INLAND NORWAY
UNIVERSITY
OF APPLIED SCIENCES

FACULTY OF APPLIED ECOLOGY, AGRICULTURAL SCIENCES
AND BIOTECHNOLOGY

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PhD Thesis

Ecology of Snow Leopards in the Central Himalayas, Nepal

PhD in Applied Ecology

2018

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Dedicated to my father and mother

Late Mon Bahadur Chetri
&
Kalika Devi Chetri

Preface

This work has been underway for a decade. Despite obstacles, I continued chasing my dream, as well as the dream of someone else: my father. He never had a chance to attend school but he was always keen that I get a good education. The place that I have reached today is largely a result of my father's love and commitment. Thank you *Baba* (dad), I hope that I have fulfilled your dreams. I always feels your presence within me.

I first traveled in snow leopard country in the year 2000, in Shey Phoksundo National Park, in the mid-western region of trans-Himalayan Nepal. There, I had an opportunity to spend several nights in one of the herder's camp, listening to the man's story. With a big smile spreading across his wrinkled face, he explained how difficult life is during the winter, and how one has to remain alert throughout the night, lest snow leopards enter the corral and harm the livestock. He also spoke of the usefulness of dogs, which provide early warning signals, by barking, as soon as they sense anything. His two massive Tibetan mastiffs were tied to stakes in the corner of his corral.

In 2002, I began my career as a conservation officer at National Trust for Nature Conservation (http://www.ntnc.org.np) and was posted in a remote unit of the Annapurna Conservation Area, in upper Mustang, which provided an opportunity to work with local communities and explore and understand the area's biodiversity. My first encounter there with a snow leopard in 2003 was quite confusing. With the naked eye, it was difficult to identify, due to its remarkable camouflage. I thought it might be a marmot, at the base of a cliff, then it disappeared in a blink. The pugmark at the base of the cliff confirmed that it could only have been a snow leopard.

In 2005, I was facing several options for my PhD research topic. That's when everything changed. One day, a colleague reported that locals in a nearby village were parading the carcass of a snow leopard around the village. They went from household to household with the furry carcass (which had been stuffed with straw) asking for money and food -- hailing their killing of this notorious enemy.

I was shocked, especially as conservation and awareness-building activities had been implemented in the region, beginning 13 years earlier. Since then, galvanized by this event, I jumped into helping local communities minimize snow leopard depredation, while helping them find alternatives means of livestock protection.

In 2012, as part of the WWF-USAID Hariyoban Program, a plan was proposed to explore the population status of snow leopard in the Annapurna-Manaslu region, and I was given the responsibility to conduct and coordinate the survey. Kamal Thapa (then Senior Program Officer at WWF Nepal), Gokarna Jung Thapa (GIS Specialist at WWF Nepal), Shanta Raj Jnawali (Hariyo Ban Program Biodiversity Coordinator) recommended setting the survey block in ACA and MCA. For the survey, we invited all the rangers and experienced field staff who had first-hand knowledge of snow leopard distribution and field survey techniques. During a one day workshop, we refined the study block, and added additional blocks based on accessibility and possibility of detecting signs and scats. We finalized 18 grid cells (each of 4x4 sq. km.) for the survey. The 2012 survey and the experience gained from it formed the basis of my Ph.D, by modifying the grid size and further extending the grid cells to cover the entire landscape. I am grateful to all involved in that workshop.

The National Trust for Nature Conservation (NTNC) granted permission to conduct this research in the Annapurna and Manaslu regions. In particular, I am indebted to Mr. Juddha Bahadur Gurung for recommending me as a Ph.D candidate under the quota program. This could not have been possible without the support of Dr. Shanta Raj Jnawali, whose support and inspiration has contributed greatly to this work.

Ganga Jang Thapa (then Executive Director of NTNC) was supportive and helpful from the beginning. My colleagues at the NTNC Central Office, namely Sarita Jnawali, Naresh Subedi, Manish Raj Pandey, Chiran P. Pokheral, were always supportive. I am also grateful to my field colleagues Shantosh Sherchan, Bidur Bikram Kuinkel, Sudip Adhikari, the field staff of UCO Lomanthang, UCO Jomsom, UCO Manang, and the Philim office of MCAP for making my stay comfortable while in the field stations.

Further, I am lucky to have Morten Odden as my supervisor, and now close friend. He not only visited my field sites, but generously shared his experience during the field work. His advice and invaluable guidance has been incredible throughout my Ph.D journey. I would also like to sincerely thank Per Wegge, my co-supervisor. Per was always keen to see that my field work data was nicely incorporated in my writings. I feel blessed by the chance to meet him twice at his favorite cabin at Varaldskogen. I am grateful to Harry Peter Andreassen for his academic support. Harry was always supportive: each and every word he spoke was like *amritha* (elixir of immortality!) to me. I am also thankful to Tom McCarthy for collaborating in this research.

I am thankful to Olivier Devineau for helping me in solving statistical problems. I am also grateful to Koustubh Sharma for helping me with SECR analysis.

Thanks also to the Government of Norway for providing me a grant through Lånekassen. And to Panthera, which supported me through the Kaplan Graduate Awards. I am also grateful to Inland Norway University of Applied Sciences for covering the laboratory expenses for fecal DNA genetic work. The Zoological Society of London (Nepal Office) also partly covered the laboratory expenses of genetic work. I am thankful to the WWF USAID Hariyo Ban Program for partly covering the field expenses.

Many others assisted in the field work, including logistic arrangements and individual interviews. Thank you all for your warm hospitality and help. Among those who helped in the field, I would especially like to thank my field colleagues Om Bahadur Gurung, Hira KC, Bhim Prasad Upadhayay, Chhang Dorje Lama, Bishnu Singh Thakuri, Buddhi Gurung, Kiran Lama and Tirtha Chaudhary. Also, Chombal BK and Sane Gurung, who were always by my side during field work in upper Mustang. Buddhi Gurung helped with surveying lower Mustang study areas, and Aitu Tamang always helped and provided rides. In Manang, Om dai was always there if I needed any assistance. I recall the day when we photographed a snow leopard nicknamed *Lapche Pothi* while she was guarding her kill (bharal). I still remember your face, you were quite scared when she stalked at us and we stood up to show her that we are not your prey, please leave us.

I am thankful to all my colleagues at Evenstad, including Kristin Evensen Gangås, Karen Marie Mathisen, Barbara Zimmermann, Henriette Wathne Gelink, Elisabeth Riseth, Eliana Ethel Bontti, Alina Lynn Evans, Torstein Storaas, Kjell Langdal, Wenche Lind, Degitu Endale Borecha, David Carricondo Sanchez, Marcel Schrijvers-Gonlag, Kaja Johnsen, Cicik Udayana, Zea Walton and Rocio Cano Martinez for your support and help. I also was blessed by new family friends and

great souls – Ragnhild Østerhagen and Mari Austeng-Jørgensen -- when I moved to Koppang. I would also like to thank Niten Skjellum and Eira Skjellum for always being kind to me and providing me a homely environment. I am grateful to Broughton Coburn for writing assistance. To the others that I met during the course of my Ph.D -- from field helpers, community people, to academic professionals and experts, I thank you all!

I am also indebted and thankful to my wife Rashmi, who single-handedly took care of our little boy Rudra, in addition to her own studies. I am grateful to have you in my life. Your positive vibes and inspiration have led me to envision a future for all of us.

Madhu Chetri
Evenstad, August 2018

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Sammendrag

Økologisk kunnskap om snøleoparden (*Panthera uncia*) er begrenset, spesielt innenfor en stor romlig skala. Årsakene til dette er knyttet til dyrenes gode kamuflasje og deres utbredelse innenfor høyereliggende fjellområder med hardt klima, noe som vanskeliggjør økologiske studier. De fleste studier av snøleoparden har derfor blitt utført innenfor små områder, eller såkalte "hotspots", og mindre enn 2% av det globale utbredelsesområdet har blitt systematisk taksert. Det er derfor viktig å skaffe grunnleggende økologisk informasjon om denne arten for å sikre at framtidig vern og forvaltning blir kunnskapsbasert. Hovedmålet med denne avhandlingen var derfor å samle inn data for å belyse viktige økologiske problemstillinger innenfor en stor romlig skala. Avhandlingen er basert på takseringer av byttedyr, innsamling av ekskrementer for studier av snøleopardens diett og bestandstetthet, og intervjuer for å kartlegge konflikter med mennesker. Studiet ble gjennomført i et 4393 km^2 stort område innenfor to verneområder (Annapurna og Manaslu) i Himalaya, Nepal. Mesteparten av feltdataene ble innsamlet i 26 ruter, hver 5x5 km store, spredt over hele studieområdet.

Snøleoparder ble identifsert til individ ved DNA-analyse av ekskrementer, og bestandstetthet ble estimert ved bruk av "spatially explicit capture-recapture-modeller" (SECR). Den gjennomsnittlige tettheten innenfor hele området inkludert i modellene (15,322 km^2) var 0.95 dyr/100 km^2 (95% konfidensintervall = 0.66 - 1.41). Den predikerte tettheten innfor samplingområdet (4393 km^2) var 1.07/100 km^2. En ekstrapolering basert på dette estimatet ga et antall på 48 individer innenfor dette området, og 140 innenfor 12.815 km^2 med potensielt snøleopardhabitat i hele Nepal. Dette er et langt lavere tall enn det offisielle estimatet for hele landet. Den beste SECR-modellen uttrykte variasjonen i tetthet som en kvadratisk funksjon av altitude, og oppdagbarhet av ekskrementer som en linær funksjon av topografi.

Analysen av dietten til snøleopard og ulv - basert på DNA-verifiserte ekskrementprøver - (snøleopard: 182 prøver, ulv: 57 prøver) viste at begge artene prefererte ville byttedyr over tamdyr. Snøleoparden prefererte ville ungulater tilknyttet bratt terreng (hovedsakelig bharal), mens ulv prefererte ungulater tilnyttet flatere grasområder (Tibetansk gaselle, kiang og Tibetansk argali). Andelene av husdyr i dietten til begge rovdyrartene var lave i forhold til tilgjengeligheten (snøleopard = 27%, ulv = 24%), og snøleopardene viste en signifikant unngåelse av husdyr. Jeg observerte sesongforskjeller i dietten til ulv, men ikke hos snøleopard, og jeg antar dette skyldtes sesongvariasjoner i tilgjengeligheten til viktige byttedyr som blant annet murmeldyr. Snøleoparder unngikk Yak trolig på grunn av deres størrelse, og prefererte hester trolig fordi disse ofte går uten tilsyn i beiteområdene. Snøleopardene prefererte geiter da disse er av optimal størrelse, og snøleopardhanner konsumerte mer husdyr enn hunner.

Mine undersøkelser av rovdyrkonflikter viste et lavt årlig tap av husdyr på ca 1% (N=428) av alle husdyr samlet. Mer enn halvparten av tapene (62%) var forårsaket av snøleoparder. Mindre husdyrarter (geit og sau) ble oftere drept av snøleopard og ulv enn større husdyrarter (yak, ku og hest). Husdyr ble tapt i alle sesonger, men en signifikant høyere andel ble drept om sommeren enn om vinteren. Snøleopardene viste imidlertid ingen sesongforskjell i motsetning til ulv og andre rovdyrarter. Blant eiere av hovedsakelig større husdyr økte sannsynligheten for tap i takt med størrelsen på flokkene, men dette var mindre markert hos eiere av små husdyr. Forholdet mellom

tettheten av ville byttedyr innenfor beiteområdene og tap av husdyr var komplisert. Sannsynligheten for tap var lavest innenfor beiteområder med relativt få husdyr og mange ville byttedyr, mens tapet var høyest der tettheten av begge artsgruppene var høye.

Denne avhandlingen har demonstrert betydningen av romlig skala innenfor forskning, overvåkning og vern av snøleoparder. Jeg fant markerte romlige variasjoner i snøleopardens bestandstetthet og diett, og dette antyder at resultater fra småskala-studier trolig varierer mye på grunn av studieområdenes ulike økologiske betingelser. Det er også åpenbart at husdyrtap var minimale, men med store lokale variasjoner. Pågående strategier for begrensning av konflikter blir utført på ad hoc-basis, og det er behov for å utvikle nye planer som tar hensyn til lokale variasjoner i tapsrisiko, samt å forbedre systemene for registrering av tap. Videre er det behov for å øke innsatsen for overvåkning utenfor verneområdene for å sikre overlevelsen til snøleopard og andre rovdyrarter i Himalaya.

Abstract

The snow leopard (*Panthera uncia*) is an elusive large carnivore distributed in the mountains of Central Asia. The highly camouflaged fur and harsh environment of the cat's habitat have made ecological studies challenging. To date, most snow leopard research have been conducted in small study areas, or "hotspots", and less than 2% of the global snow leopard distribution range has been sampled systematically. Basic ecological knowledge of the species across large landscapes is essential in order to develop effective conservation and management plans. The main aim of this thesis was therefore to provide data on some key ecological aspects of snow leopard ecology on a large spatial scale. The study was primarily based on field surveys of prey density, collection of snow leopard scats for studying diet and estimating density, and semi-structured interviews for assessing conflicts with humans. Most of the data were collected within 26 grid cells of 5x5 km^2 each, totaling 650 km^2 in a 4 393 km^2 area within two protected areas (Annapurna and Manaslu) in the central Himalayas, Nepal.

Individual snow leopards were identified from fecal DNA, and abundance and density were estimated using spatially explicit capture recapture models (SECR). The average density estimate of snow leopards for the entire projected model area (15,322 km^2) was 0.95 (SE 0.19) animals per 100 km^2 (95% CL = 0.66 - 1.41). The predicted density within the sampling area of ca. 4393 km^2 was 1.07/100 km^2. An extrapolation based on this estimate rendered an abundance of 48 individuals within our 4393 km^2 sampling area, and a country-wide abundance of 140 animals within 12815 km^2 of potential snow leopard habitat. This estimate is less than half of the current, official estimate made for the whole country (DNPWC 2017). The best SECR model described the variation in density as a quadratic function of altitude, and detection of scats as a linear function of topography.

The diet analyses of snow leopards and wolves, based on genotyped scats (snow leopards, n=182 scats; wolves n=57 scats), revealed that both species preferred wild prey. Snow leopards typically preferred cliff-dwelling wild ungulates (mainly bharal), whereas wolves preferred plain-dwellers (Tibetan gazelle, kiang and Tibetan argali). Livestock content in the diet of both predators was low compared to their availability (snow leopard = 27%; wolf = 24%) and snow leopards significantly avoided livestock. A seasonal difference in diet was noted in wolves, but not in snow leopards, and I believe this was mainly due to seasonal differences in the availability of important prey animals, such as marmots. Snow leopards avoided yaks, probably due to their large size, and preferred horses as they are often left unattended in the pastures, and also preferred goats as they are of optimal body size. Male snow leopards consumed more livestock than females.

My investigation on human-carnivore conflicts revealed that the overall losses to various carnivores was only around 1% (N=428) of the total livestock holdings. More than half of the livestock depredation events (62%) was caused by snow leopards. Small stock (goats and sheep) were killed more often by snow leopards and wolves than larger domestic animals (yak, horse, cattle). Losses occurred in all seasons, however, a significantly larger proportion of livestock depredation occurred during summer than in winter. More kills were observed in summer than in winter by wolves and by other predators. Among farmers owning large proportions of large stock (yak, horse and cow), the probability of loss increased with herd size; such a trend was not evident among farmers owning mainly small stock. The relationship between wild prey density and livestock loss was complex; the lowest loss probability occurred in areas of high wild prey density and low livestock density, but it was highest in areas where both livestock and wild prey were abundant.

This dissertation has demonstrated the importance of spatial scale in research, monitoring and protection of snow leopards. I detected marked spatial variations in snow leopard diet and density, which entails that small-scale studies may produce highly variable results due to contrasting ecological conditions. Moreover, the overall livestock loss to carnivores was minimal, but with large local variations. Ongoing conflict resolution strategies are being implemented on an ad hoc basis, and there is a need to develop new plans that take into account local variations in order minimize risk of loss, as well as to improve systems for recording losses. Furthermore, there is a need to increase monitoring efforts outside the protected areas to ensure the survival of snow leopards and other predators in the Himalayas.

Keywords: Conflicts, conservation, density, diet, Himalayan wolf, livestock losses, snow leopard, spatial scale

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List of papers

This thesis is based on the following original publications and submitted manuscripts. It was entirely based on primary field data.

Paper I:

Chetri, M., Odden, M., Sharma, K., Flagstad, Ø., and Wegge, P. Estimating snow leopard density using fecal DNA in a large landscape in north-central, Nepal. *Manuscript submitted.*

Paper II:
Chetri, M., Odden, M., and Wegge, P. 2017. Snow Leopard and Himalayan Wolf: Food Habits and Prey Selection in the Central Himalayas, Nepal. PLoS ONE 12(2): e0170549. doi:10.1371/journal.pone.0170549.

Paper III:

Chetri, M., Odden, M., Devineau, O., and Wegge, P. Patterns of livestock depredation by snow leopards and other large carnivores in the Central Himalayas, Nepal. *Manuscript submitted.*

1 Introduction

1.1 Snow leopards

1.1.1 Status and distribution

Snow leopards (*Panthera uncia*) are widely, but sparsely, distributed over the mountainous ranges of Central Asia, with core areas in the Altai (Mongolia and Russia), Tien Shan (Kyrgyzstan, Kazakhstan), Kun Lun (China), Karakoram (Pakistan), Pamirs (Afghanistan and Tajikistan), Hindu Kush (Pakistan and Afghanistan) and the Himalayan ranges of Bhutan, India and Nepal (McCarthy et al. 2016). Abundance estimates and perceived population trends are highly variable both among and within countries. However, the global snow leopard population was re-estimated recently at 7,463 to 7,980 individuals based on expert reviews (McCarthy et al. 2016). The IUCN status was also recently changed from endangered to vulnerable after 45 years (McCarthy et al. 2017), but the down-listing has been questioned (Ale and Mishra 2018; Aryal 2017). Snow leopards are also listed in Appendix I of the Convention of International Trade in Endangered Species (CITES). Poaching and illegal trade of pelts, bones, and other organs is a global conservation concern and there is a growing demand in the international market (Maheshwari and Niraj 2018; MaMing 2012). A recent study from 11 snow leopard range countries revealed a 61% increase in trade of snow leopard body parts from 1993-2002 to 2003-2012 (Maheshwari and Niraj 2018). Human-snow leopard conflict, reduction in natural prey and retributive killings are some of the other causes of their decline (McCarthy et al. 2017). Their sparse distribution in rugged mountains, coupled with logistic constraints, have made it difficult to conduct ecological studies. Most of the existing information on abundance and ecology have therefore been obtained from small study areas, often selected because of good habitat and/or high depredation of livestock. As a consequence, estimates of snow leopard abundance, prey selection and livestock depredation are highly variable (see e.g. Lyngdoh et al. 2014; Mallon et al. 2016; McCarthy et al. 2016; Mijiddorj et al. 2018; Mishra et al. 2016). Information from larger spatial scales is therefore needed for developing appropriate conservation efforts.

1.2 Sympatric carnivores

1.2.1 Himalayan wolf

One of the sympatric carnivores to snow leopards is the Himalayan wolf (*Canis lupus chanco*). Wolves used to roam the Trans-Himalayan regions of Nepal for centuries (Hodgson 1847). The recent discovery of a Himalayan subspecies in the Nepal Himalayas (Chetri et al. 2016) has drawn attention from scientists and conservationist both nationally and globally. In Nepal, the species is protected under the National Parks and Wildlife Conservation Act, 1973 of the Government of Nepal, and it is listed as Critically Endangered in the National Red List (Jnawali et al. 2011). The wolves that thrive in this landscape is smaller in size and very distinct from the European wolf both in physical appearance and mtDNA sequences (Chetri et al. 2016). The species was first re-discovered and reported from this landscape during this research. The updated information on this sub-species has not yet been published in IUCN Red list of threatened species (see Mech & Boitani 2010).

Wolves are distributed mostly in the northern fringes and in the flat undulating plains in the upper Mustang region of the Annapurna Conservation Area. Signs of wolf presence are also recorded in the central and eastern part of the study area. Very limited information is available on the ecology of this species in the Himalayas. The habitat of snow leopards and wolves are partly segregated, as the former prefer steep cliffs and rugged terrain while the latter prefer undulating plains (Chetri et al. 2017).

1.2.2 Other associated carnivores

Other carnivores associated with snow leopards and wolves in the study landscape are the Eurasian lynx (*Lynx lynx*), red fox (*Vulpes vulpes*), brown bear (*Ursus arctos*), golden jackal (*Canis aureus*) and Tibetan sand fox (*Vulpes ferrilata*). I found one genetically verified scat of Eurasian lynx in block no. 19 (see Fig.1). Locally known as *eek*, this species is very rare, and inhabits broken ridges with scrubland and bushes dominated by *Caragana* and juniper scrub. In upper Mustang of ACA, respondents from a few northern settlements showed high concern about lynx predation. However, during my study period, I found negligible losses from lynx (Paper III, Table 2). Red foxes are abundant and distributed up to 5800 m.asl.. Brown bears are rare and their digging signs were mainly seen during summer in the northern flat plains of the upper Mustang and Manaslu areas, where marmots are abundant. Golden jackals are common and widespread around settlements/villages. However, they were sighted up to 4800 m.asl. in upper Mustang. Tibetan sand foxes are rare, and prefer undulating flat plains, and thus share habitat with wolves in the landscape. I also recorded presence of common leopard (*Panthera pardus*) in forested habitat at lower elevation in lower Mustang, and in the Manang region of the Annapurna Conservation Area (ACA), as well as in the Manaslu Conservation Area (MCA).

1.3 Snow leopard abundance and density

Sign surveys were the most common method used to monitor and estimate snow leopard abundance and density in the past (Ale 2007; Chundawat 1992; Fox et al. 1991; Hussain 2003; Jackson and Hunter 1996; Mallon 1991; McCarthy and Munkhtsog 1997; Schaller et al. 1987; Schaller et al. 1988; Xu et al. 2008). Although the sign survey techniques have been updated (McCarthy et al. 2008), problems of observer bias remain, as individual assessments vary. Abundance and density estimation based on sign surveys are outdated with the advancement of new technology. Recently, non-invasive scat sampling has been more frequently used as it has the potential to cover large areas within relatively short time frames and at a lower cost compared to camera-trapping methods (Janečka et al. 2011). Genetic data also provide valuable information on genetic relatedness within and among populations, which is not possible using other methods (Janečka et al. 2011; McCarthy et al. 2008). In addition, a systematic and well-designed sampling of scats also provides information on diets, distribution, and habitat use (Schwartz et al. 2007).

