



The ecological benefit of tigers (*Panthera tigris*) to farmers in reducing crop and livestock losses in the eastern Himalayas: Implications for conservation of large apex predators

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ARTICLE INFO

Keywords:

Apex predators
Agro-ecosystems
Bhutan
Carnivore conservation
Predator guild
Trophic cascade

ABSTRACT

Ecologists have primarily focused their attention on how predator loss influences ecosystem structure and function in intact ecosystems, but rarely tested these ecological concepts in agricultural landscapes. We conducted a study in western Bhutan on the inter-specific dynamics between tigers, leopards, and dholes, and their subsequent impact on livestock and crop losses faced by agro-pastoralists. We found that when a tiger was present in forests surrounding villages, leopards and dholes occupied areas closer to village croplands and preyed on a higher relative abundance of wild herbivore crop raiders, thereby significantly reducing crop ($\beta = -2.25$, $p < .0001$) and livestock losses ($\beta = -2.39$, $p \leq .0001$). In contrast, leopards and dholes occupied areas in deep forests farther from croplands when a tiger was absent in the village vicinity, leading to increased predation on a higher abundance of untended free-ranging livestock. We posit that justifications for large predator conservation based on their iconic status is not persuasive to rural farmers residing close to their habitat and suffering crop and livestock loss. There is a need to determine ecological services from apex predators to farmers which may dissuade them from retaliatory killings. We recommend conservation practitioners conserve large apex predators to maintain optimal inter-specific interactions in a large predator guild to benefit rural socio-economy.

1. Introduction

With reduced populations and imminent extinction risk to apex predators in many landscapes, ecologists have focused on the impacts of predator loss on ecosystem structure and functions such as trophic cascades (Estes et al., 2011) and mesopredator release (Ripple et al., 2013) which are well documented in natural areas (Pace et al., 1999; Schmitz et al., 2000; Zdiilla, 2011; Newsome and Ripple, 2015). However, such influences of predator guilds have been rarely studied in agricultural landscapes where crops are damaged by wild herbivores and wild predators predate on livestock.

Paradoxically, farmers in developing and biodiversity-rich countries often experience economic loss through negative interactions with wild predators and herbivores. For instance in Bhutan, where approximately 70% of the population are subsistence farmers, annual crop and

livestock losses account for approximately 19% of annual household income (Wang and Macdonald, 2006). Such heavy losses result in major setbacks to rural economy (Sangay and Vernes, 2014) and may fuel negative sentiments toward conservation policies and jeopardize many years of conservation efforts (Wang et al., 2006). In such an environment, conservationists are challenged to rationalize carnivore protection, an action that is often viewed as animal-centric at the expense of human welfare.

Farmers' poor understanding of the ecological role of predators may also inadvertently exacerbate resentment against predator conservation. Livestock loss may consequently lead to retaliatory killings of large apex predators, such as tigers (*Panthera tigris*), leopards (*Panthera pardus*), and dholes (*Cuon alpinus*). Negative human-predator interactions have overshadowed potential benefits to the extent that the extirpation of carnivore species has been advocated (Bergstrom, 2017),

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<https://doi.org/10.1016/j.biocon.2018.01.015>

Received 13 August 2017; Received in revised form 6 January 2018; Accepted 14 January 2018

