Landscape Ecol
DOI 10.1007/s10980-015-0335-9

RESEARCH ARTICLE

Scale dependence of felid predation risk: identifying predictors of livestock kills by tiger and leopard in Bhutan

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Received: 15 May 2015 / Accepted: 29 December 2015

Abstract
Context Livestock predation by tiger and leopard in Bhutan is a major threat to the conservation of these felids. Conflict mitigation planning would benefit from an improved understanding of the spatial pattern of livestock kills by the two predators.
Objectives We aimed to identify the landscape features that predict livestock kills by tiger and leopard throughout Bhutan. Our goals were to: (1) identify the predictors that have the largest influence in determining livestock kills, (2) assess the influence of scale across the different predictors evaluated and identify the scale at which each was most important.
Methods We used livestock kills obtained from compensation records of tiger ($n = 326$) and leopard ($n = 377$) across Bhutan between 2003 and 2012 to run predation risk models with MaxEnt algorithm, using a multi-scale modeling approach (1, 2, 4, 8 and 16 km).
Results Human-presence (density of settlements and roads) and land-cover (percentage of tree cover and meadow patches) were the main variables contributing to livestock kills by both species. Livestock kills were likely driven by a trade-off between livestock density and predator ecology, and the balance of this trade-off varied with scale. Risk maps revealed different hotspots for tiger and leopard kills, and analysis showed both species preferentially killed equids over other livestock types.
Conclusions Our results highlight the importance of evaluating scale when investigating the spatial attributes of livestock kills by tiger and leopard. Our findings provide guidance for reducing conflict between humans and large felids throughout the country.

Keywords Carnivore conservation · Human–carnivore conflict · Livestock predation · MaxEnt · Multi-scale analysis · *Panthera pardus* · *Panthera tigris* · Spatial predation risk modeling · Scale optimization

Electronic supplementary material The online version of this article (doi:10.1007/s10980-015-0335-9) contains supplementary material, which is available to authorized users.

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Published online: 01 February 2016

Introduction

Most carnivore populations are in global decline largely due to habitat loss, reduction of prey populations, and persecution (Ogada et al. 2003; Wang 2008; Henschel et al. 2011; Sunarto et al. 2013; Ripple et al. 2014, 2015). Large carnivores in particular have undergone striking declines in both population size and geographic range (Dickman et al. 2013), with 61 % of the world's large carnivore species being threatened with extinction (Ripple et al. 2014). A major driver of these declines has been persecution by humans driven by real or perceived threats to human lives and/or their livestock (Woodroffe 2001; Treves and Karanth 2003; Kolowski and Holekamp 2006; Dalerum et al. 2009; Ripple et al. 2014). Such threats can prompt retaliatory and preventative killings of carnivores, cause their translocations, incur high costs for rural people, and result in negative attitudes by local people, thereby reducing support for conservation (Woodroffe et al. 2007; Goodrich 2010; Mc Manus et al. 2014). Consequently, human–carnivore conflict (HCC) constitutes one of the major threats to carnivore long-term survival (Dickman 2010), and is a crucially important conservation issue that must be addressed if large carnivores are to persist in most of their currently occupied range (Woodroffe et al. 2007; Dickman et al. 2013).

Felids in the *Panthera* genus are particularly prone to conflict (Karanth and Gopal 2005). The tiger (*Panthera tigris*) and leopard (*P. pardus*) are two of the three large felid species considered to suffer most from severe conflict (Inskip and Zimmermann 2009). For example, up to 50 % of tiger mortality has been attributed to retaliatory killings in some areas (Inskip and Zimmermann 2009). In general, the tiger is among the most vulnerable species to human-induced changes due to its large land and prey requirements (Gurung et al. 2008), and human-related killings are usually the primary mortality factor for this species (Goodrich 2010; Walston et al. 2010). Retaliatory killings, concurrently with the illegal wildlife trade, habitat loss and prey depletion, already have contributed to the extinction of three tiger subspecies (*P. t. balica, P. t. virgata and P. t. sondaica*) in the last 50 years (Chundawat et al. 2011; Macdonald et al. 2013) and a fourth subspecies (*P. t. amoyensis*) is now likely extinct in the wild (Tilson et al. 2004). Overall, the tiger has lost over 93 % of its historic range, and its global population in the wild has declined at least 50 % over the past 20 years (Dinerstein et al. 2007; Seidensticker et al. 2010; Chundawat et al. 2011). If the range contraction and population decline remains unabated, it is likely that the tiger, already listed as Endangered by the IUCN (Chundawat et al. 2011), will be at least functionally extinct by 2030 (Nyhus et al. 2010).

Similarly, the leopard is highly prone to conflict as it preferentially prey upon species within a weight range of 10–40 kg (Hayward et al. 2006; Henschel et al. 2011), which is similar to the weight range of many medium-sized livestock such as goats, pigs, and sheep (Dutta et al. 2013; Kabir et al. 2014). In addition, the leopard have the ability to inhabit a variety of forested and degraded habitats where people occur (Athreya et al. 2011; Dutta et al. 2013), thus are often persecuted by humans based on perceived or real threats, which generally leads to indiscriminate killings. Despite being the most common, versatile, and resilient *Panthera* species, the leopard has been eradicated from vast tracts of its former range (Balme et al. 2010), and persecution by humans, along with habitat loss and the depletion of native prey, has already caused >50 % decline of its historical range.

Conflict with the tiger and leopard not only represents a significant and growing threat to the population persistence of these species but to human welfare. Incidences of human-large felid conflict (HLC), here defined as tiger/leopard attacks on people or livestock, adversely affect the communities that interface with these species, as it can result in physical/financial hardship, diminished psychosocial wellbeing, and opportunity costs (e.g., time spent guarding livestock). For example, in Bhutan, tiger and leopard accounted for 82 % of the total livestock killed by carnivores in and around the Jigme Singye Wangchuck National Park (Wang and Macdonald 2006), inflicting losses on poor households that sometimes exceeded two-thirds of their annual cash income. Such losses are understandably difficult to tolerate as they threaten human livelihoods and create a spiraling antipathy towards carnivores, eroding community support for conservation efforts and prompting retaliatory killings (Chapron et al. 2008; Barua et al. 2013). This in turn jeopardizes conservation more broadly as mortality events caused by retaliation can result in consequences for the species beyond the loss of individuals, such as increased infanticide, reduced reproductive and population growth rates, and lower cub/subadult survival (Goodrich et al. 2008, 2010). In addition, the loss or decline of apex carnivores such as the tiger can affect the numbers and distributions of mesocarnivores and prey, thereby causing trophic cascades and ecosystem regime shifts (Ripple and Beschta 2006, 2007; Estes et al. 2011; Ripple et al. 2014). Finally, the decline in large felid numbers in countries like Bhutan, considered a biodiversity hotspot for wild felids (Tempa et al. 2013), can have worldwide repercussions for the conservation of these species by undermining the role of these countries as source populations (Walston et al. 2010).

Livestock predation, one of the main drivers of HCC in Bhutan (Sangay and Vernes 2008), has increased in recent years across the country, with tiger and leopard killing significantly more livestock than any other carnivore species (Wang and Macdonald 2006; Sangay and Vernes 2008). A recent increase in the country's livestock numbers, resulting from an augment in national income and living standards, together with the expansion of grazing pastures into forested areas, restrictions on the use of common grazing lands by farmers and a culture of lax livestock husbandry practices, have exacerbated the conflict (Wang and Macdonald 2006) and eroded a Buddhist ethic of tolerance towards predators. In addition, the land-sharing ethic that characterizes the regulation of Bhutanese protected areas allows natural resource use (e.g., grazing, agriculture, and collection of non-timber forest products) within park boundaries (Wang 2008), which increases the chances of HLC incidents. Accordingly, farmers in central Bhutan ranked livestock predation, together with crop damage, as the most serious threats to their livelihood, and several farmers expressed a desire to exterminate problem wildlife (Wang et al. 2006). With 79 % of the population involved in agriculture and animal husbandry (Sangay and Vernes 2008), it is a priority for conservation in Bhutan to understand the factors leading to livestock predation.

