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ORIGINAL ARTICLE

Livestock losses and hotspots of attack from tigers and leopards in Kanha Tiger Reserve, Central India

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Abstract Carnivore attacks on livestock are a primary driver of human–carnivore conflict and carnivore decline globally. Livestock depredation is particularly threatening to carnivore conservation in Central India, a priority landscape and stronghold for the endangered tiger. To strengthen the effectiveness of conflict mitigation strategies, we examined the spatial and temporal patterns and physical characteristics of livestock depredation in Kanha Tiger Reserve. We combined livestock compensation historical records (2001–2009) with ground surveys (2011–2012) and carnivore scat to identify when and where livestock species were most vulnerable. Between 400 and 600 livestock were reported for financial compensation each year, and most (91–95 %) were successfully reimbursed. Tigers and leopards were responsible for nearly all livestock losses and most often killed in the afternoon and early evening. Cattle and buffalo were most at risk in dense forests away from villages and roads, whereas goats were most often killed in open vegetation near villages. A spatial predation risk model for cattle revealed high-risk hotspots around the core zone boundary, confirming the significant risks to livestock grazing illegally in the core. Such ecological insights on carnivore–livestock interactions may help improve species-specific livestock husbandry for minimizing livestock losses and enabling coexistence between people and carnivores.

Keywords Carnivore conservation · Hotspot predation risk map · Human–carnivore conflict · Kill site · Livestock depredation · Livestock compensation

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Introduction

Large carnivore populations worldwide are rapidly declining, in part due to retaliatory killing by livestock owners following attacks on domestic animals (Woodroffe et al. 2005; Ripple et al. 2014). Much of this human–carnivore conflict occurs at the edges of protected areas where carnivores, livestock, and people overlap (Woodroffe and Ginsberg 1998; Nyhus and Tilson 2004). Many non-lethal techniques exist to help reduce livestock and livelihood losses, including livestock husbandry strategies, physical deterrents, and financial incentives for communities (Treves and Karanth 2003; Shivik 2006). Yet effective implementation of these tools requires detailed knowledge of when and where carnivores attack livestock and how risk differs between livestock species. Understanding carnivore–livestock interactions is a crucial step toward mitigating human–carnivore conflict and better enabling coexistence between people and carnivores (Treves and Karanth 2003; Goodrich 2010).

Ecological insights on the environmental factors and animal behaviors that lead to carnivore depredation on particular livestock are particularly useful for strengthening livestock husbandry techniques (Wikramanayake et al. 1998; Miller 2015). Many previous studies on human–carnivore conflict have focused on depredation by a single carnivore species (usually a high-priority species of conservation concern) on all livestock species generally, which can obscure unique risk gradients for individual livestock species from specific carnivores (Treves et al. 2011; Lichtenfeld et al. 2014; Athreya et al. 2014; Miller et al. 2015). Differences between the body sizes, anti-predator defenses, and grazing requirements of livestock species result in distinct levels of vulnerability to wild carnivores (Seidensticker 1976; Sinclair et al. 2003). For instance, in many areas smaller large carnivores like leopards, hyenas, and wild dogs primarily kill smaller-bodied livestock such as calves, sheep, and goats, whereas the largest carnivores like tigers target larger-bodied livestock such as adult cattle, buffalo, and horses (Sangay and Vernes 2008). Likewise, large carnivore species employ unique hunting strategies and segregation tactics to avoid interspecific competition that results in risks for livestock at different times and locations (Laundré et al. 2009). For example, tigers and leopards often segregate temporally or spatially to minimize interference competition (Odden et al. 2010; Harihar et al. 2011; Lovari et al. 2013), with tigers mostly attacking livestock at night and in forest while leopards attack in open agricultural areas in mid-day (Katel et al. 2014; Malviya and Ramesh 2015). Understanding the temporal and spatial patterns of interactions between different livestock and carnivore species is necessary for developing ecologically informed strategies for conflict mitigation.

We focused our study in Kanha Tiger Reserve, a protected area in Madhya Pradesh, India, where 18 % of households lose livestock to wild carnivores, primarily tigers (*Panthera tigris*) and leopards (*Panthera pardus*; Karanth et al. 2013). Kanha also serves as a source site for tiger and leopard populations throughout the central Indian landscape (Dutta et al. 2013; Sharma et al. 2013) and is thus a priority region for minimizing human–carnivore conflict. In Kanha, tigers and leopards mainly kill cattle (*Bos indicus*), buffalo (*Bubalus bubalis*), and goats (*Capra aegagrus hircus*; Negi and Shukla 2010). The Forest Department permits people to graze livestock in the multiple-use buffer zone but bans grazing inside the interior core zone of the park, except by livestock from several villages located in the core.

Local livestock owners implement distinct grazing regimes depending on the livestock species and season, which reflects trade-offs between livestock vulnerability to carnivores, herder costs, and other environmental factors. Cattle and buffalo, which often graze side-by-side in groups, are allowed to free-graze without a herder in the winter and summer months (November–June). In the monsoon (July–October), herders accompany cattle and buffalo to prevent livestock from consuming crops. In contrast, herders accompany goats year-round because goats can browse on the low-quality forage around villages, are more vulnerable to wild carnivores, and tend to wander off if unsupervised. These different temporal and spatial patterns of grazing suggest that cattle and buffalo may experience different threats from carnivores than goats. However, few studies have assessed how risk varies between domestic prey species, and this information is not available for Central India despite its importance as a Tiger Conservation Landscape (Wikramanayake et al. 1998).

Our objective was to understand the temporal and spatial patterns of risk for different livestock species and develop insights for reducing livestock losses. Using cases from the livestock compensation program, we examined historical records from 2001 to 2009 for past trends in livestock losses. We obtained more detailed insight on the temporal and spatial distribution and the physical characteristics of depredated livestock by conducting ground surveys of livestock killed in 2011–2012. We also investigated the location and prey contents of tiger and leopard scat to better understand the movement of the carnivores consuming livestock. Through combining multiple data sources, we provide an ecological perspective on carnivore–livestock interactions and develop ecologically informed recommendations for minimizing livestock vulnerability to carnivores.

