Original Research Article

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

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A R T I C L E   I N F O

A B S T R A C T

Quantifying livestock losses due to large carnivores and understanding the impact on local people is vital for formulating long-term mitigation strategies. In the large Annapurna-Manaslu landscape (6621 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 aimed at assessing how livestock losses were related to the sizes and species composition of herds as well as the ecological conditions within the grazing areas, i.e. topography, and densities of predators and wild and domestic prey. We interviewed 428 respondents - 184 were selected randomly ("random house-holds") - for estimating extent of loss due to carnivore predation, and 244 respondents were from households with known depredation losses ("conflict households"). Compared to other studies in Nepal and elsewhere, losses were quite low (i.e. 0.9% and 2.0% among random- and conflict households, respectively), presumably due to the large spatial scale of our study and large variation among villages. The large variation suggests that the human-wildlife conflict requires site-specific mitigation measures. Snow leopards were responsible for more than half of the kills (62%), while wolves killed an estimated 17%. Using generalized linear mixed effects models, we found that the probability of loss increased with herd size, more so among those owning mainly large stock (e.g. yak and horses). We suspect that this might be due to large stock herds being less attended and more dispersed while grazing. The impact of wild prey density revealed that the probability of loss was lowest in areas of high density of wild prey and low density of livestock, and highest in areas where both livestock and wild prey was abundant. This illustrates 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.

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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. 2004, 2016; 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 unfavourable environment in which local support for conservation deteriorates and management efforts ultimately lose 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; on a large scale, kill rates on domestic sheep were inversely related to the density of their main natural prey, roe deer (*Capreolus capreolus*) (Odden et al., 2013), whereas 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 has also been investigated previously, including habitat, predator density, livestock density and herding practices. Regarding the former, predation risk has 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 concluded to have 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., 2014; Oli et al., 1994). In the rural Himalayas of Nepal, the majority of the human population are traditional agro-pastoralists, 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 depredation (Aryal et al., 2014; 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., 2014; 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 (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 locations of high conflict levels, and to gain knowledge on how these should be mitigated. Hence, in our study, we assessed the extent and causes of the human-carnivore conflict across a large area of 6621 km^2 in the Central Himalayas in Nepal based on questionnaires and surveys of predator and prey density and distribution. We focussed on how vulnerability to depredation varied with the size and species composition of the livestock herds, and assessed the influence of habitat structure and abundances of livestock, natural prey and predators within the grazing areas.

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 in 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, henceforth referred to as study area, 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 grazing (summer: May to October, winter: November−April) according to a traditional grazing calendar (Fig. 1). In the study area, the density of livestock is five times higher than that of wild ungulates. (Chetri et al., 2017).

