jackson et al. 2010). In this regard, my PhD thesis reveals an urgent need to optimise the main intervention strategies applied in the Annapurna region (i.e., herding during daytime and corralling during night-time), especially as depredation patterns seem to be hardly impacted by wild ungulate densities, unlike elsewhere (e.g., Suryawanshi et al. 2013; Bagchi et al. 2020). My study results indicate that low performance of interventions could be a result of pure ineffectiveness or inconsistent application of the approaches used (e.g., shepherds being absent, animals remaining outside corrals). Either way, depredation occurred at various times of the day and throughout the year, implying the need to reduce depredation both on pastures and in night-time corrals. The latter could be achieved by constructing predator-proof corrals and enhancing traditional stone-wall huts/houses to prevent snow leopard intrusion and surplus killings (e.g., Jackson and Wangchuk 2004; Samelius et al. 2021; Thapa 2021). Such measures are currently being implemented in the Annapurna Conservation Area (National Trust for Nature Conservation 2018). The effectiveness of some other potentially useful night-time interventions deserves further investigation (see Chapter 5.2). Likewise, other studies have suggested that daytime herding practices could be improved by avoiding straggling individuals and rugged pastures (Johansson et al. 2015; Mijiddorj et al. 2018).

Admittedly, the mentioned theoretical considerations might be impractical in some parts of the Annapurna Conservation Area, and livestock owners need to trade off depredation risk against forage availability (Aryal et al. 2014d). Eventually, interventions may not be implemented due

to logistic constraints, transhumant practices, or financial limitations, or they may simply fail because a chosen approach does not prevent snow leopard access to livestock. In that case, though associated with bureaucracy and potentially causing complacency and false claims (Jackson et al. 2010), complementary compensation and insurance schemes might back up livestock owners from severe economic damages (National Trust for Nature Conservation 2018; Loch-Temzelides 2021) and, in turn, snow leopards from retaliatory killings (Nowell et al. 2016).

5.2 Future prospects: potential research and monitoring priorities

This project raises additional questions about ecological relationships in snow leopard habitats, livestock depredation patterns, and the suitability of intervention strategies. Based on our findings, I suggest several research priorities and focal areas for monitoring for the short-term and long-term management of snow leopards and other wildlife in the Annapurna region and beyond. These suggestions are detailed below.

Establishment of wildlife monitoring schemes in the Annapurna Conservation Area

Long-term monitoring is essential to detect population declines at an early stage, evaluate the effects of conservation measures, and guide future management (Holland et al. 2012). Given the important ecological role of blue sheep and continuous economic development in the Annapurna Conservation Area, I suggest establishing a long-term monitoring scheme for this ungulate in Manang and other parts of this protected area. Blue sheep could be surveyed through a participatory approach, including protected area staff and local people, to also increase environmental awareness and approval of applied conservation policies (Schmeller et al. 2017). A regular blue sheep monitoring system could be based on total counts from vantage points and along predefined fixed transects or on the double-observer approach (Nichols et al. 2000). While the former method enables wildlife managers to estimate minimum densities and detect population trends (Loison et al. 2006), double-observer counts yield more robust density estimates (Suryawanshi et al. 2012) and allow the calculation of additional parameters, such as the carrying capacity for snow leopards (e.g., Tumursukh et al. 2016). Complementarily, it would make sense to establish similar monitoring systems for species belonging to other classes (e.g., Phasianidae) and living in different habitats (e.g., Himalayan tahr, musk deer, barking deer *Muntiacus vaginalis*) to assess the effects of tourism developments on these taxa and ecosystems.

In addition to the suggested long-term monitoring schemes, (indirect) effects of tourism on blue sheep, which might have an impact after some time (Bürgi et al. 2017), could be explored by a set of additional investigations of blue sheep ecology, physiology and habitat use. These

investigations could include observational studies to examine reproductive rates (e.g., young:adult ratios; Mishra et al. 2004; Tumursukh et al. 2016) and behaviour-mediated fitness effects (e.g., vigilance behaviour; Jiang et al. 2013), telemetry studies to identify fine-scale responses to tourism and livestock (Westekemper et al. 2018), and non-invasive genetic analyses (e.g., stress levels; Zbyryt et al. 2018).

Reduction of livestock losses: assessing the ways to improve interventions and the role of secondary prey

The modest impact of the main intervention strategies applied in the Annapurna Conservation Area on livestock depredation rates calls for more research on how their performance can be improved. Although daytime losses attributed to snow leopards have been associated with habitat features like rugged pastures (Johansson et al. 2015), in-depth knowledge of exact kill sites (e.g., Krofel et al. 2021) is still rare but valuable to optimise daytime herding practices. Such data could be collected by involving reliable local people responsible for the verification of claimed depredation events and mapping exact attack locations. Moreover, we identified a number of infrequently applied but potentially useful intervention strategies that were associated with decreases in reported yak depredation during night-time. These strategies were the use of guarding dogs, deterrents (light, music playing, dung burning, and flapping tape; merged due to small sample sizes), and the (simultaneous) application of multiple interventions. Dogs and non-lethal deterrents have indicated their potential in mitigating conflicts between humans and snow leopards or other felids (Ohrens et al. 2019; Augugliaro et al. 2020; Naha et al. 2020), and the application of multiple interventions may prevent predator habituation (Khorozyan and Waltert 2019). Given the limited number of previous studies and small sample sizes in our analyses, we suggest controlled randomised experiments to validate these promising findings and quantitatively assess the short-term and long-term effectiveness of the respective interventions (Krafte Holland et al. 2018). Finally, implementing the most practical and suitable interventions would be another important step towards human-snow leopard co-existence.