In the Nepal Himalayas, pioneering research on snow leopard ecology was initiated during the early 1980's and 90's (Jackson 1996; Oli et al. 1993). These studies were conducted in small areas and in prime habitats. Based on a habitat suitability model, a population of 350-500 snow leopards was reported in Nepal (Jackson and Ahlborn 1989). Similarly, snow leopard densities were also estimated based on radio-telemetry and sign surveys (tracks and scrapes): i) 5-10 snow leopards/100km^2 in Langu Valley, Dolpo (Jackson and Ahlborn 1989) and ii) 4.8 - 6.7 snow leopards/100km^2 in Manang of Annapurna Conservation Area (Oli 1994). In addition, some information on snow leopard abundance was obtained by fecal DNA analysis and camera trapping from upper Mustang of ACA, Kanchenjunga Conservation Area, Sagarmatha National Park and Phu valley of ACA in Manang (Ale et al. 2014; Aryal et al. 2014b; Karmacharya et al. 2011a; Lovari et al. 2009; Wegge et al. 2012). However, all these studies were conducted in small areas. The current population abundance estimate of 301-400 snow leopards in Nepal and the density estimate of 1.5 to 3.2 animals per 100 km^2 (DNPWC 2017) were based on compilation of various small-scale surveys (sign surveys, camera trapping, fecal DNA sampling).

1.4 Diet and prey selection

Top carnivores such as snow leopards are important for maintaining biological energy flows and optimal functioning of ecosystems (Ripple et al. 2014). Knowledge concerning their foraging strategies and prey selection is essential for understanding their impact on their prey as well as their potential for coexistence with other members of the same guild. Snow leopards are wide-ranging animals; they patrol their territory, and transverse long distances in search of prey. They often come in conflict with the pastoral communities because of their habit of killing domestic stock (Jackson and Wangchuk 2004; McCarthy et al. 2017; Mishra 1997). A clear understanding of their food habits is therefore needed to develop effective conflict mitigating measures and conservation strategies. Some site-specific information on snow leopard diet is available (see Lyngdoh et al. 2014; Mallon et al. 2016), but many of the earlier studies were based on analyses of scat samples that had not been verified by genetic analyses. Species verification of snow leopard scats based on scat size, field experience and associated signs and markings in areas containing several other sympatric carnivores can often be misleading (Janečka et al. 2008). In fact, it has been shown that up to 50-60% of scats that were assumed to be from snow leopard were misidentified (Janečka et al. 2008; Janečka et al. 2011; Laguardia et al. 2015).This implies that some of the earlier research work on diet, prey preference, conflict etc. may be questionable (Chetri et al. 2017; Weiskopf et al. 2016). Since previous study areas were small, the results may therefore be highly site-specific and also susceptible to bias due to individual diet variation (Johansson et al. 2015).

1.5 Human-carnivore conflicts in the Himalayas

In pastoral landscapes, the presence of large carnivores is locally controversial because they kill livestock, and are thus exposed to retaliatory killings (Jackson 2015; Mishra et al. 2003; Mishra et al. 2016; Suryawanshi et al. 2014; Woodroffe et al. 2005). Persecution of carnivores occurs mainly as a result of one or both of these situations: i) a desire to rid the depredation problem permanently from the area, and ii) a response to the losses not being addressed properly by the concerned authorities. These situations further deteriorate if authorities obligate legal actions (in the case of retaliation). This creates an unfavorable social and political environment, and local support for conservation efforts can lose stability and progress (Madden 2004). As prices of livestock are increasing rapidly, more livestock depredation means more financial loss (Chen et al. 2016), which may increase negative attitudes towards carnivores. Therefore, an understanding of actual losses and the factors that determine the causes are fundamental for designing strategies for mitigating human-wildlife conflicts (Kansky et al. 2014).

Complaints about livestock losses are common and poaching and retaliatory killing cannot be avoided in remote pastoral landscapes such as the Himalayan mountains. Most of the available research on these carnivores in Central Asia have assessed livestock depredation based on interviews. Interviews can reveal peoples' perceptions, attitudes, and trends (Mishra et al. 2016; Suryawanshi et al. 2013), but may lead to bias if the losses are not monitored with a proper recording system. Also, information on attitudes and perceptions alone are not sufficient for developing long-term mitigation strategies. Some earlier studies have evaluated site-specific losses to snow leopards (Oli et al. 1994; Wegge et al. 2012), but no information is available at a larger spatial scale. Hence, to initiate a sound mitigation programme, a clear understanding of conflict patterns is essential.

2 Objectives

My study area is regarded as a priority landscape for snow leopard conservation by the government of Nepal (DNPWC 2017), as well as by conservation agencies. In this landscape, community-based conservation efforts have been in place for more than two decades. Therefore, landscape level estimates of abundance and density are needed as a baseline for long term science-based monitoring and expanded conservation efforts. Accordingly, the aim of this thesis was to obtain essential ecological knowledge of snow leopards on a large spatial scale. I focused especially on obtaining information on factors affecting spatial variation in their abundance, diet and prey selection, and their impact on local people due to livestock depredation. In **Paper I**, I estimated the density of snow leopards using fecal DNA for identification of individuals and newly developed spatially explicit capture recapture (SECR) modeling to estimate abundance and density. I explored how variation in abundance was determined by topography and habitat structure. In **Paper II**, I used scat analyses and surveys of prey density to assess prey selection of snow leopards. In particular, I studied how their use of domestic- versus wild prey varied along gradients of prey accessibility in a heterogeneous landscape. I compared the patterns of prey selection with a sympatric species, the Himalayan wolf. In **Paper III,** I assessed overall patterns of livestock losses. I also explored how snow leopards predation is influenced by the relative abundances of domestic and wild prey, livestock species composition, livestock herd size, topography, and local abundance of snow leopards.

3 Materials and methods

3.1 Study area *(Paper I - III)*

The Annapurna-Manaslu landscape (N28-29°, E83-85°) falls in the rain shadow area of the trans- and semi-trans-Himalaya, and adjoins the Tibetan Plateau in the north (Fig.1). The topography is dominated by steep slopes, massive cliffs and glaciers (Shrestha and Wegge 2008). The climate is also highly variable due to a marked variation in topography and altitudinal gradients. The area has minimal rainfall during the summer, and in winter, the area remains under snow cover for more than three months (Chetri and Gurung 2004). The micro-climatic variations, and the gradients of altitude and slope govern the composition and distribution of vegetation. Scrublands are widespread on dry and vertical slopes, and alpine grasslands are located at higher elevations (above 4,000 m. asl.). This vast landscape of ca. 5000 km^2 contains a unique assemblage of carnivores (see section 1.2.2 for a list of species). Other smaller mammals include: Himalayan marmot (*Marmota himalayensis),* wooly hare (*Lepus oiostolus),* several species of small mustelids (*Mustela* spp., *Martes* spp.), small felids (*Felis* spp., *Prionailurus* spp.), and various species of pikas (*Ochotona* spp.) and voles (*Alticola* spp.). Steppe polecat (*Mustela eversmanii*) was recorded for the first time in the country during this research (Chetri et al. 2014). Large herbivores present in the area are bharal or blue sheep (*Pseudois nayaur*), Himalayan tahr (*Hemitragus jemlahicus*), alpine musk deer (*Moschus chrysogaster*), Tibetan gazelle (*Procapra picticaudata*), kiang (*Equus kiang*) and Tibetan argali (*Ovis ammon hogdsoni*). The distribution of both wild and domestic ungulates, as well as carnivores, varies from east to west due to differences in vegetation and topography.

Local communities reside within the conservation area and their main subsistence economy is animal husbandry. Human population density is low within the region, averaging 13.8 and 5.4 per km^2 in ACA and MCA, respectively (NTNC 2018). Domestic animal densities varied throughout the study area, but averaged 35.7 (±0.1 SE) per km^2 in total (see Paper II). Goat was the most common species (16.4±0.2), followed by Yak (10.9±0.1), sheep (6.4±0.1), horse (1.2±0.1) and lulu cow (0.8±0.1). The people mostly follow Buddhism and killing animals is considered a sin in most parts of the northern settlements. Pastoral communities use all the accessible areas for livestock grazing and have their own traditional rotational grazing practices (Pokharel and Chetri 2006). Sheep *Ovis aries*, goat *Capra hircus* and lulu cow *Bos taurus* sp. are usually herded and periodically moved among different pastures, whereas yaks and horses move freely. Some nomadic families also exist in this region, and during winter they move to lower elevations with all their stock animals. The marked variation in topography, vegetation and animal species along the east-west gradient has made the study area unique for studying snow leopards in contrasting ecological settings.

3.2 Sampling design *(Paper I - III)*

A random or systematic sampling was not feasible in my study area due to logistic and cultural constraints. I placed a 5×5 km grid over a digitized map of the study area and selected 26 grid cells (650 km^2) by using the following criteria: (i) each grid cell was located within a minimum and maximum distance of 5-10 km between borders, I avoided (ii) areas with >50% of glaciers and inaccessible high mountain peaks, (iii) areas along the main trekking routes and the main road (Korolla-Jomsom highway in ACA), (iv) areas falling in and around larger settlements and areas with other cultural restrictions (e.g. only allowed to be visited in a certain times of the year by the local communities), and (v) areas below 3000 m. a.s.l., as the presence of snow leopards has not been reported in these low altitudes in this region (McCarthy and Chapron 2003). We chose to use grid cells of 5x5 km since this was the largest size that was possible to monitor within a restricted time budget of ca one week per cell. The spacing of grid cells of 5-10 km between borders was used to minimize the probability that some snow leopard home ranges were not overlapped by any grid cell, and thus not *potentially* sampled. According to recent data from Mongolia, average 95% MCP home ranges of GPS collared individuals were ca 500 km^2, and thus, it is unlikely that home ranges in our study area was too small to be covered by the sampling grid cells. I conducted a preliminary survey during April-June 2012 to validate the feasibility of the identified sampling grids before the beginning of the data collection. The selected grid cells were located within the distribution range of snow leopards (McCarthy et al. 2005; Oli 1997). Only one grid cell was outside the conservation areas, in the Bhimthang valley (Fig.1).

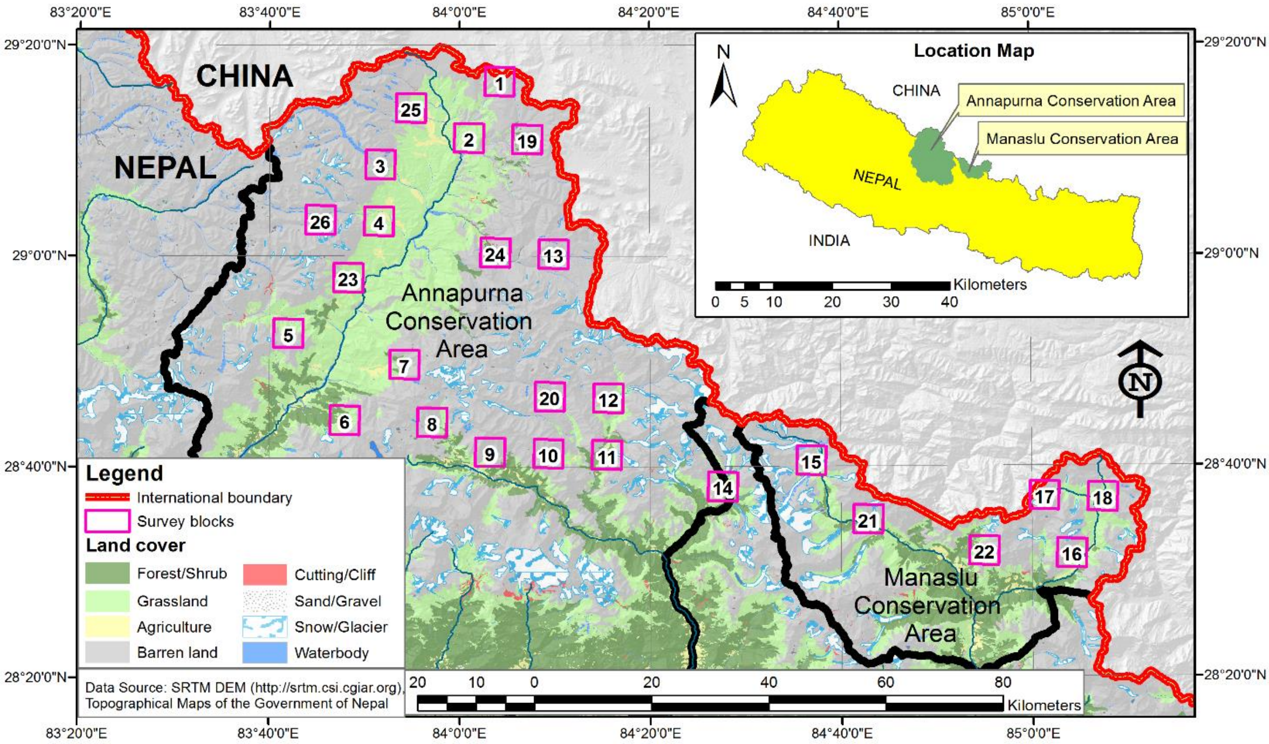

Fig.1. Study Area: Locations of survey grid cells in the Annapurna-Manaslu Landscape, Central Himalayas.

3.3 Field survey and data collection *(Paper I - III)*

I collected field data from September 2013 to September 2014. Putative snow leopard and wolf scat samples were collected from the grid cells by following 567 km of transects positioned along trails, mountain ridges, river beds and mountain passes (Jackson and Hunter 1996). The selected transect locations covered all the accessible and available habitats of snow leopard and wolf. I also collected scats encountered along the main trails during movement from one grid cell to another, and these data were recorded separately. Habitat features associated with scats, pugmarks, scrapes and kill sites were recorded using the snow leopard information management system (SLIMS) (Jackson and Hunter 1996; McCarthy 2000). When a scat was encountered, a small portion of it was put in a plastic tube and preserved in silica desiccant for fecal DNA analysis (Janečka et al. 2008; Lovari et al. 2009), and a larger portion was collected in paper envelopes for diet analyses. During my field survey, I collected altogether 809 scats from snow leopards and wolves (573 from snow leopards and 236 from wolves). However, due to limited funding, I analyzed only 347 snow leopard scats and 100 wolf scats. We disregarded scats that looked too old to contain DNA, and set an upper limit to 30 scats per grid cell. The screened samples were analyzed at the Centre for Molecular Dynamics Nepal (CMDN) for DNA extraction and individual identification.

I estimated prey abundance using the double-observer survey method (Suryawanshi et al. 2012). All ungulates encountered were also assigned to sex and age classes, whenever possible. Habitat features (slope, altitude, dominant vegetation), sighting distance, and GPS position were recorded systematically. Similarly, livestock (goat, sheep, yak, dzo, and horse) that were encountered in the grazing areas were also recorded. I mapped the seasonal grazing areas (summer, winter and year round) by observing from the vantage points, and delineated them on topographic maps (1:25000) published by the survey department of the Government of Nepal. The areas were delineated by the help of knowledgeable herders and community members, and boundaries were later digitized using ArcMap 10.3.

I used a semi-structured questionnaire survey to record livestock losses due to various predators in random (n=184) and conflict households (n=244). I also interviewed herders by visiting their herding camps or when encountered in the field. I interviewed two respondent groups; households that were known to have lost livestock to predators (conflict households) and households selected randomly (random households). I selected conflict households from lists of compensation claimants provided by the VDC level conservation area management committee leaders. Random households were located by approaching the nearest house with people present in a random direction from a visited conflict household. One respondent was interviewed from each household, i.e. one of the livestock owners. I cross-checked village level losses with herders during random interviews while visiting their herding camps or when encountered in the field (n=35), and also tallied with the livestock loss data maintained at the field office of ACA and MCA whenever applicable. More details on questionnaire survey design is provided in paper III.

3.4 Snow leopard abundance and density (Paper I)

I used Spatially Explicit Capture Recapture (SECR) analysis to estimate snow leopard abundance and density. The SECR analysis requires two datasets: i) a trap file and ii) a capture file. The trap file contains information about the sampling effort and the location of transects while the capture file provides information about captures and recaptures of identified individuals. In my case, because captures were made in the form of genetic samples collected on transects, each capture location was listed along with the coordinates of the transect line. I plotted GPS track data of each transect in ArcGIS version 10.3 and calculated the length of each surveyed transect. I created the trap file by listing each transect as a set of two or more vertices, each vertex listed in a new line. Transect length in meters was included as a measure of sampling effort (see data file in supplementary material, Paper I). Snow leopards are known to use habitat non-uniformly within their home ranges. Hence, I included topography and habitat structure as detection covariates in the trap file, as these are likely to affect both the probability of snow leopards depositing scats and the researcher detecting them. I classified the topographic features into four main categories: i) open livestock trail ii) rugged livestock trail, iii) dry riverbeds and iv) ridgelines. Similarly, I broadly classified the transects into four main habitat categories: i) grassland, ii) scrubland, iii) mixed scrubland, and iv) barren land. For covariates affecting density, I used altitude from the 30 × 30 m Digital Elevation Model from Aster Global Digital Elevation Model data and estimated a terrain ruggedness index using the terrain analysis plugin in the Quantum GIS 2.14 software. I used the package secr in R (Efford 2018) to estimate snow leopard density using Maximum Likelihood based SECR models.

3.5 Foraging ecology and prey selection (Paper II)

For the diet analysis, I used only genotyped scats. I prepared reference slides from hair samples that I collected from the remnants of wild and domestic ungulate species found in the study area. I cleaned the hair samples using soft detergent and later with diethyl ether solution. I prepared the impression on the slide using transparent nail polish as this is easily available in the market as compared to gelatin smear. I prepared a photographic key of all potential prey species (11 wild species and 5 domestic species) by taking pictures of hair structures with a microscopic camera with 10X and 40X magnification (Bahuguna et al. 2010; Oli 1993). I used a similar procedure for hair found in scat samples (see methods in Paper II). To select hairs, I used a modified version of the point frame method (Ciucci et al. 2004; Stewart 1967; Wegge et al. 2012). From each sample, I selected 50 different hairs that were closest to the intersections of an overlaid grid and compared them with the reference slides based on cuticular cell arrangements, medullary patterns and relative length (Bahuguna et al. 2010; Brunner and Coman 1974). I used generalized liner mixed models to assess factors that influenced diet composition of snow leopards and wolves. As binomial response variables, I used the presence or absence of three main food categories; i) wild ungulates, ii) livestock and iii) small mammals/birds. As explanatory variables, I used: i) the sex of the predator, ii) the season of scat collection, iii) characteristics of the sampling grid cells including latitude, iv) longitude, v) density of wild ungulates, vi) density of livestock and vii) wild prey species diversity. I used sampling grid cell ID as a random factor in all models.

3.6 Human-wildlife conflicts (Paper III)

I used a semi-structured questionnaire to record total numbers of livestock owned by individual households and the number of animals lost to predators (numbers lost, predator species and other details regarding the depredation event). To obtain predicted wild ungulate and livestock densities within each grazing area, I used density values that were obtained from double observer survey counts from the 26 survey grid cells and interpolated using inverse distance weighing (IDW) in the geostatistical analyst tools in ArcMap 10.3. (ESRI 2014). I obtained predicted snow leopard density values for each grazing area from spatially explicit capture-recapture models (SECR) based on analyses of snow leopard scat DNA collected from 490 km of transects traversing large parts of the study area (see Paper I). Using generalized linear mixed effects models, I tested factors associated with livestock losses to snow leopards. I used “loss” as a binomial response variable i.e. loss=1, no loss=0. For explanatory variables, I used : i) herd size, ii) herd composition, iii) wild ungulate density, iv) livestock density, v) snow leopard density, and vi) terrain ruggedness. For the latter variables iii-vi), I used average interpolated values for the grazing area used by the respondent. I used Village Development Committee (VDC) as a random factor in all models. A VDC is the lowest administrative unit of the government and usually contains 7-9 small clustered villages/settlements.

4 Results and discussion

4.1 Snow leopard abundance and density

I identified 34 different individuals from 81 snow leopards scat samples (20 males, 14 females). The average density of snow leopards for the entire model integration area (ca.15322 km^2) was 0.95 (SE 0.19) animals per 100 km^2 (0.66 - 1.41, 95% CL). The predicted densities varied between 0.1 and 1.9 in different parts (Fig. 2), thus highlighting the heterogeneity in densities as a function of habitat types. I found that the predicted density in Annapurna (1.07/100 km^2) was almost similar as in Bhimtang/Manaslu (1.16/100 km^2). The abundance estimates within the 4393 km^2 main study area in the Annapurna-Manaslu landscape was 48 individuals, and the predicted density was 1.07/100 km^2. The best model described the variation in density as a quadratic function of altitude and detection as a linear function of topography. Densities were highest in intermediate elevations, and the probability of detecting snow leopard scats was highest at valley bottoms, followed by ridgelines and livestock trails.

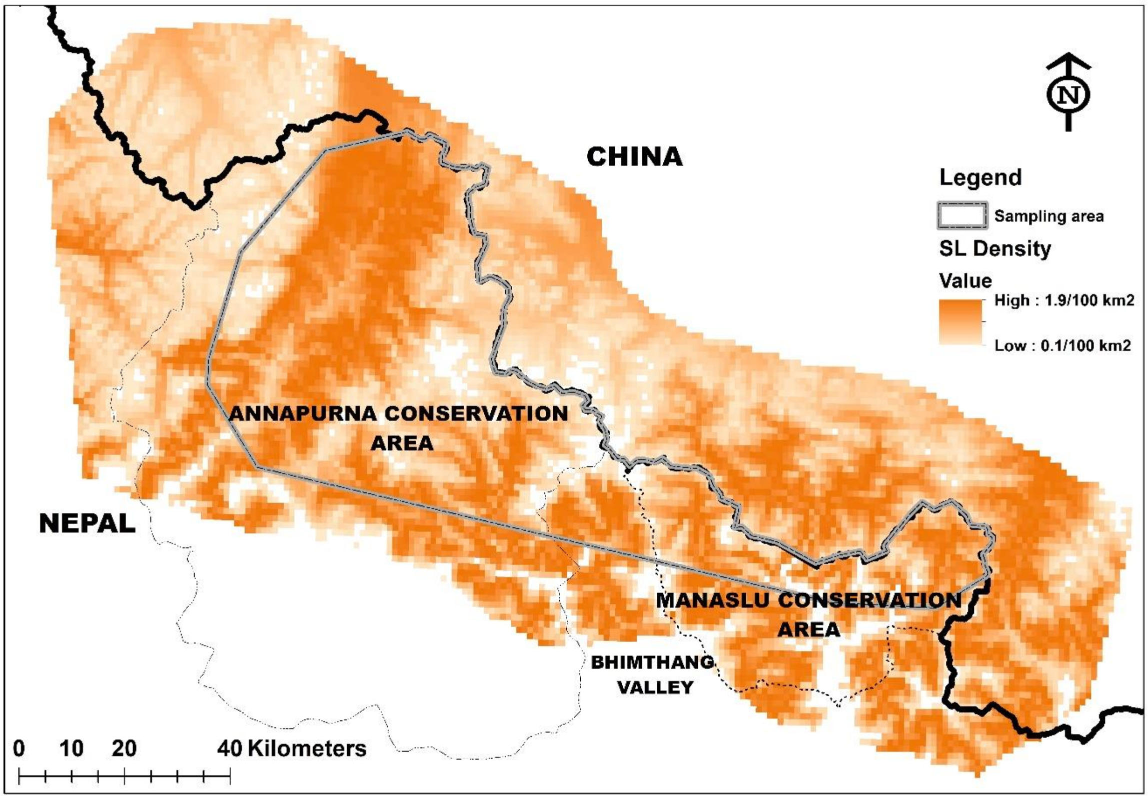

Fig. 2. Predicted snow leopard density in the landscape.