Materials and methods

The study was conducted in Kanha Tiger Reserve in Central India. This 2074 km^2 protected area consists of a 940 km^2 interior core zone, where human activities are restricted, surrounded by a 1134 km^2 buffer zone, where human residences and activities such as livestock grazing are permitted. The reserve supports stable populations of 70 tigers and 100 leopards and growing populations of 59,000 cattle, 22,000 buffalo, and 11,000 goats, which are regularly attacked by wild carnivores (Negi and Shukla 2010; Jhala et al. 2014b). In an effort to prevent livestock owners from retaliating against carnivores, the Indian Forest Department financially compensates owners for domestic animals killed by wild carnivores. To receive compensation, a livestock owner must locate and report the livestock carcass to the Forest Department within 48 h, and an officer then visits the site to record evidence of the death. Although not all livestock owners choose to report lost livestock (Karanth et al. 2012), between 400 and 600 livestock are reported for compensation each year within the tiger reserve (Negi and Shukla 2010).

Data collection at livestock kill sites

We used the compensation program to investigate patterns of livestock depredation. We analyzed Kanha Tiger Reserve Forest Department historical records of compensation cases from January 2001 through December 2009 to assess long-term trends in livestock losses. These records provided information on the incident date, livestock species, carnivore, and compensation amount. To obtain more detailed spatial, temporal, and demographic data on the livestock killed, we conducted ground surveys of freshly killed livestock reported for compensation from December 2011 through August 2012. Sampling methods are described in detail in Miller et al. (2015) and overviewed here.

At each kill site, we recorded the incident date and time (if known by the owner), livestock species and age, percent of carcass remaining, and GPS coordinates. We differentiated the kill site (where the animal was killed) from the cache site (where the animal was dragged and consumed) by trails of scuffmarks, blood, and hair. The death of each animal was attributed to a specific carnivore based on fresh signs within 50 m of the kill and cache site. Researchers were trained to identify differences in the size and shape of signs for each carnivore species following the National Tiger Conservation Authority protocol (Jhala et al. 2009). We identified carnivore signs conservatively and omitted from analysis any kill sites with ambiguous carnivore signs. A total of 90 % of all 'confirmed' kills were identified using direct sightings of the carnivore (25 % of kills), pugmarks (64 % of kills), and/or scrapes (2 % of kills), which can be clearly distinguished between tigers and leopards (Karanth and Sunquist 1995). Because the methods used to identify predators were unknown for historical records, we analyzed only ground survey data when calculating carnivore species-specific trends. Finally, we recorded the compensation amount and the day payment was issued to livestock owners.

Carnivore scat

To study tiger and leopard diet and movement, we examined the prey contents and spatial location of carnivore feces. We collected tiger and leopard scat opportunistically along roadsides and foot trails, features which individuals use often for hunting and general movement (Smith et al. 1989; Karanth and Sunquist 2000). Tiger scat and leopard scat are distinct in appearance from the scat of other carnivores in our study area (Karanth and Sunquist 2000) but can be difficult to distinguish between the two species. Scat was identified to carnivore species using genetic analysis conducted by the Wildlife Institute of India (Yumnam et al. 2014). However, because only a few scat samples (18 %) contained viable genetic material, we did not associate carnivore identity with scat for our final analysis. We identified the prey in feces by drying scat, sampling hair contents, and microscopically comparing hair width, medullary structure, and other characteristics to prey reference slides at the Wildlife Institute of India (Mukherjee et al. 1994; Bahuguna et al. 2010). We mapped the GPS coordinates of each scat to examine where carnivores moved after consuming livestock.

Landscape attributes

We examined the landscape characteristics associated with kills by sampling environmental and anthropogenic variables known to influence livestock depredation by large *Felidae* predators (Seidensticker 1976; Shrader et al. 2008; Valeix et al. 2009; Kissling et al. 2009; Karanth et al. 2012; Zarco-González et al. 2013; Soh et al. 2014). For land use, we utilized the Forest Survey of India State of the Forests 2009 map of land cover, which included non-forest (i.e., agricultural fields), water, scrubland, open forest, moderately dense forest, and very dense forest. Since the land-use map did not distinguish villages, we used heads-up digitization with Google Earth satellite imagery from 2007 to 2013 to outline village areas. We also quantified human presence using roads digitized from Survey of India topographic maps and the boundary of the reserve core zone provided by the Kanha Forest Department. Landscape variables were converted to raster format at a 20-m spatial resolution using the Spatial Analyst toolset in ArcGIS (v.10.1, ESRI, CA, USA). We then calculated the Euclidean distance between the center of each kill site pixel and the center of the nearest pixel with the landscape attribute. We limited our study area to within 4 km of village centers in the reserve since no livestock were killed beyond this distance (Miller et al. 2015).

To contextualize kills against the available landscape, we also sampled the range of landscape attribute values at randomly selected sites across the study area (Johnson et al. 2006; Manly et al. 2002). The locations of these sites were determined by generating random points stratified across a 200-m grid in ArcGIS, with one point per pixel separated by at least 200 m so as not to repeatedly sample the same area. While ground-surveying these random sites for another study (Miller et al. 2015), no wild or domestic prey carcasses were observed.

We examined linkages between livestock kills and precipitation by comparing kill frequencies to daily and monthly rainfall measured by the Kanha Tiger Reserve Forest Department in 2011–2012.

Statistical analysis and modeling

Since the 2011–2012 data on livestock characteristics and landscape characteristics were not normally distributed, we used Mann–Whitney U tests to compare groups. For livestock species with adequate sample sizes (cattle, goat, and buffalo but not pig since $n_{\text{pig}} = 2$), we investigated differences by month in the historical frequencies of livestock kills using two-way ANOVAs. We explored associations between cache distance and livestock age, and between the timing of kills and daily or monthly rainfall, using linear regression models.