2.2. Questionnaire survey

To quantify livestock losses, we interviewed 428 individuals in 85 settlements from July to September 2014 using both semi-structured and open ended questionnaires. We covered 13% of the total number of households in the survey villages (CBS, 2012). A structured questionnaire was first tested randomly with different age groups and gender (n = 10). Based on the responses, we modified the questionnaire before initiating the survey. Due to the vast landscape and remoteness of the scattered settlements/villages, most of the questionnaire survey was conducted by trained local community members managed through the Unit Conservation Offices (UCOs) of Annapurna Conservation Area (ACA) and Manaslu Conservation Area (MCA). Each interviewer was briefed clearly beforehand about the purpose of the study and trained how to fill in the information before initiating the survey. Most of the settlements/villages are clustered, and households with livestock losses are known to everyone in the village. We interviewed two different groups of respondents, i.e. (1) "conflict households" which were known to have lost livestock to predators during the last year and (2) "random households" which were selected by approaching the nearest house with people present in a random direction from a visited "conflict household". Conflict
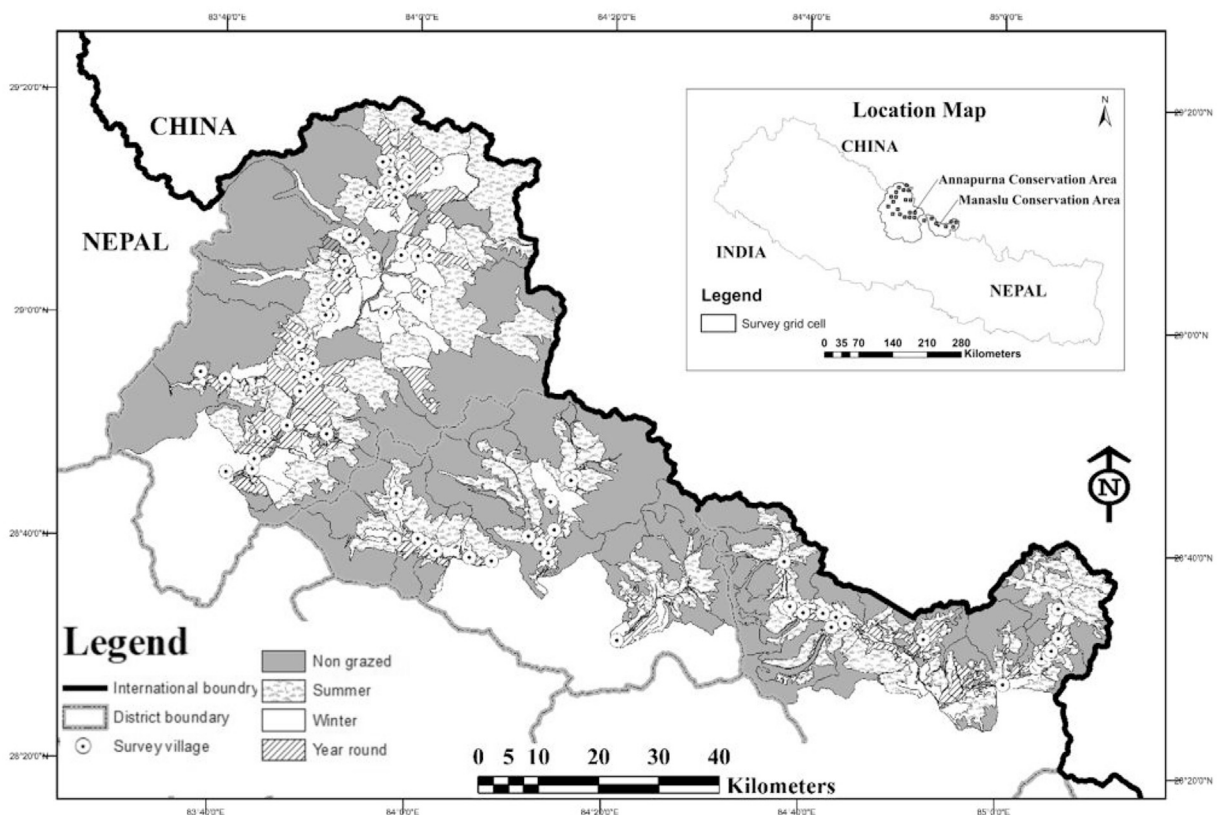

Fig. 1. Study area with location of survey villages and grazing areas.

households were identified from lists of compensation claimants provided by the VDC conservation area management committee leaders. We used two respondent groups because the proportion of randomly selected households that had experienced depredation was too low (24.5%) to obtain sufficient information on depredation events. Hence, information from "random households" was used to quantify livestock predation rates and other mortality causes. Conflict households (including random households that had experienced depredation) provided information 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 (see Supplementary Data-Appendix S1), we recorded household livestock ownership (species, numbers, sex and age) and losses due to predators, and other causes of death (disease and accidents).

Other field work relevant for this study were surveys of prey and predator abundances and grazing area mapping (see description below). A team of seven members spent 151 days conducting these surveys from September 2013 to September 2014. In this period, collection of snow leopard DNA samples and prey counts were done along 246 transects covering a total length of 490 km (Chetri et al., 2017). The transects were placed within 26 sampling blocks of 5×5 km that were spaced $5-10$ km apart throughout the study area.