Given that large felids hunt repeatedly in areas with similar landscape features (e.g., vegetation structure, prey densities, human activities, land uses) where prey is more easily killed (Hopcraft et al. 2005; Laundre et al. 2009; Miller et al. 2015), identifying the features that lead to livestock kills by tiger and leopard (i.e., livestock accessibility) can help guide conservation decision making. Ultimately, this may reduce the number of kills, thereby initiating a virtuous circle that reduces retaliatory killing and fosters the species' conservation. Spatially explicit predation risk modeling (hereafter predation risk models) is a quantitative tool for identifying the factors associated with high-risk areas and assessing gradients of prey accessibility to carnivores across landscapes (Treves et al. 2011). Predation risk models use location-specific data to predict the probability of a carnivore attack by relating the landscape attributes at kill sites and comparing them to random sites representing landscape availability. Previous studies have linked the propensity of these species to cause conflict to various factors such as physical impediments (e.g., human-caused injuries, Goodrich et al. 2011), habitat features (e.g., forest proximity, De Azevedo and Murray 2007), livestock husbandry practices (Ogada et al. 2003; Woodroffe et al. 2007), the prey's anti-predator behavior, individual predator behavior (Wang and Macdonald 2006), predator and natural prey densities (Loveridge et al. 2010), livestock type and breed, spatial distribution of both prey (wild and domestic) and other sympatric carnivores (Kolowski and Holekamp 2006), and the distance to settlements, roads, water sources and protected areas (Karanth et al. 2012; Soh et al. 2014).

Besides detecting the correct factors or drivers (Williams et al. 2012), it is also important to undertake a scaling analysis when working with species-habitat relationships (Shirk et al. 2010; Moudrý and Šímová 2012; Mateo Sánchez et al. 2013) as species generally select for different landscape characteristics at different scales (Thompson and McGarigal 2002; Wasserman et al. 2012; Rostro-García et al. 2015). Ignoring the effect of scale can cause misinterpretation of the relationship between the species and the considered parameters (Mateo Sánchez et al. 2013), thereby reducing predictive power, which can in turn misdirect management.

The aim of this study was to identify the landscape (i.e., environmental, geomorphological, and anthropogenic) features that predict livestock predation by tiger and leopard in Bhutan. We used predation risk models generated with MaxEnt species distribution modeling software (Elith et al. 2011), and spatial data on livestock kills (from national records), by using a single level, multi-scale modeling approach

(McGarigal et al. this volume), where incidents of livestock kills were examined at a landscape level, and evaluating a range of predictor variables across a range of 5 spatial scales. Our goals were to: (1) identify the predictors that have the largest influence in determining livestock kills by tiger and leopard, (2) assess the influence of scale across the different predictors evaluated and identify the scale at which each was most important. Based on previous literature, we predict that the land-cover and human-presence variables will contribute to the predation risk of livestock by both tiger and leopard, but the contributions and scale of these variables will vary by species. Our predictive models identify high-risk areas (hotspots) and the factors contributing to livestock vulnerability to tiger and leopard predation, which can be used to develop management recommendations that ultimately decrease the conflicts.

Methods

Study area

The study was carried out in the Kingdom of Bhutan (hereafter Bhutan), a landlocked South Asian country located in the eastern Himalayas, bordered by China to the north and India to the south, east and west (Choden 2009, Fig. 1). The country covers 38,394 km^2, and the human population is about 761,000 (National Statistics Bureau 2013).

Forest covers 70.5 % of Bhutan (National Statistics Bureau 2013), whereas agricultural land covers 2.9 % (Dorji and Penjor 2011). There is a pronounced south-north elevation gradient (97–7570 m.a.s.l.; Central Intelligence Agency 2009) and an inverse precipitation gradient moving north to south (500–>2000 mm) (Curriculum and Professional Support Division 2006). The climate is governed by altitude, orientation of mountain ranges, vegetation and the monsoons, ranging from sub-tropical to alpine.

Species presence data

We used records of livestock predation incidents (hereafter kills) collected across all districts (i.e., dzongkhags) of Bhutan by field staff of protected areas, and local officials in forest divisions outside protected areas, between 2002 and 2012, as part of a compensation scheme introduced in 2002 (Nature Conservation Division 2008). Each reported kill site was visited by a team comprising of a local community leader (who confirmed the claimant's ownership of the livestock), a veterinarian (who performed a post-mortem examination and confirmed that a predator had killed the animal), and a park or local forest official (who decided whether the alleged species was responsible). Information on the cause of death, predator responsible, age/gender/breed of livestock, and number of livestock owned was recorded, along with additional information. The location of the kill sites was recorded using a GPS or extracted later from maps. Predator identification was based on the examination of field signs (e.g., tracks, scats, hair remains), bite (i.e., size and distance between canine punctures) and feeding patterns on the carcass, as well as eye witness reports and, at times, camera trap records.

We tested for seasonality in the frequency of kills, based on whether they occurred during the rainy (April–October) or dry (November–March) season (Choden 2009). To assess whether tiger and leopard killed the different livestock types (i.e., cattle, yak, equids, small livestock) in proportion to their availability, we calculated the Jacobs' index D (Jacobs 1974) for each livestock type using the formula:

$$D = (r - p)/(r + p - 2rp),$$

where r is the fraction of prey used, and p is the fraction of prey available. The index, which ranges between -1 (negative selection) and $+1$ (positive selection), was calculated using all livestock owned by claimant as the fraction of "available" (i.e., p) and the livestock type and numbers killed as "used" (i.e., r). Because D-values of rare species often are biased (Klare et al. 2010), we excluded species that were <3 % used and <3 % available, thus small livestock were not considered in the analysis of tiger kills.

Data from 2002 were considered incomplete for both species, therefore only confirmed tiger and leopard kills from 2003 onwards were used for modeling. Tiger and leopard occasionally killed >1 livestock during a single attack event, but these were treated as a single kill site because our analysis focused on the characteristics of individual kill sites.

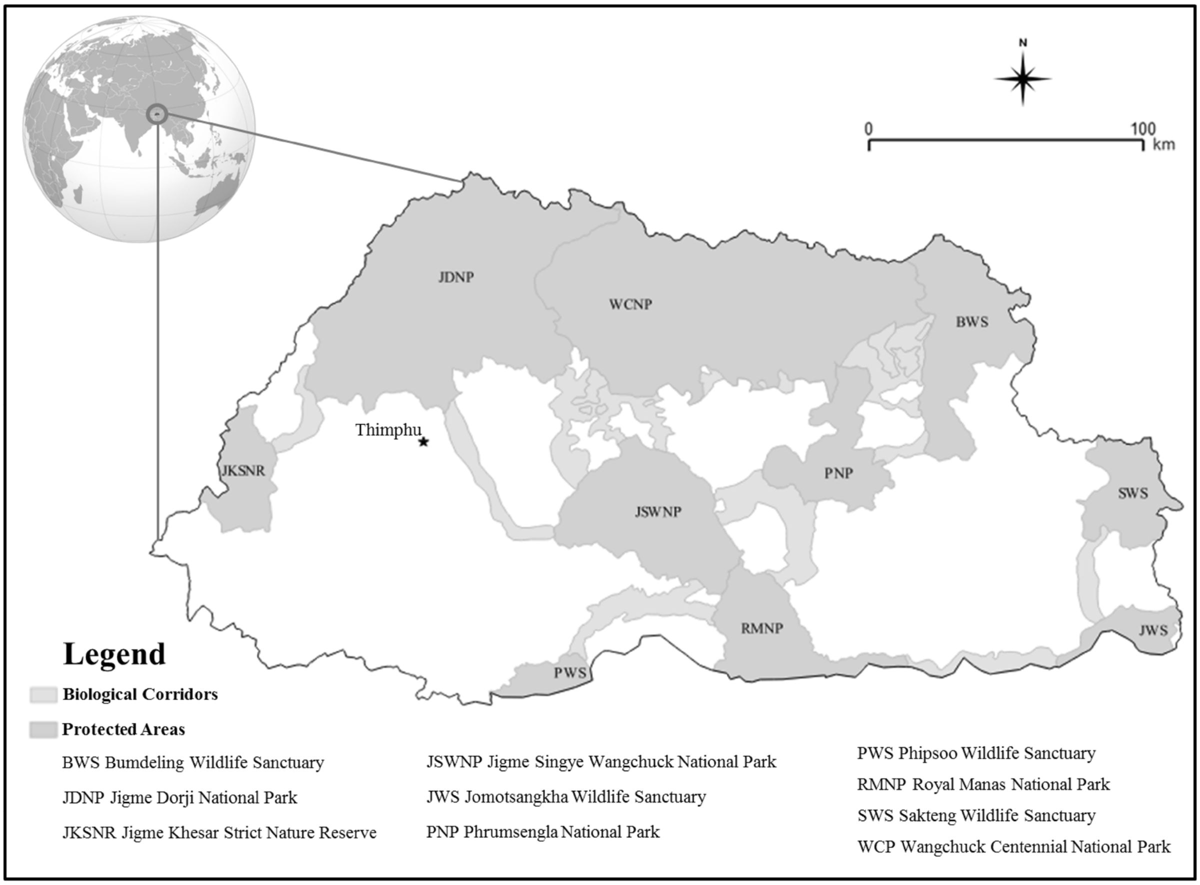

Fig. 1 Map of Bhutan showing the capital city (Thimphu), biological corridors and protected areas

Environmental data

We developed 1 km^2 resolution raster maps of Bhutan for variables that a) have been reported to have a high predictive power for felid occurrence, or were considered to be potentially good predictors of kills by tiger and leopard (e.g., elevation, land cover, topography, and human pressure), and b) were either available for the entire country from international or national datasets, or could be generated from them (Table 1). Multi-scale rasters for each of the variables were generated, in order to carry out the optimization process to select for the optimal scale of each predictor (Mateo Sánchez et al. 2013). In total, 164 variable-scale combinations were considered for model inclusion for each species (Table 1). For our analyses, all variables were re-sampled at 1000 m grid resolution and re-projected to the Bhutan DRUKref03 projection. Quantum GIS (v.2.8.1-Wien) was used to visualize and generate maps, whereas GRASS (v.6.4.3) was used for the spatial integration and development of some of the layers.