The overall density estimate was low compared with earlier estimates from the region (see Paper I). My results revealed that future snow leopard research and monitoring should be conducted in a large spatial scale and raise a question on how large areas need to be surveyed in order to obtain reliable density estimates. Bondrup-Nielsen (1983) suggested that sampling grids should be three to sixteen times larger than the average home ranges.

SECR models are highly flexible and do not require that the capture probability of all individuals should be greater than zero, which is a fundamental assumption in conventional CR models (Borchers and Efford 2008; Efford 2004; Karanth and Nichols 1998; Royle 2009). In large sampling areas that are partially inaccessible, SECR may therefore perform better, as these models are less sensitive to bias caused by uneven spacing of camera traps or fecal DNA transects. In addition, SECR may perform better in surveying elusive and wide ranging species such as snow leopards. Additionally, SECR accommodates covariates, which helps to improve model accuracy and it does not require an arbitrary designation of an effective sampling area as in the conventional CR models.

In conclusion, my results imply that the earlier abundance and density estimates of snow leopards in Nepal and elsewhere may be over-estimated. A previous country-wide assessment based on combining small scale density estimates with habitat suitability models suggested an abundance of 301-400 individuals within an area of 12815 km^2 of potential snow leopard habitat (DNPWC 2017). Based on my abundance estimates, an extrapolation would render a country-wide abundance of 140 animals. These new insights have raised questions about the validity of the earlier estimates and highlight the need for a reassessment of the country-wide estimate of snow leopard abundance and density using refined sampling and analytical methods.

4.2 Food ecology and prey preferences

Prey density and distribution

I found a marked variation in the distribution of both wild and domestic ungulates among the study grid cells. Across the landscape, livestock were generally more evenly distributed (except the lulu cow) than the wild ungulates. Among the various livestock species, goat density was highest, followed by yak, sheep, horse and the lulu cow. The overall density of wild ungulates ($7.41 \pm 0.09/km^2$) was much lower than that of domestic livestock ($35.74 \pm 0.10/km^2$). The most commonly encountered wild ungulate was the bharal. Tibetan argali, Tibetan gazelle and the kiang were found only in two grid cells in the northwestern part of upper Mustang of ACA. The Himalayan marmots, wooly hare and Royle's pika were present in more than 65% of the grid cells.

Diet comparison between snow leopards and wolves

The scats of snow leopards consisted of 73% wild prey and 27% of domestic animals (Fig. 3). Among the wild prey, cliff-dwelling ungulates (bharal and Himalayan tahr) dominated the diet (57.4% of remains in scats), and the most commonly identified species was the bharal. Plain-dwelling ungulates (kiang, Tibetan argali and Tibetan gazelle) were almost absent in the scats (0.8%), whereas small mammals constituted 12.6% of scat contents. Among domestic animals, the highest proportion in the scats was from goats, followed by horses, sheep, yak and lulu cow.

Wolf diet content was dominated by small mammals (37.6%) and plain dwelling ungulates (30.8%). Only a small proportion of the scat material (4.4%) was from cliff dwelling ungulates. Among domestic animals (23.8% of scat contents), the highest proportion in the wolf scats was from goats, followed by horses, lulu cow, yak and sheep. Fischer exact tests revealed significantly different proportions of cliff-dwelling ($P=0.001$) and plain-dwelling wild ungulates ($P=0.001$) between snow leopards and wolves. Domestic animals was significantly higher in snow leopards scats ($P=0.025$), whereas a higher number of wolf scats contained small mammals, but the difference was not significant ($P=0.081$). I found little diet overlap between snow leopards and wolves (Pianka index = 0.4) as compared to earlier studies, i.e. 0.9 (Jumabay-Uulu et al. 2013; Wang et al. 2014). Both previous studies attributed the high diet overlap to low prey diversity. My results concur with this explanation, as species richness was relatively high in the northwestern part of our study area where the two carnivores overlapped in distribution.

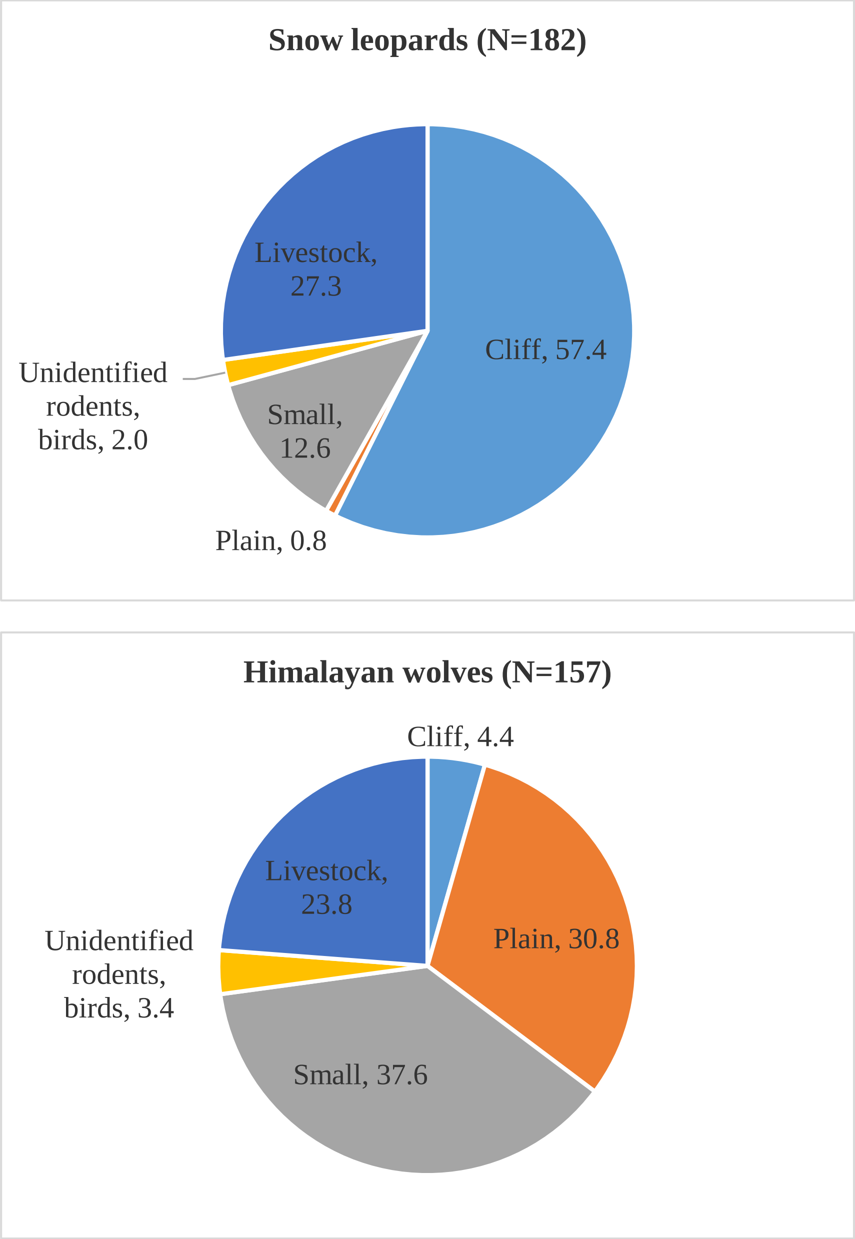

Fig. 3. Diets of snow leopard and wolf: proportions (%) of wild and domestic prey in scats. Cliff=bharal, Himalayan tahr; Plain=Tibetan argali, Tibetan gazelle and kiang; Small=Himalayan marmot, woolly hare, royle’s pika; Livestock=yak, horse, lulu cow, goat and sheep.

Prey selection

I compared patterns of prey selection among the three categories of ungulates, i.e. cliff dwellers, plain dwellers and livestock. Prey selection differed markedly between snow leopards and wolves, i.e. snow leopards significantly preferred cliff-dwelling wild ungulates and avoided livestock, whereas wolves significantly preferred plain dwelling wild ungulates and avoided cliff dwelling ungulates, and livestock was taken according to their availability. Among livestock species, snow leopards significantly preferred horses and goats and avoided yaks. In the case of wolves, I failed to test selection among the different livestock species due to a low sample size. A higher frequency of attacks on horses than on other livestock has also been observed in a previous study (Mishra 1997), and may be caused by horses often being left unattended in the pastures. Yaks are also unattended, but they are generally too large to be killed by snow leopards. Goats and sheep are prey of optimal size for snow leopards, but only the former was significantly preferred. Both species are attended by herders, but goats are often more dispersed than sheep and therefore probably more vulnerable.

Factors influencing diet composition

In order to determine the occurrence of main food categories in the snow leopard scats, I tested for the relative influence of scat collection season, the scat locations (latitude and longitude), sex of the predator, wild prey species diversity and densities of livestock and wild ungulates. Regarding the occurrence of wild ungulates, two candidate models had ΔAIC values <2 (see Table 5, Paper II), and both included the term “sex”. The highest ranking model included latitude (Y-coordinate) whereas the second best model included longitude (X-coordinate). I found that a larger proportion of samples from female snow leopards (70%) contained wild ungulates compared to males (48%). The parameter estimates from the best model showed that wild ungulate occurrence in scats was negative for longitude and positive for latitude (Table 1). This reveals that the occurrence of wild ungulates decreased from west towards east and increased from south towards north. The parameter estimate for latitude was negative, which indicates that a large number of scats collected from the southern part of the study area had higher livestock contents (Table 1).

Regarding the occurrence of livestock in snow leopard scats, the best model included the terms sex and latitude. The occurrence of livestock in male scats (47%) was more than double the occurrence of livestock in scats from females (21%), and the frequency increased from north to south. A recent study in Mongolia revealed that that the proportion of livestock kills by males were more than double that of females (Johansson et al. 2015). Such patterns of livestock killing among males has also been observed in several other carnivores species (Linnell et al. 1999), but has never been confirmed based on scat analysis. It has been suggested that male biased livestock killings in carnivores is caused by higher encounter rates because of their wider ranging movements (Linnell et al. 1999). Also among males, sexual selection have favored a high risk-high gain strategy (Odden and Wegge 2005; Sukumar 1991), which involves killing of easily accessible domestic prey even though it may impose a greater mortality risk.

In the food category “small mammals/birds”, the best model of occurrence in snow leopard scats included only the wild prey species diversity index (see Table 7, Paper II). Samples containing this food category were found within grid cells with higher diversity indices (Table 1, see also Table 7, Paper II).

In wolf scats, the occurrence of domestic animals did not differ seasonally. However, wild ungulates occurred more frequently in scats from the cold season (78%) than from the warm season (33%), whereas an opposite pattern was recorded for small mammals/birds i.e., 74% in summer samples and 22% winter samples, respectively. The seasonal differences in wolf scat contents were probably due to the winter hibernation of marmots, an important prey animal.

Table 1 Parameter estimates and test statistics of Generalized Linear Mixed Models of diet composition of snow leopards and wolves in the Central Himalayas. Response variables were the occurrence of wild ungulates (Ungulate), Livestock and small mammals/birds (Small) in scats. SW indicates wild prey species diversity expressed as the Shannon-Wiener Diversity Index.

Species	Response variable	Predictor variable	Estimate	SE	Z-value	P
Snow leopards	Ungulate	Intercept	-1.96	0.62	-1.54	0.120
		Sex	0.90	0.35	2.57	0.010
		Latitude (Y)	0.59	0.29	2.02	0.040
	Livestock	Intercept	0.94	0.6	1.56	0.118
		Sex	-1.14	0.36	-3.20	0.001
		Latitude (Y)	-0.59	0.27	-2.22	0.026
	Small mammals	Intercept	-2.16	0.41	-5.30	0.000
		SW	0.94	0.36	2.27	0.024
Wolves	Ungulate	Intercept	3.19	1.18	2.70	0.000
		Seasons	-0.95	0.66	-2.94	0.000
	Small mammals	Intercept	-3.58	1.27	-2.82	0.000
		Seasons	2.30	0.72	3.20	0.000

4.3 Human-wildlife conflict

Livestock ownership and mortality patterns

I found that the annual predation rate of livestock was very low in randomly selected households (<1%), and differed markedly among livestock species (Fig. 4). The predation rate was highest in horses (4.2%) and lowest in yak and yak hybrids (0.3% and 0%). The mortality rate due to disease and accidents was negligible (0.3% and 0.1%). My estimates were low when compared to earlier studies from the same landscape (Aryal et al. 2014a; Oli et al. 1994; Wegge et al. 2012) as well as in other parts of central and south Asia, i.e. 1.3 to 12.0% (Alexander et al. 2015a; Din et al. 2017; Hussain 2000; Jackson and Wangchuk 2004; Li et al. 2013; Mishra 1997; Namgail et al. 2007; Schaller et al. 1987; Wang and Macdonald 2006), and in parts of north America, Europe and Africa, i.e. 3.0 to 18.0% (Thirgood et al. 2005).

Livestock depredation

In my study area, more than half of the reported kills (62.0%) was done by snow leopards and the second highest loss was caused by wolves (16.8%) (see Table 2 Paper III). A significantly larger proportion of livestock depredation events occurred during the summer than in winter (Table 2). This pattern was common among wolves and the group of "other predators" (jackal, Eurasian lynx, common leopard, brown bear, black bear and feral dog), but not among snow leopards. The seasonal difference in livestock depredation can be partially explained by the herding practice. During summer, livestock are moved to the high altitude pasture and grazed in large flocks where the probability of encountering predators such as wolves and brown bear are higher. Furthermore, bears hibernate during winter. Seasonal variations in wolf attacks and livestock kills have also been documented elsewhere (Musiani et al. 2005; Nelson et al. 2016).

The probability of experiencing livestock loss to snow leopards depended on an interaction between livestock herd size and herd composition, and an interaction between wild and domestic ungulate density in the grazing areas (Fig.5 and 6). Surprisingly, snow leopard density and landscape ruggedness had a small effect on loss probability. The loss probability increased with herd size, but to a much greater extent among owners of mainly large stock than among small stock owners (Fig. 5). This was probably caused by differences in herding practices; small stock was grazed in groups with a herder present and losses were therefore probably less dependent on herd size. On the contrary, large stock was often left unattended and the risk of snow leopard attacks probably increased when herds were large. These herding practices are common among pastoralists also in other countries such as Bhutan (Wang and Macdonald 2006), China (Alexander et al. 2015a), and Mongolia (Mijiddorj et al. 2018).

The effect of wild and domestic ungulate density on loss probability was complex, i.e. wild ungulate density had opposite effects depending on domestic animal density (Fig.6). In areas of low livestock density, the model predicted that the probability of livestock loss would decrease along a gradient of increasing wild ungulate densities. However, an opposite scenario was predicted in areas of high livestock density. In the first scenario, livestock probably contributed little to the total prey base, i.e. below a threshold proportion where snow leopards almost solely consumed natural prey. In the second scenario, the high livestock loss in areas of high wild prey density may be caused by an aggregation effect, i.e. risk of loss was higher because the probability of encountering snow leopards increased where natural prey was abundant. These results illustrate that the relationship between livestock loss and natural prey abundance is context dependent, and it is therefore difficult to predict the outcome of management actions aimed at enhancing the natural prey base.

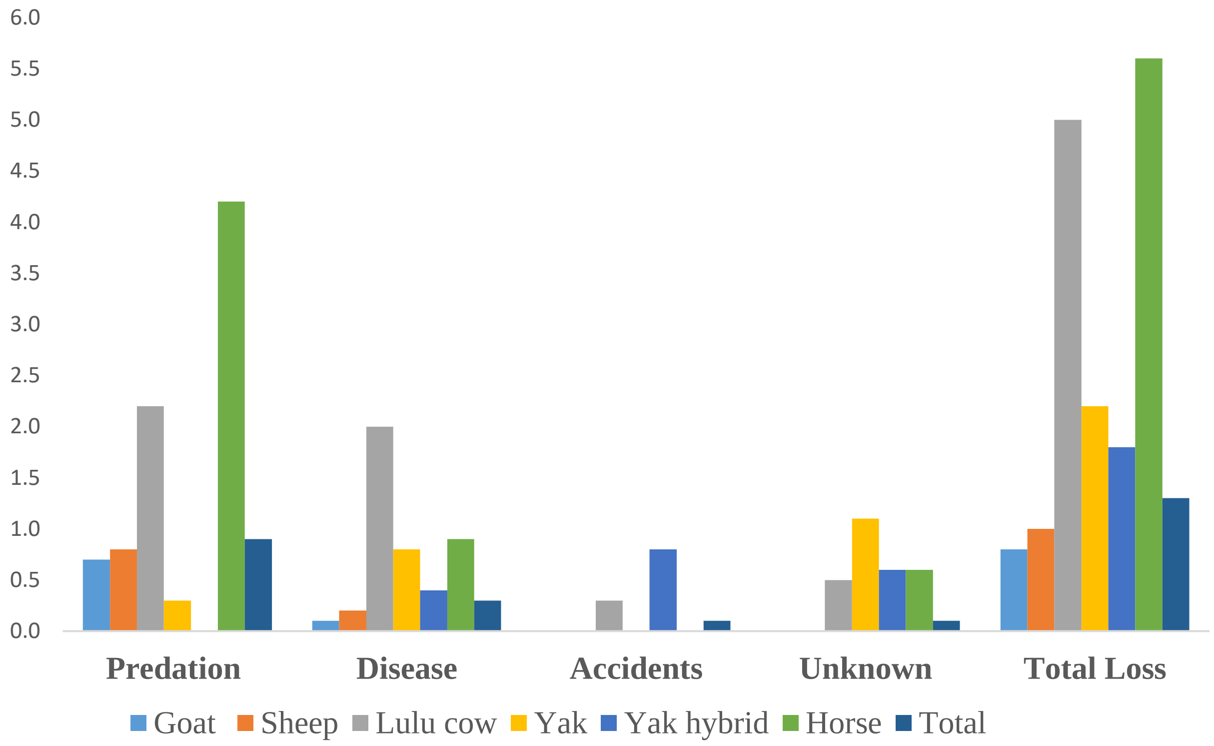

Fig.4. Annual livestock mortality (%) due to predation and other causes (%) in randomly selected households.

Table 2 Percentage of total livestock loss according to snow leopards, wolves and other predators, by season. Other predators' category excludes snow leopards and wolves losses.

	Percentage of total livestock loss (%)			
Category	Summer	Winter	χ2	p-Value
All predators	59.5	40.5	10.25	0.001
Snow leopards	51.9	48.1	0.20	0.656
Woves	77.6	22.5	14.93	0.001
Other predators	67.2	32.8	6.93	0.008

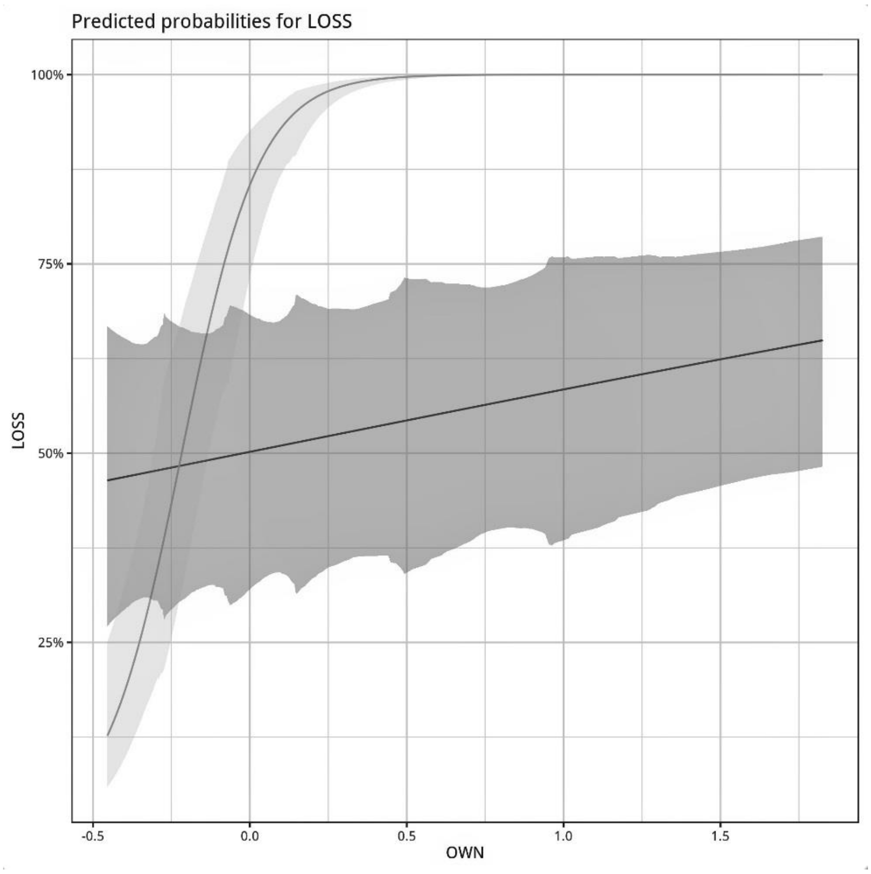

Fig. 5. Probabilities of experiencing livestock loss due to snow leopards based on the best Generalized Linear Mixed-Effects Model (see fig. 2, Paper III). The figure illustrates the impact of herd size (OWN) given two different values of livestock species composition; the grey line represents owners of only large stock and the black line represents only small stock.

