



# Unraveling the complexity of human–tiger conflicts in the Leuser Ecosystem, Sumatra

M. I. Lubis<sup>1,2</sup> , W. Pusparini<sup>1,4</sup>, S. A. Prabowo<sup>3</sup>, W. Marthy<sup>1</sup>, Tarmizi<sup>1</sup>, N. Andayani<sup>1</sup> & M. Linkie<sup>1</sup> 

1 Wildlife Conservation Society, Indonesia Program, Bogor, Indonesia

2 Asian School of the Environment, Nanyang Technological University, Singapore, Singapore

3 Natural Resource Conservation Agencies (BKSDA), Banda Aceh, Aceh Province, Indonesia

4 Wildlife Conservation Research Unit and Interdisciplinary Center for Conservation Science (ICCS), Department of Zoology, University of Oxford, Oxford, UK

## Keywords

human–tiger conflict; large carnivore; livestock; *Panthera*; poaching; research–implementation gap; retaliatory killing.

## Correspondence

Muhammad I. Lubis, Asian School of the Environment, Nanyang Technological University, Singapore.

Email: muhammad439@e.ntu.edu.sg

Editor: Julie Young

Associate Editor: Zhongqiu Li

Received 23 August 2019; accepted 18 March 2020

doi:10.1111/acv.12591

## Abstract

Conserving large carnivores that live in close proximity to people depends on a variety of socio-economic, political and biological factors. These include local tolerance toward potentially dangerous animals, efficacy of human–carnivore conflict mitigation schemes, and identifying and then addressing the underlying causes of conflict. The Leuser Ecosystem is the largest contiguous forest habitat for the critically endangered Sumatran tiger. Its extensive forest edge is abutted by farming communities and we predict that spatial variation in human–tiger conflict (HTC) would be a function of habitat conversion, livestock abundance, and poaching of tiger and its wild prey. To investigate which of these potential drivers of conflict, as well as other biophysical factors, best explain the observed patterns, we used resource selection function (RSF) technique to develop a predictive spatially explicit model of HTC. From 148 conflict incidences recorded from 2008 to 2018 across the Leuser Ecosystem, the areas that were closer to villages and with lower occurrence of wild prey were most susceptible to tiger attacks. From 18 districts monitored, 6 stood out for having disproportionately high levels of HTC. We recommend that these areas be prioritized with increased support from conflict mitigation teams to prevent further injuries to people, livestock or tigers; district governments address one underlying cause of HTC by supporting improved animal husbandry practices, such as tiger-proof livestock pen construction; and, an increase in ranger patrol effort to recover wild prey populations. This type of priority setting approach has wide application for better determining the required management response to reduce conflicts between people and large carnivores in both tropical and temporal landscapes.

## Introduction

Large carnivores are in trouble across most of their global range (Ripple *et al.*, 2014). They are often persecuted in retaliation to attacks on people or their livestock, or because of a perceived threat from their presence (St. John *et al.*, 2018). Many of these carnivore species are also in demand to supply the illegal wildlife trade and such conflict situations are often exploited by wildlife traffickers seeking to precipitate their capture (Linkie *et al.*, 2018).

The severity of human–carnivore conflict tends to be positively and significantly correlated with species body mass (Inskip & Zimmermann, 2009), which partly justifies the research bias toward large carnivores (Lozano *et al.*, 2019).

The underlying causes of conflict occurrence, such as increasing scales of habitat loss and livestock grazing, add to this complexity but require locally appropriate, targeted and practical solutions (Knight *et al.*, 2008; Dickman *et al.*, 2014). All this is highly relevant to the critically endangered Sumatran tiger *Panthera tigris sumatrae*.

Sumatra is the sixth largest island in the world. Its rain-forest tigers, a unique subspecies, were once widespread across the island until two major interlinked waves of deforestation occurred. Decentralization of power in the natural resource sector from the national government to provincial governments in 1998 resulted in rampant illegal logging of tropical hardwood trees (McCarthy, 2000). This was closely followed by large-scale expansion of oil palm and acacia

plantations and smallholder cash crop farms, especially in areas that had been previously degraded by illegal logging and were outside of the protected area network (Gaveau *et al.*, 2009). This forest fragmentation and loss also brought tigers and people into closer contact, although this situation would also apply to jaguar *Panthera onca*, leopard *Panthera pardus* and other carnivore species (Michalski *et al.*, 2006; Dar *et al.*, 2009).