Using surveyed kill sites and landscape attribute data, we built a multivariate logistic regression model to predict and map the probability of carnivore predation of cattle (Miller 2015). We focused on cattle exclusively because they are the most depredated livestock species in Kanha, and because the numbers of buffalo and goats killed in 2011–2012 were not adequate to build a validated model. We modeled combined risk from tigers and leopards for cattle because we felt the output risk map would be most helpful to managers and owners for understanding and mitigating risk to cattle generally. Following a use-availability design (Johnson et al. 2006), the response variable in the model featured binary values, with 0 for random sites and 1 for kill sites. Incidences where a carnivore killed multiple livestock during the same predation event ($n = 36$) were treated as single kill sites to focus the spatial models on units of kill sites rather than individual animals and avoid pseudoreplication. We generated univariate linear regression models to examine which landscape attributes were strong predictors of kill probability. Following standard methods (Garamszegi 2010; Treves et al. 2011), we ran Spearman correlations between variables and built global models for livestock species that included the variables that were significant in the univariate regression and not correlated with more significant variables ($r_s < 0.6$). These requirements excluded the variable distance to non-forest, which was correlated with distance to village ($r_s = 0.7$) and distance to very dense forest ($r_s = 0.7$). Based on field observations, we suspected that roads, villages, scrubland, and very dense forest would have a threshold relationship with kill risk such that effects might decrease in a nonlinear direction at some distance. Furthermore, we found that including the quadratic structural form of these variables lowered the global model AIC by ≥ 2 (Draper and Smith 1993; Burnham and Anderson 2002). The global model were used to generate and rank models with all combinations of the eligible variables based on the corrected Akaike's information criterion (AIC_c) to account for small sample size (Burnham and Anderson 2002). Since no one top model emerged ($\text{AIC}_c \leq 2$), we averaged models to produce a final model.

We used the model to investigate the effect of each landscape attribute on the kill probability by predicting risk while varying the attribute of interest and holding all other variables constant at their means. We then mapped the model in ArcGIS to observe hotspots in carnivore kill risk across the study area. Finally, we validated whether the model could predict future kills by conducting a randomization test against an independent dataset of kills (detailed methods in Appendix S1 and Figure S1). Statistical analyses were conducted using R (v.2.15.3, R Project Development Team, www.r-project.org) with the MASS, MuMIN, and R DAAG packages.

Results

Historical records from 2001 to 2009 contained 4561 livestock reported for compensation, consisting of 72 % cattle, 16 % goats, 10 % buffalo, 2 % pigs, and <1 % horses. All cases were attributed to a specific carnivore: 64 % were attributed to tiger attacks, 34 % to leopard, 1 % to unknown carnivores, and <1 % to wild dog and wolf. However, since the methods used to identify carnivores are unknown and 30 % of ground-surveyed kills in 2011–2012 did not contain conclusive evidence about the carnivore, carnivore identity data should be interpreted with care. Between December 2011 and August 2012, we ground-surveyed 449 livestock carcasses, which totaled 92 % of all reported kills in Kanha during the study period. Livestock consisted of 76 % cattle, 14 % goats, 9 % buffalo, and <1 % pigs. Based on carnivore signs, we were able to confidently identify the predator at 71 % of kills, of which we attributed 57 % to tiger and 43 % to leopard.

Ground surveys indicated that tigers and leopards selected different size classes for livestock ($U_{430} = 7357$, $p < 0.001$; Fig. 1a–c). Leopards killed more young cattle (aged 1–4 years) and buffalo (3 years) than tigers, whereas tigers killed more older cattle (5–11 years) and buffalo (6–10 years). Only leopards killed goats, which ranged from 1 to 6 years. The ages of depredated pigs could not be identified.

Historically, 95 % of livestock were accepted for compensation (note that the Forest Department did not record cases that did not meet program requirements, such as injured livestock). The Forest Department paid a total of INR 81,46,842 in compensation over the eight-year period, ranging INR 8,78,471–16,28,150 per year. In 2011–2012, the Forest Department similarly paid INR 21,42,650 for 91 % of reported kills, which it distributed to owners within an average of 17.4 ± 0.9 days (mean ± SE; based on 120 cases with data on payment date).