3. Data analysis

We used generalized linear mixed effects models (GLMMs) to assess factors associated with the probability of households experiencing livestock loss to snow leopards. Here we included data from both random- and conflict households. We excluded other predators from this analysis due to very few 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 holding that also included goats and sheep), (iii) wild ungulate density, (iv) livestock density, (v) snow leopard density, and (vi) terrain ruggedness. For the four latter variables (iii-vi), we extracted values from the delineated year-round grazing areas of the VDC that the respondent belonged to: Wild ungulate density (iii) and livestock density (iv) were estimated in 26 different 25 km^2 sampling blocks distributed throughout the whole study area, as described in Chetri et al. (2017). To obtain wild ungulate and livestock densities within each grazing area, we interpolated values from the 26 sampling blocks using inverse distance weighing (IDW) in the geostatistical analyst tools in ArcMap 10.3 (ESRI, 2014). IDW is a method commonly used for interpolating for instance animal density values to non-surveyed locations based on known density values from scattered survey locations. The assigned values are calculated based on a weighted average of the values available from survey locations (see e.g. Lu and Wong, 2008). We obtained interpolated snow leopard density values (v) for each grazing area from spatially explicit capture-recapture models (SECR) based on snow leopard scat DNA collected from transects across large parts of the study area (Chetri et al., 2019). The IDW- and spatially explicit models predicted density values for 1×1 km^2 pixels covering the whole study area, and in our analyses, we used the average predicted value for each grazing area. Terrain ruggedness (vi) 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 (see Supplementary Data-Appendix S2).

4. Results

4.1. Livestock ownership and mortality patterns

Among the randomly selected households, the average number of 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 other large stock species than random households (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). Among conflict households, the annual predation rate was 2.0%. Of all livestock species, horses had the highest annual predation rates in both groups of respondents. Goat was the most commonly owned livestock species, with annual depredation rates varying between 0.7% and 1.4% among random and conflict households, respectively. Mortality due to disease and accidents was negligible in both household groups (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). However, taking into

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)

account the relative proportions owned of the two livestock categories (large stock = 18.3%, small stock = 81.7%), large stock were killed significantly more frequently than small stock (large stock = 38.6%, small stock = 61.4%, $\chi^2 = 71.93$, df = 1, p < 0.001). A similar patterns was observed among predator species categories - snow leopards, wolves and the other predators combined all killed larger numbers of small stock, but more large stock than expected from a random selection among the two prey categories (snow leopard: $\chi^2 = 34.18$, df = 1, p < 0.001; wolf: $\chi^2 = 29.80$, df = 1, p < 0.001, others: $\chi^2 = 11.24$, df = 1, p < 0.001). However, in the category of other predators, we observed differences in livestock predation among species; i.e. jackals, Eurasian lynx and feral dogs predominantly killed small stock, whereas brown bears, black bears and common leopards killed mainly large stock (Table 2). A significantly larger proportion of livestock depredation events occurred during summer (59.5%) than during winter (40.5%, $\chi^2 = 10.25$, 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%, $\chi^2 = 0.20$, df = 1, p = 0.656), but more kills were observed in summer by wolves (summer = 77.6%, winter = 22.5%, $\chi^2 = 14.93$, df = 1, p < 0.001) and by the other predators grouped (summer = 67.2%, winter = 32.8%, $\chi^2 = 6.93$, df = 1, p = 0.008).

4.3. Probability of livestock loss from snow leopards

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 herd size 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

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

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., 2019). Per capita, we have no reason to believe that there were marked differences in livestock killing between snow leopards and 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 leopards were distributed across the whole study area, both during winter and summer, thus rendering smaller seasonal differences in livestock vulnerability to attacks by this species.