Previous analyses of human–tiger conflict (HTC) in Sumatra, which have been based on the compilation of unpublished reports, reveal two salient points (Nyhus & Tilson, 2004; Kartika, 2017). First, they reflect an uneven monitoring effort among provinces, which suggests that an unknown number of HTC events go unreported. This would further suggest that the actual loss of tigers is higher than the reported 8–18 individuals/year from 1978 to 2016. Second, while the loss of tigers over the past decades may seem low, for a highly threatened animal that numbers around 500 individuals, this loss is disproportionately high especially when considering its fragmented population distribution and variable viability (Pusparini *et al.*, 2017). These circumstances stress the importance of using a science-based approach to understand the site-based occurrence and causes of HTC so that appropriate responses are made where they are most needed.

In this study, we use a decade of HTC field data that has been systematically collected from the Leuser Ecosystem, a global priority for the long-term survival of tigers (Walston *et al.*, 2010). We aim to identify the drivers of HTC by developing a spatially explicit model to test four hypotheses that may, individually or in combination, explain the occurrence of conflict: (1) lack of wild prey causes tigers to attack livestock; (2) abundance of unprotected livestock increases tiger attacks; (3) villages are more susceptible to tiger encounters and tiger attacks; and (4) deforestation leading to farmland encroachment and habitat fragmentation increases tiger encounters and conflict with people and livestock. We use these results to make management recommendations to mitigate future conflicts, describe how these recommendations have subsequently been implemented on the ground and discuss the wider applicability of our methodological approach for understanding the drivers of conflict for other threatened carnivore species.

## Materials and methods

### Study area

The 25 000-km<sup>2</sup> forested Leuser Ecosystem spans the provinces of Aceh and North Sumatra and includes the 8282-km<sup>2</sup> Gunung Leuser National Park. Besides tigers, it is also home to Sumatran rhino *Dicerorhinus sumatrensis*, Sumatran orangutan *Pongo abelii* and Asian elephant *Elephas maximus*. Wild boar *Sus scrofa* and sambar *Rusa unicolor* constitute the principal Sumatran tiger prey. The Leuser Ecosystem ranges from carbon-rich deep peat swamp lying at sea level in the west through the main Sumatran rainforest types of lowland, hill, submontane and montane, up to the

peak of Mount Leuser which is 3466 m above sea level. This wide expanse and high elevation covers 37 watershed forest areas (MoEF, 2019) that provide essential ecosystem services to around 6–7 million people (BPS Aceh, 2018; BPS North Sumatra, 2018) situated on the flatter terrain located in the lowlands (Beukering *et al.*, 2009). These communities typically grow coffee, rice and other cash crops as their main source of income, and some keep a small number of livestock, but this is either for their own consumption or for cash. Livestock are generally available all year round where they are typically left to graze in the open, including near the forest edge. Buffalos are usually on a long leash, whereas goats roam free or are put in feeding pens when they need to be fattened before sale. In the northeastern area, industrial oil palm plantations and dryland agriculture are a common feature and a source of encroachment into the forest (Lubis *et al.*, 2019).

### Data collection

HTC data were collected by five Wildlife Response Unit (WRU) teams (Fig. 3) which responded to community and government reports of human–wildlife conflict. Team composition included personnel from Wildlife Conservation Society (WCS), local government, local NGO and local communities. The teams were placed to provide complete coverage across the Leuser Ecosystem whilst being in close proximity to the districts with a history of conflict. Travel times to conflict sites took from 1 to 6 hours by car or motorbike.

A widespread community informant network reported HTC incidents by phone directly from the affected village. The informants are varied; the majority are village head, local government staff, local NGO staff or villagers who live in the affected communities. Since 2008, the mitigation teams have been frequently visiting villages around the forest edge, particularly those located in the HTC hotspot areas, to prepare the village leaders and local communities in how to respond and to report HTC when it occurs in their village. However, for very remote villages, informants might need to travel for up to an hour to obtain phone coverage to report an incident. The fuel cost and phone credit used by these informants is reimbursed by the team. Upon receiving a report, the team would visit the site to verify where the conflict incident had occurred, including looking for evidence of tiger presence (pugmarks, scats and injured livestock of carcasses). This would determine the subsequent response, such as monitoring the forest boundary for 1–2 weeks, educating local communities about better animal husbandry practices and/or repelling or removing the tiger from the wild.

The types of HTC include tiger attacks on people, livestock attacked, tigers injured or killed by people and tigers approaching farmland or settlements, which can generate fear within the community who subsequently call for the tiger to be repelled or removed. From 2008 to 2018, the mitigation teams received and responded to 206 HTC reports. Of these, 58 reports were removed from our analysis because they lacked sufficient evidence to demonstrate that a HTC incident had occurred, that is, the information was outdated,

there were no signs of conflict having occurred or the information was inaccurate. To investigate the drivers of HTC, all conflict types ( $n = 148$ ) were combined into one dataset and were used to model the conflict incidents in the Leuser Ecosystem.