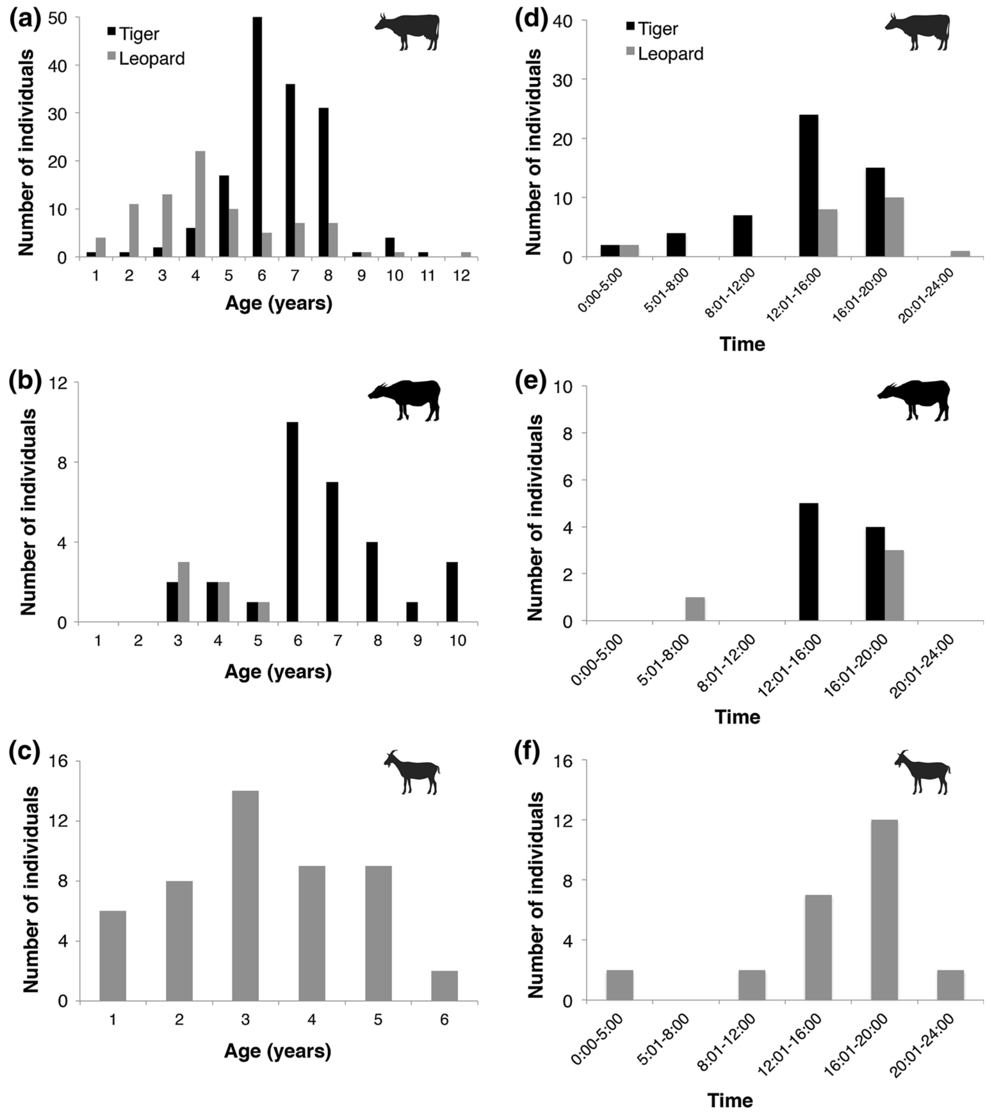


Fig. 1 Age (*left*, **a–c**) and attack time (*right*, **d–f**) of livestock killed by tigers (*black*) and leopards (*gray*) for (**a**, **d**) cattle, (**b**, **e**) buffalo, and (**c**) goats (**c**, **f**)

Tiger and leopard hunting behavior

Most livestock carcasses were cached away from the site where they were killed. Tigers cached 71 % of cattle kills and leopards cached 63 %, and both carnivores dragged carcasses similar distances (mean ± SD for tigers was 50 ± 54 m and leopards was 51 ± 94 m; $U_{155} = 2324$, $p = 0.154$). Tigers and leopards cached 61 and 50 % of buffalo kills, respectively, and varied more in the length of their drags (average distance of 36 ± 26 m for tigers and 116 ± 86 m for leopards), but these differences were not statistically significant ($U_{19} = 38$, $p = 0.203$). Leopards cached 52 % of goat carcasses, dragging them an average of 192 ± 229 m, and cached both pig kills ($n = 2$), moving one carcass 8 m and the other 470 m. For each carnivore, smaller-bodied livestock species were cached farther from kill sites, and overall cache distance was significantly but weakly correlated with livestock age ($R^2 = 0.066$, $F_{1,269} = 18.86$, $p < 0.001$). In only 45 % of cases were carnivores able to consume more than half the carcass before the Forest Department burned the body (Fig. S2).

We collected 133 tiger and leopard scat distributed across the reserve (Fig. 2), 69 (52 %) in the core zone and 64 (48 %) in the buffer zone. The majority of scat (67 %) contained only wild prey animals, 29 % contained only domestic animals (cattle and buffalo), and 4 % contained both wild and domestic prey (Fig. S3). Since hair from wild and domestic pig appears identical under the microscope, we conservatively categorized all pig hairs as wild prey for our analysis. Out of the 44 scat containing livestock, only eight were found in the park core zone, five of which were located close (<2 km) to the core-buffer boundary. Genetic analysis confirmed that two of the five near the boundary

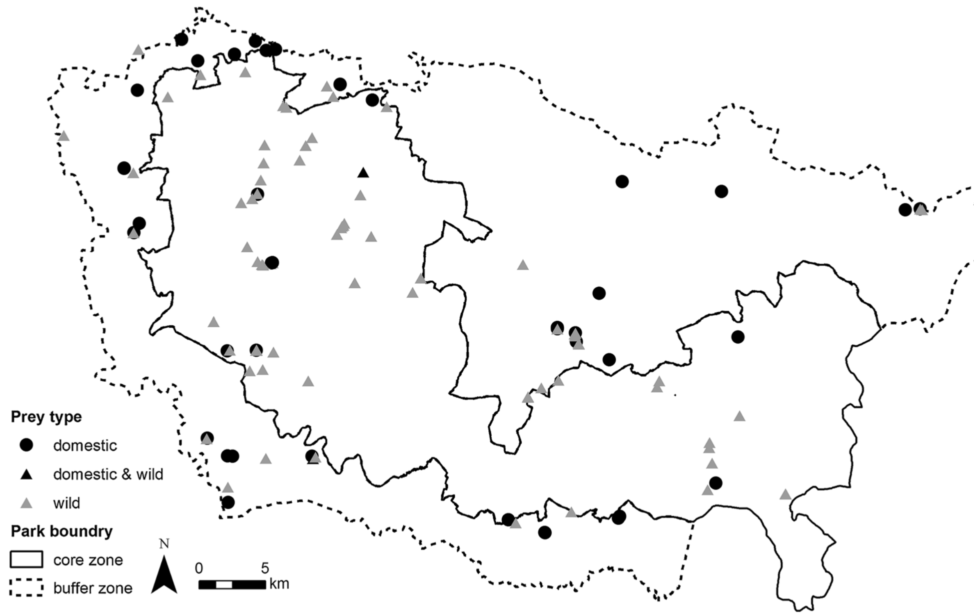


Fig. 2 Locations of tiger and leopard scat collected across Kanha Tiger Reserve, showing the distribution of domestic and wild prey contents with respect to the reserve core and buffer zones. Villages are primarily located in the buffer zone

were tiger and one was leopard. Three scats containing livestock were found deep within the core interior (3.5–7.2 km from the boundary).

Temporal patterns

From 2001 to 2012, the frequency of livestock depredations varied substantially by year but did not consistently increase or decrease over time (Fig. 3). The number of kills did not significantly differ between month for cattle ($F_{1,106} = 0.106$, $p = 0.746$), buffalo ($F_{1,106} = 0.039$, $p = 0.845$), goat ($F_{1,106} = 1.664$, $p = 0.200$), pig ($F_{1,106} = 1.492$, $p = 0.225$), or horse ($F_{1,106} = 0.716$, $p = 0.399$). A distinct peak in compensated livestock occurred each year sometime between July and September during the monsoon (Fig. 3). However, the number of kills was not associated with monthly ($R^2 = 0.137$, $F_{1,7} = 1.112$, $p = 0.327$) or daily ($R^2 = 0.002$, $F_{1,210} = 0.392$, $p = 0.532$) rainfall.

Most livestock were killed in the afternoon and evening between 12:00 and 20:00 hour (Fig. 1d–f). Both tigers and leopards attacked cattle during this period and tigers also frequently killed cattle throughout the morning (05:00–12:00 hour). Leopards killed goats throughout the day and especially in the early evening (16:00–20:00 hour).