Available online 02 February 2018

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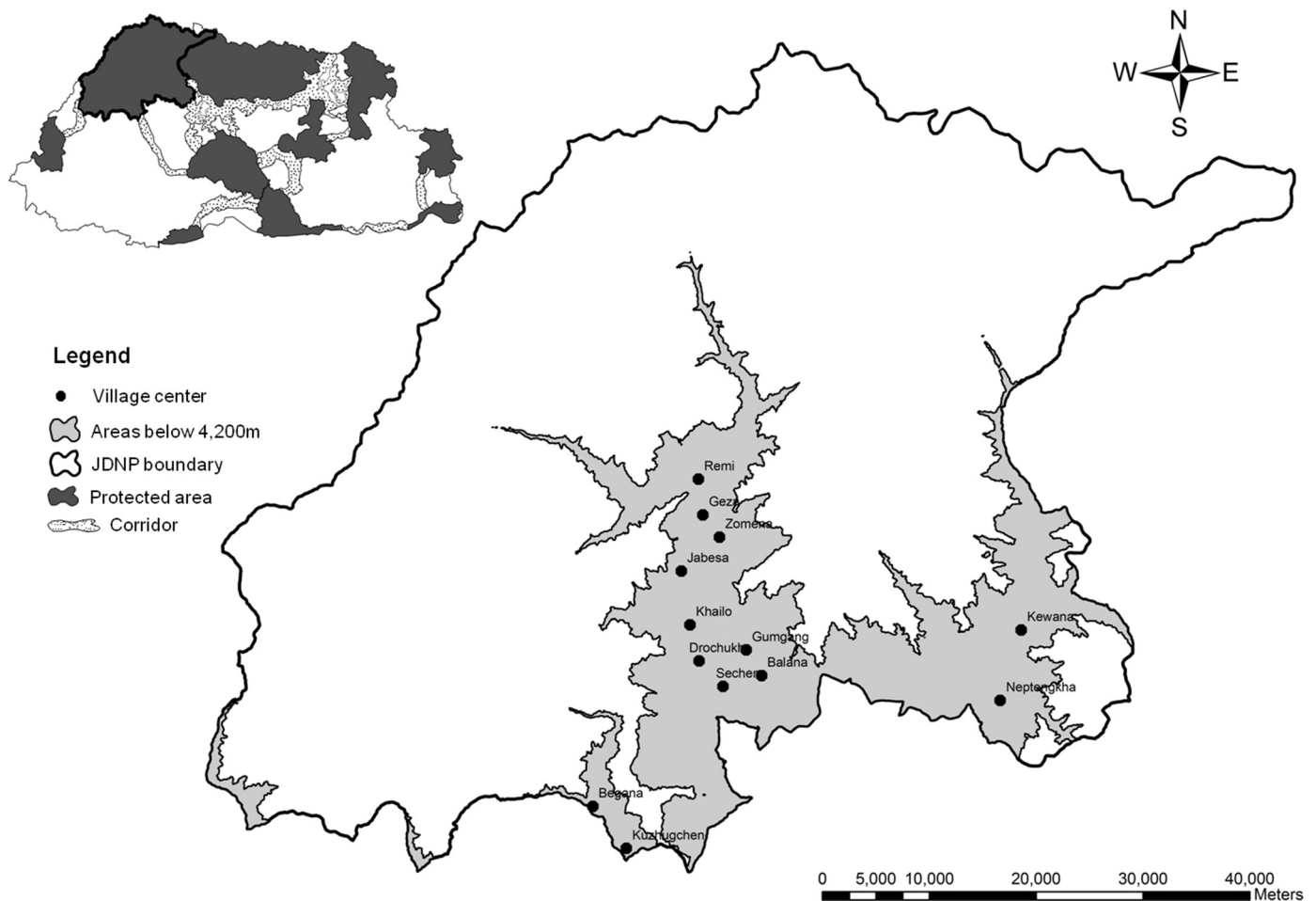


Fig. 1. Map of Jigme Dorji National Park showing location of study villages in the park. The inset shows a map of protected areas and biological corridors within Bhutan.

potentially depriving humans of valuable ecosystem services and functions from predators. Mass extermination of wild predators has been globally documented (Carbyn, 1989; Fritts et al., 1997; Gibbons and Dorcas, 2002; Wangchuk, 2004), mainly because predators have been deemed undesirable because of competition with humans for game animals, associated economic losses, and safety concerns. In many cases, these actions have been counterproductive. For instance, farmers in Bhutan almost extirpated dholes (*Cuon alpinus*) in the early 1990s hoping to reduce livestock losses. A decade later, wild pig (*Sus scrofa*) populations dramatically increased, resulting in massive unprecedented agricultural crop loss across the country (Wangchuk, 2004; Thinley et al., 2011). Likewise, wolf (*Canis lupus*) extermination from many areas in the eastern United States and Canada has been associated with the subsequent increase in white-tailed deer populations that destructively foraged on forest understory, leading to changes in plant communities and subsequent impact on forest regeneration (Horsley et al., 2003; Tremblay et al., 2006; Martin et al., 2010; Levi et al., 2012; Levine et al., 2012).

However, humans have allowed carnivores to thrive if negative impacts were tolerable. Additionally, proponents of large carnivore conservation programs have advocated and championed the cultural and aesthetic value of large carnivores, instead of emphasizing their key ecological importance. Given increasing negative human-predator interactions (Woodroffe and Ginsberg, 1998; Wang and Macdonald, 2006) in agro-ecosystems, there is an increasing need to investigate ecological concepts related to large predators, such as trophic cascade and top-down control, to maintain ecologically viable populations of apex predators (Woodroffe and Ginsberg, 1998; Wang and Macdonald, 2006). Practical application of predator-based ecological concepts may

not only facilitate the use of science in conservation decision-making (Cook et al., 2013), but may also strengthen environmental education and garner enhanced public support for nature conservation (Espinosa and Jacobson, 2012).