### Spatial covariates

We constructed a wild prey distribution model to use as a covariate in the HTC model. Combined data for sambar and wild boar, collected from the Sumatra-wide survey conducted from 2007 to 2009 (Wibisono *et al.*, 2011), were used. Within 1x1 km sampling units, the detection (1) or non-detection (0) of prey were recorded along 100 m segments (spatial replicates), adjusted for topography using a GIS (ArcMap v10.4.1), to create detection histories.

Data were analyzed as a single species (wild prey), single season occupancy model (MacKenzie *et al.*, 2002) using RPresence package in R (R Core Team, 2017). We modelled detection probability, as well as the probability of occupancy with the inclusion of the following covariates: elevation; Terrain Ruggedness Index; distance from forest edge in 2009; distance from river; Normalized Difference Vegetation Indices (NDVI); and proportion of forest (Table S1). All covariates were standardized using a Z transformation. We then created a spatially explicit map of wild prey occurrence using the most parsimonious model that is the model with as few predictor variables as possible (see supplementary materials).

To predict HTC patterns, the wild prey probability of occurrence layer resulted from a separate analysis and was tested with distance from recent deforestation, village livestock density and distance from village. The minimum distance from recent deforestation was calculated based on deforested areas (forest in 2000 that had been converted into non-forest areas by 2017; MoEF, 2018). We only selected deforested areas larger than 100 ha and calculated the minimum distance using the Euclidean Distance tool in ArcMap 10.4. Minimum distance from village was calculated using point locations of settlement data (Indonesia Geospatial Agency, 2017). Predicted livestock densities (heads/km<sup>2</sup>) combined for cow, buffalo, goat, sheep and pig were taken from Robinson *et al.* (2014). The continuous covariates were also standardized and resampled to a 1-km spatial resolution (Table S1; Fig. S1).

### Data analysis

Collinearity between the independent variables was tested using a Pearson's correlation test, with a threshold coefficient of  $\pm 0.5$  (Tables S2 & S4), so that no model combinations included correlated variables. We also used a variable inflation factor (VIF) to test for multicollinearity using a threshold of three. We used an RSF technique to determine the HTC correlates (Boyce *et al.*, 2002) by first using a generalized linear model (GLM) to characterize HTC presence and pseudo-absence (i.e. from suitable to unsuitable habitats for tiger). The available data points were drawn

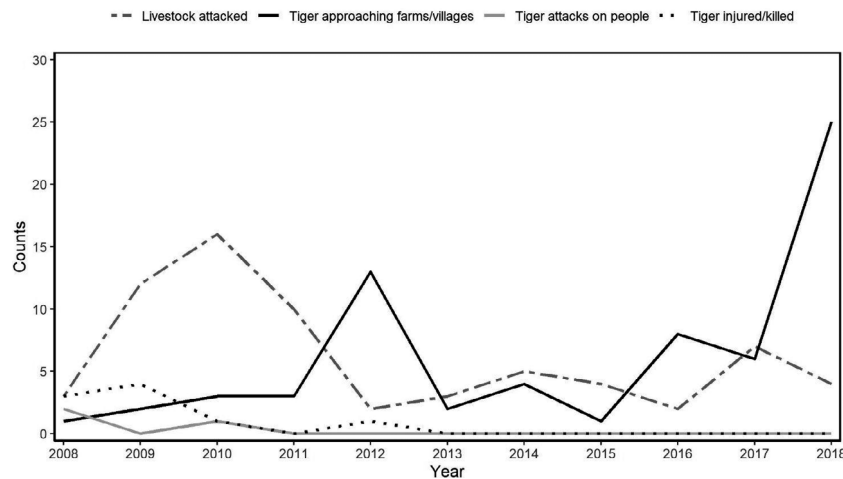
from the distribution of used HTC locations. Around each HTC location, we randomly selected five available points within a 17-km buffer – the putative home range size of an adult male Sumatran tiger (Wibisono *et al.*, 2011). There were 740 available points to compare with the 148 HTC points from 2008 to 2018 which were used to develop the models.