In that respect, we also found some evidence that the presence of Himalayan marmots, unlike blue sheep densities, reduced reported depredation rates of sheep and goats, which accounted for the majority of livestock killed by snow leopards. In light of monitoring constraints, unaltered seasonal depredation patterns and characteristics of marmot habitats, this finding should not be overstated. Nevertheless, these rodents play a notable role in the diet of snow leopards (Lyngdoh et al. 2014; Chetri et al. 2017) and also affect the regional and seasonal dependence of snow leopards on livestock (e.g., Lhagvasuren and Munkhtsog 2002; Bagchi and Mishra 2006). Therefore, the influence of marmots and other secondary prey species, such as pikas, on livestock depredation patterns warrants further research.

Notwithstanding the above suggestion, the protection of marmot populations, which have declined in Upper Mustang over the past decade and which compete with livestock for limited food resources (Aryal et al. 2015b; R. P. Lama, personal communication), should benefit ecosystem integrity thus indirectly benefitting snow leopard populations.

Further steps to improve the monitoring of cryptic snow leopards

Cryptic behaviour, hardly accessible terrain, and low population densities prevent snow leopard monitoring based on direct observations (e.g., Hunter et al. 2016). In this PhD study, we followed the Snow Leopard Information Management System (SLIMS) protocol to estimate snow leopard relative abundance based on sign surveys (Jackson and Hunter 1996). Though this approach is commonly used and considered a useful indicator of snow leopard relative abundance when accounting for potential sources of bias (Snow Leopard Network 2014; Valentová 2017), its robustness has rarely been tested empirically (McCarthy et al. 2008). Therefore, I suggest further studies investigating relationships between densities of snow leopard signs (SLIMS surveys) and densities of populations (camera trapping). As limited funding and legal transboundary difficulties often hinder the usage of modern techniques like camera traps and genetic analyses (e.g., Hunter et al. 2016; Weckworth 2021), such studies would be valuable and could further support the suitability and application of the SLIMS approach to monitor snow leopard populations in remote landscapes.

5.3 Closing remarks

Clearly, the success or failure of snow leopard conservation will eventually depend on a multitude of factors as well as on major efforts by numerous stakeholders on various levels. Effective intervention strategies alone will not safeguard the snow leopard if its habitats and wild prey resources diminish. Likewise, the preservation of intact high-mountain ecosystems will not be sufficient if poaching and retaliatory killing continue. Further, pure research will not make any difference if conservation implications disappear into scientific journals rather than being put into practice. It appears indisputable that effective outcomes require consultation and close cooperation with local people rather than top-down decision-making. Finally, I hope that the insights obtained from this PhD study and its conclusions provide knowledge and mechanisms to support wildlife managers, decision makers, and local authorities in setting conservation priorities and actually implementing measures that benefit snow leopards, their wild prey species, and human-snow leopard co-existence. It is my sincere wish that this PhD project provides another ‘piece of the puzzle’ on the path towards snow leopard conservation, allowing also people in the distant future to get a glimpse of the ‘ghost of the mountains’ in its wonderful natural habitats.

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Curriculum Vitae

Marc Filla, born on 9 April 1991 in Kempen, Germany

Education and scientific career

2018 - Present	Doctoral studies in *Biological Diversity and Ecology*, University of Göttingen
2017 - 2018	Research assistant, Workgroup on Endangered Species, University of Göttingen
2014 - 2017	Master of Science & Master of International Nature Conservation in *International Nature Conservation*, University of Göttingen, Germany & Lincoln University, New Zealand
2011 - 2014	Bachelor of Science in *Biology*, Heinrich Heine University Düsseldorf
1997 - 2010	Katharinenschule and Städtisches Gymnasium Straelen (Primary and Secondary School), Straelen

Work experience

01 - 07/2016	Research activities, Bavarian Forest National Park
08 - 12/2015	Internships, Centro de Rescate Amazónico, Peru & Pró-Tapir, Brazil & Universidad Nacional del Sur, Argentina
09/2013	Internship, Alfred Wegener Institute Sylt, List
07 - 12/2010	Civil service, LBV-Umweltstation Altmühlsee, Muhr am See
02 and 07/2008	Internships, Veterinary medicine of Zoo Krefeld, Krefeld

Voluntary activities

2021 - Present	Active member, Foodsharing, Göttingen
2017 - Present	Active member, German Federation for the Environment and Nature Conservation (BUND), Göttingen
2017 - 2019	Youth coach, SC Hainberg, Göttingen
04 - 06/2015	Assistance in wildlife monitoring and conservation measures, Lincoln University, New Zealand & Hastings Caves State Reserve, Australia
03 - 04/2013; 01/2016	Participation in conservation measures, Nature and Biodiversity Conservation Union (NABU)
2011 - 2013	Youth coach, SV Straelen, Straelen

Skills

Languages	Mother tongue: German Fluent: English Conversant: Spanish, French Basic knowledge: Latin, Dutch, Finnish

Fieldwork	Wildlife monitoring (e.g., telemetry, camera trapping) Habitat mapping
Computing	Microsoft Office: *Word*, *Excel*, *PowerPoint* Coding language: *R* Geographic information systems: *ArcGIS*, *ArcView*, *QGIS*
Diving	SSI Open Water Diver (since 2011)

Publications

Soofi, M., Qashqaei, A. T., Mousavi, M., Hadipour, E., Filla, M., Kiabi, B. H., Bleyhl, B., Ghoddousi, A., Balkenhol, N., Royle, A., Pavey, C. R., Khorozyan, I., Waltert, M. (2022). Quantifying the relationship between prey density, livestock and illegal killing of leopards. *Journal of Applied Ecology*, Accepted Author Manuscript.

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Personal interests

Activities	Ball sports, Travelling, Mountaineering, Jogging, Cycling

Göttingen, 4 April 2022