Despite attention to global livestock loss (Rajaratnam et al., 2016), the intricate relationships between sympatric carnivores, prey species, and associated wildlife damage to humans and their property (e.g., crop damage, livestock losses, and human injury) have been largely unstudied. The complex trophic structures and dynamics associated with predator and prey diversity can provide ecosystem stability and resilience (Soluk, 1993; Soule et al., 2003; Estes et al., 2011), and greater knowledge of these complex interactions can give wildlife managers and conservationists the tools to make better informed management decisions. However, there have been few studies on inter-specific predator interactions and their cascading impact on prey populations (Losey and Denno, 1998; Bjorkman and Liman, 2005). Indeed, interactions among various predators may influence food web dynamics by determining the distribution and control of prey populations (Vanbuskirk, 1988; Denno and Finke, 2006), prey selection (Karanth and Sunquist, 1995; Wang and Macdonald, 2009a), and space use by specific guild members at various spatial scales. Additionally, interactions between large carnivores may benefit agro-pastoralists through enhanced ecosystem services such as reduced crop damage by wild ungulates and fewer livestock losses to wild carnivores.

In this study in Bhutan, we examine the distribution of two mid-sized predators (leopards and dholes) in the presence or absence of a large apex predator (the tiger) in relation to distance from village croplands. We further investigate how crop and livestock losses vary with tiger and leopard presence/absence in agro-ecosystem landscapes

where dholes are extant.

2. Methods

2.1. Study area

We conducted the study in Bhutan's Jigme Dorji National Park (JDNP), which is approximately 4316 km² in size (11% of the country's total area) and situated between 27°32'52.8" and 28°14'45.6" latitudes and 89°15'10.8" and 90°17'6" longitudes (Fig. 1). The park is rich in biodiversity, containing 40 species of mammals, 328 bird species, and 1450 plant species (Thinley et al., 2015c). Major carnivore species present in the park at lower elevations [< 4000 m above sea level (a.s.l.)] include the tiger, leopard, and dhole, while the snow leopard (*Panthera uncia*) occupies areas above 4000 m a.s.l. The park also houses a diverse ungulate community, including sambar (*Rusa unicorn*), muntjac (*Muntiacus muntjak*), and wild pig. The elevation in the park ranges from 1200 to 7200 m a.s.l. Approximately 5000 people from 35 villages reside in the park, the majority of whom are agro-pastoralists (growing crops and raising livestock) at elevations lower than 3500 m a.s.l. where the landscape consists of a mosaic of croplands within a matrix of largely undisturbed forest. We focused our research on communities where a household's average livestock holding was 15 animals (inclusive of cattle and horses), and the average land holding was 1.3 ha in size, and randomly selected 13 agro-pastoralist villages. All selected villages experienced crop losses to wild pig, sambar, and muntjac and livestock losses to tigers, leopards, and dholes.

2.2. Study design and data collection

We selected tiger, leopard, and dhole as our focal predator species, because they have reportedly killed and injured many livestock in the park and elsewhere in the country (Wang and Macdonald, 2006; Sangay and Vernes, 2008). They are also natural predators for the major herbivores that impact crops (Wang and Macdonald, 2009a). Because there have been no reports of livestock losses to other medium-sized predators, such as clouded leopard (*Neofelis nebulosa*), Asiatic golden cat (*Pardofelis temminckii*), and marbled cat (*Pardofelis marmorata*), they were excluded as focal predators in our study. Similarly livestock and crop losses to Himalayan black bears (*Ursus thibetanus*) were also excluded from our study because the number of cases was very low ($n = 2$). We also excluded snow leopards (*Panthera uncia*) as there was no documentation of their predation on herbivore crop depredators and they were mainly found in areas above 4200 m (Thinley, 2013) where their principal prey was blue sheep (*Pseudois nayaur*) and occasionally domestic yaks (*Bos grunniens*) (Leki et al., 2017).

Villagers in the study villages were thoroughly briefed and requested to promptly report any incidence of crop and livestock loss to the nearest park office. When a livestock loss was reported, a verification team comprising the local park ranger, village headman, livestock extension officer, and claimant visited the kill-site to authenticate and assess the loss. Likewise, the same group with an agriculture extension officer substituting for the livestock extension officer verified crop losses to wild herbivores. The livestock and crop loss data were collected from January to December 2012, based on reports submitted by agro-pastoralists in the study villages. Because crop losses were hard to quantify, we recorded the frequency of crop loss incidences as a measure of crop loss to ungulates (Thinley et al., 2017). Standardized forms were developed to record and assess losses. We recorded livestock losses as the actual number of animals killed, along with ancillary data, such as location and probable date of the kill.