The average annual livestock mortality from predation was less than 1% in random households and 2% in conflict households, 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. 2.3–4.0% (Aryal et al., 2014; Oli, 1994; Wegge et al., 2012). From other parts of central and south Asian mountains, highly variable losses between 1.3 and 12% have been recorded (Alexander et al., 2015; 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 is primarily due to the spatial extent of our study. While most 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 the probability of livestock loss from predation by snow leopards depended on an interaction between the size and the species composition of herds; the loss probability increased with herd size, but a much higher probability was observed among households owning mainly large stock. A probable explanation for the impact of herd size is that larger herds are both easier to detect by the predator and more difficult to protect by herders. A similar explanation can be applied for 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 are more scattered and usually unattended in the pastures. Irrespective of herd size, small stock is therefore relatively easy to oversee and guard from attacks, compared to large stock herds. In Bhutan (Wang and Macdonald, 2006), China (Alexander et al., 2015), Nepal (Jackson et al., 1996) and south Gobi Mongolia (Mijiddorj et al., 2018), the herding practice of releasing large stock more or less unattended in the pastures is common among pastoralists. 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 stricter herding practices have high potential as a mitigating measure against livestock losses to predators.
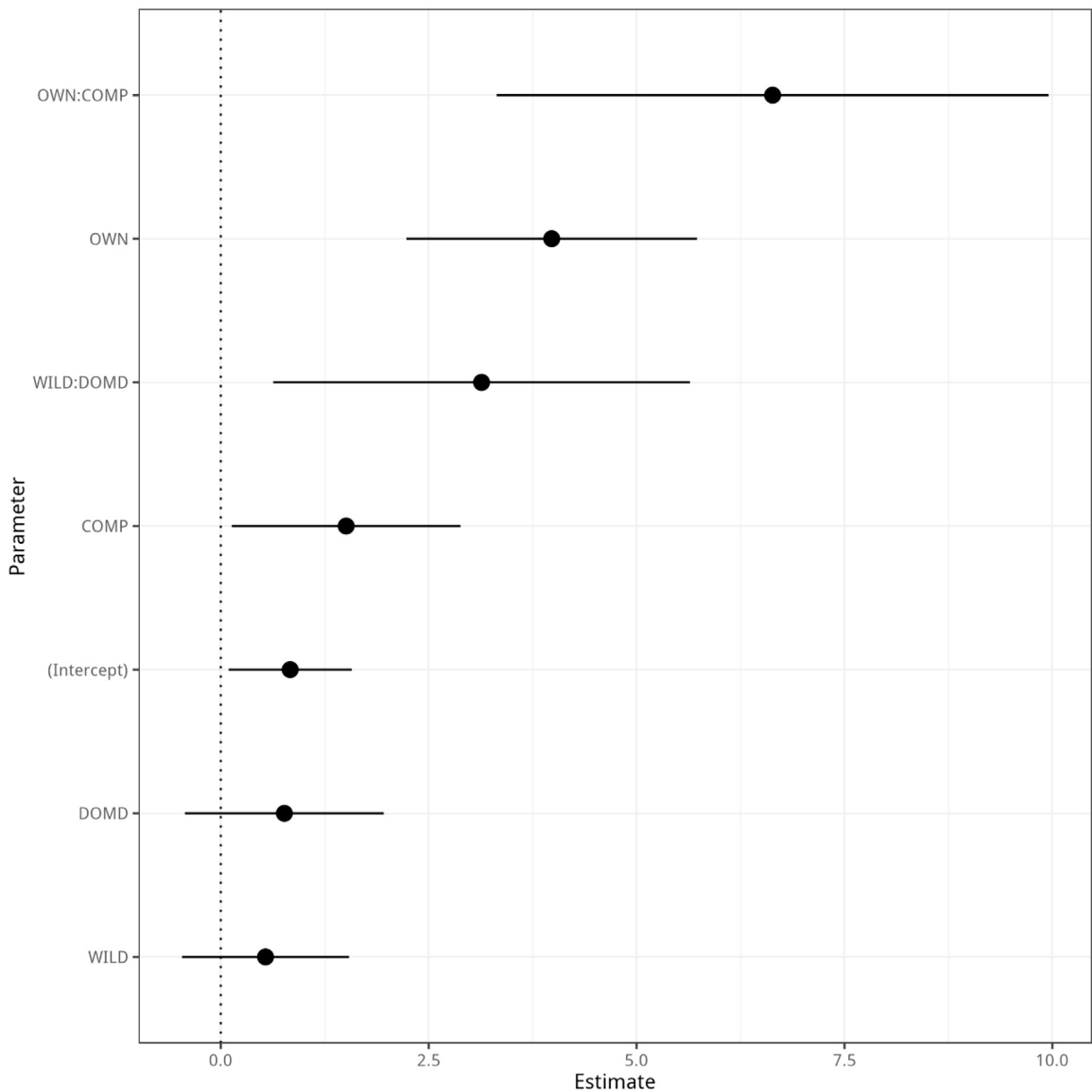
Fig. 2. Parameter estimates (dots) and 95% confidence intervals (solid lines) from the best Generalized Linear Mixed-Effects Model of factors affecting livestock loss to snow leopards. The strength of the effect of parameters is indicated by the distances between the solid horizontal lines and the dotted 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.