The MODerate-resolution Imaging Spectroradiometer (MODIS) Vegetation Continuous Fields (VCF; 250 m resolution) was used as the source of tree cover for the years 2002 and 2010 (www.landcover.org). VCF reports the percentage of each pixel's area covered by woody vegetation, herbaceous vegetation and bare ground (DiMiceli et al. 2011). The tree cover layers from the study period were used to calculate the tree cover change (i.e., % loss or increase) within each grid cell over this period using GRASS. This was done using the following formula, (A-B)/A, where A is percentage of tree cover in 2002, and B percentage of tree cover in 2010. Water and missing data in both A and B were replaced by null values beforehand. The resultant layer (C) was later reclassified into areas with >25 and <25 % cover,

Table 1 Variables considered for analyzing livestock kills by tiger and leopard in Bhutan

Covariate	Short name	Type	Native Spatial Resolution (m)	Metrics calculated	Scale (km)	Produced with/generated in	Source
Elevation ASTER GDEM 30 m	E	Topographic	30	Focal mean (FM)	1, 2, 4, 8, 16	r.neighbors/GRASS v.6.4	http://asterweb.jpl.nasa.gov/gdem.asp
Global Human Influence Index	HII	Anthropic	1000	Focal mean (FM)	1, 2, 4, 8, 16	r.neighbors/GRASS v.6.4	http://sedac.ciesin.columbia.edu/data/set/wildareas-v2-human-influence-index-geographic
Forest Loss: 0, 1	FL	Land cover	200	Radius of Gyration Area-Weighted Mean (GYR) Patch density (PD) Percentage of landscape (PLAND)	1, 2, 4, 8, 16	FRAGSTATS 4.1	Generated in GRASS v.6.4
Landcover Class-Level: Agriculture (A), Forest (F), Meadows (M), Urban (U)	LCL	Land cover	100	Radius of Gyration Area-Weighted Mean (GYR) Patch density (PD) Percentage of landscape (PLAND)	1, 2, 4, 8, 16	FRAGSTATS 4.1	WCD
Landcover Landscape-Level:	LLL	Land cover	100	Aggregation Index (AI) Contrast-weighted edge effect (CWED) Edge density (ED) Patch density (PD) Shannon Diversity Index (SHDI)	1, 2, 4, 8, 16	FRAGSTATS 4.1	
Landcover type: corridors (C), non protected areas (NP), protected areas (PA)	LT	Land cover	100	Radius of Gyration Area-Weighted Mean (GYR) Patch density (PD) Percentage of landscape (PLAND)	1, 2, 4, 8, 16	FRAGSTATS 4.1	
Rivers-streams density	RSD	Land cover	100	Focal mean (FM)	1, 2, 4, 8, 16	v.kernel (250 m)-r.neighbors/GRASS v.6.4	
Road density	RD	Anthropic	100	Focal mean (FM)	1, 2, 4, 8, 16		
Settlement density	SD	Anthropic	100	Focal mean (FM)	1, 2, 4, 8, 16		
Slope	S	Topographic	30	Focal mean (FM)	1, 2, 4, 8	r.neighbors/GRASS v.6.4	Derived from ASTER GDEM 30 m
Terrain ruggedness index	TRI	Topographic	30	Focal mean (FM)	1, 2, 4, 8, 16		Derived from ASTER GDEM 30 m
Vegetation Continuous Fields	VCF	Land cover	250	Focal mean (FM)	1, 2, 4, 8, 16		http://glcf.umd.edu/data/vcf/

whereas A was reclassified (A_r) into areas with >50 and <50 % cover. The final layer (Forest Loss) was a binary map (0–1) which was created by selecting areas that had both experienced a >25 % tree cover loss between 2002–2010 and had originally >50 % tree cover (i.e., were conservatively considered to be forests in 2002). We calculated class-level metrics of Forest Loss at five scales (1, 2, 4, 8, and 16 km) with FRAGSTATS v4 (McGarigal et al. 2012).

The Global Human Influence Index (Geographic), v2 (1995 – 2004) was used to quantify anthropogenic impacts on the environment. This global dataset of 1 km grid cells takes into account nine global data layers covering human access (coastlines, roads, railroads, navigable rivers), population pressure (population density), land use and infrastructure (built-up areas, night-time lights, land cover) (Wildlife Conservation Society 2005). We calculated the focal mean (FM) of Human Influence Index at five different scales of radii 1, 2, 4, 8 and 16 km.

Information about land cover classes, settlements, road network, rivers-streams and Bhutan's protected areas and corridors was provided by the Department of Forests and Park Services (DoFPS), Ministry of Agriculture and Forests, Royal Government of Bhutan. We calculated the FM density of settlements, rivers-streams, and road network at five scales of radii 1, 2, 4, 8, and 16 km (Table 1). Because no precise estimates of wild prey number and distribution were available, we considered protected areas also as an index of wild prey availability in our analyses, and calculated class-level metrics of protected areas at five scales (1, 2, 4, 8, and 16 km) with FRAGSTATS.

The land cover types provided by the DoFPS were reclassified into five categories: forest, agricultural lands, meadows, urban and non-habitat. FRAGSTATS was used to calculate metrics quantifying different aspects of landscape fragmentation and habitat connectivity patterns at the landscape level and class (land cover type) level. At the landscape level, five metrics characterizing landscape composition, configuration, and edge contrast were calculated, whereas at the class level, three composition and configuration metrics were calculated (Table 1). This was done for the four land cover classes that were considered to be particularly important with regards to their habitat use: forest (blue pine, broadleaf, broadleaf/conifer, chir pine, conifer, fir, mixed conifer, plantation broadleaf, plantation conifer, scrub); agricultural lands (crops, cultivated fields, and orchards); meadows (improved pastures, marshy areas, meadows); and urban (settlements). Each of the metrics was calculated at five different scales using circular windows with radii 1, 2, 4, 8, and 16 km.

Elevation was obtained from the 30 m resolution global digital elevation model of the Advanced Spaceborne Thermal Emission and Reflection Radiometer (ASTER GDEM). For every 30 m cell, we calculated the mean of surrounding elevation values at five different scales of radii 1, 2, 4, 8 and 16 km. This was also done for slope and terrain ruggedness index, both derived from ASTER GDEM 30 m using Quantum GIS. All the FM calculations were done rounding up to the nearest grid cell integer, resulting in a summarized area near the size of the desired scale/radii (e.g., a neighbourhood average function with a neighbourhood size of 17 was used to obtain the 2 km scale VCF).

The different radii distances were selected to represent the ecological responses of tiger and leopard across scales relevant to meet their daily requirements: from the extent of the species reported home ranges (tiger: 20–450 km^2, Chundawat et al. 2011; leopard: 5–487 km^2, Norton and Lawson 1985; Odden and Wegge 2005) to resources within habitat patches.