We used fivefold cross-validation technique to train and assess model performance by separating data into training and testing sets as suggested by Boyce *et al.* (2002). The training set (a random selection of 80% of the data) was used to train the model and create its spatial prediction while the testing set (a random selection of 20% of the data) was used to evaluate the performance of the models produced by the training dataset. We developed five candidate models based on our initial hypothesis and performed a GLM analysis and assessed model parsimony using the AIC corrected for small sample sizes (AICc) using the full dataset. The spatial predictions were constructed for each fold of the data using the raster package (Hijmans & van Etten, 2013) in R (R Core Team, 2017) and then classified into 10 equal areas based on quartile ranges. The Spearman-rank correlation between area-adjusted frequency of cross validation points within individual bins and the RSF bin rank was calculated. A model with good predictive performance will have strong positive correlation that is close to 1.0. Finally, we created the spatially predictive RSF model from the top ranked model using the full dataset (HTC 2008–2018) and classified this into 10 equal areas/bins, similar to the previous approach.

### Results

From 2008 to 2018, the conflict mitigation teams responded to 148 reported cases of HTC ( $13.4 \pm 7.2$  annually). Conflict frequency underwent annual fluctuations with the highest number of cases occurring in 2018 and the lowest in 2013 and 2015 (Fig. 1). The main conflict types were tiger approaching a farm or village (45.9%), livestock attacked (45.9%) and tiger injured or killed (6.1%). Tiger attacks on people were uncommon ( $n = 3$ ; 2.0%) and only occurred in Aceh Selatan district where one person was injured and two died. Ten problem tigers were killed in retaliation outside of the forest over the study period, with the last recorded case being in 2010 from the districts of Aceh Selatan. There were 68 incidents of livestock attacks on 156 animals, consisting of 91 goats, 19 cows, 30 buffaloes, 14 dogs and 2 domestic pigs, which peaked in 2010 and decreased steadily thereafter (Fig. 1).

HTC occurred in 12 of the 18 districts monitored, including 47 subdistricts and 84 villages. Aceh Selatan district was noteworthy for having a disproportionately high number of incidents (47.9%), followed by Gayo Lues (8.1%), Langkat (7.4%), Subulussalam (7.4%), Aceh Tenggara (6.7%) and the remaining 7 districts with <6% each. In Aceh Selatan, conflicts occurred in 29 villages, with the highest frequency of conflicts occurring in Panton Luas (18 incidents) and Jambo Papeun (14).



**Figure 1** Annual patterns of reported human–tiger conflict types in the Leuser Ecosystem.

The 148 conflict incidents recorded from 2008 to 2018 were used to model HTC and from the top three ranked models, the highest covariate summed model weights were: distance to village (100%), wild prey occupancy (100%), livestock density (39%) and distance from recent deforestation (11%; Table 1). HTC was most likely to occur in areas closer to villages and with lower wild prey occupancy, with a smaller influence from having a higher livestock density and then from being closer to recent deforestation (Fig. 2).

There was little variability in the strength and significance of HTC and its environmental variables coefficients between full data and each fold of data indicated that distance from villages and prey occupancy are good predictors of HTC in this tiger landscape (Table S5). The Spearman-rank correlation values were high (mean  $Rho > 0.85$ ) for the top ranked model, which suggests that there was a strong association between RSF bin ranks from the spatial predictive layers with the HTC data from the test sets. The spatial predictive surface resulting from the top ranked RSF model (Fig. 3) indicated that HTCs were distributed at the edge of the Leuser Ecosystem where villages are more highly concentrated.

## Discussion

Our study provides the first reliable rates of HTC across the Leuser Ecosystem. These rates were lower than might be expected for one of the largest tiger landscapes in Southeast Asia yet they were widespread, reflecting the wide occurrence of tigers (Wibisono *et al.*, 2011). The spatial patterns of HTC were disproportionately higher in six districts (Aceh Selatan, Aceh Tenggara, Subulussalam, Aceh Singkil, Gayo Lues and Langkat) and primarily explained by two of our four hypothesized parameters, namely closer proximity to villages and lower wild prey occupancy, with a small effect from livestock density. Distance to recent deforestation had little influence on the likelihood of HTC in our study area, but we stress that habitat loss remains a serious threat to tiger population viability in Sumatra and the pernicious nature of this threat is seen for other critically endangered wildlife in the Leuser Ecosystem (Linkie *et al.*, 2006). For example, in the north-eastern section of the ecosystem large-scale conversion of forest to oil palm plantations has resulted in the death of at least 10 Sumatran elephants over the past four years (2014–2017; WCS, 2018).