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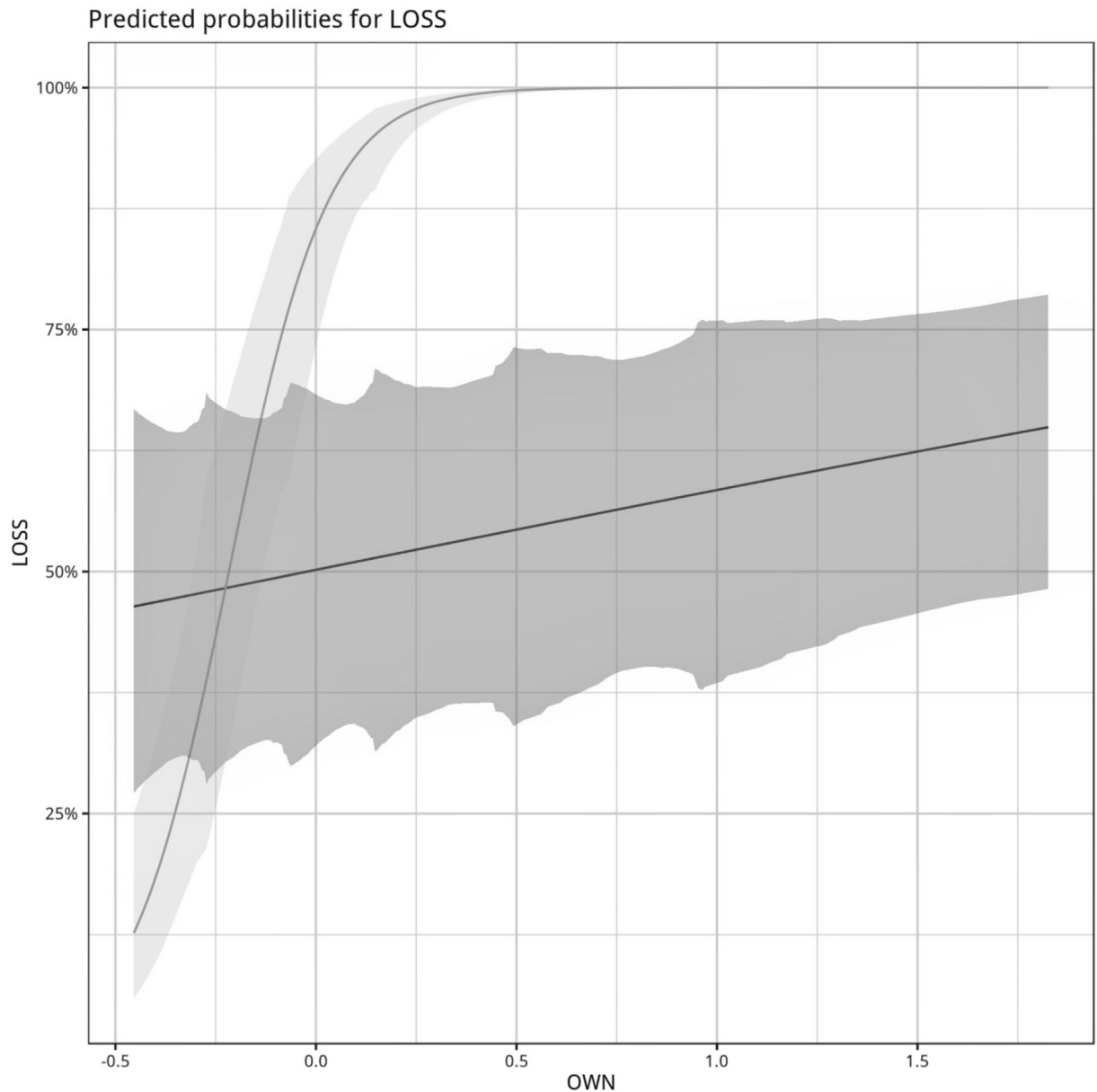
Fig. 3. Probabilities of experiencing livestock loss due to snow leopards based on the best Generalized Linear Mixed-Effects Model (see Fig. 2). The figure il-lustrates the impact of herd size (OWN) given two different values of livestock species composition; the grey line represent owners of only large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