We documented predator occurrence using a combination of camera-traps (Reconyx™, Holmen, WI, USA), location of livestock kill sites, and sign surveys around study villages from January – December 2012. In each village, five camera-traps were positioned at randomly selected incremental distances from the croplands. Camera-traps were

concurrently deployed throughout the study period (January – December 2012), resulting in a trapping effort of 23,725 trap-nights. Camera-traps were regularly monitored by field staff; each month, batteries were replaced, data on memory cards were transferred to a laptop computer, and overhanging tree branches and leaves were removed to ensure cameras remained operational. Because local people were made aware of the significance of the study, and because park staff regularly checked cameras during monthly resource patrolling and other field activities, we did not lose any camera-trap during the study. We also surveyed human trails in the forests surrounding study villages once in each season (i.e., four times in a year) and recorded the locations of predator signs, such as tracks, scats, fresh scratch marks, and fresh scent marks. After each sign survey, tracks were covered and scats were removed from the trails to avoid double counting in the next survey season. We ensured that signs were unmistakably assigned to specific predator species. Tiger scats were differentiated from leopard scats by size and distance between constrictions; tiger scats had larger diameters with longer distance between constrictions (Wang and Macdonald, 2009a). We also ascertained a leopard track (6–8 cm length) from that of a tiger cub or a sub-adult tiger by the added presence of an adult (mother) tiger's track (8–10 cm length). Dhole scats were easily distinguishable by their size (2–3.5 cm diameter) and presence in latrines (Thinley et al., 2011).

We grouped livestock and crop losses by villages. We further segregated patterns of predator occurrence (where D = dhole, L = leopard, and T = tiger) in the village vicinity by season and village, classifying different predator combinations as dhole only (D), tiger present (DT and DLT), and tiger absent (D and DL). There were no villages where predator combinations of leopard only (L), tiger only (T), and leopard and tiger only (LT) occurred.

Predator locations in terms of distance from cropland boundaries were recorded using GPS (Garmin eTrex Vista® HCx, Olathe, KS, USA) points for all predator positive camera-traps, predator occurrence signs, and livestock kill sites, with locations assigned to the different predator combinations. We then plotted these locations in ArcGIS 10.3™ for spatial analysis.

2.3. Data analysis

To model crop and livestock losses, we first examined the data for any noticeable difference in the central tendencies of crop or livestock losses in the presence and absence of a tiger. Based on the distributions of the response variables of crop and livestock losses, we developed a generalized linear mixed model (GLMM) using a Poisson distribution and log link function (O'Hara, 2009) to assess the effects of tiger presence/absence by season. We used a Poisson model because the response variables were count data; we did not use Quasi Poisson or negative binomial regression models (Hoef and Boveng, 2007) because the mean crop and livestock losses were almost equal to their variances, and were thus not over-dispersed. Because we were interested in determining only the differences in crop and livestock losses associated with tiger presence/absence across all villages, we treated the predictor 'village' as a random-effect variable since study villages were randomly selected as a representative sample of all villages in the park. All other predictor variables were treated as having fixed effects. In selecting the most desirable model, we first ran the model containing only the main effect variables without any interaction terms (M1, Table 1). We then eliminated the main effect variable ('season' in our case) that had no significant effect on the response variables (M2, Table 1). Using the forward selection method, we progressively added the interaction term (tiger x season interaction; M3, Table 1) to the reduced model (M2, Table 1). In each step, we compared the subsequent model with the previous model using a likelihood-ratio test. We used the lowest Akaike Information Criterion (AIC) values to select the best (or parsimonious) model at each step (Wagenmakers and Farrell, 2004). All statistical operations were performed in R version 3.3.3 (R Core Team), using the

Table 1

Generalized linear mixed models using Poisson distribution for effects on crop and livestock loss^a in the presence and absence of a tiger (*Panthera tigris*) in 13 villages^b inside Jigme Dorji National Park, Bhutan.

Models with predictor variables and their coefficients (SE)	AIC	ΔAIC ^c	Likelihood ratio p-value (model pair)
(a) Effect on crop loss			
M1 2.39(0.13)Int ^{***} + 0.2(0.15)Sp + 0.12(0.15)Su + 0.04(0.15)Wi - 0.78(0.11)T ^{***}	247.2	0	Not applicable
M2^d 2.5(0.06)Int^{***} - 0.81(0.1)T^{***}	244	- 3.2	.4240 (M1 and M2)
M3 2.5(0.06)Int ^{***} - 0.97(0.16)T ^{***} + 0.42(0.24)T:Sp + 0.11(0.21)T:Su + 0.42(0.26)T:Wi	245.6	1.6	.2196 (M2 and M3)
M0 2.15(0.08)Int ^{***}	300.9	56.9	< .0001 (M2 and M0)
(b) Effect on livestock loss			
M1 0.97(0.25)Int ^{**} + 0.57(0.27)Sp [*] + 0.26(0.29)Su + 0.46(0.28)Wi - 0.69 (0.2)T ^{***}	178.9	0	Not applicable
M2 1.4(0.1)Int^{***} - 0.87(0.18)T^{***}	177.8	- 1.1	.1778 (M1 and M2)
M3 1.4(0.1)Int ^{***} - 1.21(0.3)T ^{***} + 0.63(0.44)T:Sp + 0.33(0.39)T:Su + 0.8(0.46)T:Wi	180.1	2.3	.2964 (M2 and M3)
M0 1.05(0.08)Int ^{***}	201.5	23.7	< 0.0001 (M2 and M0)