Livestock kill distribution modeling

In order to identify the scale at which each variable best predicted tiger and leopard kill sites, we first ran univariate MaxEnt (v.3.3.3k) models with each scale for the different variables. MaxEnt is a software package that uses the maximum entropy algorithm for modeling species distributions (Phillips et al. 2006; Phillips and Dudík 2008) and characterizing species-habitat associations from presence-only data (i.e., when no direct information about absences is available). This software package uses only presence records and landscape data to estimate habitat preferences, which is achieved by comparing the locations of known use sites with those throughout the region modelled, also known as background (Merow and Silander 2014; Guillera-Arroita et al. 2015). MaxEnt is widely used and is considered one of the most effective presence-only models (Phillips et al. 2006; Hernandez et al. 2008; Elith et al. 2011; Zarco-González et al. 2013), due to the software's capacity to deal with both continuous and categorical variables, and their interactions, as well as to generate distribution models (Phillips and Dudík 2008). MaxEnt, the most popular presence-only model (>3000 citations; Phillips et al. 2006), has been widely used to predict species' distribution (Wilting et al. 2010; Rodríguez-Soto et al. 2011; Clements et al. 2012), as well as zones of carnivore predation risk (Zarco-González et al. 2012, 2013; Behdarvand et al. 2014). However, this method has also been criticized mainly for producing poorly defined indices that are not directly related to the probability of occurrence (OP), and for generating extreme under-predictions when compared to estimates produced by other methods (Royle et al. 2012; Yackulic et al. 2013). Because MaxEnt is restricted to modeling relative occurrence probabilities or relative occurrence rates (ROR), another method based on conventional likelihood, MaxLike, was developed and proposed as a way of obtaining a formal statistical inference about the species OP (Royle et al. 2012). MaxLike has been shown to reliably predict absolute OP for very large data sets, where OP approximately spanned [0,1] in the landscape (Merow and Silander 2014). However, for smaller data sets, the uncertainty of predicted OP (e.g., large variances, and wide confidence intervals) by MaxLike has been shown to be very large and the instability of the intercept estimates (high variability) can lead to large average percentage error in predicted OP (Merow and Silander 2014; Pauli et al. 2015). Therefore, due to the small sample size available and the parametric assumptions imposed (Hastie and Fithian 2013), we decided not to use MaxLike, and instead use MaxEnt's predictions, which despite providing relative rates that can be less informative than OP, are more accessible, and available from presence-background data (Hastie and Fithian 2013), and much less biased (i.e., lower percentage error) for smaller sample sizes (Merow and Silander 2014). In this case, MaxEnt was used to obtain a ROR of tiger and leopard kill sites of livestock in Bhutan, by comparing the predictor variables at sites where livestock were reported to be killed by tiger or leopard with those throughout the modelled region.

MaxEnt models were run using the auto features option, which uses an algorithm to determine the most suitable complexity based on the number of presence records (Syfert et al. 2013). The default regularization settings were used (Phillips and Dudík 2008); a convergence threshold of 0.00001, 5000 iterations, 10 replicates and 20,000 background data points. A random subset of 25 % of the data was held out as a testing data set. For each variable, model performance at each scale was assessed comparing the area under the receiver operating characteristic curve (AUC; Fielding and Bell 1997). MaxEnt uses a modified version of the AUC that, instead of being used for the problem of classifying presence versus absence, it is used for classifying presence versus background points (Yackulic et al. 2013), which are generated by MaxEnt. We used the same number of background points in each of the analyzed scales, thus AUC was used as a relative value for comparing the performance of the different models (i.e., different scales) based on the same data (Golicher et al. 2012; Yackulic et al. 2013). The AUC ranges from 0.5 (random) to 1.0 (perfect discrimination). Models with AUC values 0.7–0.9 can be considered of moderate discrimination, whereas values >0.9 indicate high discrimination. For each variable, we selected the scale with the best performance (highest AUC value) for consideration in the multi-variable models. We tested for possible correlation (Pearson; R v.3.1.3) in order to exclude highly correlated variables ($r > 0.69$ or $r < -0.69$), using AUC values. This resulted in the inclusion of 22 out of the 164 initial variables for tiger and 20 out of the 164 initial variables for leopard (Table 3). Although the number of included variables could have been reduced, these potential predictors were used based on a priori predictions derived from previous studies, covariates that we assumed could influence the risk of livestock kills available for the area, and considering that landscape differences can influence the risk of kills differently.

We ran multi-variable models in MaxEnt on the final scaled variable pool. We considered MaxEnt's heuristic estimates of the relative contribution of the variables to the models, together with the results of the jack-knife test, to evaluate the contribution of each variable in the models. We used the same model settings (e.g., 25 % test data) as with the univariate models and obtained the logistic output to ease interpretation and comparisons. However, because knowledge of the probability of the species (i.e., occurrence and predation event) under average conditions was not available, the resulting probability of kills were likely biased considering that MaxEnt arbitrarily assumes the probability at an average site is 0.5 (Royle et al. 2012; Yackulic et al. 2013). For this reason, we also obtained the raw output, which was proportional to density of kills (i.e., expected number

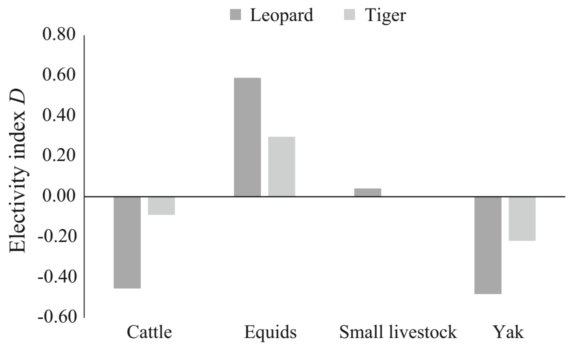

Fig. 2 Jacobs' electivity index (D) of livestock based on number of individuals killed by tiger and leopard in households in Bhutan. These data come only from households that experienced livestock losses to tiger and leopard

of kills per unit area; Merow et al. 2013; Yackulic et al. 2013). The raw output can be interpreted as OP re-scaled by a constant, which is the sum of predictions over the background cells (Merow and Silander 2014). The response curves were examined for those variables with a higher predictive value (>5 %). These plots illustrate how the logistic and raw prediction changes with each of the studied variables. The best performing multi-scale models were compared with single-scale (i.e., all non-correlated variables at 1 km) models to assess how scale optimization affected the predictive performance of the resultant models (e.g., Mateo Sánchez et al. 2013).

Results

We obtained records of 329 confirmed livestock kills by tiger and 385 by leopard, spanning from September 2002 to October 2012. These records were obtained from 15 of the 20 administrative districts of Bhutan (Fig. 3). For the tiger, nearly a third of kills (32.5 %, $n = 107$) occurred in Trongsa, whereas for the leopard the kills were mostly concentrated in Trashigang (25.7 %, $n = 99$), and Trashiyangtse (20.3 %, $n = 78$). Tiger killed 299 cattle, 50 equids (i.e., horse, donkey or mule), 22 yaks and 1 small livestock, with a mean (±SE) of 1.12 ± 0.03 animals per event. Tiger killed equids more frequently than their availability ($D = +0.30$), whereas it killed yak and cattle less than their availability ($D = -0.22$ and $D = -0.09$, respectively; Fig. 2). Leopard killed 199 cattle, 195 equids, 12 yaks and 21 small livestock, with a mean (±SE) of 1.11 ± 0.04 animals per event. Leopard killed equids more frequently than their availability ($D = +0.59$), followed by small livestock ($D = +0.04$), whereas cattle and yak were killed less than expected ($D = -0.45$ and $D = -0.48$, respectively; Fig. 2). There was a significant difference in the

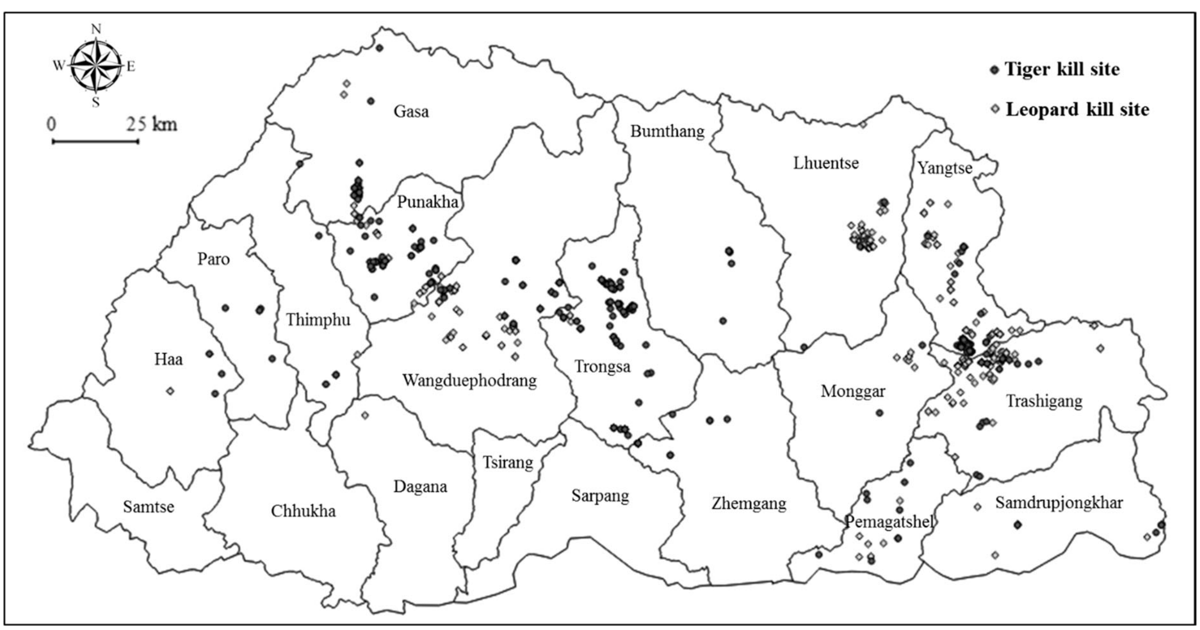

Fig. 3 Map of Bhutan showing confirmed tiger and leopard kills on livestock by district (i.e., Dzongkhag) reported to the Nature Conservation Division between 2003 and 2012