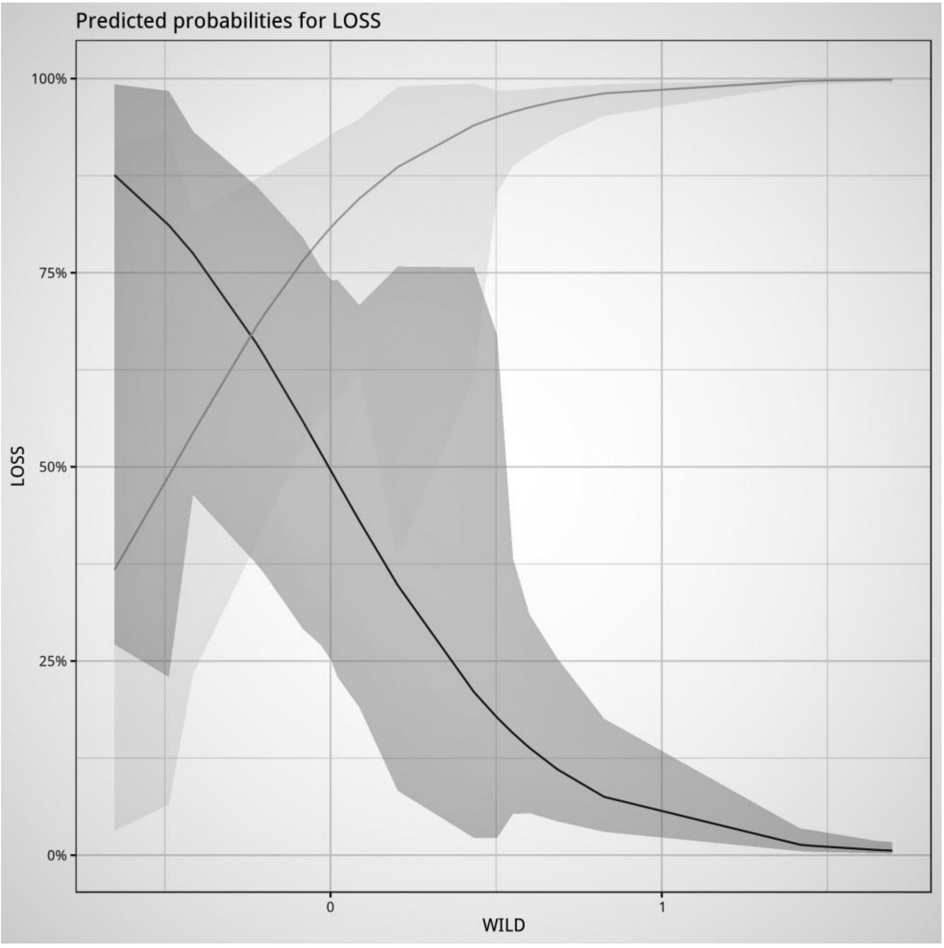

Fig. 6. Probabilities of experiencing livestock loss due to snow leopards based on the best Generalized Linear Mixed-Effects Model (see fig. 2, Paper III). The figure illustrates the impact of wild prey density in the grazing areas given two different values of livestock density; the grey line represents the highest recorded livestock density (86.5 per km^2) and the black line represents the lowest density (2.9 per km^2).

5 Conclusions and Future Perspectives

In this thesis, I have addressed some key aspects of snow leopard ecology. First, I covered a large spatial scale, and I detected marked spatial variations in snow leopard density, diet and conflicts. This suggests that studies of smaller spatial scale are apt to produce variable results due to contrasting ecological conditions. Moreover, the diet study was based on genetically verified scats and therefore I avoided biases due to misidentification of predator species (Janečka et al. 2008). In the study of conflict, I assessed both conflict and random households and obtained a better picture of the overall patterns of livestock losses than some previous studies which sampled only conflict households. Until now, this is the largest study area sampled for estimating snow leopard density, demonstrating the potential of using non-invasive methods for large-scale studies of snow leopards as well as other elusive species of similar nature.

Still, many important ecological questions remain unanswered. Snow leopard density was low (Paper I), which raises a question concerning the earlier national estimates (DNPWC 2017). Considering the contrasting results between my study and earlier work, and with the current downlisting of the species from endangered to vulnerable in the IUCN red list of threatened species (McCarthy et al. 2017), there is a need for a nationwide survey to generate a more reliable population estimate. In Paper II, I studied the diet of snow leopards and wolves, but it is also important to investigate how their diets and habitats are partitioned with respect to other sympatric carnivores, and to understand how each species functions in the Trans-Himalayan ecosystems. One crucial part, which was outside the range of this study, is to conduct rangeland assessments and grazing management. Rangelands are integral components for sustaining local livelihoods, and they are important habitats for a large number of important prey species of snow leopards and other predators.

In my study of human-wildlife conflict (Paper III), the average annual losses were quite low. However, site-specific losses were sometimes high, and occasionally, mass killings occurred due to negligence of the herder/owner. The system of monitoring of losses and verification is poor and not uniform across the landscape. Long-term monitoring of livestock losses will be important in order to develop maps of high and low predation risk zones. In the future, such information will help the management authorities in formulating and focusing conflict mitigation measures.

Future research should also investigate the movement patterns of snow leopards in order to assess their use of both protected and non-protected areas. Outside of the protected areas, there may be a higher risk to be killed by poachers or in retaliation due to the absence of conservation and management authorities. A holistic effort (e.g. including conservation programs, awareness outreach activities, conflict mitigation programs, research and monitoring) is required in order to conserve snow leopards and their prey both within and outside the protected areas.

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PAPER I

Estimating snow leopard density using fecal DNA in a large landscape in north-central Nepal

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Abstract

Although abundance estimates have a strong bearing on the conservation status of a species, less than 2% of the global snow leopard distribution range has been sampled systematically, mostly in small survey areas. In order to estimate snow leopard density across large landscapes, we collected 347 putative snow leopard scats from 246 transects (490 km) in twenty-six 5x5km sized sampling grid cells within 4393 km^2 in Annapurna-Manaslu, Nepal. From 182 confirmed snow leopard scats, 81 were identified as belonging to 34 individuals; the remaining were discarded for their low (<0.625) quality index. Using maximum likelihood based spatial capture recapture analysis, we developed candidate model sets to test effects of various covariates on density and detection of scats on transects. The best models described the variation in density as a quadratic function of altitude and detection as a linear function of topography. The average density estimate of snow leopards for the area of interest within Nepal was 0.95 (SE 0.19) animals per 100km^2 (0.66 - 1.41 95% CL) with predicted densities varying between 0.1 and 1.9 in different parts, thus highlighting the heterogeneity in densities as a function of habitat types. Our density estimate was low compared to previous estimates from smaller study areas. Probably, estimates from some of these areas were inflated due to locally high abundances in overlap zones (hotspots) of neighboring individuals, whose territories probably range far beyond study area borders. Our results highlight the need for a large-scale approach in snow leopard monitoring, and we recommend that methodological problems related to spatial scale is taken into account in future snow leopard research.

Keywords: *Panthera uncia*, density, Annapurna-Manaslu landscape, topography, spatial scale.

1. Introduction

Snow leopards *Panthera uncia* are sparsely distributed over the mountainous regions of twelve countries in Central Asia (McCarthy et al. 2016). Although widely distributed, world-wide population numbers are believed to be quite low. Main threats to the species are retaliatory killing due to livestock loss, poaching, and shrinkage and degradation of habitat due to poorly planned developmental activities (e.g. mining, dams, roads, railway lines etc.) and global climate change (Maheshwari and Niraj 2018; McCarthy et al. 2017). The snow leopard is listed as vulnerable in the International Union for the Conservation of Nature and Natural Resources (IUCN) Red List of Threatened Species (McCarthy et al. 2017). It is also listed in Appendix I of the Convention of International Trade in Endangered Species (CITES).

According to the most recent figures, the global snow leopard population size is estimated to count between 4,678 and 8,745 individuals with a mean density of 0.9-1.8 leopards per 100 km^2 (McCarthy et al. 2016). Although abundance estimates have a strong bearing on the conservation status of a species, global abundance estimates might be inaccurate, as the remote and rugged mountain habitats have rendered snow leopard population surveys challenging. Till date, less than 2% of the global snow leopard distribution range has been sampled systematically, and surveys have often been focused on sampling the best habitats (Jackson and Ahlborn 1989). The Bishkek Declaration 2017 and the Kathmandu Resolution 2017, both endorsed by governments of all the 12 snow leopard range countries, identify the need to estimate global snow leopard populations as a priority.

Sign surveys using Snow Leopard Information Management System (SLIMS) were widely propagated to estimate snow leopard abundance and distribution (Jackson et al. 2006). However, sign surveys alone were deemed unfit to derive quantitative population estimates (McCarthy et al. 2008). Development of capture-recapture analyses based on identification of individuals within a population has been promising tools for estimating absolute abundance and density (Karanth et al. 2006). Non-invasive sampling like camera trapping and genetic sampling by DNA analysis of scats are now widely applied in capturing and identifying individuals living within a population (e.g. (Ale et al. 2014; Jackson et al. 2006; Janečka et al. 2011; Sharma et al. 2014; Waits and Paetkau 2005; Wegge et al. 2012). An advantage of these methods is that they do not require direct contact with the animals, and are therefore favored when studying rare and endangered species (Janečka et al. 2011). The technique is particularly well-suited for snow leopards as they are extremely elusive, inhabit typically dry habitats where scats are often well preserved, and have reasonably predictable marking sites (Jackson and Ahlborn 1989). Non-invasive scat sampling also has the potential of enabling large-scale distribution and abundance surveys of felids at low costs, but identifying individuals from DNA samples is sometimes challenging due to poor DNA quality (Janečka et al. 2011).

The population estimate of 350-500 snow leopards in Nepal reported by Jackson and Ahlborn (1989) was derived from a model based on habitat suitability (low, medium, high and unsuitable) that assumed relative snow leopard densities in different habitat categories (low=0.5/100km^2, medium=2.5/100km^2 and high=5.0/100km^2). High snow leopard densities were estimated in different areas based on radio-telemetry and distribution of sign (tracks and scrapes): a) 5-10 snow leopards/100km^2 in Langu Valley, Dolpa (Jackson and Ahlborn 1989) and b) 4.8 - 6.7 snow leopards/100km^2 in Manang of

Annapurna Conservation Area (Oli 1997). Similarly, relatively high densities were later reported from studies based on sign surveys, camera trapping and DNA analysis of scats

(DNPWC 2017). However, a common problem with these studies is the small sizes of the survey areas. In fact, none of these areas were larger than the average home range size of GPS collared snow leopards in Mongolia (MCP 95% = 503 km^2±286, LoCoH 95% = 179 km^2±80, (Johansson et al. 2016), thus compromising the validity of capture-recapture analyses. Conventional capture-recapture analyses typically need sampling to be done in areas that are much bigger than the average home range size to prevent positive bias (Foster and Harmsen 2012).

Recent developments in analysis of genetic data coupled with advances in spatial capture-recapture analysis that allow variability in effort, detectability and density within sampled sites are promising in their ability to sample large areas with substantial inherent heterogeneity. Nepal is one of the 12 snow leopard range countries with up to 20-30% of its entire territory representing snow leopard habitat. The country's snow leopard habitat has been broadly divided into three conservation landscapes (DNPWC 2017). We sampled snow leopard population across the Annapurna-Manaslu Landscape (AML) as it has a potential to maintain a viable population due to an assemblage of diverse prey species of their choice (see Chetri et al. 2017). Here, we report the first ever comprehensive snow leopard population estimates from the AML that incorporates potential heterogeneity in snow leopard density and detectability across space.

2. Methods

2.1. Study area

The study area in the Annapurna-Manaslu landscape (28-29°N, 83-85°E) falls in the rain shadow of the Trans and semi-Trans Himalayas, Nepal. The northern part of the landscape adjoins the vast Tibetan Plateau (Fig. 1). The major proportion falls within the two conservation areas - the Annapurna Conservation Area (ACA) and the Manaslu Conservation Area (MCA); a smaller proportion is located in the Bhimthang valley between these two protected areas. We defined the borders of our study area by delineating a minimum convex polygon around all scat sampling transects (Fig. 1), except in the northern section, where we used the Nepal-China international boundary. The size of the total area covered by the polygon was 4,661 km^2. However, the habitats of snow leopards lie above the tree line at an altitude ranging from 3,000 to 6,000 m (SnowLeopardNetwork 2014). Hence, we removed the area that was either above or below this altitude range, after which the size of the area of potential snow leopard habitat was recalculated to 4,393 km^2. Climate in the region is highly seasonal, and the area harbors several importance species of global significance. The landscape is inhabited by agro-pastoralists, and accessible areas are used for livestock grazing. A detailed description of the study area is given in Chetri et al. (2017).

2.2. Field sampling

We sampled scats mainly within 26 grid cells of 5×5 km that were distributed across the landscape with 5-10 km between nearest neighboring cells. This represented about 15% of the total study area. However, we also collected scats along trails connecting the cells and along some trails extending beyond grid cell borders (Fig. 1). We avoided placing grid cells in areas that were inaccessible due to high elevation or ruggedness, near human habitation, areas with cultural restrictions and near main trekking trails and roads. Details concerning sampling design are described by Chetri et al. (2017). All the selected cells were located within the distribution range of snow leopards (McCarthy et al. 2005; Oli 1997). Transects were positioned covering trails, mountain ridges, river beds and mountain passes (Jackson and Hunter 1996). Selected transect locations covered all the accessible snow leopard habitat types and available habitat features in the region. We broadly classified each transect into four main habitat categories: i) grassland-dominated by *Carex* and *Kobresia* spp. ii) scrubland-dominated by *Caragana* and *Rosa* spp. and sometimes mixed with Juniper scrub iii) mixed scrubland-grassland, and iv) barren land (loose soil, gravel or boulders with scarce vegetation). We also classified four main topographic categories: i) open livestock trail (in open landscapes encompassing grassland, scrubland, mixed scrubland and alpine meadows); ii) rugged livestock trail (passing through broken cliffs), iii) dry riverbeds and iv) ridgelines.

Once a putative snow leopard scat was encountered, a small portion of the outer dried layer was extracted using twigs or sharp-edged grits and then preserved in a plastic tube with silica desiccant for DNA fecal analysis (Janečka et al. 2008). Altogether, 573 putative snow leopard scats were collected throughout the survey period from November 2013 to October 2014. At each scat location, we left nearly half of the scat in order to avoid influencing the territorial marking behavior of the snow leopards (Lovari et al. 2009). We revisited 108 of these sites after an interval of 205 ± 10 days (SD) in order to assess scat degradation over time. All but one scat had disappeared during this period, thus suggesting that most of the collected scats were less than ca 6 months old during the time of collection.

2.3. Laboratory analyses

The collected samples were submitted to the Central for Molecular Dynamics, Nepal for individual identification. Due to economic limitations, the samples were screened before submission to the laboratory as described by Chetri et al. (2017). The screened scat samples (n=347) were analyzed to identify species following the methods described by Karmacharya et al. (2011b). In total, 182 (52.4%) samples were successfully verified as snow leopard scats (Chetri et al. 2017).

The verified scats were analyzed further for individual identification using a panel of six microsatellite markers specifically designed for snow leopard (Janečka et al. 2008). Two multiplex panels of PCR amplification were used, i.e. (1) PUN124, PUN229, PUN1157 and (2) PUN132, PUN894, PUN935, in 10 µl reactions with PCR conditions and profiles described in Karmacharya et al. (2011b). All genotyping reactions were run in at least three independent replicates. We never accepted single-locus genotypes before it had showed at least three identical homozygote profiles or two identical heterozygote profiles, which is in accordance with Janečka et al. (2008). As an additional quality control, we calculated the quality index described by Miquel et al. (2006) for all samples. Following the recommendations of Miquel et al. (2006), we discarded all samples with a quality index of < 0.625 from the data set.

Of the 182 verified snow leopard samples, 86 samples had one or more loci missing. Only 101 samples had all six matching loci and 81 samples (80.2 %) gave reliable results according to the above-mentioned criteria. Based on the observed allele frequencies of the identified individuals, the probability of identity (PI) were estimated to 5.1×10^{-5} for unrelated individuals and 1.9×10^{-2} for siblings, suggesting that different individuals could be distinguished reliably in the study area (see Waits et al. 2001).

2.4. Data preparation

Spatial Capture Recapture analyses require data about where identified individuals were located during the sampling period. While the capture file provides information about the captures and recaptures of identified individuals, the trap file contains information about sampling effort and locations of traps. In our case, since captures were made in the form of genetic samples collected on transects, each capture was listed along with coordinates that corresponded with the coordinates of the transect line. We plotted GPS track data of each transect in ArcGIS version 10.3 and calculated the length of each surveyed transect. The trap file was created by listing each transect as a set of two or more vertices, each vertex listed in a new line. Transect length in meters was included as effort (see Supplementary data). Snow leopards are known to use habitat non-uniformly within their home ranges. Accordingly, we included detection covariates (e.g. topography and habitat) in the trap file that were likely to affect the probability of snow leopards depositing scats and that of the researchers detecting them (see above). For covariates affecting density, we used altitude from the 30 × 30 m Digital Elevation Model from Aster Global Digital Elevation Model data, and estimated terrain ruggedness index from the altitude data using the terrain analysis plugin in the Quantum GIS 2.14 software.

3. Data analysis

We used the package SECR (Efford 2018) in R to estimate density using maximum likelihood based spatially explicit capture recapture models. The spatial capture recapture process estimates the density of unknown activity centers by numerically integrating them across the area of interest, i.e. by summing up all locations of detected animals, and weighing each of them by its detection probability (Borchers and Efford 2008). To restrict attention to an ecologically meaningful size, an area of integration needs to be defined as the region (mask) within which probability weights get close to zero. The mask boundary was defined by a polygon drawn with a buffer of 20 km outside the polygon, binding all transects that were sampled to collect genetic data. The assumption was that animals with activity centers beyond this buffer distance would have negligible probability of leaving scats in the transects that were sampled. We used a pixel size of 1km x 1km to estimate the density distribution of activity centers of individual ranges of snow leopards within the entire mask. We excluded areas above 6,000 m and 3,000 m below sea level. The assumption was that since these areas represented glaciers and forested habitats that are not used by snow leopards, and hence the chances of any snow leopard activity centers being placed in these were negligible (SnowLeopardNetwork 2014).

Density and detection probability were estimated as constant across space and as functions of covariates with the help of multiple models. For detection probability, we parameterized the expected encounter rate at distance zero from the activity center ($\lambda 0$) and ranging parameter (σ). We tested the effect of topography and altitude on the encounter rate at the activity center. Density was modeled as a function of altitude and ruggedness and compared with models assuming homogenous density across the study area. A total of 9 candidate models were prepared and run using combinations of the variables used in the global model. Each candidate model represented a specific hypothesis examining the relationship between snow leopard density, detection and explanatory variables. We used Akaike Information Criteria (AIC) for model selection (Burnham and Anderson 2002). All SECR analyses were implemented using a dual Intel Xeon E5-2687 server with 32 cores and 256GB RAM using multi-core processing to facilitate parallel processing and hence speed up the analysis from a mask that spread across 15, 322 km^2. We used model-averaging of the density surfaces from the top models to estimate the most plausible abundance and density estimates from areas of primary interest.

4. Results

We identified 34 different individuals from the fecal DNA extraction and analysis, of which 20 were males and 14 were females (Table 1). Only two different individuals were identified in the eastern section of the study area, i.e. Bhimtang valley and Manaslu, while 32 were in the western part, Annapurna. The total number of animals that were recaptured one or mre times was 23. Among recaptured individuals (N=23), the maximum relocation distances averaged 6.3 km SE = 1.0 km, min = 0.2 km, max = 16.2 km). The top model of snow leopard density had an AIC weight of 0.33, and the next two models were close contenders with AIC weights of 0.26 and 0.22 respectively. Ninety-five% of the AIC weights were distributed across five of the nine models (Table 2), and we therefore used model averaging to estimate snow leopard density and abundance in the entire landscape (Fig. 2).

The total number of snow leopards estimated in the entire area of 15, 322 km^2 included in the SECR analyses was 144 (SE = 28.2, 95% CL = 101.1 - 214.3). The average density estimate of snow leopards for this entire area was 0.95 animals per 100km^2 (SE = 0.19, 95% CL = 0.66 - 1.41) with predicted densities varying between 0.1 and 1.9 snow leopards per 100 km^2 within the area (Fig. 2), thus highlighting the heterogeneity in densities as a function of habitat types (altitude and topography). Region-wise, the predicted density in Annapurna was 1.07 animals/100km^2 (95% CL =0.71-1.62) was slightly lower than in Bhimthang-Manaslu, i.e. 1.16 animals/100km^2 (95% CL = 0.73-1.87), and the predicted density within the 4393 km^2 large sampling area was 1.07 animals/100km^2 (95% CL = 0.70-1.63). Density as the quadratic function of altitude scored as the top model, indicating that density increased with altitude until a certain threshold and declined above that. The second and third best models estimated density as a function of altitude, and as a constant respectively. The probability of detecting snow leopard scats was highest at dry riverbeds, followed by ridgelines and livestock trails.

5. Discussion

Our overall density estimate of 0.95 (SE 0.201) snow leopards per 100 km^2 is lower than most recorded estimates from snow leopard ranges (see e.g. Alexander et al. 2015b; Alexander et al. 2016; Chen et al. 2016; DoFPS 2016; Jackson et al. 2006; Janečka et al. 2011; Kachel et al. 2017; McCarthy et al. 2008; Suryawanshi et al. 2017; WCNP 2016). Previously reported densities varied between low and quite high estimates, indicating that high densities could be an artifact from sampling in small study areas of very good snow leopard habitats. Remarkably, the ungulate prey density in our landscape (Chetri et al. 2017) was relatively high compared to other study areas where both snow leopard and prey densities have been recorded (Kachel et al. 2017; McCarthy et al. 2008; Suryawanshi et al. 2017). As is evident from the variation in predicted snow leopard density of more than two orders of magnitude within our study area, small areas are more likely to end up with high densities unless chosen randomly. It is noteworthy that positive bias in density estimates from small study areas has also been observed in several other species (see e.g. Cuellar et al. 2006; Dillon and Kelly 2007; Zimmermann et al. 2013).

Using GPS-telemetry, Johansson et al. (2016) demonstrated that snow leopard home range sizes were between 6-44 times larger than previous VHF-based estimates. The VHF-telemetry studies indeed show suspiciously small snow leopard home ranges considering that sizes are somewhat equivalent to those of common leopards in far more productive environments (Jackson and Ahlborn 1989; Odden et al. 2014; Odden and Wegge 2005; Oli 1997). The average 95% MCP home range estimates from Johansson et al. (2016) were ca 500 km^2, thus larger than most study areas where snow leopard densities have been estimated previously (Alexander et al. 2015b; Alexander et al. 2016; Chen et al. 2016; Jackson et al. 2006; Janečka et al. 2011; Oli 1994; Suryawanshi et al. 2017). Although home ranges in our study area may have been smaller than those reported from Mongolia, the new insight into the spatial ecology of snow leopards entails that the appropriate scale for snow leopard monitoring areas is probably in the order of thousands rather than hundreds of km^2. Because snow leopards are rare, and researchers have often relied on preliminary surveys to identify appropriate sites to conduct thorough surveys, smaller study areas are more likely to be located in relatively prey rich "hot spots". To address this bias, it is important that either the inherent variability of density as a function of habitat is modeled, or sampling areas are large enough to make design-based inference.

Although most scat samples were deposited within a shorter time period, some might have been up to six months old. This raises the question of population closure; some animals might have died during this period, and scats from some pre-dispersing sub-adults might have been included in the analysis. However, owing to the large spatial scale of our study, such factors - and any migration in and out of the sampling area or long-distance movements of non-residents (transients) - have probably had minimal effect on the density estimate.