Spatial patterns of livestock kills and attack risk

The majority of livestock were killed in the buffer zone of the reserve (82 %), where most villages and livestock grazing occur. The remaining 18 % were killed in the core zone and were concentrated around the villages in the core zone or close to the core-buffer boundary. Comparisons between kill and random sites revealed that carnivores tended to kill cattle and buffalo closer to forests and farther from non-forest (agricultural fields) and villages than random (Table 1). In contrast, goats were killed closer to

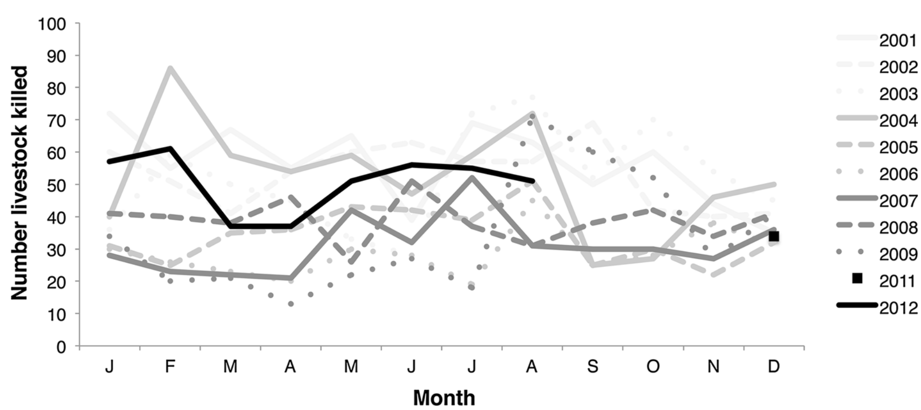


Fig. 3 Number of livestock killed each month in Kanha Tiger Reserve from 2001 to 2009. No records were available for 2010

Table 1 Mann–Whitney U test comparisons between mean values ± standard error of landscape attribute variables at sites where tigers and leopards killed livestock (kill site) and random sites in the study area in Kanha Tiger Reserve

Variable	Random sites (n = 435)	Cattle (n = 193)		Goat (n = 39)		Buffalo (n = 32)	
		Kill sites	p value	Kill sites	p value	Kill sites	p value
Distance to core (km)	0.5 ± 0.1	2.0 ± 0.2	**0.023**	1.1 ± 0.2	**0.023**	2.1 ± 0.6	0.412
Distance to road (km)	2.5 ± 0.3	0.7 ± 0.4	**<0.001**	0.5 ± 0.7	0.708	0.7 ± 0.9	0.058
Distance to village (m)	827 ± 40	956 ± 47	**<0.001**	501 ± 79	**0.042**	975 ± 84	**0.002**
Distance to water (km)	2.6 ± 0.8	2.9 ± 0.1	**0.036**	3.9 ± 0.2	**<0.001**	3.0 ± 0.3	0.195
Distance to non-forest (m)	303 ± 23	362 ± 23	**<0.001**	83 ± 20	**0.024**	511 ± 80	**<0.001**
Distance to scrubland (km)	6.7 ± 0.2	6.9 ± 0.2	0.128	5.8 ± 0.5	0.419	7.4 ± 0.7	0.251
Distance to open forest (m)	362 ± 16	289 ± 19	**0.048**	285 ± 39	0.342	301 ± 58	0.189
Distance to moderately dense forest (m)	234 ± 17	68 ± 8	**<0.001**	197 ± 35	0.41	55 ± 11	**0.003**
Distance to very dense forest (m)	495 ± 36	173 ± 39	**<0.001**	532 ± 101	0.182	104 ± 29	**<0.001**

P values in bold are significant ($p < 0.05$)

fields and villages. Both cattle and goats (but not buffalo) were killed at farther distances from water and the park core boundary than random sites. Carnivores killed cattle (but not goats or buffalo) farther from roads.

We built a predation risk model using 435 random sites and 193 cattle kills with confirmed predators. The model predicted the probability of a tiger or leopard killing a cattle given an encounter, ranging from 0 (low risk) to 0.93 (high risk). The contribution of each variable to predictions of predation risk was measured by its relative importance in the model. Most variables played a strong role in predicting risk (importance >0.70), including all human presence and dense forest variables (Table 2). Randomization tests revealed that model predictions performed better than random (Fig. S4). The model accurately identified 69 % of validation sites (88 out of 128 known kill sites) as kills, which is greater than would be expected by random chance ($p < 0.001$).