Table 2 Scale optimization of the independent variables considered for analyzing livestock kills by tiger and leopard. The bold values represent the scale with the highest AUC

Covariate-metric	Tiger					Leopard				
	1 km	2 km	4 km	8 km	16 km	1 km	2 km	4 km	8 km	16 km
E	**0.794**	0.785	0.784	0.773	0.783	0.722	0.783	0.781	0.791	**0.794**
FL-GYR-0	0.690	0.690	0.704	0.679	**0.721**	0.684	0.678	0.654	0.692	**0.750**
FL-GYR-1	0.709	0.715	**0.721**	0.717	0.705	0.706	0.713	0.706	0.711	**0.737**
FL-PD-0	**0.691**	0.648	0.663	0.681	0.679	0.678	0.654	0.655	0.645	**0.696**
FL-PD-1	0.647	0.664	0.617	0.621	**0.675**	0.615	0.666	0.637	0.647	**0.681**
FL-PLAND-0	0.719	0.717	0.711	0.724	**0.772**	0.707	0.734	0.710	0.742	**0.789**
FL-PLAND-1	0.737	0.730	0.720	0.720	**0.767**	0.707	0.743	0.706	0.736	**0.790**
HII	0.618	0.625	**0.693**	0.651	0.657	0.738	0.724	**0.752**	0.734	0.735
LCL-GYR-A	0.789	**0.802**	0.775	0.739	0.751	**0.803**	0.796	0.770	0.723	0.783
LCL-GYR-F	0.723	0.713	0.716	**0.729**	0.714	**0.746**	0.713	0.733	0.710	0.704
LCL-GYR-M	0.591	0.630	0.720	0.741	**0.747**	0.592	0.640	0.689	0.746	**0.781**
LCL-GYR-U	0.570	0.612	**0.676**	0.663	0.638	0.547	0.583	0.630	**0.653**	0.650
LCL-PD-A	0.770	**0.794**	0.765	0.757	0.759	0.779	**0.788**	0.754	0.754	0.724
LCL-PD-F	0.641	0.647	0.585	0.640	**0.684**	0.656	0.646	0.602	0.674	**0.709**
LCL-PD-M	0.576	0.601	0.704	0.718	**0.721**	0.591	0.615	0.668	0.709	**0.739**
LCL-PD-U	0.564	0.615	0.669	0.658	**0.706**	0.549	0.587	0.619	0.622	**0.741**
LCL-PLAND-A	0.803	**0.804**	0.768	0.769	0.779	0.796	**0.805**	0.772	0.759	0.791
LCL-PLAND-F	0.749	**0.759**	0.730	0.726	0.756	0.772	**0.785**	0.721	0.719	0.755
LCL-PLAND-M	0.577	0.628	0.675	**0.750**	0.741	0.587	0.627	0.688	0.758	**0.771**
LCL-PLAND-U	0.566	0.604	**0.682**	0.675	0.676	0.558	0.576	0.614	0.666	**0.721**
LLL-AI	0.767	**0.785**	0.646	0.638	0.705	0.774	**0.801**	0.722	0.705	0.695
LLL-CWED	0.799	**0.814**	0.766	0.678	0.678	0.799	**0.806**	0.802	0.759	0.742
LLL-ED	0.766	**0.768**	0.715	0.641	0.704	0.756	**0.785**	0.768	0.708	0.653
LLL-PD	0.748	**0.757**	0.732	0.702	0.752	0.740	**0.756**	0.734	0.744	0.740
LT-GYR-C	0.546	0.566	0.569	0.606	**0.646**	0.561	0.573	0.535	0.580	**0.621**
LT-GYR-NP	0.627	0.642	0.649	0.641	**0.670**	0.596	0.612	0.604	0.656	**0.747**
LT-GYR-PA	0.617	0.612	0.616	0.615	**0.667**	0.587	0.600	0.597	**0.651**	0.634
LT-PD–C	0.524	0.542	0.544	0.558	**0.600**	0.520	0.533	0.554	0.562	**0.623**
LT-PD-NP	0.615	0.619	0.630	**0.642**	0.639	0.560	0.567	0.586	0.656	**0.674**
LT-PD-PA	0.601	0.588	0.566	0.605	**0.641**	0.557	0.589	0.633	**0.643**	0.635
LT-PLAND-C	0.547	0.556	0.561	0.557	**0.600**	0.570	0.584	0.595	0.597	**0.639**
LT-PLAND-NP	0.639	0.630	0.657	0.650	**0.695**	0.576	0.588	0.614	0.656	**0.711**
LT-PLAND-PA	0.606	0.608	0.608	0.660	**0.687**	0.601	0.606	0.639	0.637	**0.651**
RD	0.704	0.748	0.776	**0.786**	0.770	0.645	0.666	0.725	0.770	**0.797**
RSD	0.667	**0.679**	0.669	0.642	0.649	0.635	0.653	0.632	0.658	**0.702**
SD	**0.837**	0.825	0.795	0.761	0.743	0.831	**0.833**	0.804	0.775	0.795
TRI	**0.731**	0.700	0.718	0.692	0.724	0.655	0.654	0.683	0.683	**0.725**
VCF	0.760	0.743	0.727	0.740	**0.779**	0.762	0.776	0.760	0.786	**0.815**

For each variable and scale, the area under the ROC curve (AUC) given by MaxEnt is reported. Refer to Table 1 for covariate-metric descriptions

Table 3 Variables used and area under the ROC curve (AUC) values obtained for the different models tested

Variable used	Leopard			Tiger		
	Single-scale	Multi-scale LO	Multi-scale RO	Single-scale	Multi-scale LO	Multi-scale RO
E	✔	✔	✔	✔	✔	✔
HII	✔			✔		
FL						
GYR-0					✔	✔
PD-0	✔			✔	✔	✔
PLAND-0						
GYR-1					✔	✔
PD-1	✔			✔		
PLAND-1		✔	✔			
LCL						
GYR-A	✔					
PD-A	✔	✔	✔	✔	✔	✔
PLAND-A	✔	✔	✔	✔	✔	✔
GYR-F	✔	✔	✔		✔	✔
PD-F	✔	✔	✔	✔		
PLAND-F						
GYR-M		✔	✔	✔	✔	✔
PD-M	✔	✔	✔	✔		
PLAND-M						
GYR-U		✔	✔			
PD-U		✔	✔		✔	✔
PLAND-U	✔			✔	✔	✔
LLL						
AI		✔	✔		✔	✔
CWED	✔	✔	✔	✔	✔	✔
ED						
PD		✔	✔		✔	✔
LT						
GYR-C					✔	✔
PD–C					✔	✔
PLAND-C		✔	✔	✔		
GYR-NP	✔					
PD-NP		✔	✔		✔	✔
PLAND-NP				✔		
GYR-PA	✔					
PD-PA						
PLAND-PA					✔	✔
RSD	✔	✔	✔	✔	✔	✔
RD	✔	✔	✔	✔	✔	✔
SD	✔	✔	✔	✔	✔	✔
TRI	✔	✔	✔	✔	✔	✔
VCF	✔	✔	✔	✔	✔	✔
AUC	0.959	0.980	0.981	0.966	0.981	0.981

number of kills reported per season ($\chi^2 = 16.8289$; df 1; $P < 0.0001$), with nearly 73 % of reported kills occurring in the wet season. For the modeling analysis we used 326 tiger and 377 leopard kills spanning from 2003 to 2012 (Fig. 3).

Scale optimization

The scale optimization showed high sensitivity between the scale of analysis (used for all variables examined) and kills by tiger and leopard (Table 2). Also, there was a difference in the predictive performance between the multi-scale and single-scale models, with the former showing a higher discrimination ability (higher AUC) for both species (Table 3). Therefore, only the results from the multi-scale models are described.

Model predictions of livestock kills

At a fine scale (i.e., 1–4 km), the features that contributed most to predicting livestock kills by both tiger and leopard were density of settlements and contrasted weighted edge density (LLL-CWED). Specifically, the risk of livestock kills by tiger and leopard increased as the density of settlements increased. However, this occurred up to a threshold, after which the chance ok kills reached a plateau (Fig. S1a, S1c). Similarly, livestock kills by both species increased with an increase in LLL-CWED up to a threshold (ca. 35 m per ha) after which the kills reached a plateau (Fig. S1b, S1d).