There are obvious logistic constraints associated with intensive sampling of large areas, particularly in snow leopard habitat. A fundamental question is thus how large areas need to be surveyed in order to obtain reliable density estimates? According to Bondrup-Nielsen (1983), sampling grids should be at least 16 times larger than the average home range size to avoid positive bias. A more conservative recommendation of study areas three to four times larger than average home ranges was suggested by Maffei and Noss (2008). However, while Maffei and Noss (2008) used conventional CR, a comparable simulation study concluded that SECR models are far more flexible regarding sampling design, and that models performed well as long as trapping arrays were similar to or larger than one average home range (Sollmann et al. 2012). Regarding model flexibility, SECR does not require that the capture probability of all individuals should be greater than zero, which is a fundamental assumption in conventional CR models (Borchers and Efford 2008; Efford 2004; Karanth and Nichols 1998; Royle 2009). SECR may therefore perform better in large sampling areas, as these models are less sensitive to bias caused by scat survey transects or camera trap positions being spaced too far apart to cover the home ranges of all inhabitants. Furthermore, in elusive and wide ranging species such as snow leopards, SECR may perform better, as these models are less sensitive to low capture probabilities (Blanc et al. 2013; Sollmann et al. 2012).

The patterns of predicted snow leopard densities and the distribution of individuals recognized from scat DNA differed markedly. The SECR model predicted a slightly higher density in the eastern section, Manaslu/Bhimtang (1.16/100km^2), than in the western part, Annapurna (1.07/100 km^2). The distribution of different individuals recognized from scat DNA showed an opposite pattern, i.e. only two individuals in Manaslu/Bhimtang and 32 in Annapurna. The difference in predicted densities basically reflects regional variation in the covariates included in the SECR models, i.e. terrain ruggedness and altitude. The contrast between model predicted densities and distribution of recognized individuals may reflect a strong influence of other factors – like local diversity and density of wild and domestic prey - that were not included in our models. Furthermore, more efforts have been aimed at snow leopard conservation activities in the western part, including public awareness programs and actions aimed at reducing livestock losses. Accordingly, poaching of snow leopards may be more common in the east, but unfortunately there are no available data to evaluate this. However, given a total estimated abundance of only 48 snow leopards in our large sampling area, it is implicit that relatively few instances of poaching may have substantial population effects.

In this paper we demonstrate the importance of considering spatial scale in future monitoring of snow leopards. Moreover, we show that non-invasive genetic sampling can be used to estimate snow leopard populations at a large spatial scales. A consequence of our study is that the abundance of snow leopards in Nepal, and perhaps elsewhere, may be over-estimated. Given that our large scale study provided a lower density estimate than the relatively small scale studies that was the basis for the country-wide assessment in Nepal (DNPWC 2017), the abundance of snow leopards in Nepal is likely to be lower than previously assumed. According to the Snow leopard conservation action plan for Nepal (2017-2021), the country has 12815 km^2 of potential snow leopard habitat containing 301-400 individuals. An extrapolation based on our estimated abundance of 48 individuals within our 4393 km^2 sampling area would render a country-wide abundance of 140 animals. These new insights have serious consequences for the conservation of snow leopards and highlights the need for more surveys using refined sampling and analytical methods.

Supplementary materials

Supplementary data (Appendix S1: Trap file database and Appendix S2: Detection file database).

Acknowledgements

National Trust for Nature Conservation, WWF USAID funded Hariyo Ban Program, Inland University of Applied Sciences, Panthera-the Kaplan Graduate Award and the Zoological Society of London (Nepal Program Office) for funding. The Center for Molecular dynamics Nepal analyzed the scats. We sincerely thank field staffs of ACA and MCA and local communities for support during field work. We are grateful to Prof. David Borchers, University of St. Andrews for his excellent advice on SECR data analysis. We thank Philip Le Fuevre from Centre for Research in Ecological and Environmental Modelling, University of St. Andrews for his assistance with providing access to the mainframe computer that facilitated multi-model analysis.

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Table 1 Number of individuals, sex and capture rates of snow leopards identified by fecal DNA analysis of scats collected in the central Himalayas, Nepal.

Number of individuals	**Sex** **Male**	 **Female**	**Number of captures**
11	8	3	1
13	7	6	2
5	1	4	3
2	2	0	5
2	1	1	6
1	1	0	7

Table 2 Candidate spatial capture recapture models of snow leopard density based on fecal DNA collected in the central Himalayas, Nepal.

SN	**Model**	**k**	**Log Likelihood**	**AIC**	**AIC Wt**
1	D~Altitude + I (Altitude^2) lambda0~Topography sigma~1	8	-955.96	1927.91	0.33
2	D~Alt lambda0~Topography sigma~1	7	-957.20	1928.39	0.26
3	D~1 lambda0~Topography sigma~1	6	-958.34	1928.68	0.22
4	D~Ruggedness + Altitude lambda0~Topography sigma~1	8	-957.17	1930.35	0.10
5	D~Ruggedness lambda0~Topography sigma~1	7	-958.34	1930.70	0.083
6	D~1 lambda0~Altitude sigma~1	4	-964.15	1936.30	0.01
7	D~1 lambda0~Habitat sigma~1	6	-967.04	1946.07	0
8	D~1 lambda0~1 sigma~1	3	-975.32	1956.63	0
9	D~Altitude lambda0~1 sigma~1	4	-974.97	1957.94	0

Altitude = Altitude of the point in the mask for which density is estimated; Altitude^2 = Square of Altitude (Combination of Alt and Alt^2 used to test an increasing and then decreasing relationship between snow leopard density and altitude); Ruggedness = Ruggedness of the point in mask for which density is estimated; D = Snow leopard density; lambda0 = encounter rate of snow leopard at distance zero from activity center (surrogate for detection probability); sigma = Spatial scale of detection function for snow leopards.

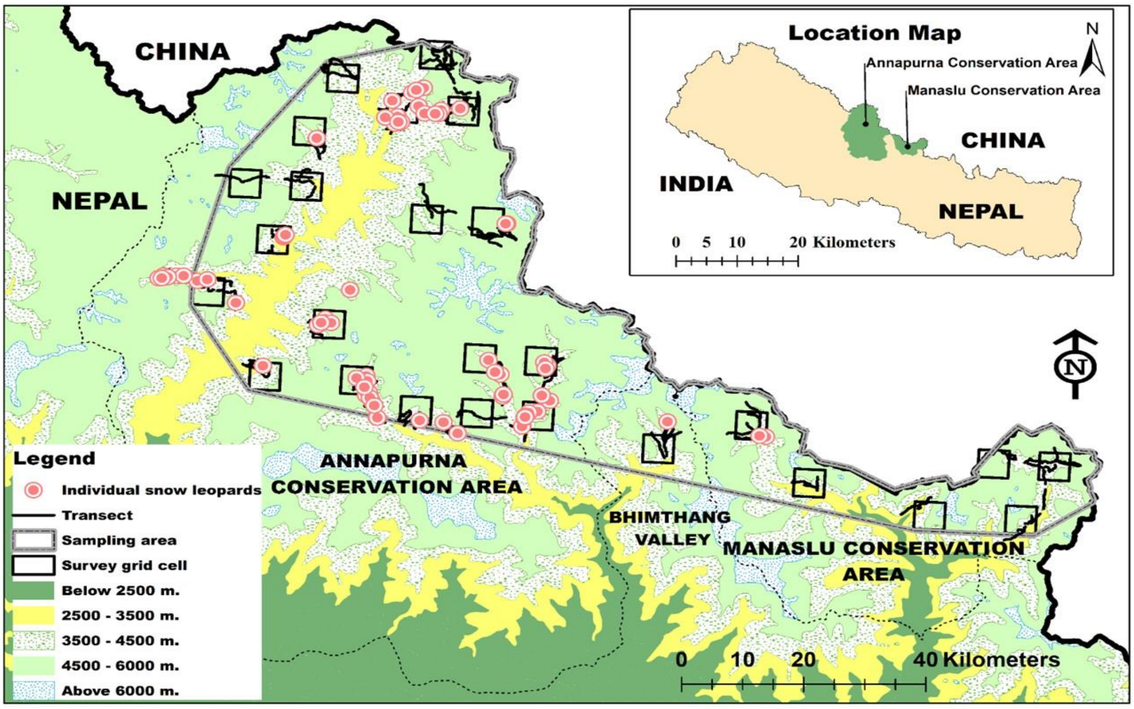

Fig. 1. Study area with location of grid cells, transects and genetically verified individual snow leopards.

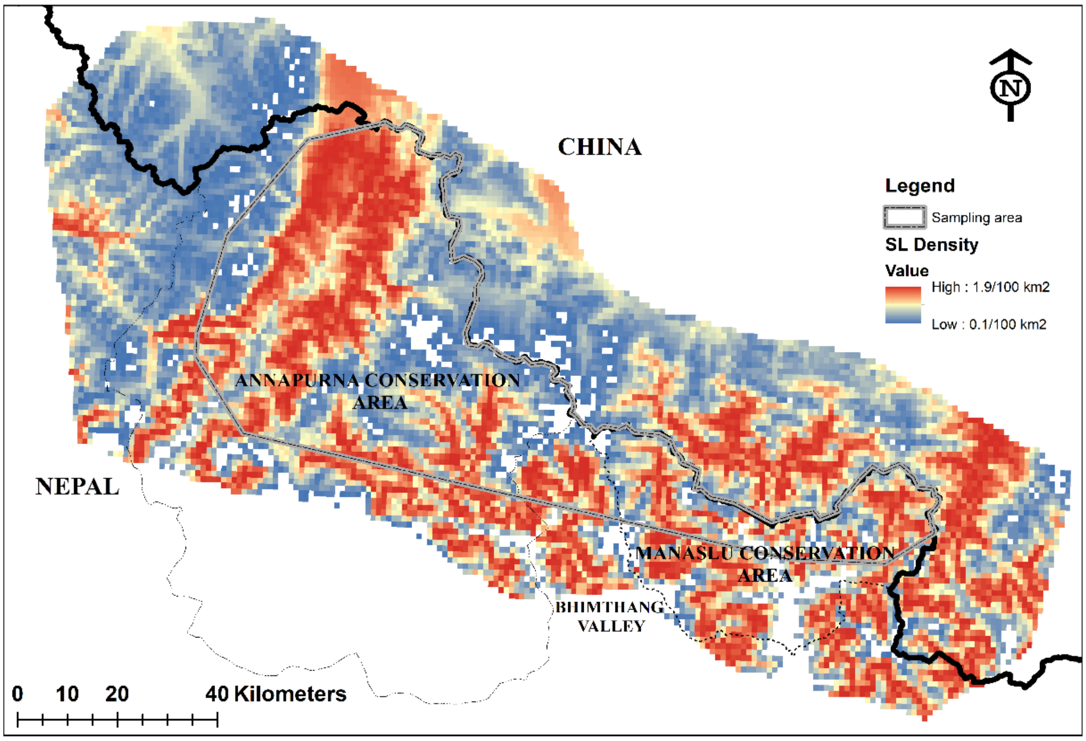

Fig. 2. Predicted snow leopards density in the landscape based on the top model as a quadratic function of altitude.

PAPER II

RESEARCH ARTICLE

Snow Leopard and Himalayan Wolf: Food Habits and Prey Selection in the Central Himalayas, Nepal

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Citation: Chetri M, Odden M, Wegge P (2017) Snow Leopard and Himalayan Wolf: Food Habits and Prey Selection in the Central Himalayas, Nepal. PLoS ONE 12(2): e0170549. doi:10.1371/journal.pone.0170549

Editor: Marco Festa-Bianchet, Université de Sherbrooke, CANADA

Received: November 9, 2016

Accepted: January 6, 2017

Published: February 8, 2017

Data Availability Statement: All relevant data are within the paper and its Supporting Information files.

Funding: The United States Agency for International Development funded Hariyo Ban Program, Panthera-Kaplan Graduate Awards and National Trust for Nature Conservation supported logistic cost for the field work to MC. Inland Norway University of Applied Sciences and the Zoological Society of London (Nepal Program Office) funded the laboratory cost for the genetic part. The funders had no role in study design, data

Abstract

Top carnivores play an important role in maintaining energy flow and functioning of the ecosystem, and a clear understanding of their diets and foraging strategies is essential for developing effective conservation strategies. In this paper, we compared diets and prey selection of snow leopards and wolves based on analyses of genotyped scats (snow leopards n = 182, wolves n = 57), collected within 26 sampling grid cells (5×5 km) that were distributed across a vast landscape of ca 5000 km^2 in the Central Himalayas, Nepal. Within the grid cells, we sampled prey abundances using the double observer method. We found that interspecific differences in diet composition and prey selection reflected their respective habitat preferences, i.e. snow leopards significantly preferred cliff-dwelling wild ungulates (mainly bharal, 57% of identified material in scat samples), whereas wolves preferred typically plain-dwellers (Tibetan gazelle, kiang and argali, 31%). Livestock was consumed less frequently than their proportional availability by both predators (snow leopard = 27%; wolf = 24%), but significant avoidance was only detected among snow leopards. Among livestock species, snow leopards significantly preferred horses and goats, avoided yaks, and used sheep as available. We identified factors influencing diet composition using Generalized Linear Mixed Models. Wolves showed seasonal differences in the occurrence of small mammals/birds, probably due to the winter hibernation of an important prey, marmots. For snow leopard, occurrence of both wild ungulates and livestock in scats depended on sex and latitude. Wild ungulates occurrence increased while livestock decreased from south to north, probably due to a latitudinal gradient in prey availability. Livestock occurred more frequently in scats from male snow leopards (males: 47%, females: 21%), and wild ungulates more frequently in scats from females (males: 48%, females: 70%). The sexual difference agrees with previous telemetry studies on snow leopards and other large carnivores, and may reflect a high-risk high-gain strategy among males.

collection and analysis, decision to publish, or preparation of the manuscript.

Competing Interests: The authors have declared that no competing interests exist.

Introduction

Top carnivores play an important role in maintaining energy flow and functioning of ecosystems. They traverse large areas to fulfill their energy demands, and their wide ranging movements and killing of domestic stock create conflicts with pastoral communities [1]. Hence, a clear understanding of diets and foraging strategies of top predators is essential for developing effective conservation strategies. The snow leopard (*Panthera uncia*) is categorized as Endangered on the IUCN Red List, and it is listed in Appendix I of CITES. Retaliatory killing, poaching for wildlife trade, habitat degradation and prey depletion are considered key factors leading to population decline [2]. In contrast, wolves are listed in the category Least Concern. However, in the Himalayas, wolves are very rare, and a recent genetic study confirmed that they belong to the ancient Himalayan wolf lineage (*Canis lupus chanco*) [3]. Ecological information about wolves in this landscape is practically non-existent. However, the preferred habitat of wolves in mountain ranges, i.e. open grassland and alpine meadows [4], is frequently used by pastoral herding communities, and wolves are potentially vulnerable to retaliations due to livestock depredation.

Little is known about the nature of the coexistence of snow leopards and wolves, but recent studies in Kyrgyzstan and northwestern China revealed pronounced interspecific diet overlap [4, 5], and therefore a potential for exploitative competition. However, interspecific competition probably varies among regions depending on several interacting factors, such as prey abundance, prey species diversity and habitat heterogeneity, as these are known to promote interspecific coexistence through niche segregation [6–8]. In general, snow leopards prefer steep terrain, ridges, broken cliffs and gullies associated with alpine and sub-alpine pastures [9], whereas wolves prefer open undulating pastures associated with alpine meadows [10]. Hence, given that preferred habitats are available to both species, coexistence may be enhanced by spatial avoidance and the utilization of different prey species that are associated with these habitats.

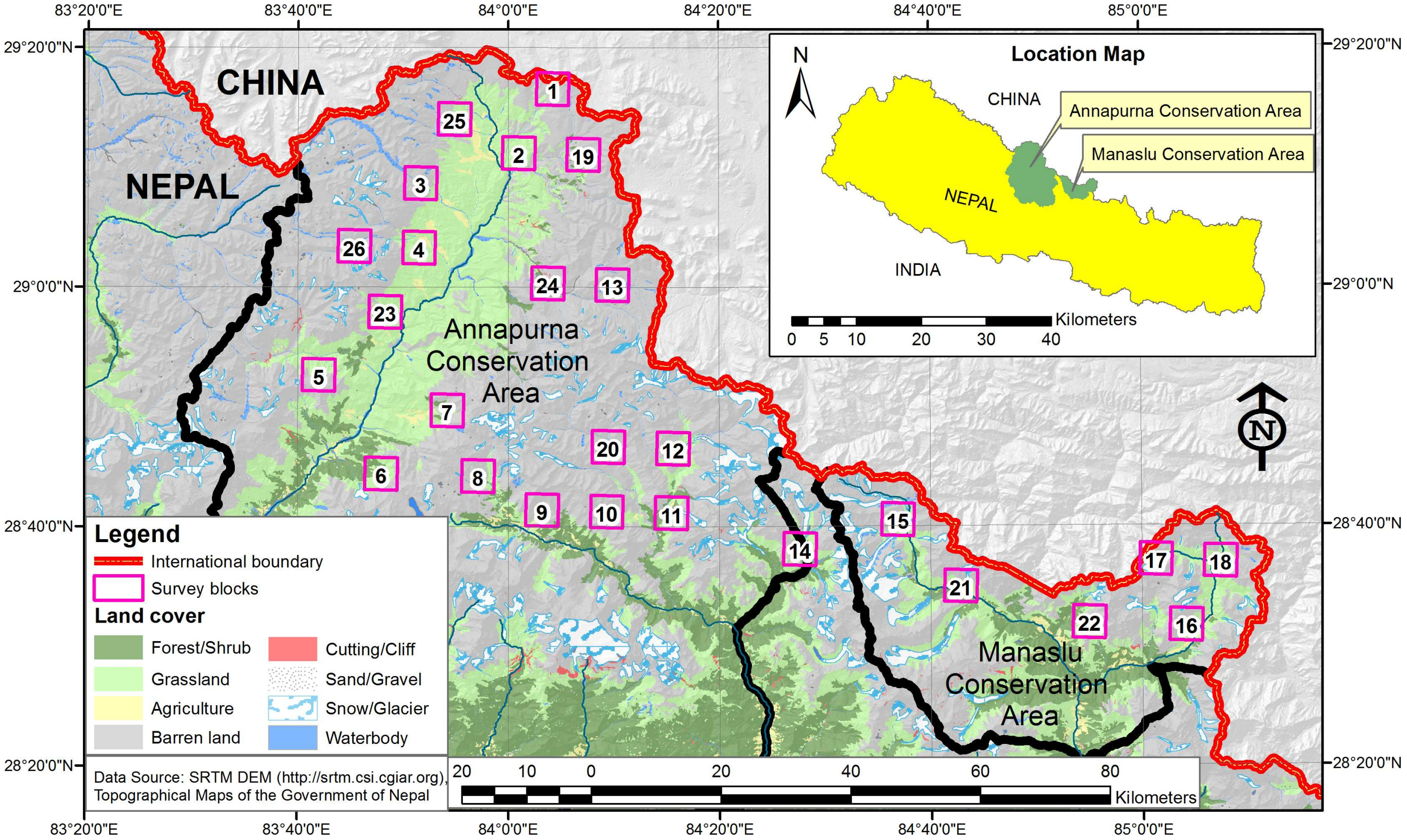
A recent review and meta-analysis of prey preferences of snow leopards revealed a relatively narrow dietary niche breadth despite marked diet differences among regions [11]. A general trend was a preference for prey species within the size range of 36–76 kg, and if available, Siberian ibex (*Capra sibirica*), bharal (or blue sheep/naur *Pseudois nayaur*) and Himalayan tahr (*Hemitragus jemlahicus*) were identified as key prey species [11]. In the absence of preferred larger prey, snow leopards consume a larger proportion of various smaller species of sub-optimal size [11]. The wolf, on the other hand, appears to be a more generalist forager than the snow leopard [12]. Although information on wolf diets are completely lacking from the Central Himalayas, food habits have been studied extensively in North America and Europe [13]. The studies reveal that wolves are opportunistic predators, with diets varying widely among regions due to different prey availability. Hence, wolves exploit a wide range of prey species from large to medium-sized wild and domestic ungulates, to berries and fruits and even garbage [13]. However, although wolves exhibit a wide food niche, their degree of diet specialization seem to vary among regions [14]. In a manner similar to snow leopards, wolves tend to widen their foraging niche in areas where preferred larger ungulates are few [15].

In our study, we assessed factors associated with variation in diets and selection of prey among snow leopards and wolves on a large spatial scale (ca 5000 km^2) to reveal the nature of their coexistence and their dependence on wild and domestic prey. Based on analyses of scats and the distribution and abundances of prey, we investigated four predictions regarding spatio-temporal patterns of diet composition. We predicted that the interspecific differences in habitat selection between wolves and snow leopards should be reflected in their diets and prey selection (i), wolves select typical plain-dwelling ungulates e.g. livestock, Tibetan argali (*Ovis* *ammon hogdsoni)*,kiang (*Equus kiang*), whereas snow leopards select typical cliff-dwellers e.g. bharal and Himalayan tahr. Furthermore, we predicted that scats from areas with low wild ungulate densities contain larger proportions of small mammals/birds and livestock (ii), and diet contents should differ with respect to season of scat collection (iii) due to a changing prey availability caused by the winter hibernation of marmots, an important prey species in the Central Himalayas [11, 16]. Lastly, we expected diet contents to differ between sexes (iv), as males seem more prone to kill livestock, which is a pattern observed among GPS collared snow leopards [17] and several other carnivore species such as lynx [18] and common leopards [19].

Study Area

The study area encompassed the Annapurna-Manaslu landscape (N28-29°, E83-85°, Fig 1), situated in the rain shadow of the Trans and semi-Trans Himalayas and adjoining the vast Tibetan Plateau in the north (Fig 1). A major proportion falls within the Annapurna Conservation Area (ACA) and the Manaslu Conservation Area (MCA), and a smaller proportion is in the Bhimthang valley which is situated between ACA and MCA.

For more than two decades, the National Trust for Nature Conservation (NTNC) has implemented a holistic conservation model for improving the rural livelihoods and conserving biodiversity in the two conservation areas. Climate in the region is highly variable with annual temperatures ranging from a minimum of -40°C in winter to a maximum of approximately



Data Source: SRTM DEM (http://srtm.csi.cgiar.org), Topographical Maps of the Government of Nepal

Fig 1. Study area: Location of survey grid cells in the Annapurna-Manaslu landscape.

doi:10.1371/journal.pone.0170549.g001

30˚C in summer. The total annual rainfall is <200 mm and more than half of the total precipitation is snow during the winter months [20]. The northern part of the landscape is treeless and contains flat undulating plains dominated by graminoids (*Carex* spp. and *Kobresia* spp.) (Fig 1). The central part is dominated by cliffs and rugged terrain composed of limestone rocks, interspersed by open areas with scrub vegetation and rangelands. The area is unique in terms of both faunal and floral species whose distributions are mainly determined by vertical topography, altitudinal gradient and the aspect of slopes. The large mammalian fauna include bharal, Himalayan tahr, Tibetan argali, kiang, Tibetan gazelle (*Procapra picticaudata)*, Himalayan serow (*Capricornis thar*), and alpine musk deer (*Moschus chryogaster*). Predator species include snow leopard, Himalayan wolf, brown bear (*Ursus arctos*), Eurasian lynx (*Lynx lynx*), red fox (*Vulpes vulpes*), Tibetan fox (*Vulpes ferrilata*) and golden jackal (*Canis aureus*). Other smaller mammals are Himalayan marmot (*Marmota himalayensis)*, Wooly hare (*Lepus oiostolus)*, different species of small mustelids (*Mustela* spp., *Martes* spp.), small felids (*Felis* spp., *Prionailurus* spp.), and several species of pikas (*Ochotona* spp.) and voles (*Alticola* spp.).