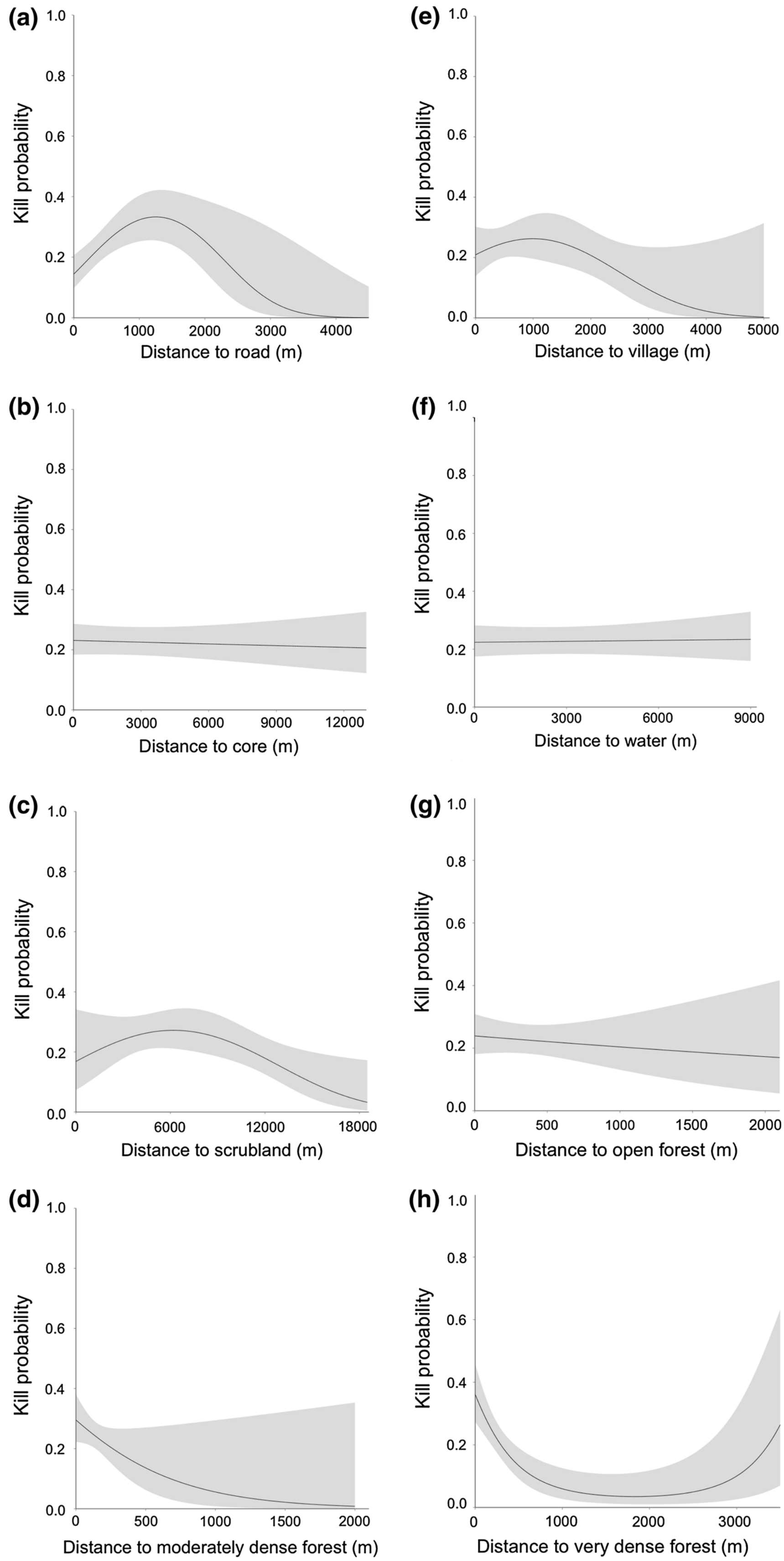
The risk to cattle was greatest in moderate and very dense forests and at intermediate distances from roads, villages, and scrubland (Fig. 4). Risk did not substantially change with increasing distance from water or the core zone boundary. Kill probability showed a negative quadratic relationship to the distance to road, village, and scrubland, with cattle vulnerability increasing at farther distances up to a threshold point and thereafter decreasing. Cattle were most vulnerable to carnivores 1.2 km from roads, 1.0 km from villages, and 6.1 km from scrubland (Fig. 4a, c, e, respectively). The distance to very dense forest showed a negative quadratic relationship, with the greatest risk directly within (0 km) or far from (>4 km) very dense forests (Fig. 4i). The predation risk map

Table 2 Statistics from the predation risk model for cattle, showing the relative importance, coefficient (β), and standard error (SE) of variables in the final averaged model

Variables	Importance	β	SE
Intercept		−1.16	0.63
Distance to very dense forest^2	1.00	8.24E−07	1.75E−07
Distance to very dense forest	1.00	−3.02E−03	7.10E−04
Distance to road	1.00	1.74E−03	5.00E−04
Distance to road^2	0.99	−6.98E−07	2.37E−07
Distance to scrub^2	0.96	−1.67E−08	8.15E−09
Distance to village^2	0.92	−3.31E−07	1.82E−07
Distance to moderately dense forest	0.88	−2.23E−03	9.43E−04
Distance to scrub	0.84	2.36E−04	1.20E−04
Distance to village	0.75	7.99E−04	4.70E−04
Distance to open forest	0.43	−4.73E−04	4.02E−04
Distance to core	0.35	−3.24E−05	3.67E−05
Distance to water	0.28	2.26E−05	5.66E−05

Relative importance values range from 0 to 1, with a value of 1 indicating a strong contribution to the model

Fig. 4 Probability of carnivore depredation on cattle with increasing distances to landscape attributes as predicted by the predation risk model. The 95 % confidence intervals are shown in *gray*



revealed the highest risk levels in forest patches adjacent to the park core boundary and the lowest levels in agricultural areas near villages and roads (Fig. 5).

Discussion

Kanha has one of the highest rates of livestock depredation from tigers and leopards in India (Kala and Kothari 2013; Karanth et al. 2013; Singh et al. 2015) yet is also renowned as one of the most successful and stable sites of tiger conservation (Post and Pandav 2013; Jhala et al. 2014a). The low frequency of retaliations against depredating carnivores in Kanha is largely due to the Forest Department's prompt livestock compensation program, which in 2011–2012 distributed payment on average about 2.5 weeks after livestock were attacked. This is considerably faster than other reported compensation time frames from India (Madhusudan 2003) and on par with championed programs (Nyhus et al. 2005). The compensation program also offers tractable long-term data that can be used for assessing the temporal and spatial patterns and physical characteristics of livestock losses. Kill data offer exclusive fine-scale spatial information about the sites where livestock are vulnerable to livestock, offering a unique perspective not otherwise captured by household surveys, which have been the basis of many previous studies on human–carnivore conflict (e.g., Wang and Macdonald 2006; Nugraha and Sugardjito 2009; Karanth et al. 2012; Katel et al. 2014; Bhattarai and Fischer 2014).

Our study confirmed that tigers and leopards were the primary depredating carnivores, with tigers responsible for killing slightly more livestock than leopards. This contrasts with reports from Corbett Tiger Reserve in northern India and Bhutan, where leopards kill substantially more livestock than tigers (Wang and Macdonald 2006; Sangay and Vernes 2008; Malviya and Ramesh 2015). We suspect this difference may be related to the lower availability of free-grazing adult cattle in Corbett (where ~30 % of households stall-feed livestock; Malviya and Ramesh 2015) and the lower density of tigers in Bhutan (Sanderson et al. 2006). We did not find evidence of attacks from other carnivores, which the Forest Department had reported in previous years, and we urge authorities to train field staff to make accurate predator identifications in order to prevent false perceptions about threats from other carnivores (Dickman 2010; Suryawanshi et al. 2013). Cattle were killed most frequently, followed by goats, buffalo, and pigs, respectively. Compensation cases are likely biased against small-bodied livestock (goats and pigs) because these animals are more often cached further and more completely eaten, and thus more difficult for livestock owners to locate and report. These strong associations between certain sized livestock and certain carnivore species suggest that segregating livestock by body size and age, and grazing cohorts in habitats less conducive to attacks by their main predator (e.g., open vegetation for tigers and dense forests for leopards), might discourage depredation (Wang and Macdonald 2006; Goodrich 2010).