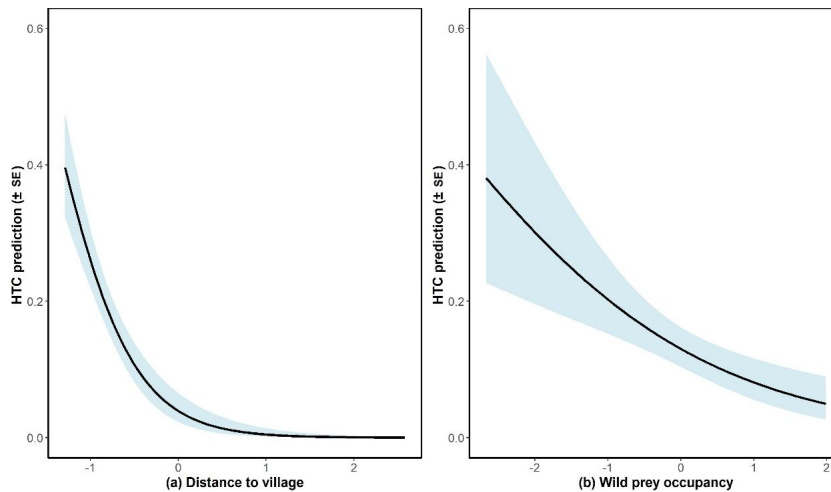
**Table 1** Resource Selection Function models for human-tiger conflict in the Leuser Ecosystem

Model	Variable/ $\beta$ (SE), $p$ -value				Mean rho	AICc	$\Delta$ AICc	$w_i$
	Dist. village	Prey occupancy	Livestock	Dist. deforestation				
Model 1	−2.15 (0.29)***	−0.53 (0.12)***	—	—	0.86	619.29	0.00	0.61
Model 2	−2.14 (0.29)***	−0.52 (0.14)***	0.07 (0.1) <sup>a</sup>	—	0.84	620.86	1.57	0.28
Model 3	−2.14 (0.30)***	−0.51 (0.14)***	0.07 (0.1) <sup>a</sup>	−0.04 (0.15) <sup>a</sup>	0.84	622.81	3.51	0.11
Model 4	−2.56 (0.30)***	—	0.12 (0.1) <sup>a</sup>	—	0.84	633.35	14.05	0.00
Model 5	−2.58 (0.29)***	—	—	−0.03 (0.14) <sup>a</sup>	0.83	634.67	15.38	0.00

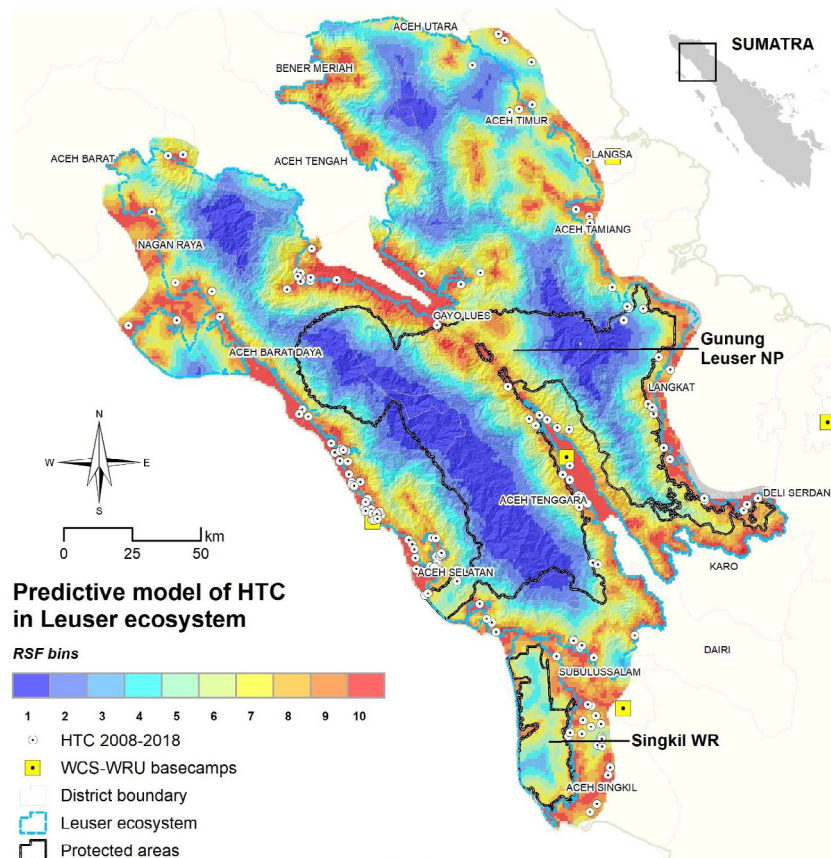
Mean rho: Cross-validated Spearman-rank correlation between RSF bin ranks and area-adjusted frequencies over 5 Cross-Validation folds. Robust standard errors in parentheses.

<sup>a</sup>Non-significant.

\*\*\*Significant at  $< 0.01$ .



**Figure 2** Relationship between predicted human–tiger conflict (HTC) and the two key predictors of (a) distance to village and (b) wild prey occupancy from the top ranked HTC model.