Animal husbandry is the main subsistence economy of the local communities. Pastoral communities use all the available rangelands for their traditional rotational grazing practices and move to different pastures according to their traditional calendar [21]. The livestock assemblage includes goat (*Capra hircus*), sheep (*Ovis aries*), yak (*Bos grunniens*), cattle-yak hybrids (dzo, jhopas, *Bos* spp.), lulu cows (*Bos taurus* sp.) and horses (*Equus ferus caballus*). Although the available grazing land has been used by nomads for centuries, nomads are now less common, and most of the families are settled in villages [22].Sheep, goats and cows are usually herded and periodically moved among different pastures according to seasons. Milking yak cows are brought back to the corrals/pens in the afternoon or in the morning on a regular basis. Male yaks and horses are left free in the pasture and are visited at an interval of 1–3 months for salt feeding depending on the pasture types, season and accessibility. During summer livestock are taken to higher elevation for grazing, and in winter, they move to lower elevations due to the harsh weather conditions.

Methods

Ethics statement

Relevant permits required to carry out the research were obtained from the National Trust for Nature Conservation, Nepal.

Sampling design

A random or systematic selection of sampling areas was not feasible due to logistic and cultural constraints. Hence, we placed a 5×5 km grid over a digitized map of the study area and used the following selection criteria: (i) Each of the 5×5 km sampling grid cells were situated with a minimum distance of 5 km and a maximum of 10 km to the border of the nearest grid cell, (ii) we avoided using grid cells with more than 50% of glaciers and inaccessible high mountain peaks, (iii) we avoided areas falling in and around larger settlements and areas with other cultural restrictions (e.g. only allowed to be visited in certain seasons by local communities), (iv) we avoided areas along the main trekking routes and the main road (Korolla-Jomsom highway in ACA), and (v) we avoided areas below 3000 m a.s.l., as snow leopard presence had not been reported in these low altitudes in this region [9]. A preliminary survey was conducted during April-June 2012 to validate the feasibility of the identified sampling cells before the beginning of the data collection. All the selected cells were located within the distribution range of snow leopards [23, 24]. Only one of the grid cell was outside the conservation areas, in the Bhimthang valley. Altogether, the grid cells covered 650 km^2, 13% of the total study landscape.

Scat collection

We collected scats during the warmer (May-October) and the colder (November-April) seasons in each of the 26 grid cells (Fig 1). Putative snow leopard (N = 573) and wolf scats (N = 236) were collected along trails, mountain ridges, river beds and mountain passes [25]. Altogether, 567 km were covered during 151 days of field work, rendering an average of 22 km in each grid cell (min = 5.83, max = 39.92, SD = 9.06). Once a scat was encountered, a small part was placed in a plastic tube with silica desiccant [26] for DNA fecal analysis. Larger parts were stored in paper envelopes for diet studies. We left ca half of the scat in the field to avoid disturbing the regular movements and territorial marking of the predators [27].

Scat analyses

We screened the samples prior to genotyping. First, we disregarded scats that seemed too old to contain DNA material, i.e. scats that were cracked, with a white or light yellowish color, had no odor, or were infected by fungus. Secondly, due to economic limitations, we set a maximum upper limit of 30 scats/grid cell. Scats were genotyped to identify species and sex following the methods described by Karmacharya et al.[28] and Kocher et al.[29]. Among a total of 347 and 100 snow leopard- and wolf scats analyzed, only 182 and 57 were successfully verified. The majority of the other samples had too low DNA quality, and some wolf scats were identified as feral dogs (1 scat), lynx (1 scat) and brown bear (1 scat).

Reference hair samples of potential prey were collected from the remains of kills found in the study area, and we collected hair of livestock from the villages nearby. Guard hair from different parts of the body were put in paper envelopes and annotated systematically. We prepared a photographic identification key of 16 wild and domestic animals following the methods described in Oli et al.[16] and Bahuguna et al.[30]. The genotyped scat samples were first oven-dried for 24 hours at 90˚C and then washed using detergents and sieved under running water. We placed two sieves on top of each other to extract hairs, one with a mesh size of 0.8 mm for larger/regular hairs and 0.5 mm below for small mammal hairs [4]. Substances such as bones, claws, bird feathers, stones, and plant material were manually separated, and then dried and stored in plastic bags. In order to prepare hairs for species identification, we followed the same procedure as described above. To select hairs, we used a modified version of the point frame method [31–33]. Using a gridded tray, we selected 50 different hairs closest to grid intersections and compared them with the prepared reference slides based on cuticular cell arrangements, medullary patterns and relative lengths [30, 34]. Small rodents and birds were not identified to species, but grouped in two different categories. For snow leopard and wolf scats, we were unable to identify 3.6% and 1.9% of the analyzed material, respectively.

Prey abundance

Among the different methods of abundance estimation of ungulate populations, distance sampling is a widely used method in tropical and temperate forests [35], but in the Himalayas, this method is not feasible due to the ruggedness of the landscape [36–38]. Instead, we used the double-observer survey method, as this technique has been evaluated as statistically robust and sufficiently precise for estimates of mountain ungulates [38, 39]. Within each grid cell, we followed trails made by humans and livestock and stopped at vantage points for scanning the area for 15–20 minutes. Two groups counted animals along the same trail with a time interval of 45–60 minutes. All wild and domestic ungulates, and smaller mammals (marmots and wooly hares), were recorded using binoculars and spotting scopes. For each observed group of prey, we noted the GPS location, the time of day, age and sex (if possible), vegetation, aspect, slope and altitude. After each survey, the two groups met to compare the data to confirm the unique identity of each sighted group [39]. Within each grid cell, we systematically mapped the actual areas covered by the survey (areas seen) by using 1:25.000 topographic paper maps, and the areas that were inaccessible from the trails and vantage points (areas not seen) were subtracted. This was done to avoid overestimating the size of the area surveyed, and thereby avoiding underestimation of animal densities.

Statistical analyses

We used the program R (version 3.2.5) for all statistical analyses, except for the analyses of prey selection where we used the SCATMAN software [40].

Prediction 1. For direct comparisons of scat contents between snow leopards and wolves, we only used samples that had been collected in six grid cells in the northwestern part of the study area where genotyped scats from both predators have been found (snow leopard: n = 27; wolf: n = 47). This was done to ensure that observed differences was due to selection of different prey species rather than differences in prey availability. We compared the proportions of four food categories between the two species using Fisher's exact tests, i.e. cliff- dwelling wild ungulates (bharal and Himalayan tahr), plain-dwelling wild ungulates (Tibetan argali, Tibetan gazelle and kiang), livestock and small mammals/birds. Before the tests were executed, we converted the relative proportions of recognized prey material into "Whole Scat Equivalents" (WSE) by multiplying the proportional occurrence of each food category (the proportions relative to all analyzed material) in all scats with the total number of scats [41]. This method allows for comparisons of proportions of food items in scats without altering the total sample size. For instance, if 100 scats all contained 10% of small mammals; they would convert into 10 scats of small mammals and 90 scats of other material. In the tests, we compared the WSEs of each food category vs. other material. We used Pianka's index [42] to assess diet overlap (DO) between the two predators; $DO = \frac{\sum PijPik}{\sqrt{\sum P^2 ij + \sum P^2 ik}}$ where Pij is the proportion of prey category i in the diet of predator j; Pik is the proportion of prey category i in the diet of predator k. The values range between 0 (no overlap) and 1 (complete overlap).

We analyzed prey selection based on the whole scat material (snow leopard: n = 182; wolf: n = 57) comparing observed and expected relative proportions of food items in scats with likelihood ratio tests (G-tests) [43], and a parametric bootstrapping procedure to obtain the p-values [44]. We specified the proportional occurrences in scats of three food categories; cliff- and plain-dwelling wild ungulates and livestock, and their estimated densities with standard errors. We also included estimates of scat production rates for each food category by using conversion equations for snow leopards ($Y = 1.980 + 0.035X$, where Y = the biomass of prey consumed to produce a scat, and x = the average body weight of each prey species) [45] and for wolves ($Y = 0.439 + 0.008X$) [46]. This was done to take into account that the relative amount of scats produced per ingested volume of different prey items varies with the size of the prey. Smaller prey produces more scat material per weight unit than larger prey due to a larger ratio of surface/volume [45]. As indices of prey selectivity, we used the Jacobs index [47] i.e. $D_i = (r_i—a_i)/(r_i+a_i-2r_ia_i)$, where r_i = proportional occurrence of prey items in the scats, a_i = proportional availability of a given prey item relative to all available prey. The value of Di ranges from +1 (maximum preference) to—1 (maximum avoidance).

Predictions 2–4. We assessed factors influencing diet composition of snow leopards and wolves with Generalized Linear Mixed Models (GLMM). As binomial response variables, we used the presence or absence of three main food categories; wild ungulates, livestock and small mammals/birds. We used sampling grid cell ID as a random factor in all models. We used the following explanatory variables: The sex of the predator, the season of scat collection, and characteristics of the sampling grid cells including latitude, longitude, density of wild ungulates, density of livestock and wild prey species diversity (Shannon-Wiener index: $H' = -\sum_{i=1}^{s} pi \ln pi$, where pi = proportion of individuals of i-th species, s = number of species). We started by investigating models with the terms sex, season, sex + season, and the NULL model with only the intercept and the random factor, by comparing their Akaike Information Criterion values [48]. We selected the most parsimonious model with the lowest AIC value and added the different grid cell specific variables listed above, one at the time. For wolf scats we only investigated the influence of season, as samples were found in only six grid cells and the number of scats with known sex was small. We also used the AICc instead of AIC due to a small sample size.

Throughout the text, scat contents are presented either as percentages (%) of each identified food item relative to all recognized material, or as frequencies of occurrence (FO). The latter is the percentage (%) of scats that contain a given food item.

Results

Prey density and distribution

The most commonly encountered cliff-dwelling wild ungulate was the bharal, which occurred in high densities in the majority of the study grid cells (Table 1). The other cliff-dwelling ungulate, the Himalayan tahr, was only found in four grid cells in the eastern part (MCA). Tibetan argali, Tibetan gazelle and the kiang were found only in two grid cells in the northwestern part (Upper Mustang of ACA), and their densities were low (Table 1). Domestic animals were generally more evenly distributed (except the lulu cow, Table 1) than the wild ungulates. The highest average density was recorded for goats (Table 1), followed by yak, sheep, horse and the lulu cow. The overall density of domestic livestock (35.74 ± 0.10/km^2) was far higher than that of the wild ungulates (7.41 ± 0.09/km^2). We did not attempt to estimate densities of smaller mammals. However, the most commonly observed species, Himalayan marmots, wooly hare and Royle's pika were present in 69.2%, 65.4% and 100% of the grid cells, respectively.

Diet comparison between snow leopards and wolves

Overall, the scats of snow leopards consisted of 73% prey of wild origin and 27% of domestic animals. Among the different categories of wild prey, cliff- dwelling ungulates (bharal and

Table 1. Average densities of wild and domestic ungulates in 26 study grid cells (5×5 km each) in the Central Himalayas.

Species	Density (No/km^2±SE)	Biomass (kg/km^2)	Species presence in grid cells (%)
Wild ungulates			
Bharal	5.97 ± 0.10	202.98	88.46
Himalayan Tahr	0.85 ± 0.22	42.50	15.38
Tibetan argali	0.24± 0.40	19.20	7.69
Tibetan gazelle	0.09 ± 0.14	1.80	7.69
Kiang	0.25 ± 0.12	25.00	7.69
Livestock			
Goat	16.39 ± 0.16	409.75	65.38
Sheep	6.36 ± 0.09	190.80	65.38
Horse	1.24 ± 0.06	136.40	73.08
Yak/Chauri	10.92 ± 0.14	1638.00	92.31
Lulu Cow	0.83 ± 0.04	83.00	42.31

doi:10.1371/journal.pone.0170549.t001

Himalayan tahr) dominated the diet (57% of remains in scats), and the most commonly identified species was the bharal (Table 2). Plain-dwelling ungulates (kiang, Tibetan argali and Tibetan gazelle) were almost absent in the scats (1%), whereas small mammals constituted 13%. Among domestic animals, the highest proportion in the scats was from goats, followed by horses, sheep, yak and lulu cow (Table 2). Altogether, five scats contained twigs of tamarisk *Myricaria* spp..

Small mammals was the most common food category found in wolf scats (41%) followed by plain dwelling ungulates (31%). Only a small proportion of the scat material (4%) was from cliff dwelling ungulates. Among domestic animals (24%), the highest proportion in the wolf scats was from goats, followed by horses, lulu cow, yak and sheep (Table 2). Three wolf scats contained plant material (*Kobresia* sp. and *Pennisetum* sp.), and two scats contained plastic material.

Fisher exact tests revealed significantly different proportions of cliff-dwelling (P = 0.001) and plain-dwelling wild ungulates (P = 0.001) between snow leopards and wolves (Table 3). The proportion of domestic animals was significantly higher in scats of snow leopards than among wolf scats (P = 0.025), whereas small mammals tended to be higher in wolf scats, but not significantly (P = 0.081). The Pianka index value was 0.44, thus indicating a relatively small diet overlap between the two species.

Table 2. Diets of snow leopard and wolf: proportions (%) of wild and domestic prey in scats, and estimated proportions of biomass and individuals consumed.

Species	Snow leopard (N = 182)			Himalayan wolf (N = 57)		
	Proportions in scats (%)	Relative biomass consumed (%)	Relative number of prey individuals consumed (%)	Proportions in scats (%)	Relative biomass consumed (%)	Relative number of prey individuals consumed (%)
Wild prey						
Cliff						
Bharal	56.85	56.16	18.32	4.42	4.09	1.76
Himalayan tahr	0.55	0.64	0.14	-	-	-
Plain						
Tibetan argali	0.78	1.16	0.16	8.95	12.57	2.30
Tibetan gazelle	0	0.00	0.00	11.05	8.62	6.31
Kiang	0	0.00	0.00	10.84	17.48	2.56
Small						
Himalayan marmot	6.55	4.47	8.26	32.11	20.36	49.66
Wooly hare	3.52	2.33	6.45	4.81	2.95	10.79
Royle's pika	2.53	1.57	58.02	0.67	0.38	18.78
Unidentified rodents	0.89	-	-	3.05	-	-
Unidentified birds	1.09	-	-	0.32	-	-
Livestock						
Yak	2.2	4.96	0.37	4.18	8.92	0.87
Horse	6.31	11.46	1.16	5.26	9.03	1.20
Lulu cow	0.41	0.70	0.08	4.6	7.42	1.09
Goat	13.99	12.45	5.52	8.53	7.10	4.15
Sheep	4.35	4.11	1.52	1.23	1.09	0.53

doi:10.1371/journal.pone.0170549.t002

Table 3. Selection of ungulate prey among snow leopards and wolves in the Central Himalayas.

Species	Category	Obs	Exp	χ2	P-value	Jacob's index
Snow leopards (n = 49)	Cliff	104	20	418.3	0.000	0.9
	Plain	1	3	1.7	0.196	-0.6
	Livestock	49	131	344.8	0.000	-0.8
Wolves (n = 14)	Cliff	3	15	18.4	0.000	-0.8
	Plain	17	1	171.5	0.000	0.9
	Livestock	14	17	1.1	0.316	-0.2

doi:10.1371/journal.pone.0170549.t003

Prey selection

Patterns of selection among the three categories of ungulates, i.e. cliff dwellers, plain dwellers and livestock, differed markedly between snow leopards and wolves. Snow leopards exhibited a significant preference for cliff-dwelling wild ungulates and a significant avoidance of livestock (Table 3). The selection index for plain dwelling ungulates was negative, thus indicating avoidance, but the difference in between use and availability was not significant (Table 3). The wolves exhibited a significant preference for plain dwelling ungulates and an avoidance of cliff dwellers, whereas livestock was consumed according to their availability (Table 3). The sample size of wolf scats was too small to test for selection among different livestock species. However, snow leopards significantly preferred horses and goats, and avoided yaks (Table 4). No selection was observed for sheep and lulu cows.

Factors influencing diet composition

For the occurrence of main food categories in the snow leopard scats, we tested for the relative influence of the sex of the predator, the season of scat collection, the latitude and longitude of the scat locations, the densities of wild ungulates and livestock, and wild prey species diversity (Table 5, data in S1 Appendix). Among the models for wild ungulate remains, two out of 14 candidate models had ΔAIC values <2, thus indicating small differences in performance between them. However, both models included the term "sex", and the highest ranking model (M5, Table 5) also included latitude (Y-coordinate), whereas the second best model (M4) included longitude (X-coordinate). Wild ungulates occurred in a larger proportion of samples from females (70%) than those from males (48%). The parameter estimates from the best model of wild ungulate occurrence (M4, Table 6) were negative for longitude and positive for latitude. This means that the occurrence of wild ungulates increased from south towards north and decreased from west towards east.

The best model of livestock occurrence in snow leopard scats included the two predictor variables "sex" and "latitude" (M5, Table 5). The second best model (M2), with a ΔAIC value of 3.5 included only the term sex. The parameter estimate for latitude was negative, indicating that livestock occurred more frequently in scats collected in the southern part of the study area

Table 4. Selection of livestock by snow leopards in the Central Himalayas.

Species	Livestock	Obs	Exp	χ2	P-value	Jacob's index
Snow leopards (n = 50)	Horse	12	3	35.1	0.000	0.7
	Goat	25	17	5.4	0.032	0.3
	Sheep	8	7	0.0	0.836	0.0
	Yak	4	21	24.0	0.000	-0.8
	Lulu	1	2	0.2	0.630	-0.2

doi:10.1371/journal.pone.0170549.t004

Table 5. Generalized linear mixed models of factors influencing diet composition of snow leopards in the Central Himalayas.

Model	Explanatory variables	Ungulates		Livestock	
		ΔAIC	W	ΔAIC	W
M1	Sex+Season	3.7	0.05	5.5	0.04
M2	Sex	3.2	0.07	3.5	0.10
M3	Season	10.2	0.00	15.0	0.00
M4	Sex+X	0.2	0.31	5.3	0.04
M5	**Sex+Y**	**0.0**	**0.34**	**0.0**	**0.61**
M6	Sex+ DD	4.8	0.03	3.6	0.10
M7	Sex + DU	4.8	0.03	5.3	0.04
M8	Sex + SW	2.3	0.11	5.4	0.04
M9	X	6.2	0.01	15.0	0.00
M10	Y	4.7	0.03	8.4	0.01
M11	DD	10.4	0.00	12.4	0.00
M12	DU	10.7	0.00	15.0	0.00
M13	SW	8.7	0.00	15.2	0.00
M14	NULL	9.1	0.00	13.3	0.00

The binomial response variables were the presence of wild ungulates and livestock in scats. X and Y indicates longitude and latitude coordinates (standardized UTM X and UTM Y values). DD = density of livestock; DU = density of wild ungulates; SW = wild prey species diversity expressed as the Shannon-Wiener Diversity Index. ΔAIC = the difference in Akaike Information Criteria between each model and best model with the lowest AIC; W = Akaike weight.

doi:10.1371/journal.pone.0170549.t005

(Table 6). Furthermore, livestock occurred more than twice as frequently in scats from male snow leopards (47%) than in scats from females (21%). Regarding the food category "small mammals/birds", the best model included only the wild prey species diversity index (M13, Tables 6 and 7). Samples containing this food category were found within grid cells with higher diversity indices (Tables 6 and 7). None of the other candidate models performed better than the NULL model, as their ΔAIC values were only marginally different.

Table 6. Parameter estimates and test statistics of Generalized Linear Mixed Models of diet composition of snow leopards and wolves in the Central Himalayas.

Species	Response variable	Predictor variable	Estimate	SE	Z-value	P
Snow leopards	Ungulate	Intercept	-1.96	0.62	-1.54	0.120
		Sex	0.90	0.35	2.57	0.010
		Latitude (Y)	0.59	0.29	2.02	0.040
	Livestock	Intercept	0.94	0.6	1.56	0.118
		Sex	-1.14	0.36	-3.20	0.001
		Latitude (Y)	-0.59	0.27	-2.22	0.026
	Small mammals	Intercept	-2.16	0.41	-5.30	0.000
		SW	0.94	0.36	2.27	0.024
Wolves	Ungulate	Intercept	3.19	1.18	2.70	0.000
		Seasons	-0.95	0.66	-2.94	0.000
	Small mammals	Intercept	-3.58	1.27	-2.82	0.000
		Seasons	2.30	0.72	3.20	0.000

Response variables were the occurrence of wild ungulates (Ungulate), livestock and small mammals/birds (Small) in scats. SW indicate wild prey species diversity expressed as the Shannon-Wiener Diversity Index.

doi:10.1371/journal.pone.0170549.t006

Table 7. Generalized linear mixed models of factors influencing the occurrence of small mammals/ birds in snow leopard scats in the Central Himalayas.

		Small mammals	
Model	**Explanatory variables**	**ΔAIC**	**W**
M1	Sex+Season	5.0	0.02
M2	Sex	4.3	0.03
M3	Season	3.3	0.05
M4	Seson+X	4.5	0.03
M5	Season+Y	5.3	0.02
M6	Season+ DD	3.6	0.04
M7	Season + DU	5.3	0.02
M8	Seson + SW	1.8	0.10
M9	X	2.9	0.06
M10	Y	4.5	0.03
M11	DD	2.7	0.07
M12	DU	4.5	0.03
M13	**SW**	**0.0**	**0.25**
M14	NULL	2.5	0.07

X and Y = longitude and latitude coordinates (standardized UTM X and UTM Y values). DD = density of livestock; DU = density of wild ungulates; SW = wild prey species diversity expressed as the Shannon-Wiener Diversity Index. ΔAIC = the difference in Akaike Information Criteria between each model and best model with the lowest AIC; W = Akaike weight.

doi:10.1371/journal.pone.0170549.t007

The occurrence of domestic animals in wolf scats did not differ among seasons, as the null model had the lowest AICc-value (data in S2 Appendix). For wild ungulates, the AICc of the null model was 3.60 (Parameter estimate = -1.95±0.66SE), and for small mammals/birds it was 6.09 (Parameter estimate = 2.30±0.72SE). The models including the predictor variable "season" performed better in both cases (Table 6). Wild ungulates occurred far more frequently in scats from the cold season (78%) than from the warm season (33%). An opposite pattern was evident for small mammals/birds, as these occurred markedly more frequently in samples from the summer (74%) than from winter (22%).