At a broader scale (i.e., 8 and 16 km), livestock vulnerability to tiger and leopard kills varied according to different land-cover types. For example, livestock kills peaked at about 50 % tree cover (Figs. S2a, S3a). For the tiger, risk of kills peaked in areas that contained about 10 % of protected areas (Fig. S3b), whereas for the leopard risk of kills peaked in areas with about 20 % of agricultural fields (Fig. S2b). For both species, risk of kills were more likely to occur as the density of roads increased (Figs. S2c, S3c) and in landscapes with a large component of coverage by meadows (Figs. S2d, S3d). Risk of kills was high in areas with approximately 1000 m correlation length of

Table 4 Percentage of contribution and permutation importance of variables predicting leopard kills based on logistic and raw outputs

Logistic output			Raw output		
Variable	% Contribution	Permutation importance	Variable	% Contribution	Permutation importance
SD	22.6	9.4	SD	21.1	6.8
LCL-PD-M	13.7	5.8	LCL-PD-M	13.8	9.2
VCF	10.8	26.8	LLL-CWED	11.8	9.4
LLL-CWED	10.2	8.2	VCF	9.6	22.6
TRI	7.9	2.5	TRI	7.5	2.5
LCL-PLAND-A	6.1	1.7	LCL-PLAND-A	5.8	1.7
RD	5	2.8	RD	5.4	3.3
LCL-PD-U	3.5	1.9	LCL-GYR-M	3.7	2.2
E	3.4	4.8	LCL-PD-A	3	1.3
RSD	2.8	1	E	2.9	4.4
FL-PLAND-1	2.6	17.4	LCL-PD-U	2.6	1.2
LT-PLAND-C	2	2.2	RSD	2.5	0.6
LCL-GYR-M	2	2	LT-PLAND-C	2.2	3
LCL-GYR-F	1.7	1	FL-PLAND-1	1.8	17.6
LT-PD-NP	1.2	1.2	LT-PD-NP	1.5	1.3
LCL-PD-F	1.1	2.2	LLL-AI	1.2	4
LLL-AI	1	2.9	LCL-GYR-F	1.1	1.6
LLL-PD	0.9	2.8	LCL-PD-F	1	3.4
LCL-GYR-U	0.8	1.7	LCL-GYR-U	0.8	2
LCL-PD-A	0.7	1.6	LLL-PD	0.7	2

Table 5 Percentage of contribution and permutation importance of variables predicting tiger kills based on logistic and raw outputs

Logistic output			Raw output		
Variable	% Contribution	Permutation importance	Variable	% Contribution	Permutation importance
SD	26.4	7	SD	23.9	2.7
LLL-CWED	9.4	8.3	RD	8.2	9.7
LT-PLAND-PA	8	9.1	LT-PLAND-PA	7.1	11.5
VCF	7.2	10.7	VCF	6.8	13.3
LCL-GYR-M	5.7	7.5	E	6.1	10.9
RD	5.6	6.5	LCL-GYR-M	5.7	6.1
E	5.3	9.8	LCL-PD-A	5.6	3.8
TRI	4.3	3.3	LLL-CWED	4.6	4.8
LCL-PD-U	4.2	2.7	TRI	4.3	3.7
LT-GYR-C	3.4	3.1	LCL-PLAND-A	4.1	3.4
RSD	2.9	1.5	LCL-PD-U	3.7	2.6
FL-GYR-1	2.8	3.4	RSD	3.4	1.9
FL-GYR-0	2.6	4	FL-GYR-1	3.2	3.3
LCL-GYR-F	2	4.4	FL-GYR-0	2.9	3.5
LCL-PD-A	1.8	2.9	LT-GYR-C	2.4	2.4
LCL-PLAND-A	1.7	3	LLL-AI	1.6	3.4
LLL-AI	1.4	4.1	LT-PD–C	1.3	1.7
FL-PD-0	1.2	2.1	LCL-PLAND-U	1.3	0.1
LT-PD–C	1.1	2.3	LCL-GYR-F	1.1	4.1
LLL-PD	1.1	3	FL-PD-0	1.1	2.3
LT-PD-NP	0.9	1	LLL-PD	1.1	3.7
LCL-PLAND-U	0.8	0.1	LT-PD-NP	0.9	1.1

meadow for tiger, and meadow patch density of ca. 0.25 per 100 ha for leopard. Topography influenced risk of kills by tiger at a fine scale, with risk of kills peaking in areas with elevations from 1000 to 3000 m (Fig. S1e), whereas it influenced kills by leopard at a broad scale, with most kills occurring in areas with TRI between 11 and 14 (Fig. S2e). In general, the raw outputs were similar to the logistic outputs, with the difference that the features that contributed most to predicting kills by both tiger and leopard had different percentage contributions (Tables 4, 5).

The predictive maps of livestock kills by tiger and leopard across Bhutan suggest that the areas of highest relative predation risk are located in the central and eastern part of the country (Figs. 4, 5). More specifically, Trongsa and Yangtse have the highest risk of kills by tiger and leopard, with a mean kill risk of 9.9 and 15.13 %, respectively. In contrast, Tsirang and Zhemgang have the lowest kill risk by tiger and leopard, with a mean kill risk of 0.2 and 0.8 %, respectively.

Discussion

Retaliation for livestock predation is one of the major threats to large felids in Bhutan. Despite this, systematic data on the topic are scarce, and consequently the impact that conflict could have in large felid conservation is not yet known. By analyzing existing compensation records for livestock predation, we provide a nation-wide model of predation risk by tiger and leopard which can aid conflict mitigation measures. Our models identified conflict hotspots, which should receive priority by wildlife managers, and landscape features associated with livestock kills, which should be considered by local people when developing animal husbandry methods.

Our analyses revealed that human-presence and land-cover variables affected livestock kills by tiger and leopard, which supported our prediction. In particular, our results suggest that attacks on livestock are driven by a trade-off between livestock density and predator ecology, and the balance of this trade-off varied with scale. The most important predictor for both species was density of settlements at a fine scale, with a higher risk of kills at medium settlement density. This likely was due to livestock density being positively associated with density of settlements, and indeed such correlation has been reported in the country (Wang and Macdonald 2006; Sangay and Vernes 2008). The density of settlements incorporated both rural and urban households, which probably accounts for the higher confidence intervals in kill risk by both predators at the higher range. Also, since settlements were not weighted by size, area or surroundings, this variable may be an inappropriate proxy for human disturbance, which may be better indicated by class-level metrics of urban areas. The tiger have been shown to avoid human settlements in other areas (Harihar et al. 2007; Sunarto et al. 2012), suggesting it was livestock numbers that attracted large felids to human settlements, but only at "tolerable" levels of human disturbance. Future research that incorporates livestock density and fine scale rural settlement layers in the analysis is needed to confirm this hypothesis.

Tiger and leopard were most likely to kill in landscapes characterized by a mosaic of habitat patches. Specifically, at a fine scale the contrasted weighted edge density (LLL-CWED) was an important predictor of livestock kills by both species, which is likely because both predators preferentially used habitat edges, with forest-meadow probably being the most important edge type for these species. Habitat edges are known to be used by predators (Andrén 1995), including large felids which use cover when stalking and ambushing prey (Balme et al. 2007; Palmeira et al. 2008; Rostro-García et al. 2015). In contrast, at a broad scale, the risk of kills by tiger and leopard was highest when the land was covered by meadow patches and by approximately 50 % forests. Increased livestock kills by both tiger and leopard in areas with meadows was likely due to livestock preferring to graze in this habitat type, whereas the need for 50 % forest cover is consistent with felid hunting behavior (Murray et al. 1995). For example, although forest cover likely increases the success of attacks by these stalk-and-ambush predators, too much cover can reduce the chance of encountering prey or impede the progress of a stalk. The apparent requirement of habitat heterogeneity by both felid species at a broad scale may be related to prey catchability, similar to that shown for other large felids (Balme et al. 2007; Rostro-García et al. 2015). In general, tiger presence is known to be positively affected by forest cover (Sunarto et al. 2012), whereas livestock were shown to be more accessible to tiger near patchy forest (Miller et al. 2015). The leopard, known to prefer hunting in habitats with high prey catchability (Balme et al. 2007), also could be positively selecting for mosaic habitats where not only prey could be killed, but larger predators such as the tiger could be detected. Among carnivores, subordinate species, such as the African wild dog (*Lycaon pictus*), have been shown to prefer habitats that allow greater visibility of more dominant carnivores (Fuller and Kat 1990).