**Figure 3** The spatial prediction of human–tiger conflict (HTC) in the Leuser Ecosystem using the top-ranked resource selection function model for field data from 2008 to 2018. The map was classified into 10 equal areas (bins) which was used to test the predictive accuracy of the model, and higher bin ranks denote a higher probability of HTC occurrence.

Our community-based reporting system and the frequent visits by the conflict mitigation teams to forest-edge communities give confidence that HTC was systematically

monitored and reported across the entire Leuser Ecosystem. Temporal patterns of HTC fluctuated, but the general trend after 2012 was a declining rate of attacks on livestock and

people, which for the latter has been zero for the past 9 years. This may subsequently explain why no problem tigers have been killed in retaliation since 2012, especially as large carnivore attacks on people are likely to be fatal and evoke calls for the capture of the culprit animal (Marchini & Macdonald, 2012). We cannot completely rule out that there was no retaliatory killing of problem tigers in our study area because it is an illegal action, which removes the incentive to report it as shown for lions (*Panthera leo*) and spotted hyenas (*Crocuta crocuta*) in Tanzania (Dickman *et al.*, 2014). Nevertheless, WCS also operates a community informant network across the entire Leuser Ecosystem and it detected no such retaliatory killings, which gives a greater confidence that this was not the case.

From our study, the 2017 upturn in livestock attacks is curious and difficult to explain but may relate to an increase in wild prey snare traps set near villages, as recorded by ranger patrols conducted from 2014–2017 (WCS, 2019). Lower availability of wild prey was an important determinant of increased HTC in our study. Across Sumatra, local people typically not only use snares as a control measure for crop-raiding animals, such as wild boar, but also to sell their meat for domestic consumption (Luskin *et al.*, 2014). Similarly, overhunting of wild ungulates by people was found to be the single greatest predictor of Persian leopard *Panthera pardus saxicolor* and grey wolf *Canis lupus* attacks on livestock in Iran (Soofi *et al.*, 2019). More broadly, over-hunting of wild tiger prey is predicted to increase the likelihood of tigers supplementing their diet with livestock. In the Russian Far East, most attacks on livestock occur in the winter, when harsh weather physically stressed Amur tigers (Goodrich *et al.*, 2011).

Numerous studies have highlighted the disconnect between research and action, known as the ‘research-implementation gap’ (Knight *et al.*, 2008). This also applies to addressing human-carnivore conflicts (Gray *et al.*, 2019). Here, we make three key management recommendations based on the main findings from our study and describe how they are being implemented by NGO-government-community partners in the field.

First, the conflict mitigation teams should increase their support to conflict prone districts (Aceh Selatan, Aceh Tenggara, Gayo Lues, Subulussalam, Aceh Singkil and Langkat) to prevent further injuries to people, livestock and tigers, especially in light of the overall increase in HTC recorded since 2013. From our experience, having greater presence in affected villages builds trust and provides clear channels of communication so that conflict situations can be quickly addressed, preventing escalation and retaliation. The presence of response teams also prevents opportunistic poachers from taking advantage of such situations by offering to capture the real or perceived problem tiger. There may also be social costs associated with conflict as found in central Sumatra, where several ethnic groups believe that tigers act as a village guardian and punish those who transgress a moral code, thereby stigmatizing the victim (Mckay *et al.*, 2018). This may provide a novel way to mitigate HTC.

Second, local governments responsible for the at-risk districts identified in our study could reduce HTC rates by improving animal husbandry practices. This could include allocating government financed village funds to establish community HTC mitigation teams or support the construction of tiger-proof livestock pens, a successful initiative started by WCS in 2008 (WCS, 2018). It would also be useful to quantify what the loss of livestock represents to a rural household. For example, studies have shown that even relatively small losses from snow leopard in Nepal and grey wolf in India can represent a significant loss of household income and result in retribution killings (Dickman *et al.*, 2011).

Support from the village fund scheme in Indonesia could be extended further though local governments rewarding villages practicing these better husbandry techniques with veterinary care for their livestock in the form of disease prevention, which is responsible for a greater loss of livestock than tiger attacks. In the neighboring forests in Aceh province, vaccination of >3000 goats and buffaloes directly addressed a critical and unmet need of rural communities and generated substantial local support for wildlife conservation activities thereafter (FFI, 2014). Conversely, rural communities dissatisfied with veterinary services in Iran suffered higher livestock losses to leopard, suggesting that unvaccinated animals were weaker and therefore more susceptible to attacks (Khorozyan *et al.*, 2015).