^a We used crop loss and livestock loss as the response variables for models in groups ‘a’ and ‘b’ respectively. Tiger presence (T = 1; present and T = 0; absent), and different seasons (Fa = Fall, Su = Summer, Sp = Spring, Wi = Winter) were used as fixed predictor variables.

^b We considered ‘village’ as a random predictor variable.

^c ΔAIC represents change in Akaike Information Criterion value when the predictor variables were added or removed from the model.

^d Best models are highlighted in bold. For correct interpretation of the slopes, they need to be back transformed using e^{β} , where $e = 2.71828$.

^e Significance codes can be interpreted as: *** ($p < .0001$), ** ($p < .001$), and * ($p < .01$).

packages ‘lme4’ version 1.1–12 for running GLMM and ‘lsmeans’ version 2.25 to compare mean crop and livestock losses in the presence or absence of a tiger. The significance level was determined by $p < .05$.

3. Results

3.1. Distribution of dholes and leopards relative to tiger presence and absence

We observed that predator (where D = dhole, L = leopard, and T = tiger) combinations differed spatially across the 13 study villages. Dholes occurred in all 13 villages, but *dhole only* (D) occurred in five villages and the remaining predator combinations – *tiger present* (DT and DLT), *tiger absent* (D and DL) – occurred differentially in the remaining eight villages.

Although all our three focal predators spatially overlapped in our study area, we found that dhole and leopard occurrence relative to distance from croplands was influenced by the presence or absence of tigers. For instance, when tigers were present around villages, they mostly occupied areas farther away from crop fields or village

boundaries at an average distance of $1823 \text{ m} \pm 117 \text{ m}$ (range: 900 m – 2800 m) (Fig.2). When a tiger was present in the vicinity of study villages, leopards and dholes occupied areas closer to croplands, at an average distance of $581 \text{ m} \pm 85 \text{ m}$ (range: 140 m – 1200 m) for the leopard and $635 \text{ m} \pm 32 \text{ m}$ (range: 332 m – 1020 m) for the dhole, from the crop field edge (Fig. 2). Contrastingly, when a tiger was not present in the vicinity, leopards ($1982 \text{ m} \pm 209 \text{ m}$; range: 1000 m – 3500 m) and dholes ($2047 \text{ m} \pm 254 \text{ m}$; range: 980 m – 3680 m) occupied forests farther away from croplands (Fig. 2).

3.2. Crop and livestock losses associated with a tiger's presence and absence

In the presence of a tiger across all seasons, frequency of crop loss was reduced by a magnitude of 2.25, which is based on the significant regression coefficient ($\beta = -2.25, p < .0001$) for the best model (back transformed from Table 1(a), Model 2). This shows that when tigers were present along with dholes and leopards, the frequency of crop loss was lower than when tigers were absent. Livestock loss measured as the number of animals lost (Table 1(b), Model 2), was also significantly reduced in the presence of a tiger ($\beta = -2.39, p < .0001$).