Within this mosaic landscape however, there were differences between the kill sites of the two species, which probably reflects their ecological differences. The tiger was more likely to attack livestock near protected areas, whereas the leopard in more human dominated landscapes (i.e., ~ 20 % agricultural areas). This difference also may reflect their differential tolerance to human disturbance. Higher chances of tiger attacks on livestock have been associated with protected areas and tiger aversion to human presence (Miller et al. 2015). Alternatively, this could also be correlated with higher tiger numbers in these areas due to higher levels of protection, or lax herding practices in large and remote protected areas where livestock are more difficult to monitor. This is in accordance with Wang and Macdonald (2006) who reported a significantly greater frequency of reported livestock losses to carnivores in the inner zone of the Jigme Singye Wangchuck National Park than on the buffer zone areas.

Intraguild competition between the two felids is another possible explanation for the observed differences in kills between the species, because the leopard may be displaced from some areas by the more dominant tiger. For instance, in India and Nepal the leopard was shown to avoid optimal habitat where there was high risk of encountering tiger, often causing the leopard to be more common near park boundaries and buffer zones (Seidensticker et al. 1990; Odden et al. 2010; Harihar et al. 2011). This relationship may increase human–leopard conflicts near park boundaries, especially because the leopard was reported to be the most damaging species in several protected areas in India (Karanth et al. 2013a). Accordingly,

(a)

(b)

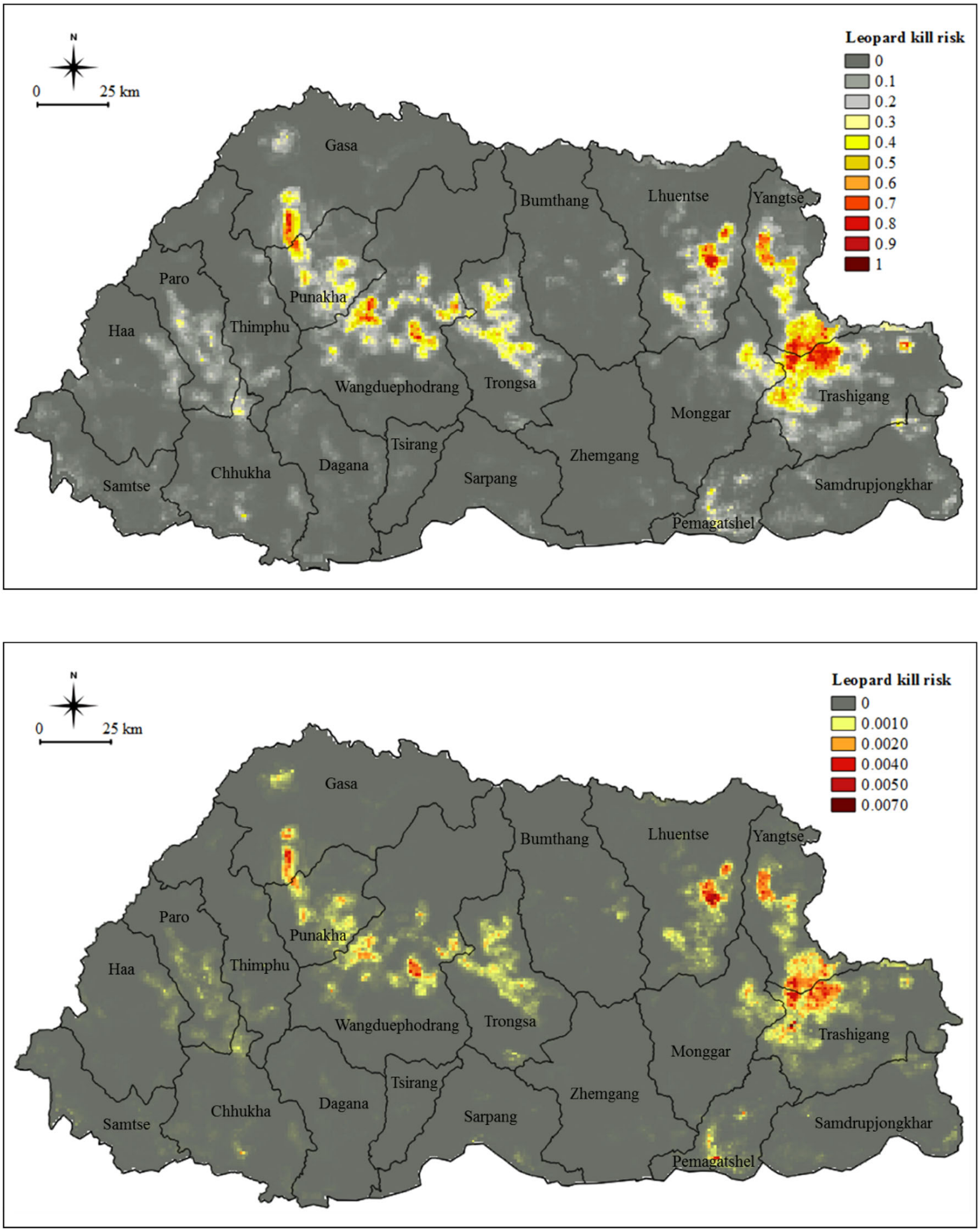

Fig. 4 Predicted risk of leopard kills on livestock across Bhutan (**a** logistic output, **b** raw output). The *color gradient* indicates livestock vulnerability, with *warmer colors* representing the areas in which kills are most likely to occur. The risk of predation is shown for the different districts. (Color figure online)

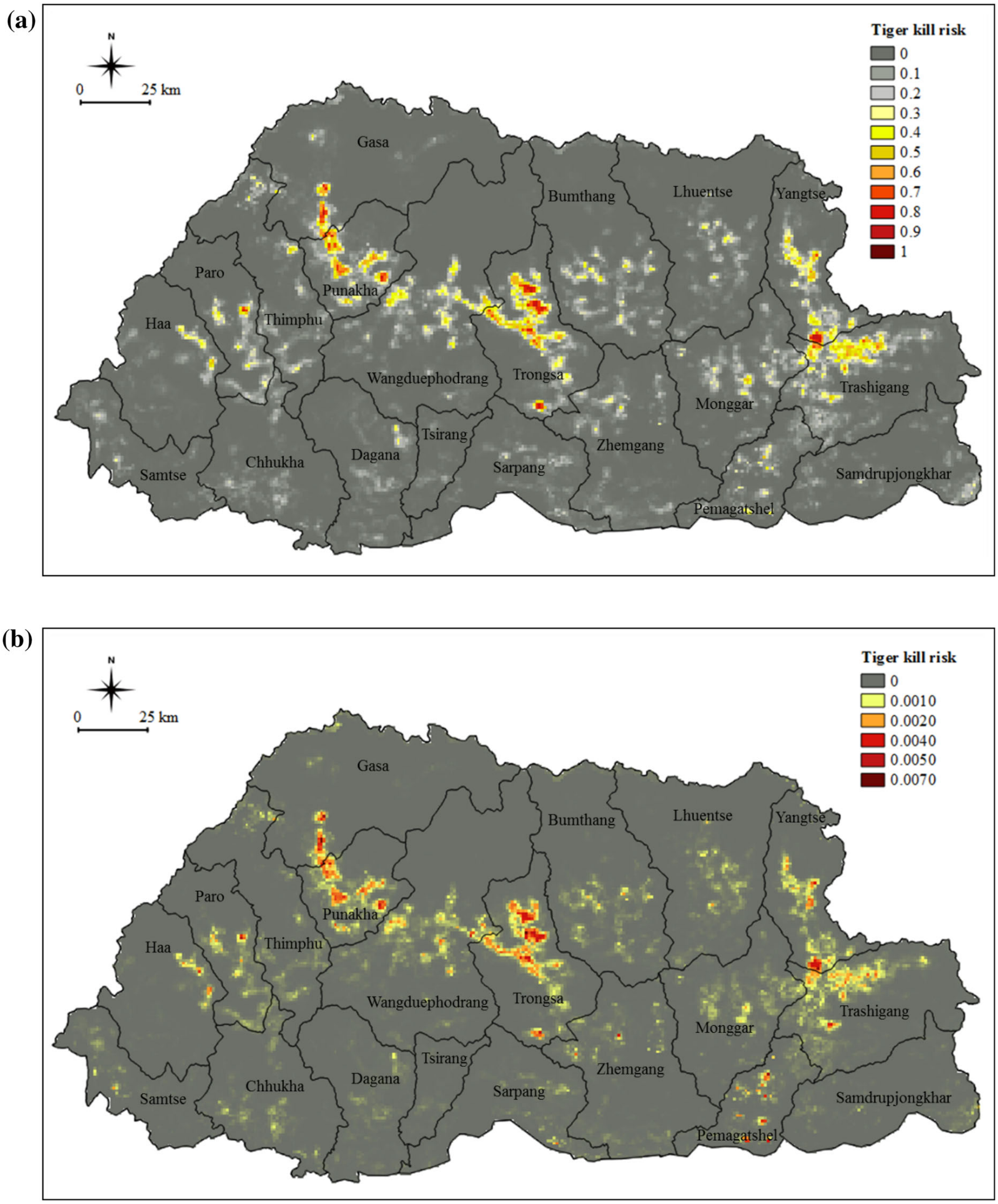

Fig. 5 Predicted risk of tiger kills on livestock across Bhutan (**a** logistic output, **b** raw output). The *color gradient* indicates livestock vulnerability, with *warmer colors* representing the areas in which kills are most likely to occur. The risk of predation is shown for the different districts. (Color figure online)

most predation cases in this study where reported to be from the leopard, despite this species being part of the compensation scheme for a shorter period than the tiger.