Our final recommendation is to recover the wild prey base in forest patches that have low (<0.5) occupancy because such areas are likely to incur increased HTC rates. This approach offers an additional benefit because prey recovery is also a principal driver of tiger population recovery (Karanth *et al.*, 2004). The protection afforded to tigers and their prey has been strengthened with an increase in the number of government–community–NGO ranger teams from 13 to 22 units and a corresponding increase in patrol effort from 2 455 km/year (2014) to 6 773 km/year (2018). The patrol teams have been effectively distributed based on areas identified as hotspot of illegal activities that are usually located in the border areas of Gunung Leuser NP, which were associated with the HTC hotspots found in this study (WCS, 2019; Fig. 3). To sharpen the law enforcement response, all patrol data are stored and analyzed within a single adaptive management system (System Monitoring and Reporting Tool – SMART) that is now being used to strategically guide patrolling. Integrating HTC data with patrol data should help to better define the link between better patrol effort, prey recovery and reduced HTC rates. Clearly, such an approach will help better protect other carnivore species that are at risk of poaching, especially potential conflict species that are also in demand for the illegal wildlife trade, such as jaguar (Fraser, 2018).

## Conclusion

In protected area landscapes with strong law enforcement, such as Bukit Barisan Selatan National Park, recovering tiger populations are recolonizing parts of their former range and

this is also predicted to increase HTC (Pusparini *et al.*, 2017). Under such a scenario, HTC mitigation teams will form an essential part of the solution, especially in empowering communities to better respond to conflicts. These teams also bring benefit to other wildlife, such as elephants, and the spatially explicit modeling approach developed in our study should be applied to other threatened species to better understand the drivers of conflict so as to direct conservation investments. The predictive modeling used in our study could be used to map the recovery of large carnivore species across large forested landscapes, aid in identifying critical forest corridors for restoration, and target the areas where livestock protection is most needed (Harihar & Pandav, 2012; van Eeden *et al.*, 2018). Finally, the tolerance of people who live close to large carnivores has been shown to be driven by a complex number of interacting factors that include spirituality, tolerance, perceived risk of attack, as well as susceptibility to attack (Struebig *et al.*, 2018; McKay *et al.*, 2018). Thus, future work should also focus on integrating social data within the predictive modeling to enable a more nuanced approach giving it a greater utility (Beck *et al.*, 2019).

## Acknowledgements

WCS is grateful to the Indonesian Ministry of Environment and Forestry for permission to conduct the human–wildlife conflict mitigation work. We thank the U.S. Fish & Wildlife Service, Liz Claiborne and Art Ortenberg Foundation, Panthera, Fondation Segré, UNDP/GEF, IUCN/KfW, Disney Conservation Fund and USAID LESTARI for supporting this work. We thank Dale Miquelle and Janice Ser Huay Lee for commenting on the manuscript.