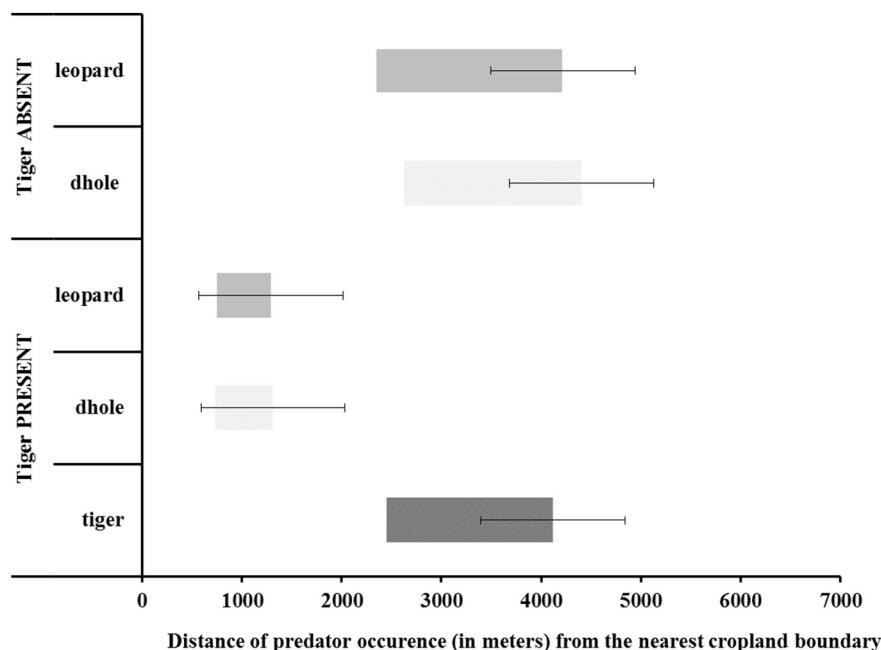


Fig. 2. Occurrence of dholes and leopards from the nearest cropland boundary in the presence and absence of a tiger around 13 villages inside Bhutan's Jigme Dorji National Park (JDNP) from January to December 2013. Boxes are based on medians (50th percentile) and whiskers are the error bars.

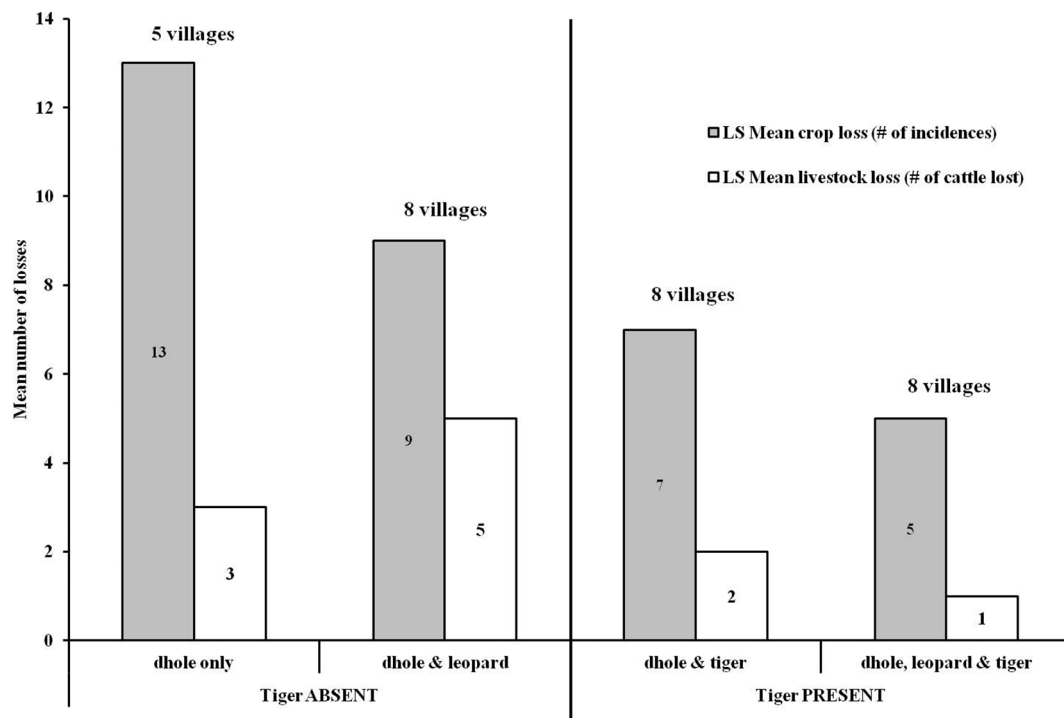


Fig. 3. Observed differences in least square mean incidences of crop losses and number of livestock losses (computed after *post-hoc* analysis on the best models in Table 1) associated with the presence or absence of a tiger around 13 villages inside Bhutan's Jigme Dorji National Park from January to December 2013. Gray and white bars represent mean incidences of crop loss and mean number of livestock losses, respectively. The number of villages in which the predator combinations occurred is shown above the bars.

Post-hoc analyses using pair-wise comparison of least square means yielded a significant difference in mean livestock losses (Fig. 3) between tiger absent and tiger present (z ratio = 5.0771, $p < .0001$).

4. Discussion

We are aware that predator density and abundance play significant roles in the reduction of prey populations, and subsequently on crop losses. This could also influence livestock depredation. However, limited by time and resources, we could not quantify the abundance of tigers and leopards near each study village. Moreover, camera-trap images in some villages were not adequate to allow the identification of specific individuals. Nevertheless, analysis of camera-trap images in a different study (Thinley et al., 2015a) yielded seven individual tigers and three leopards in our study area. Counting the number of scats per latrine, we found that pack size of dholes ranged from three to 12 in our study area, which is consistent with our previous findings for some villages in the study area (Thinley et al., 2011). We recommend that in the future studies, the quantitative relationship between predator density and crop or livestock damages should be evaluated.