Temporal patterns

Tigers and leopards killed livestock at all hours of the day, particularly in the afternoon and evening. Our analysis found a high number of attacks by tigers in the afternoon

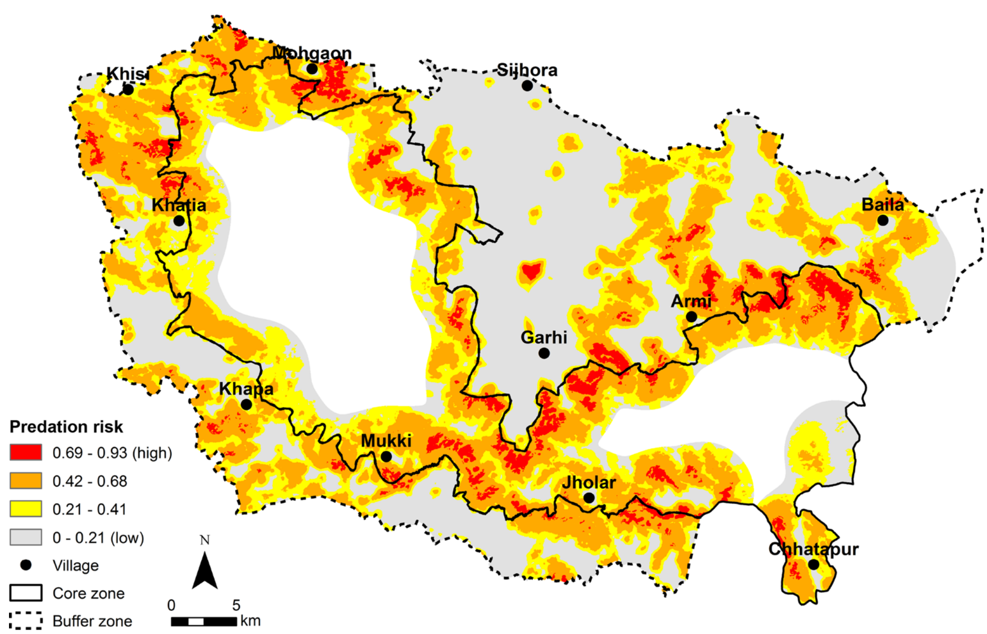


Fig. 5 Distribution of tiger and leopard predation risk for cattle in Kanha Tiger Reserve. Values represent the kill probability given an encounter between a tiger or leopard and cattle. Low-risk areas primarily occur in agricultural fields and village areas, whereas high-risk hotspots occur in dense forest away from human activity. Notable villages are shown for orientation (not all villages are marked). The study area was designated within 4 km of village centers and did not include *white areas* shown on the map (see 'Materials and methods' for details)

(12:00–16:00 hour), likely because this was when livestock were farthest from the village and in dense vegetation where tigers often attack livestock (Soh et al. 2014; Malviya and Ramesh 2015; Miller et al. 2015). Furthermore, tigers (and leopards) are most active and hunting in the early morning, late afternoon, evening, and night and avoid much activity mid-day (Karanth and Sunquist 2000). Our results did not reveal temporal separation between tiger and leopard or a tendency toward nocturnal hunting in either predator as found in previous studies (Seidensticker 1976; Karanth and Sunquist 2000; Malviya and Ramesh 2015), probably due to the nature of our dataset, which depended on people witnessing attacks.

We observed a spike in livestock losses each year during the monsoon, which echoes similar findings from other protected areas in South Asia (e.g., Bhadauria and Singh 1994; Sangay and Vernes 2008; Singh et al. 2015). However, the number of livestock kills did not closely follow monthly rainfall throughout the year as reported from Africa (Kolowski and Holekamp 2006). This may indicate that the rise in depredations during monsoon is due to human-induced changes, such as herders leading cattle and buffalo away from crops to graze in denser forests with greater predation risk. If so, monsoon may be an ideal season in which to implement alternative grazing strategies since humans have more control over livestock movement.

Spatial patterns

Results revealed distinct risk distributions by livestock species, which to our knowledge has not been examined for tiger and leopard depredation. The predation risk model found that threats from both carnivores combined were highest for cattle near dense forests and lowest near agricultural fields, villages, and roads. These results are comparable to previous conflict studies on tigers that likewise observed most attacks on livestock in forest and away from roads (Wang and Macdonald 2006; Soh et al. 2014). The risk map for cattle closely resembles general tiger risk for all livestock (Miller et al. 2015), likely because cattle are the most frequent species killed by tiger and thus most strongly represented in the tiger risk model. Risk hotspots occurred 1–2 km from the core zone boundary in both the buffer zone and the interior of the core zone, corroborating previous findings from Central India that livestock depredation increases with close proximity to protected areas (Karanth et al. 2013). The high kill probabilities inside the core zone reiterates the need for strict enforcing to eliminate grazing livestock in the core, which has been emphasized as a priority for reducing human–tiger conflict in the past (Goodrich 2010). To reduce livestock losses, livestock owners could minimize cattle presence in dense forests and favor grazing routes close to open vegetation and human areas. If grazing routes are adapted to reduce risk, carnivores should also be initially monitored for behavioral feedbacks to ensure that they are not drawn into closer contact with people (Miller 2015).

Similarities in the landscape attributes associated with cattle and buffalo kill sites suggest that buffalo may experience comparable distributions of predation risk as cattle. However, results showed opposite trends for goats, which were more vulnerable in open vegetation and village areas. These distinctions may be related to grazing patterns since herders may restrict goats to the open vegetation and village areas that are most convenient for human access, whereas cattle and buffalo graze unrestrained farther from villages for most of the year. Our data do not enable us to discern whether these risk distributions are shaped more by carnivores or by livestock and people, but we encourage future studies to directly pursue the mechanisms behind depredation.