Discussion

Wolf scats contained larger proportions of plain dwelling ungulates and smaller portions of cliff dwellers than scats from snow leopards. Similarly, wolves significantly selected plain dwellers, whereas snow leopards selected cliff dwellers. Hence, prediction one was supported by our data. These predictions were founded on previously observed patterns of habitat selection among the two species, i.e. that wolves prefer open undulating plains associated with alpine meadows, whereas snow leopards are adapted to rugged terrain and cliffs [4, 9, 10]. Our results concur with these previous findings, as wolf scats were found mainly in the northwestern sampling grid cells where plain dwelling ungulates were most common. Apparently, the differences between the two species in diets and habitat use are associated with their hunting strategies and social behaviors. The hunting success of the snow leopard and other solitary and stalking/ambushing predators depends on access to cover to reduce attack distances [49]. Coursing and pack hunting predators are typically less dependent on cover, and their hunting success have been attributed to several factors such as pack sizes and physical characteristics of the prey [50, 51].

In our interspecific diet comparison, we found that snow leopard scats contained a larger proportion of livestock than wolf scats. Nevertheless, the prey selection analyses revealed significant avoidance of livestock among snow leopards, but not among wolves. These seemingly contrasting results are probably caused by the interspecific comparison being based on samples from areas where both species were present, whereas prey selection was analyzed based on the whole scat material. Both species were present in the northwestern part which contained relatively large areas of alpine meadows and less rugged terrain. Hence, the prime prey of snow leopards in our study area, the bharal, was few, and this may have caused a relatively high utilization of livestock among snow leopards compared to wolves. Regarding selection among livestock species, snow leopards preferred horses, but avoided yaks. A higher attack frequency on horses has also been observed in previous studies [52], and it may be caused by horses often being left unattended in the pastures. Yaks are also unattended, but they are generally too large to be killed by snow leopards. Goats and sheep are prey of optimal size for snow leopards, but only the former was significantly preferred. Both species are attended by herders, but goats are often more dispersed than sheep and therefore probably more vulnerable. Regarding interspecific diet overlap, the Pianka index value of 0.44 was much smaller than in two previous comparisons between the two species, i.e. 0.91 [4] and 0.87 [5]. Both previous studies attributed the high diet overlap to low prey diversity. Our results concur with this explanation, as species richness was relatively high in the northwestern part of our study area where the two carnivores overlapped in distribution.

We predicted that scats from areas with low wild ungulate densities should contain larger proportions of small mammals/birds and livestock, due to a lower degree of diet specialization towards preferred wild ungulate prey in these areas. However, this prediction was not supported, as the best models of small mammal and livestock occurrence in scats did not include wild prey abundance. For small mammals, the best model only included the term "wild prey diversity", and the association was positive, but relatively weak. The Shannon-Weiner diversity index gives high values when the numbers of prey species are high and with relatively even densities. Hence, a low density of a dominating prey species in these areas, such as bharal, may have given high index values. As a consequence, the consumption of small mammals and birds may have been positively associated with the species diversity index due to a lower availability of the preferred bharal.

We observed seasonal diet differences among wolves, but not among snow leopards. Hence, prediction iii was only partially supported. Wolves consumed more small prey during summer and more wild ungulates during winter. Marmots was the most common small prey species in wolf scats, and the seasonal diet differences is probably caused by changes in the accessibility of marmots due to their winter hibernation. Although livestock are distributed in different altitudes during the warmer and colder months, we did not detect any seasonal difference in their occurrence in predator scats. Presumably, seasonal differences in the accessibility of livestock was not high enough to cause significant diet shifts.

Among snow leopards, scat contents differed between the sexes, i.e. females had a higher proportion of wild ungulates and males a higher proportion of livestock. Hence, prediction iv was supported and the results concur with a telemetry study of snow leopards in Mongolia, which showed that the proportion of livestock among located kills were more than twice as high among males than females [17]. More frequent livestock killing among males than females has also been observed among several other carnivore species [53], but to our knowledge, it has never before been revealed based on scat analyses. Male biased livestock killing in carnivores has been suggested to be caused by higher encounter rates among males due to their wider ranging movements [53]. It has also been suggested that sexual selection have favored a high risk-high gain strategy among the males [19, 54], which involves the depredation of easily accessible domestic prey even though it may impose a greater mortality risk due to retaliatory killing.

Livestock depredation and the associated conflicts with humans is a main challenge for the conservation of both snow leopards and wolves [15, 55]. In this context, an interesting aspect is whether management aimed at enhancing the wild prey base will lead to reduced predation rates on domestic animals [56]. In a study of Eurasian lynx, livestock depredation was inversely related to wild ungulate prey density [18]. Furthermore, a recent review revealed a somewhat similar relationship among larger felids [57], i.e. that the proportion of livestock in diets abruptly increased when wild prey biomass decreased below a threshold value. In our study, we did not detect any influence of wild prey density on the occurrence of livestock in snow leopard scats even though wild prey biomass within sampling grid cells ranged both above and below the suggested threshold value of 545 kg/km^2 [57]. The lack of a relationship in our study may be partially due to a confounding effect of the wide ranging movements of snow leopards. Recently, snow leopards in Mongolia was shown to move within home ranges of several hundred km^2 [58], and this entails that some individuals in our study area may have utilized several different sampling grid cells. Although thresholds in livestock depredation may exist, we believe that more research is needed to the potentially interacting effects of livestock- and wild prey abundance on the probability of livestock killings.

Supporting Information

S1 Appendix. Snow leopard diet data for logistic models (Snowleopardsdiet.txt).
(TXT)

S2 Appendix. Wolf diet data for logistic models (Wolfdiet.txt).
(TXT)

Acknowledgments

The Center for Molecular dynamics Nepal genotyped the scats. We sincerely thank officers and rangers of Jomsom and Lomanthang Unit Conservation Offices of Annapurna Conservation area and Manaslu Conservation area for support during field work. We are also grateful to local communities for their great help and support during the field work. We thank Nawa Raj Chapagain for preparing the study area map.

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PAPER III

Patterns of livestock depredation by snow leopards and other large carnivores in the Central Himalayas, Nepal.

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Abstract

Quantifying livestock losses due to large carnivores and understanding the impact on local people is vital for formulating long-term mitigation strategies. In a large area (≈5000 km^2) in the central Himalayas, Nepal, we conducted a semi-structured questionnaire survey to quantitatively assess livestock losses due to snow leopards, wolves, and other carnivores. We interviewed 428 respondents in 21 village development committees across the Annapurna-Manaslu landscape; 184 respondents were selected randomly and 244 were from households with known depredation losses. Livestock predation mortality was low among random households (i.e. 0.9%), but it varied markedly among villages, thus suggesting that site-specific mitigation measures are required. Snow leopards were responsible for more than half of the kills (62%). Using generalized linear mixed effects models, we found that loss probability increased with herd size, but more among those owning mainly large stock (e.g. yak and horses). We suspect this is due to large stock herds being less attended and more dispersed while grazing. The impact of wild prey density in the grazing areas on loss probability was complex; the lowest loss probability occurred in areas of high wild prey density and low livestock density, but was highest in areas where both livestock and wild prey was abundant.

Keywords: *Panthera uncia, Canis lupus chanco*, human-wildlife conflict, large carnivores, trans-Himalayas.

1. Introduction

The presence of large carnivores in pastoral landscapes is controversial because of the associated conflicts with human livelihoods (Treves and Karanth 2003). Harm to humans and livestock from carnivore attacks instigate negative attitudes towards their conservation, and the conflicts often lead to retaliatory killings, which is a serious concern globally (Jackson 2015; Mishra et al. 2016; Mishra et al. 2004; Suryawanshi et al. 2014; Woodroffe et al. 2005). Persecution of carnivores typically occurs either to get rid of the depredation problem permanently or when the losses have not been adequately addressed by the concerned authorities. These situations further deteriorate if authorities obligate legal actions in case of retaliation. This creates an unfavorable environment in which local support for conservation deteriorates and management efforts ultimately loses stability and progress (Hill et al. 2002; Madden 2004). In order to reduce negative impacts of conflicts, both for local people and carnivores, it is important that mitigation strategies and management interventions are evidence-based, and take into account location-specific cultural and ecological conditions (van Eeden et al. 2018). Otherwise, it is difficult to evaluate the extent of the conflicts and whether or not mitigation measures have the desired effect.

Available literature reveals highly contrasting results and conclusions regarding factors associated with livestock depredation. For instance, depredation is assumed to decrease if the abundance of natural prey increases (Mizutani 1999), and enhancing the natural prey base is therefore often recommended to mitigate livestock losses (Mishra et al. 2003). Although intuitively logical, few studies have managed to provide clear evidence for this relationship. However, a review by Khorozyan et al. (2015) showed that livestock depredation by big cats typically increases when wild prey declines below minimum threshold values. On the other hand, a study of snow leopards in the Indian Trans-Himalaya and in south Gobi, Mongolia, revealed that an increase in wild prey abundance accelerated livestock depredation due to aggregative responses of carnivores (Suryawanshi et al. 2017). A study of Eurasian lynx (*Lynx lynx*) predation on domestic sheep in Scandinavia revealed scale-dependent responses of wild prey density (Odden et al. 2008; Odden et al. 2013). On a large scale, kill rates on domestic sheep was inversely related to the density of their main natural prey, roe deer (*Capreolus capreolus*) (Odden et al. 2013). However, on a smaller scale, a seemingly contrasting pattern emerged, i.e. domestic sheep were more often killed in relatively good roe deer habitat (Odden et al. 2008). Two models were proposed to explain the different effects; according to the “attraction model”, livestock depredation increases where natural prey is locally abundant due to higher encounter rates between carnivores and livestock, whereas the “energetic model” predicts that in regions of high natural prey density, these encounters more rarely lead to livestock being killed (Odden et al. 2013).

The impact of several other factors on livestock depredation loss has also been investigated previously, including habitat, predator density, livestock density and herding practices. Regarding the former, predation risk have been shown to increase in or near habitat types that are selected by the predators (see e.g. de Azevedo and Murray 2007; Johansson et al. 2015). Interestingly, although aggregation effects by predators may influence livestock loss (Suryawanshi et al. 2017), predator density was evaluated as having limited influence in two reviews (Graham et al. 2005; Kaczensky 1999) . Likewise, livestock density and herding practices have been reported to have both negligible and high impact on losses (Graham et al. 2005; Kaczensky 1999; Mijiddorj et al. 2018; Ogada et al. 2003).

The socio-economic consequences of livestock depredation are particularly severe in economically marginal communities that are to a large extent dependent on pastoralism (Aryal et al. 2014a; Oli et al. 1994). In the rural Himalayas of Nepal, the majority of the human population are traditional agro-pastoralist, and animal husbandry is the main source of income. All accessible land is used for grazing, and grazing areas overlap with several large carnivore species known to prey on livestock, with snow leopards (*Panthera uncia*) and wolves (*Canis lupus*) being responsible for most of the cases (Aryal et al. 2014a; Chetri et al. 2017). The potential for human-carnivore conflicts is therefore high in this region, and previous studies have revealed high - but variable – levels of loss (Aryal et al. 2014a; Jackson et al. 1996; Mishra 1997; Oli 1994; Wegge et al. 2012). Some of this variation may be attributed to the studies being conducted in relatively small study areas with highly site-specific levels of loss due to contrasting ecological conditions (Jackson et al. 1996; Mishra 1997; Oli 1994; Wegge et al. 2012). Little is known about the relative importance of different determinant factors causing spatial variation in losses at larger spatial scales. Such information is clearly needed in order to improve our ability to predict potential locations of high conflict levels, and to gain knowledge on how these should be mitigated. Hence, in our study, we assessed the extent of the conflict and its influential factors across an area of 5000 km^2 in the Central Himalayas in Nepal. We focused mainly on how vulnerability to depredation depended on the size and species composition of herds, and assessed the influence of ecological conditions within the grazing areas, including habitat structure and the abundances of livestock, natural prey and predators.

2. Methods

2.1. Study area

The study area was located within the Annapurna Conservation Area (ACA) and the Manaslu Conservation Area (MCA) (N28-29°, E83-85°) in the rain shadow area of the trans- and semi-trans Himalayas. The ca. 9292 km^2 of ACA and MCA represent 27% of the protected areas in Nepal (http://www.dnpwc.gov.np). The interviews were conducted 21 Village Development Committees (VDCs) covering the northern section of ACA and MCA. A VDC is the lowest administrative unit of the government and usually contains 7-9 small clustered village/settlements. The 21 VDCs have separate designated grazing areas of 6621 km^2 (summer gazing area=1631 km^2, winter gazing area=721 km^2, year round=582 km^2, non-grazed area=3687 km^2) in the northern section of ACA and MCA (Fig. 1). The area is rich in both floral and faunal diversity, governed by altitudinal gradients, topography, microhabitats and high climatic variation. Large ungulate assemblages include bharal (*Pseudois nayaur*), Himalayan tahr (*Hemitragus jemlahicus*), Tibetan argali (*Ovis ammon hogdsoni*), kiang (*Equus kiang*), and Tibetan gazelle (*Procapra picticaudata*).The main predators are snow leopards and wolves, other carnivores include golden jackal (*Canis aureus*), red fox (*Vulpes vulpes*), Himalayan black bear (*Ursus thibetanus*), Tibetan sand fox (*Vulpes ferrilata*), brown bear (*Ursus arctos*), Eurasian lynx and several species of weasel (*Mustela* spp.), and marten (*Martes* spp.). The presence of common leopard (*Panthera pardus*) has been recorded near the tree line up to 4000 m. Snow leopards and wolves are mainly distributed within an altitudinal range of 3000 – 6000m asl., which comprises the grazing areas of livestock (summer, winter and year round). Animal husbandry is the main source of livelihood, with livestock consisting of yaks (*Bos grunniens*), cattle-yak hybrids (dzo, jhopas, *Bos* spp.), lulu cows (*Bos taurus* sp.), horses (*Equus ferus caballus*), goats (*Capra hircus*) and sheep (*Ovis aries*). All accessible areas are used for seasonal livestock grazing (summer: May to October, winter: November-April) according to a traditional grazing calendar (Fig. 1). The density of livestock is five times higher than that of wild ungulates in the study area (Chetri et al. 2017).

2.2. Questionnaire survey

To quantify livestock losses, we interviewed 428 individuals in 85 settlements using both semi-structured and open ended questionnaires. We covered 13% of the total number of households in the survey villages (CBS 2012). We interviewed two different groups of respondents, i.e. “conflict households” which were known to have lost livestock to predators during the last year and “random households” which were selected by approaching the nearest house with people present in a random direction from a visited “conflict household”. We selected conflict households from lists of compensation claimants provided by the VDC level conservation area management committee leaders. We used two respondent groups because the proportion of randomly selected households experiencing depredation was too low (24.5%) to obtain sufficient information on depredation events. Hence, information from “random households” was used to assess the probability of experiencing depredation and to quantify livestock predation rates and other mortality causes. Conflict households (including random households that had experienced depredation) provided data on the relative contribution of different predator species, their selection of livestock species, and circumstances of livestock killing. Field verification is crucial as interview data sometimes lead to bias if the carnivore species is disliked by the communities (Mishra et al. 2016). Some pastoralists also intentionally exaggerate the numbers of livestock killed, perhaps in the hope of getting higher compensation from the concerned authorities (Namgail et al. 2007). Accordingly, we cross checked and tallied our questionnaire data with the livestock loss data maintained at the field offices of ACA and MCA whenever applicable. We also cross-verified village-level losses with herders during random interviews and discussions in the field (n=35). In the questionnaire, we recorded household livestock ownership (species, numbers, sex and age) and losses due to predators, and other causes of death (disease and accidents).

3. Data analysis

We used generalized linear mixed effects models (GLMMs) to assess factors associated with the probability of households experiencing livestock losses to snow leopards. We excluded other predators from this analysis due to the very small number of recorded depredation events. We used a binomial response variable, i.e. whether the respondent had experienced livestock loss or not, and VDC was set as a random effect. As explanatory variables, we used (i) ownership (total livestock holdings), (ii) herd composition (the proportion of large stock, i.e. horses, cattle, yak and lulu cow, in their total holdings, (iii) wild ungulate density, (iv) livestock density, (v) snow leopard density, and (vi) terrain ruggedness. For the four latter variables (iii-vi), we used extracted values from the delineated year-round grazing areas of the VDC that the respondent belonged to. (iii) Wild ungulate density and (iv) livestock density was estimated using the double observer method in 26 different 25 km^2 sampling blocks distributed throughout the whole study area, as described in Chetri et al. (2017). To obtain predicted livestock densities within each grazing area, we interpolated values from the census blocks using inverse distance weighing (IDW) in the geostatistical analyst tools in ArcMap 10.3. (ESRI 2014). (v) We obtained predicted snow leopard density values for each grazing area from spatially explicit capture-recapture models (SECR) based on analyses of snow leopard scat DNA collected from 490 km of transects traversing large parts of the study area (Chetri et al. *submitted*). (vi) Terrain ruggedness values for the grazing areas were obtained from 40m interval contour lines from a digital topographic map, defined as the average length of contour lines per km^2.

4. Results

4.1. Livestock ownership and mortality patterns

Among the randomly selected households, average total livestock holdings was 61 (SD=83.2), and thus smaller than among the conflict households (average=99, SD=89.3, Table 1). Relative proportions of small stock and large stock were similar among the two respondent groups, but conflict households owned a larger proportion of yak and smaller proportions of the other large stock species (Table 1). The annual predation rate of livestock owned by random households was very low, i.e. 0.9%, and it differed markedly among species (Table 1). Horses had the highest annual predation rates (4.2%), whereas predation rates of yak and yak hybrids (0.3% and 0%) were the lowest among the livestock species. Mortality due to disease and accidents was negligible in both random- and conflict households (Table 1).

4.2. Livestock depredation

Snow leopards were responsible for more than half of the predation losses (61.9%); the remaining were from Himalayan wolf (16.8%) and other predators (21.3%) including feral dogs, brown bear, black bear, Eurasian lynx, jackal and common leopard (Table 2). All predators combined killed larger numbers of small stock than large stock (Table 2). A significantly larger proportion of livestock depredation events occurred during summer (59.5%) than during winter (40.5%, χ^2= 10.25, df = 1, p = 0.001). However, we detected differences among the predator species in their seasonal patterns. Snow leopards showed no seasonal difference (summer = 51.9%, winter = 48.1%, χ^2 = 0.20, df = 1, p = 0.656), but more kills were observed in summer by wolves (summer = 77.6%, winter =22.5%, χ^2= 14.93, df = 1, p < 0.001) and by the other predators grouped (summer = 67.2%, winter = 32.8%, χ^2 = 6.93, df = 1, p = 0.008).

We compared 20 candidate models to investigate factors affecting the probability of experiencing livestock loss due to snow leopards. According to the best model, the probability of livestock loss depended on an interaction between livestock ownership (total herd size) and herd composition, and an interaction between wild and domestic ungulate density in the grazing areas (Table 3, Fig.2). Loss probability increased with ownership and was higher among farmers owning larger proportions of large stock. The interaction between herd size and composition (Fig.3) showed that among farmers owning mainly small stock, herd size had a small effect on loss probability, whereas a strong effect of herd size was evident among large stock owners. The impact of wild and domestic ungulate density on loss probability was complex, i.e. wild ungulate density had opposite effects depending on domestic animal density (Fig. 4). Where domestic animal density was high, increasing wild prey densities lead to higher losses. In contrast, the lowest loss probability occurred in areas of low livestock densities and high wild prey densities. Surprisingly, neither snow leopard density nor landscape ruggedness appeared in the best model.

5. Discussion

Snow leopards were responsible for more than half the kills followed by wolves and other predators. Seasonal differences in predation was evident for wolves and for the group of "other predators" (all except snow leopards and wolves), but not for snow leopards. The dominating role of snow leopards may be explained by their wider distribution and higher abundance in the study area compared to the other species (Chetri et al. *submitted*). Per capita, it is unlikely that snow leopards killed more livestock than for instance wolves, as a recent study in the same area showed that their diets contained quite similar proportions of livestock (Chetri et al. 2017). Concerning seasonal patterns of loss, differences between winter and summer are logical consequences of winter hibernation among black- and brown bears, and for wolves, that their distribution was limited to the northwestern section of the study area which was only used for grazing during summer (Chetri et al. 2017). On the contrary, snow leopard distribution covered the entire study area, both winter and summer pastures, thus rendering smaller seasonal differences in livestock vulnerability to attacks by this species.

The average annual livestock mortality from predation was less than 1%, and although spatial variation was large, it did not exceed 3% in any of the VDC's. Our estimated losses were small compared with previous studies of snow leopards and other large carnivores in the mountain ranges of Nepal, i.e. 2.3 to 4.0% (Aryal et al. 2014a; Oli 1994; Wegge et al. 2012). From other parts of central and south Asian mountains, highly variable losses between 1.3 to 12% have been recorded (Alexander et al. 2015a; Din et al. 2017; Hussain 2000; Jackson and Wangchuk 2004; Li et al. 2013; Mishra 1997; Namgail et al. 2007; Wang and Macdonald 2006). Hence, to our knowledge, livestock mortality due to predation was the lowest ever recorded in the whole region. We believe this may be caused primarily by the aim and the spatial extent of our study. While many studies have focused on obtaining a thorough understanding of the nature of conflicts in smaller areas, or "hotspots", we aimed to assess and identify sources of spatial variation by including a large area with variable levels of loss.

Our analyses revealed that loss probability depended on an interaction between the size and the species composition herds; loss probability increased with herd size, but a much stronger effect was observed among households owning mainly large stock. An obvious explanation to the impact of herd size is that larger herds are both easier to detect by the predators and more difficult to protect by herders. A similar explanation can be applied to the difference in the impact of herd size among owners of small stock and large stock. Small stock is usually far less dispersed than large stock, which often moves scattered and unattended in the pastures. Irrespective of herd size, small stock is therefore relatively easy to oversee and guard from attacks, as compared to large stock herds. The herding practice of releasing large stock more or less unattended in the pastures is common among pastoralists for instance in Bhutan (Wang and Macdonald 2006), China (Alexander et al. 2015a), Nepal (Jackson et al. 1996) and south Gobi Mongolia (Mijiddorj et al. 2018). In accordance with our results, Mijiddorj et al. (2018) reported that losses increased with herd size and that herding practice had a strong effect. We agree with the conclusion of Mijiddorj et al. (2018) that there is a strong potential in aiming attention to herding practices when mitigating livestock losses to predators.