We are also conscious about the difficulties in disentangling correlation from causation in this type of observational study (Jaffee et al., 2012). However, we were highly certain that the observed patterns of dhole and leopard distribution were due to tiger presence or absence, not because of other confounding factors such as hunting pressure and retaliatory killing. Hunting or killing of any animal is prohibited by the Forest and Nature Conservation Act of Bhutan 1995, which is strictly enforced by park staff. During our study, we did not record any case of hunting or poisoning of predators in our study area. Farmers in our study area tolerate livestock losses to predators, largely influenced by Buddhist sentiments and also by the huge penalties associated with killing of tigers. Moreover, almost all livestock herders in the study area received cash compensation from the government for livestock losses (Tshering and Thinley, 2017).

Tigers, leopards, and dholes are sympatric across much of their

distributional range (Selvan et al., 2013). They spatially overlapped in our study area similar to observations by Karanth and Sunquist (2000) in India's Nagarhole National Park and more recently in Thailand's Kuiburi National Park (Steinmetz et al., 2013). Dholes are the most widely distributed among the three predators in JDNP (Thinley et al., 2015b) which is corroborated by their presence in all villages in our study area. However, our spatial pattern of tiger occurrence concurs with the finding from Nepal's Chitwan National Park (Carter et al., 2012) where tigers were detected in areas farther away from human settlements. This is because tigers are generally found to occupy areas with lower human disturbance (Karanth and Stith, 1999). Furthermore, a camera-trap study in Bhutan's Jigme Singye Wangchuck National Park by Wang and Macdonald (2009b) also found that tigers occupied areas farther away from human settlements, while leopards occurred closer to human settlements.

Although it appears that tigers and leopards are sympatric at the landscape scale, we found them to be spatially segregated at finer scales in our study area. Similar to our spatial pattern reported here, leopards avoided areas frequented by tigers in Nepal's Chitwan National Park (Seidensticker, 1976). Additionally, Odden et al. (2010) found significantly higher leopard sign near the periphery of a tiger's home range in Nepal's Bardia National Park, rather than closer to the tiger's core area. We postulate that the spatial segregation between tigers and leopards is a consequence of ecological dominance displayed by tigers (Morse, 1974; Steinmetz et al., 2013). Furthermore, none of the camera-traps photographed all predators at the same location, on the same day, or during the same two-week sampling occasion, providing further support for these predators being allopatric at finer spatial scales.

Tiger influence on reduced crop loss frequency can be attributed to their displacement of leopards and dholes from deep forests to areas closer to cropland boundaries where they preyed on crop raiders such as wild pig (*Sus scrofa*), sambar (*Rusa unicolor*), and muntjac (*Muntiacus muntjac*) which were found in high relative abundance (Thinley et al., 2017). Steinmetz et al. (2013) similarly recorded leopards and dholes

avoiding tigers and favoring areas with higher prey availability in Thailand's Kuiburi National Park.

It is a common herding practice to graze livestock unattended in forests near villages in Bhutan (Rajaratnam et al., 2016; Tshering and Thinley, 2017). In the absence of a tiger in the vicinity, leopards and dholes occupied areas farther away from cropland boundaries where they heavily preyed on untended livestock (Tshering and Thinley, 2017). Although tigers do occasionally attack livestock (Sangay and Vernes, 2008; Rajaratnam et al., 2016), leopards and dholes are known to be principal predators of livestock, especially domestic cattle (Sangay and Vernes, 2008; Thinley et al., 2011). As such, the severity and frequency of livestock losses to predation in the forests is reduced in presence of a tiger in the vicinity because leopards and dholes were displaced much closer to cropland boundaries where relative livestock abundance is lower (Thinley et al., 2017). In contrast to our finding and based on scat analysis, Wang and Macdonald (2009a) reported that livestock comprised 44.5% of tiger diet in comparison to 73.4% and 15.9% of leopard and dhole diet, respectively. Their result indicates that tigers prey on livestock approximately three times higher than dholes. However, their study is not comparable with our study because it did not investigate the spatial interaction between tigers, leopards, and dholes, and the spatial distribution of livestock and natural prey relative to distance from human settlements. Additionally, our study did not analyze the relative diets of these predators. As such, we could not directly equate the presence or absence of tigers, leopards, and dholes in the environs of our study villages with the propensity for livestock predation revealed through dietary analysis. We instead based our livestock losses from reports submitted by agro-pastoralists, with livestock losses further segregated by the presence or absence of a tiger in the village environs. Furthermore, our study was closely aligned with a wild ungulate study (Thinley et al., 2017) which reported a higher relative abundance of wild ungulates near croplands compared to areas farther away in deep forest. In essence, we point to the increased predation of livestock by dhole and leopard in the absence of a tiger within the vicinity of a village.