It is currently unknown whether the individual tigers and leopards predating on livestock are resident or dispersing, but our scat results offer some insight into carnivore movement. Though scat contents indicated that tiger and leopard diets primarily consisted of wild prey, 33 % of all scat (buffer and core zone) and 42 % of scat found in the buffer contained domestic livestock, which is a surprisingly large proportion considering the high abundance of wild prey available in the core zone (Jhala et al. 2014b). Twelve percent of scat found in the core zone contained livestock remains, and 10 % was found 3–7 km from the core-buffer boundary in the interior of the core. Although this scat may have been deposited by young tigers or leopards dispersing through the reserve, it is also possible that resident carnivores may visit the buffer zone to supplement their diet with livestock. Considering the extensive home ranges of tigers ($\sim$10–100 km^2; Sharma et al. 2010) and leopards ($\sim$10–60 km^2; Odden et al. 2014), livestock depredation may not be restricted to transient individuals as commonly believed. Furthermore, if resident individuals are regularly attracted out of the park core zone to kill livestock, they may be susceptible to human threats in the buffer zone and non-protected areas (Balme et al. 2010). However, our limited sample size and opportunistic (rather than systematic) sampling of scat limit the scope of our conclusions. Greater efforts in the future must be dedicated to identifying which individual carnivores kill livestock, especially since this answer may help more fully elucidate the drivers behind livestock depredation.

Implications for human–carnivore conflict mitigation

The call to reduce human–carnivore conflict by avoiding predator hotspots has been sounded before (Wang and

Macdonald 2006; Goodrich 2010), and our study contributes insight to help identify when and where different livestock species are most vulnerable to tigers and leopards. Middle-aged cattle (4–8 years) were the most vulnerable to tigers and leopards and were attacked primarily in the afternoon and early evening (12:00–20:00 hour) near dense forests and at moderate distances from road, village, and scrub forests. Buffalo were mostly killed by tigers, which tended to attack middle-aged individuals (6–8 years) during the afternoon and early evening (12:00–20:00 hour) in dense forests and away from open habitat and villages. To reduce losses, we recommend the use of herders year-round, instead of only during the monsoon, to enable greater control over cattle and buffalo routes and timing to minimize high-risk grazing in forests. Middle-aged goats (2–6 years) were most at risk from leopards during the early evening (16:00–20:00 hour) in open vegetation and village areas. Rather than shift goat grazing routes to denser forest to reduce risk, which might increase threats from tigers, owners could consider protecting goats earlier in the day (before 16:00 hour) in reinforced, leopard-proof enclosures. Furthermore, to decrease losses with all livestock species, owners living in high-risk areas could consider implementing additional mitigation techniques such as trained guard dogs, predator-proof enclosures and fencing, deterrents, and sensory stimulants, especially during the highest risk season (monsoon), to further reduce attacks from carnivores (Shivik 2006). Previous research in Central India (Karanth et al. 2013) and in east Africa (Kolowski and Holekamp 2006) found that guard animals and fencing were especially useful in mitigating attacks. Finally, we encourage managers worldwide to regularly update predation risk models and maps to monitor conflict, and to develop results into relevant education and outreach materials to assist livestock owners in understanding risks near their villages (Miller 2015).

This paper demonstrates that livestock compensation programs generate data that can be useful for understanding and preventing conflict. Financial compensation systems play a particularly important role in supporting livestock owners that live in the 'diffuse edge' buffer zones of protected areas where the majority of human–carnivore conflict often occurs (this study; Nyhus and Tilson 2004). This is the case in Kanha, one of the few tiger reserves in India with a functional buffer zone, where the livestock compensation program is key to minimizing retaliations against carnivores. Compensation programs also present opportunities for villagers to develop stronger relationships with the Forest Department, which can impact human–carnivore conflict given that local trust in authority is directly linked to attitudes toward conservation (Treves et al. 2006; Dickman 2010; Carter et al. 2012). To build trust and local engagement, it is important that authorities ensure that livestock owners understand and can meet the regulations related to livestock compensation (Nyhus et al. 2005). Most surveyed livestock losses (91 %) in Kanha from 2011 to 2012 were compensated within several weeks if basic requirements were met. These levels greatly differ from the lower success rates (29 %) reported just outside the buffer of Kanha (Karanth et al. 2012), where compensation is mandated but often overlooked by governing authorities in the absence of the high-profile tiger. This discrepancy has sparked confusion and intolerance in some livestock owners (Karanth et al. 2013), who may be more prone to retaliate against wild carnivores that depredate livestock. We encourage managers to maintain consistency and generously award compensation whenever possible (while taking care to avoiding false claims, corruption, and perverse incentives; Nyhus et al. 2005). This is important both within and outside of protected areas, especially since carnivore dispersal outside of parks is essential for maintaining resilient populations (Yumnam et al. 2014).

The results of this paper face several potential limitations. First, compensation data may not have evenly represented the spatial distribution of livestock depredations if village remoteness or villager–authority relationships biased the reporting of kills. Because Forest Department beat camps (where owners go to report kills) are evenly distributed across the Kanha buffer and core, and because we were not aware of negative social tensions during nine months of extensive field visits, we do not expect that results were significantly biased. Second, though the presence of herders grazing cattle during the monsoon months may change the distribution of predation risk from the rest of the year, our cattle risk models did not address season-wise differences. This is because our goal in modeling cattle risk was to understand year-round predation risk to offer managers simple guidance for decision-making, but we do recognize that risk will shift with different grazing practices and resource distribution and encourage future studies to more closely examine such short-term shifts. Finally, the cattle risk model portrays combined risks for tigers and leopards, which offers managers and owners a tool for strategizing protection for cattle but may limit inferences on the spatial distribution of risk from each species.

Conclusions

The first increase in the tiger population recently reported from India (Jhala et al. 2014a) offers hope that collective efforts worldwide can reverse carnivore declines. Yet even if carnivore populations stabilize, expanding human development guarantees that natural resource managers and livestock owners will continue to face challenges in mitigating human–carnivore conflict (Treves and Karanth

2003; Ripple et al. 2014). Understanding the temporal and spatial factors that underlie ecological interactions between specific carnivore and livestock species will be essential for developing strong mitigating methods that ultimately make coexistence possible.

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