We previously described contrasting views on how natural prey abundance affects levels of livestock depredation (Khorozyan et al. 2015; Mizutani 1999; Suryawanshi et al. 2017). Two opposing scenarios are (i) livestock depredation increases when wild prey increases due to an aggregation response by predators, and (ii) livestock loss declines when natural prey increases due to a diet switch by the predators. The difference between the two scenarios is the relative contribution of numerical- (i) and functional (ii) response of a predator to increasing prey density (Holling 1959). Our best model of loss probability partially supported both of these views. We observed that the densities of wild ungulates and livestock in the grazing areas had negligible effect, independently, but that the effect of their interaction was strong (Fig. 2). Markedly different impacts of wild ungulates occurred in areas of low and high livestock density. Where livestock density was high, loss probability was highest in areas with high wild ungulate densities. As in scenario (i) above, this could be caused by an aggregation effect. On the contrary, as in scenario (ii) above, livestock loss probability declined with increasing wild ungulate density in areas where livestock was low. This is probably explained by livestock contributing relatively little to the total prey base in these parts, i.e. below a threshold proportion where snow leopards almost solely focus on natural prey. Our findings illustrate that the relationship between livestock loss and natural prey abundance is complex and context dependent, and it is therefore difficult to predict the outcome of management actions aimed at enhancing the natural prey base.

In this paper, we have shown that livestock losses were low in our study area, and that a large proportion (76%) of randomly selected households had never experienced loss at all. Hence, the overall conflict potential seemed low compared to previous studies from the region. However, since losses varied markedly among villages, and based on earlier studies (Jackson et al. 1996; Oli et al. 1994; Wegge et al. 2012), it seems that conflict “hotspots” do exist. Plans for managing livestock conflicts should therefore focus on identifying and mapping these specific areas so that appropriate mitigation measures can be initiated. Furthermore, the low proportion of losses in our study does not reflect an absence of severe impact on local economy. Several instances of mass killings of livestock have been reported during the last years. In our own records, two cases of 11 sheep and 17 goats being killed in a single attack occurred. After the data collection ended, one unfortunate herder lost all his 104 goats in two consecutive nights. According to the current management system in our study area, only a small fraction of ca 4-6% of the economic cost is compensated (Chetri pers. comm.). Experiencing mass killings thus entails a severe economic impact, and improved systems are needed for aiding these farmers.

Funding

The first author’s fieldwork was supported by the Panthera-the Kaplan Graduate Award. Fieldwork was also partly funded by the National Trust for Nature Conservation through its USAID funded Hariyo Ban Program.

Acknowledgements

We thank the National Trust for Nature Conservation for permission to carry out the study. We sincerely thank the survey participants, the field staff of ACA and MCA, and the local communities for their support and collaboration during the field surveys.

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Table 1 Ownership and annual mortality of livestock among interviewed households in the Central Himalayas, Nepal.

	Small stock		**Large stock**				
	Goat	**Sheep**	**Lulu cow**	**Yak**	**Yak hybrid**	**Horse**	**Total**
Random households (N = 184)							
Owned (SD)	43.7 (73.7)	6.2 (18.9)	3.3 (2.3)	3.5 (8.6)	2.8 (5.4)	1.8 (1.4)	61.3 (83.2)
Predation (%)	0.7	0.8	2.2	0.3	0.0	4.2	0.9
Disease (%)	0.1	0.2	2.0	0.8	0.4	0.9	0.3
Accidents(%)	0.0	0.0	0.3	0.0	0.8	0.0	0.1
Unknown (%)	0.0	0.0	0.5	1.1	0.6	0.6	0.1
Total Loss (%)	0.8	1.0	5.0	2.2	1.8	5.6	1.3
Conflict households (N = 244)							
Owned (SD)	71.8 (83.5)	9.0 (20.8)	3.6 (2.6)	10.4 (23.4)	1.5 (2.4)	2.5 (1.7)	98.8 (89.3)
Predation (%)	1.4	2.5	2.7	4.4	4.0	8.0	2.0
Disease (%)	0.0	0.3	1.6	0.2	0.3	1.0	0.2
Accidents(%)	0.0	0.0	0.3	0.4	0.0	0.0	0.1
Unknown (%)	0.0	0.0	0.5	0.1	0.0	0.2	0.0
Total Loss (%)	1.4	2.8	5.1	5.1	4.3	9.1	2.3

Table 2 Number of livestock deaths due to depredation by various carnivores between July 2013 and June 2014 based on questionnaire survey in the central Himalayas. A=Adult, J=Juvenile.

Species	**Goat**		**Sheep**		**Lulu cow**		**Yak**		**Yak-cow hybrid**		**Horse**		**Total (%)**
	A	**J**	**A**	**J**	**A**	**J**	**A**	**J**	**A**	**J**	**A**	**J**	
Snow Leopard	168	18	37	2	9	2	10	69	4	5	21	17	362 (61.9)
Himalayan wolf	25	17	9	1	8	5	0	10	1	1	11	10	98 (16.8)
Jackal	23	17	4	1	4	2	0	1	0	0	0	0	52 (8.9)
Eurasian Lynx	6	0	4	0	1	0	0	0	0	0	0	0	11 (1.9)
Common Leopard	0	0	0	0	0	0	0	5	0	0	0	0	5 (0.9)
Brown bear	0	0	0	0	0	0	0	5	0	0	0	4	9 (1.5)
Black bear	0	0	0	0	1	0	6	4	5	0	0	0	16 (2.7)
Feral dog	14	8	3	2	0	4	0	0	0	0	0	1	32 (5.5)
Total (%)	236 (40.3)	60 (10.3)	57 (9.7)	6 (1.0)	23 (3.9)	13 (2.2)	16 (2.7)	94 (16.1)	10 (1.7)	6 (1.0)	32 (5.5)	32 (5.5)	585 (100.0)

Table 3. Model selection for loss due to snow leopard. All continuous variables were standardized by 2 standard deviations as per (Gelman and Hill 2007) and all models included a varying intercept on VDC (i.e. VDC included as a random effect). OWN: number of domestic animals owned, COMP: composition of the herd, WILD = Wild ungulate density, DOMD= Domestic animal density, SLD = Snow leopard density, RIS = Ruggedness index.

Model	df	logLik	AICc	delta	weight
OWN * COMP + WILD * DOMD	8	-215	447	0	0.49
OWN * COMP + WILD * DOMD + SLD	9	-215	449	2.04	0.18
OWN * COMP + WILD * DOMD + RIS	9	-215	449	2.08	0.17
OWN * COMP + WILD * DOMD + RIS + SLD	10	-215	451	4.11	0.06
OWN * COMP + WILD + DOMD	7	-218	451	4.27	0.06
OWN * COMP + WILD + DOMD + SLD	8	-218	453	6.18	0.02
OWN * COMP	5	-222	454	6.64	0.02
OWN * COMP + SLD	6	-222	456	8.65	0.01
OWN + COMP + WILD * DOMD + SLD	8	-225	466	18.96	0
OWN + COMP + WILD + DOMD	6	-228	469	22.01	0
OWN + COMP + WILD + DOMD + SLD	7	-228	470	23.51	0
OWN	3	-236	478	30.89	0
COMP	3	-238	482	35.37	0
WILD * DOMD	5	-240	490	43.43	0
WILD * DOMD + SLD	6	-240	492	45.37	0
DOMD	3	-247	500	52.63	0
RIS	3	-248	503	55.55	0
WILD	3	-249	505	57.83	0
NULL	2	-251	506	58.61	0
SLD	3	-251	507	60.44	0

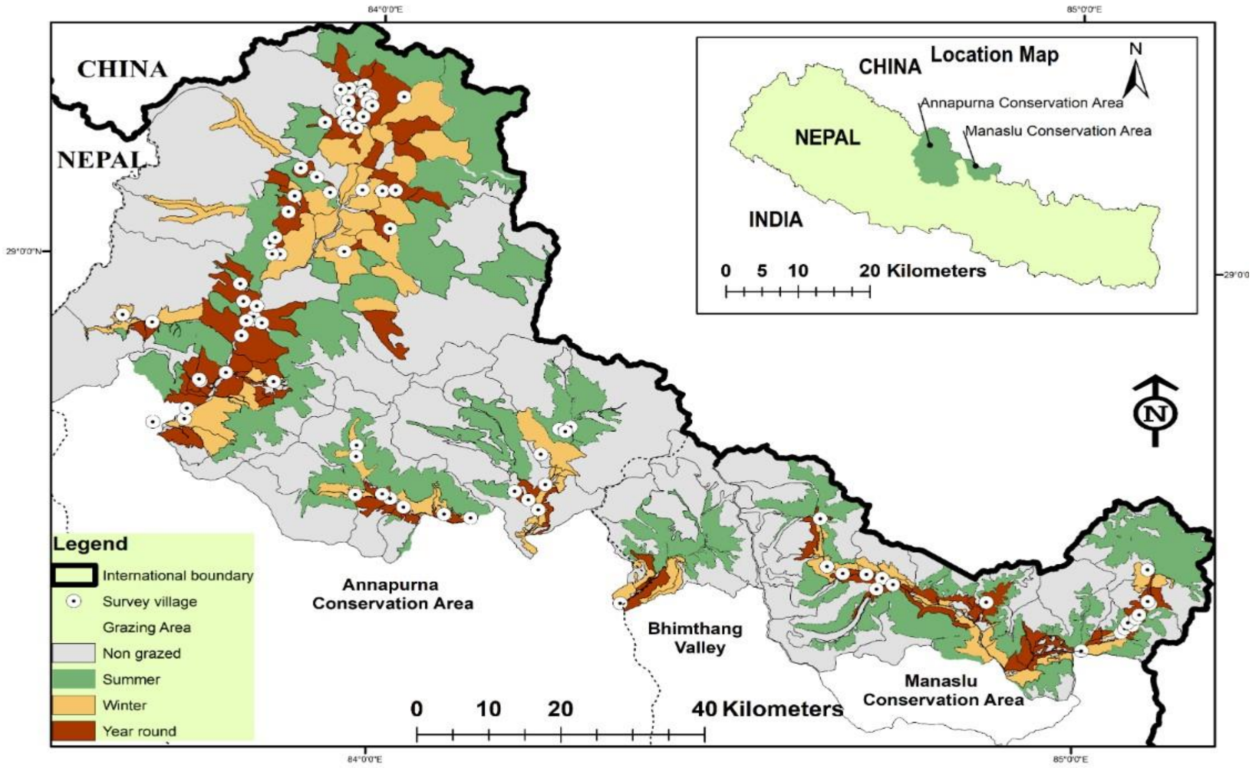

Fig.1. Study area with location of survey villages and grazing areas.

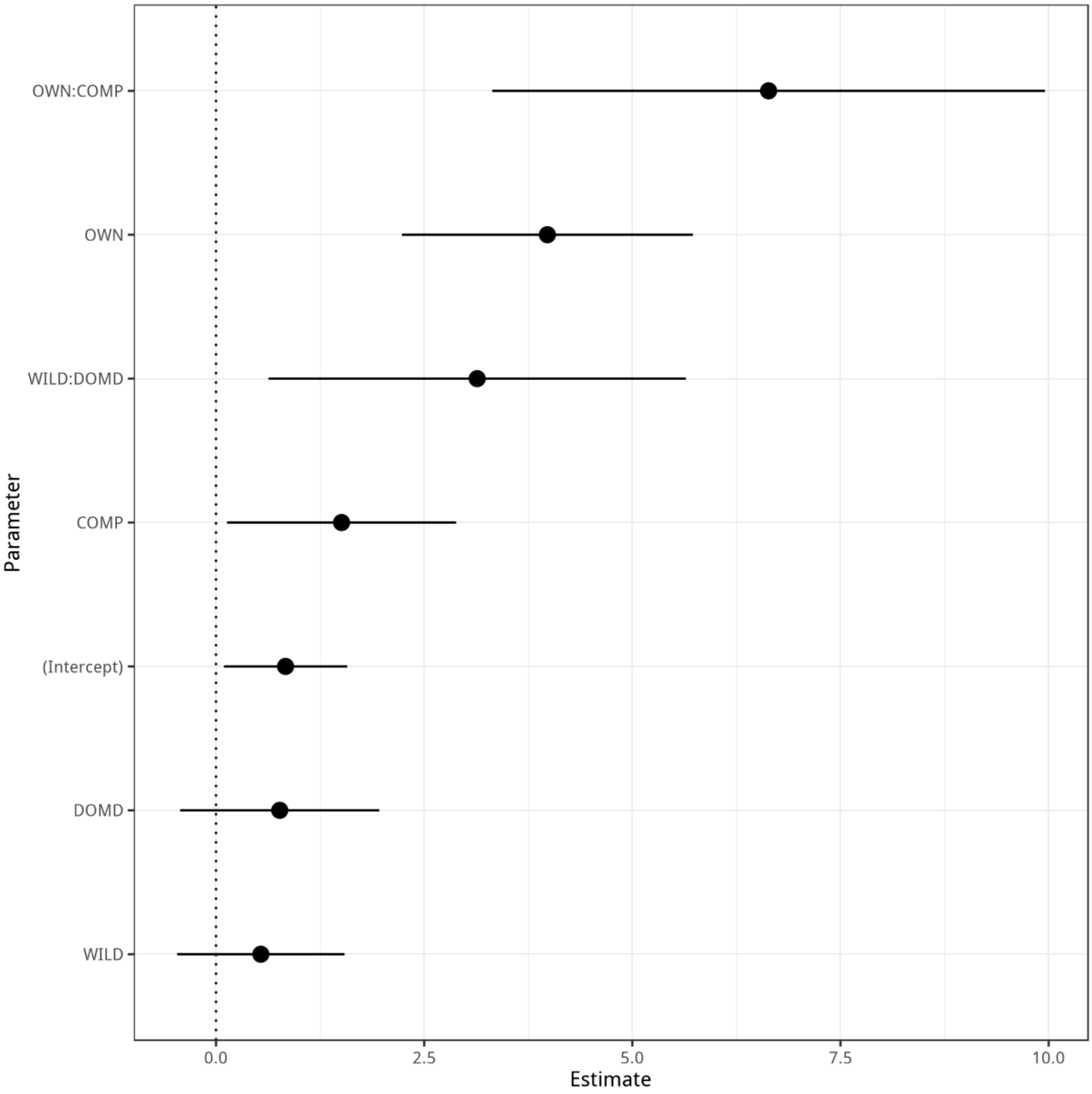

Fig. 2. Parameter estimates (dots) and 95% confidence intervals (solid lines) from the best Generalized Linear Mixed-Effects Model of factors affecting livestock loss to snow leopards. The strength of the effect of parameters is indicated by the distances between the solid horizontal lines and the dotted vertical line. OWN=Total herd size, COMP= livestock species composition, i.e. the proportion of large livestock in the herds, DOMD=Domestic livestock density in the grazing areas, WILD=Wild ungulate density in the grazing areas, OWN:COMP=interaction between total herd size and livestock species composition, and WILD:DOMD=interaction between wild ungulate density and domestic livestock density in the grazing areas.

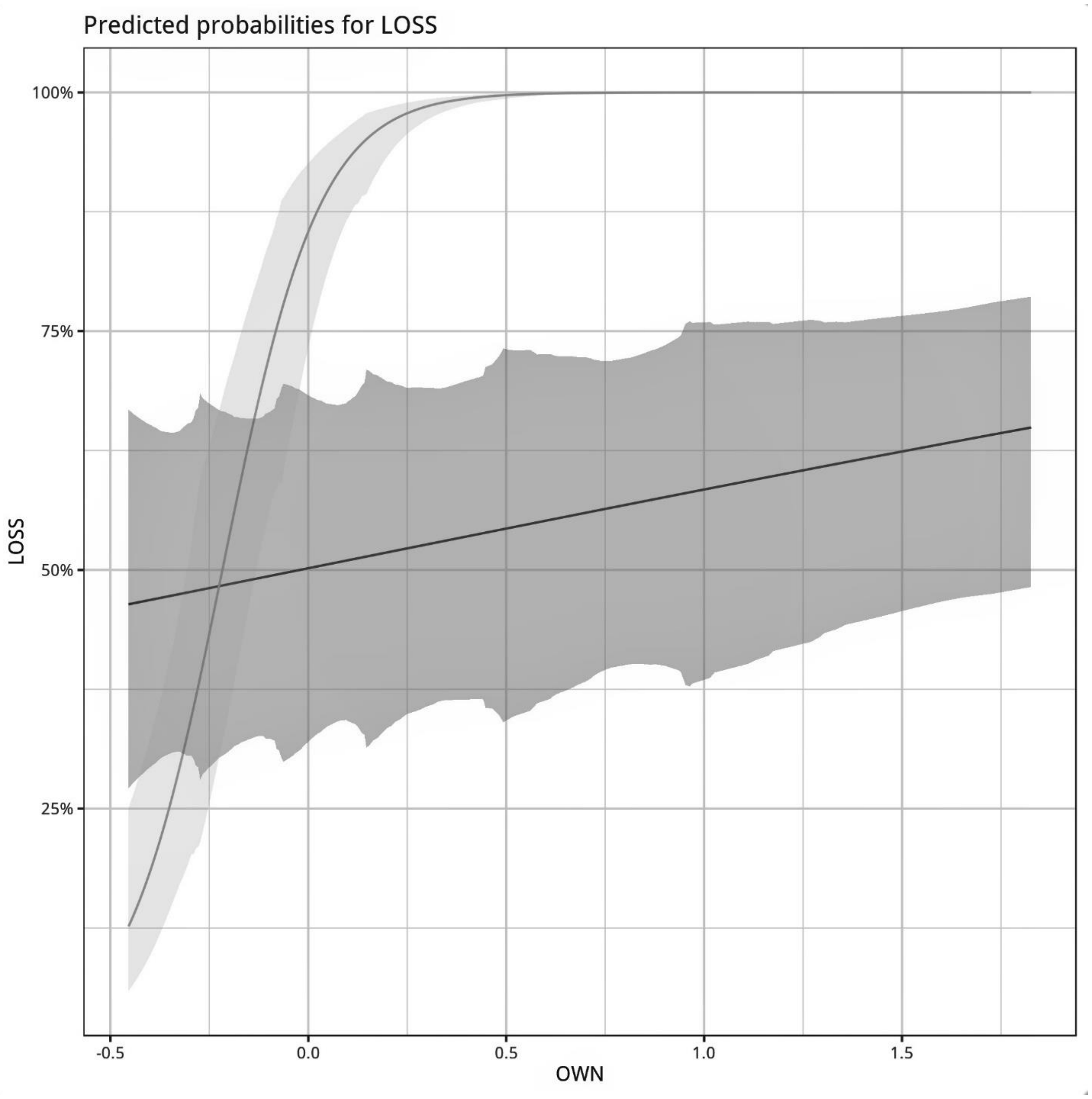

Fig. 3. Probabilities of experiencing livestock loss due to snow leopards based on the best Generalized Linear Mixed-Effects Model (see fig. 2). The figure illustrates the impact of herd size (OWN) given two different values of livestock species composition; the grey line represent owners of only large stock and the black line represent only small stock.

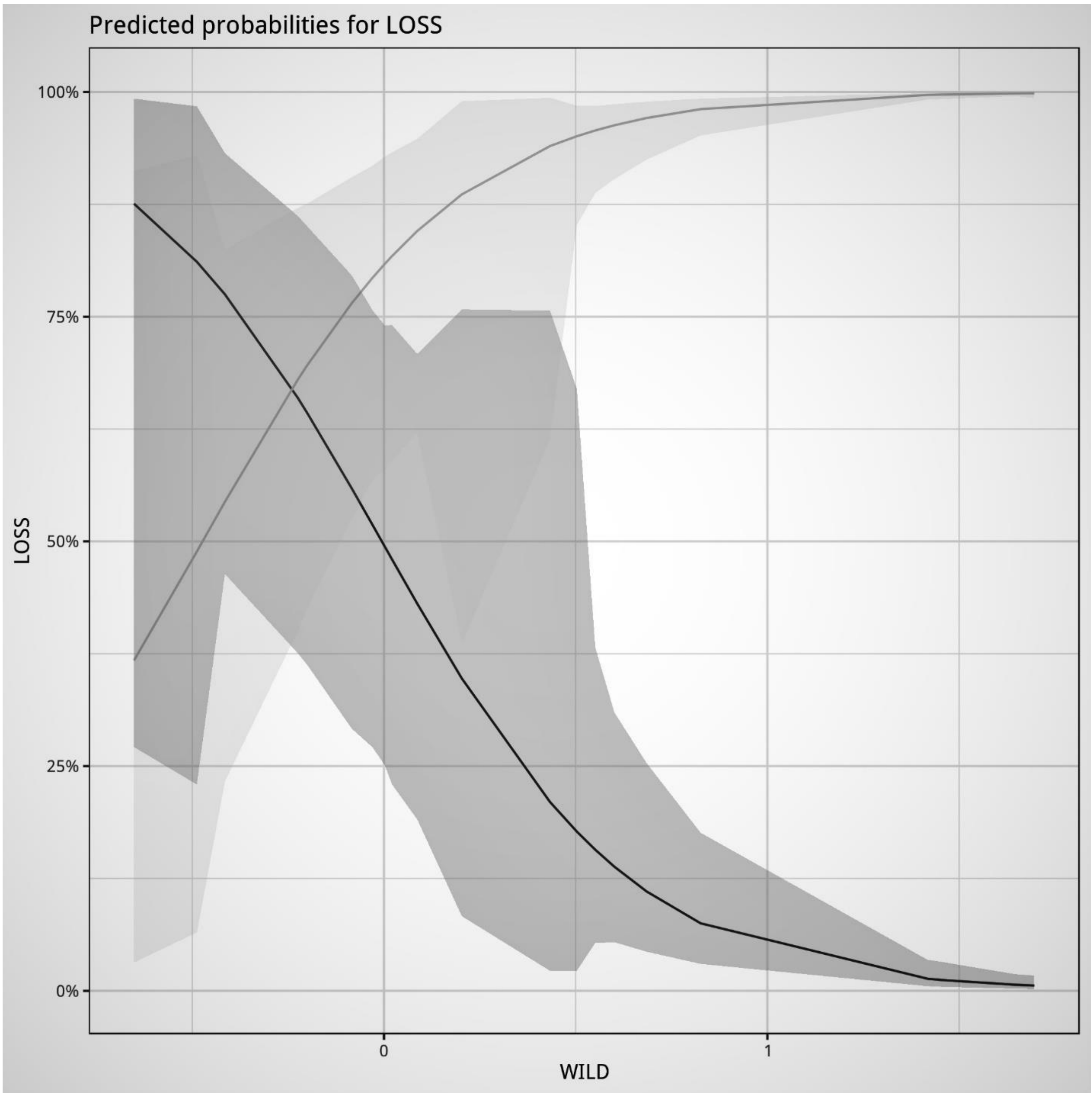

Fig. 4. Probabilities of experiencing livestock loss due to snow leopards based on the best Generalized Linear Mixed-Effects Model (see fig. 2). The figure illustrates the impact of wild prey density in the grazing areas given two different values of livestock density; the grey line represent the highest recorded livestock density (86.5 per km^2) and the black line represent the lowest density (2.9 per km^2).