The “green world hypothesis” proposed by Hairston et al. (1960), which states that presence of a predator leads to reduction in the population of prey, thereby resulting in flourishing of a plant community, needs to be re-examined in the context of human-dominated landscapes, where livestock are preyed by tigers, leopards, and dholes (Sangay and Vernes, 2008; Wang and Macdonald, 2009a). Based on our results, we posit that the hypothesis is applicable to agricultural ecosystems, but the mere presence of a single predator species does not necessarily imply lower crop and livestock damage. Rather, when an apex predator, such as the tiger, is present along with other predators, such as dholes and leopards, there may be cascading effects that may lead to a reduction in livestock predation and agricultural crop loss.

Our research finding potentially translates into substantial annual economic benefits for Bhutanese agro-pastoralists. Using our best model (Table 1(a), Model 2), we calculated a magnitude of 2.25 times reduction in crop loss frequency per farm household per year, in the presence of a tiger. In monetary terms, this is equivalent to saving US \$450, based on an average income loss of US \$200 per incidence of crop loss, as documented in Jigme Dorji National Park (Leki, Park Ranger, pers. comm). Similarly, based on the model developed for livestock loss (Table 1(b), Model 2), the number of livestock lost would be reduced by 2.4 animals per farm household per year in the presence of a tiger. This reduction translates to a savings of approximately US \$1120, using an average loss of US \$500 for each head of livestock (including horse and cattle) lost. Thus, the total potential savings in the presence of a tiger influencing the spatial distribution of leopards and dholes approximately equates to US \$1570 annually for an agro-pastoralist in JDNP. This represents a very substantial rural household saving in Bhutan which is 70% of the average per capita income of US \$2230, based on a 2014 gross national income and population estimate (NSB (National Statistics Bureau), 2015).

5. Implications for conservation of large apex predators

Our study benefits global conservation and supports the recovery of large apex predators, because it highlights a tangible ecological service by an apex predator such as the tiger to rural farmers through minimizing crop and livestock loss. It further elucidates the beneficial effects from ecological interactions among a predator guild composed of a large apex predator and two mid-sized predators. Our study is timely, because many apex predators are endangered in the face of increasing negative interactions with humans (Stier et al., 2016). It is especially relevant at the current tiger conservation crossroad where tiger scientists, conservation donors, and leaders of the tiger range countries commit to doubling tiger numbers (Wikramanayake et al., 2011) amidst subsequent suspicions as to whether such a measure would be compatible with humans, particularly those who live close to tiger habitats. Conservation practitioners can use our significant finding to educate and dissuade rural farmers in developing countries from retaliating against apex predators, such as the tiger, in the event of livestock depredation. We also posit that justifications for large predator conservation based on their iconic status is not persuasive to rural farmers residing close to their habitat and suffering crop and livestock loss. There is a need to determine ecological services from apex predators to farmers which may dissuade them from retaliatory killings. We recommend that conservation practitioners promote and conserve wide-ranging apex predators to maintain optimal inter-specific interactions in a large predator guild which can benefit rural socio-economy. Conservation efforts must focus on adequate habitat protection, rigorous anti-poaching activities, education programs to agro-pastoralists, better livestock husbandry practices (Tshering and Thinley, 2017) and livestock compensation and or insurance schemes (Rajaratnam et al., 2016).

6. Conclusion

Large apex predators such as the tiger are declining within their geographical range. Justifications for their conservation based on their iconic status is not a persuasive argument with rural farmers living close to tiger habitat and suffering frequent crop and livestock loss from wildlife. There is, therefore, a strong need to determine whether apex predators provide any ecological services to farmers, which in turn, may dissuade them from retaliatory killings. We found that areas with tigers experienced significantly fewer incidences of crop and livestock losses compared to those without tigers. The complex interactions between tigers, sympatric mid-sized carnivores, and wild herbivores potentially reduce crop and livestock losses. As such, conserving a full predator guild maximizes socio-economic benefits to agro-pastoralists.

Acknowledgements

This study was conducted as part of the management zoning for Jigme Dorji National Park. We thank Bhutan Government's Department of Forests and Park Services for providing funding and administrative support. We remain immensely grateful to the dedicated park staff for their unwavering support and cooperation in data collection of such a magnitude. We thank the anonymous reviewers for their thorough reviews and comments.

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