contrary, as in scenario (ii) above, livestock loss probability declined with increasing wild ungulate density in areas where livestock was low. This can probably be 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 the overall conflict potential seemed to be 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 clear that conflict "hotspots" do exist. For instance, in the Phu valley (located within our larger study area), annual losses of 4% were recorded by Wegge et al. (2012). Plans for managing livestock predation 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
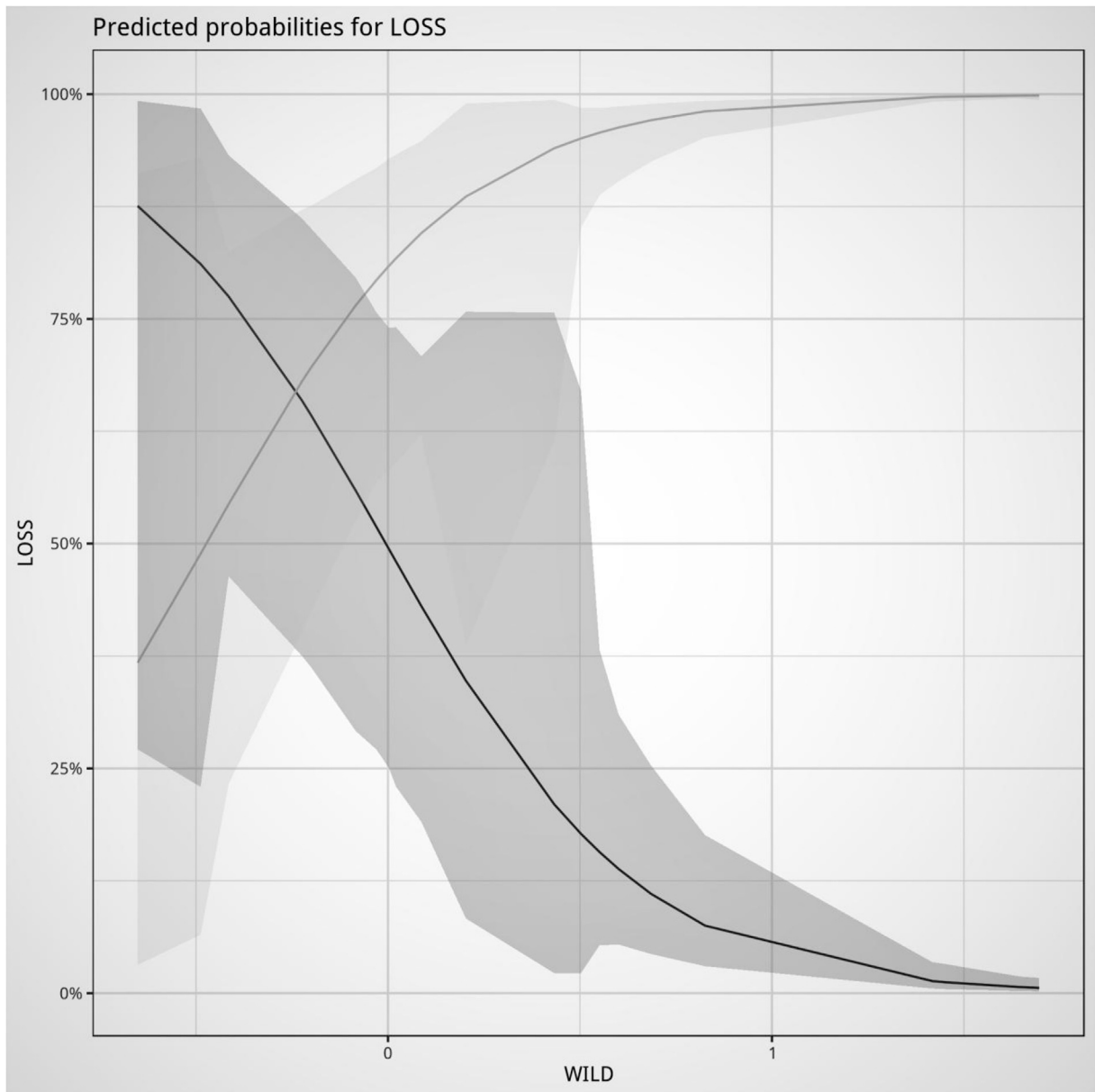
Fig. 4. Probabilities of experiencing livestock loss due to snow leopards based on the best Generalized Linear Mixed-Effects Model (see Fig. 2). The figure illustrates the impact of wild prey density in the grazing areas given two different values of livestock density; the grey line represent the highest recorded livestock density (86.5 per km^2) and the black line represent the lowest density (2.9 per km^2).

an absence of severe impact on the local economy. Several instances of mass killings of livestock have been reported during the last years. In our own records, two cases of snow leopard attacks led to loss of 11 sheep and 17 goats, respectively. After our data collection ended, one unfortunate herder lost all his 104 goats (male = 56, female = 48) in two consecutive nights. According to the current management system in our study area, only ca 4–6% of the economic loss from livestock depredation is compensated. Improved systems are therefore needed for aiding farmers with severe losses.

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Appendix A. Supplementary data

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