The risk of livestock kills by tiger and leopard also was influenced by topography although at different scales and with different factors. At a fine scale, tiger kills were more likely to occur in areas between 1000 and 3000 m, which could be related to places with higher number of livestock, or higher tiger densities, given that the breeding habitat of this species in Bhutan is below 3000 m (McDougal and Tshering 1998). On the contrary, at a broad scale, leopard kills were positively associated with terrain ruggedness, which could be due to livestock being more vulnerable to ambush by the leopard in relatively rugged areas.

The selection for equids by both predators in our study is consistent with previous studies in Bhutan and the Indian trans-Himalaya, where horses were reportedly preyed upon significantly more than their availability (Mishra 1997; Sangay and Vernes 2008), which was attributed to the herding practices for these animals. The preference for this livestock type could reflect a lower economic return of such animals compared to cattle, thereby resulting in more lax herding practices (e.g., untended when grazing and untethered at night), which increases their vulnerability to felid kills (Sangay and Vernes 2008). Alternatively, preference for equids could result from a differential use of habitat and social behavior (e.g., grazing in smaller numbers may reduce their ability to detect predators) compared to cattle, or functional availability. The roughly proportional predation of cattle to that of their availability observed in our data is in accordance to the findings of Sangay and Vernes (2008), who reported a correlation in the number of cattle lost per district to the district's total livestock population. This proportional predation, together with the apparent lack of preference for cattle by both species previously reported in central Bhutan (Wang and Macdonald 2009), suggests that livestock predation might be reduced by increasing wild prey numbers through better livestock management and habitat protection, given the same number of large felids.

Our results highlight the difference in the features selected for livestock kill sites compared to those reported to be selected for within home ranges, which would not be apparent without multi-scale analysis. For instance, at a fine scale the probability of habitat use by tiger in Sumatra co-varied negatively with human settlements (Sunarto et al. 2012), however at the same scale in our study this feature was positively associated with reported kill sites. Previous studies showed that habitat selection by felids varied with the evaluated scale (Zarco-González et al. 2012; Miller et al. 2015; Rostro-García et al. 2015). Also, the shifts in the predictors' importance at different scales suggest that both tiger and leopard use landscape attributes differently at different scales, highlighting the importance of testing for scale-dependent differences when managing areas to decrease livestock predation. Similar to previous studies (Thompson and McGarigal 2002; Shirk et al. 2010; Wasserman et al. 2012), our results suggest that explicitly optimizing the scale of each variable independently improved single-scale models in both model performance and spatial prediction.

Several modeling constraints should be noted when considering generalizing our findings. Although MaxEnt has been found to provide the best performance and greater accuracy when compared to other algorithms (e.g., Zarco-González et al. 2013), this method has been criticized for producing poorly defined indices that are not directly related to the OP, and that could hence lead to inferential errors and under-predictions (Royle et al. 2012) by producing more conservative distribution areas (Rodríguez-Soto et al. 2011). Also, MaxEnt, like other presence-only modeling, assumes that detection probability is constant across sites, however heterogeneity in detection probabilities of the studied species is expected. In addition, model-based inferences in presence-only analyses require a random or landscape representative sample of presence locations (Yackulic et al. 2013), thus model predictions could have been biased if this assumption was violated. Similarly, we assumed that, despite possible sampling effort variations (e.g., ability of villagers to report kills), the spatial distribution of sampling intensity was similar throughout the landscape given that most people in Bhutan were aware of the compensation scheme. Given the area covered in our analyses (i.e., country-wide) and the available data, the models were built from 1 km onwards. Nevertheless, because variables could be highly spatially heterogeneous, we suggest that data should be gathered and models built at a finer resolution (<100 m) as this has been shown to have a higher accuracy when predicting tiger kill sites

(Miller et al. 2015). Also, decreasing cell size in the discretized landscape can help ensure that the assumption of random distribution of individuals made by MaxEnt becomes equivalent to a random distribution in space, which allows the prediction of relative OP (Merow and Silander 2014).

Because felid predation data are the result of a strict scrutiny at multiple levels, we considered them a conservative estimate of livestock predation in the country. However, livestock kills were more likely reported for species with a higher economic (e.g., cattle) or utility (e.g., horses) value, compared to small livestock (Karanth et al. 2013b). Hence, the impact of leopard predation in our study may have been underestimated and thus also the identified risk areas. Additionally, due to the exhaustion of compensation funds, cases of livestock killed by leopard were dropped from the compensation scheme after January 2006, and thus the farmers stopped reporting such cases soon thereafter. Therefore, we recommend gathering more information on leopard kills, particularly on small livestock. Despite the constraints, we believe our analysis adequately showed the variables that influenced livestock kills by both tiger and leopard considering data availability (only presence data was available). However, when compared to occupancy-detection or presence–absence data, presence-only data is the least rich type of data in terms of information content, providing only likelihoods of occurrence instead of actual probabilities (Guillera-Arroita et al. 2015). For this reason, while recent advances in presence-only modeling allow users to precisely approximate trends in the data, future efforts should be directed towards the collection of more informative survey data.

The Bhutanese economy is closely associated with animal husbandry and agriculture, which not only contributes to the country's gross domestic product (33 %) but also provide livelihoods to a substantial part of the population (Sangay and Vernes 2008). Considering that animal husbandry significantly contributes to rural economy, HLC must be minimized wherever possible and careful management provided in order to strengthen both economic livelihood and wildlife conservation. One of the most important mitigation measures would therefore be to alter traditional grazing and animal husbandry practices in areas where conflict hotspots are known to exist, thereby diminishing livestock vulnerability to felid attacks. For example, livestock owners could use herders to guard livestock when they are grazing in forests away from villages, and livestock should be corralled at night. Previous research in Bhutan showed that livestock consumption by dholes (*Cuon alpinus*) was eliminated during the dry season when livestock were brought closer to villages (Thinley et al. 2011). Similarly, our results showed reported livestock predation incidents by large felids were highest in the wet season, when livestock are usually left unguarded in the forests away from villages, indicating changes in herding practices would likely reduce livestock kills. Clear zoning within protected areas should also be developed and enforced, which would reduce livestock grazing in core areas, reducing the chances of conflict incidents and allowing an increase in wild prey numbers due to decreased competition with livestock.

Finally, it should be realized that all maps are partial truths, and their ability to approach reality can only be judged when ground-truthed. Thus, we emphasize the importance of ground-truthing the information and communicating with experts before any practical intervention (e.g., mitigation or preventative measure) is applied in the field to reduce the number of livestock killed by tiger and leopard. Also, efforts to lower HLC through practical interventions should be paired with community engagement and educational campaigns in order to achieve a successful implementation of strategies. Effective interventions would contribute to lower HLC throughout Bhutan and thus aid in the conservation of these iconic species in one of the most natural and intact ecosystems remaining in South Asia.

Conclusions

Our study emphasizes the value of considering the optimal scale of variables in spatial predation risk models, as this can detect variations in data that single-scale models may fail to capture. We also highlight the importance of reducing livestock kills by tiger and leopard in Bhutan, and suggest practical strategies that can be adopted. This is especially important in Bhutan because the country is home to significant populations of globally threatened felids, and livestock raising is central to the livelihoods of a majority of the country's population. The information generated by predation risk models can aid in communicating to different stakeholders about the predictors associated with areas of higher kill risk. As such, our findings were shared with local wildlife authorities via a workshop in 2014, with the goal of helping national and regional authorities to develop targeted measures to both reduce livestock predation and assist large felid conservation.

Acknowledgments We thank the Department of Forest and Park Services, Royal Government of Bhutan for making the livestock predation records available to us for the purposes of this study. We are also grateful to the park and forest officials, veterinarians and community leaders involved in gathering the data. Thanks to Arjun Gopalaswamy, Jan F. Kamler and anonymous reviewers for providing feedback. Funding for the digitizing of the records and disseminations of the preliminary findings of the study was provided by the Rufford Foundation (Rufford Small Grant funding scheme). This work was done primarily while SRG was at WildCRU undertaking the International Postgraduate Diploma in Practical Wildlife Conservation Practice at the Recanati-Kaplan Centre.

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