## References

- Beck, J.M., Lopez, M.C., Mudumba, T. & Montgomery, R.A. (2019). Improving human–lion conflict research through interdisciplinarity. *Front Ecol Evol* **7**, 1–8.
- van Beukering, P., Grogan, K., Hansforth, S.L. & Seager, D. (2009). *An economic valuation of Aceh's forests: the road towards sustainable development* Amsterdam: Institute for Environmental Studies, 44.
- van Eeden, L.M., Eklund, A., Miller, J.R.B., López-Bao, J.V., Chapron, G., Cejtín, M.R., Crowther, M.S., Dickman, C.R., Frank, J., Krofel, M. & Macdonald, D.W. (2018). Carnivore conservation needs evidence-based livestock protection. *PLoS Biol.* **16**, 1–8.
- Boyce, M.S., Vernier, P.R., Nielsen, S.E. & Schmiegelow, F.K.A. (2002). Evaluating resource selection functions. *Ecol. Model.* **157**, 281–300.
- BPS Aceh. (2018). Aceh in Figures 2018. Badan Pusat Statistik Provinsi Aceh. Retrieved from <https://aceh.bps.go.id/>.
- BPS North Sumatra. (2018). North Sumatra in Figures 2018. Badan Pusat Statistik Provinsi Sumatera Utara. Retrieved from <https://sumut.bps.go.id/>
- Dar, N.I., Minhas, R.A., Zaman, Q. & Linkie, M. (2009). Predicting the patterns, perceptions and causes of human–carnivore conflict in and around Machiara National Park, Pakistan. *Biol. Cons.* **142**, 2076–2082.
- Dickman, A.J., Macdonald, E.A. & Macdonald, D.W. (2011). A review of financial instruments to pay for predator conservation and encourage human–carnivore co-existence. *Proc. Natl Acad. Sci. USA* **108**, 19836.
- Dickman, A.J., Hazzah, L., Carbone, C. & Durant, S.M. (2014). Carnivores, culture and ‘contagious conflict’: Multiple factors influence perceived problems with carnivores in Tanzania’s Ruaha landscape. *Biol. Cons.* **178**, 19–27.
- FFI. (2014). The community ranger programme. World Bank implementation completion report. Jakarta.
- Fraser, B.Y.B. (2018). China’s lust for jaguar fangs imperils big cats. *Nature* **555**, 13–14.
- Gaveau, D.L.A., Epting, J., Lyne, O., Linkie, M., Kumara, I., Kanninen, M. & Leader-Williams, N. (2009). Evaluating whether protected areas reduce tropical deforestation in Sumatra. *J. Biogeogr.* **36**, 2165–2175.
- Goodrich, J.M., Seryodkin, I., Miquelle, D.G. & Berezuk, S.L. (2011). Conflicts between Amur (Siberian) tigers and humans in the Russian Far East. *Biol. Cons.* **144**, 584–592.
- Gray, S.M., Booher, C.R., Elliott, K.C., Kramer, D.B., Waller, J.C., Millsbaugh, J.J., Kissui, B.M. & Montgomery, R.A. (2019). Research–implementation gap limits the actionability of human–carnivore conflict studies in East Africa. *Anim. Conserv.* 1–11.
- Harihar, A. & Pandav, B. (2012). Influence of connectivity, wild prey and disturbance on occupancy of tigers in the human-dominated western Terai Arc landscape. *PLoS ONE* **7**, e40105.
- Hijmans R.J. & van Etten J. (2012). raster: Geographic analysis and modeling with raster data. R package version 2.0-12. <http://CRAN.R-project.org/package=raster>
- Indonesia Geospatial Agency. (2017). Retrieved from <http://ta.nahair.indonesia.go.id/portal-web>.
- Inskip, C. & Zimmermann, A. (2009). Human–felid conflict: a review of patterns and priorities worldwide. *Oryx* **43**, 18–34.
- Karanth, K.U., Nichols, J.D., Kumar, N.S., Link, W.A. & Hines, J.E. (2004). Tigers and their prey: predicting carnivore densities from prey abundance. *PNAS* **101**, 4854–4858.
- Kartika, E.C. (2017). Spatio-temporal patterns of human tiger conflicts in Sumatra 2001–2016. Direktorat KKH - KLHK. Jakarta.
- Khorozyan, I., Soofi, M., Hamidi, A.K., Ghoddousi, A. & Waltert, M. (2015). Dissatisfaction with veterinary services is associated with leopard (*Panthera pardus*) predation on domestic animals. *PLoS ONE* **10**, 1–10.
- Knight, A.T., Cowling, R.M., Rouget, M., Balmford, A., Lombard, A.T. & Campbell, B.M. (2008). Knowing but not doing: Selecting priority conservation areas and the research–implementation gap. *Conserv. Biol.* **22**, 610–617.

- Linkie, M., Chapron, G., Martyr, D.J., Holden, J. & Leader-Williams, N.I.G.E.L. (2006). Assessing the viability of tiger subpopulations in a fragmented landscape. *J. Appl. Ecol.* **43**, 576–586.
- Linkie, M., Martyr, D., Harihar, A., Mardiah, S., Hodgetts, T., Risdianto, D., Subchaan, M. & Macdonald, D. (2018). Asia's economic growth and its impact on Indonesia's tigers. *Biol. Cons.* **219**, 105–109.
- Lozano, J., Olszańska, A., Morales-Reyes, Z., Castro, A.A., Malo, A.F., Moleón, M., Sánchez-Zapata, J.A., Cortés-Avizanda, A., von Wehrden, H., Dorresteijn, I. & Kansky, R. (2019). Human-carnivore relations: a systematic review. *Biol. Cons.* **237**, 480–492.
- Lubis, M.I., Hussein, S., Hadi, A.N., Rumampea, E.E., Yasin, A., Trihangga, A., Tarmizi, & Marthy, W. *et al.* (2019). *Monitoring of forest cover changes in Gunung Leuser National Park between 2000 and 2017*. Bogor: Gunung Leuser National Park and Wildlife Conservation Society.
- Luskin, M.S., Christina, E.D., Kelley, L.C. & Potts, M.D. (2014). Modern hunting practices and wild meat trade in the oil palm plantation-dominated landscapes of Sumatra, Indonesia. *Hum. Ecol.* **42**, 35–45.
- MacKenzie, D.I., Nichols, J.D., Lachman, G.B., Droege, S., Royle, J.A. & Langtimm, C.A. (2002). Estimating site occupancy rates when detection probabilities are less than one. *Ecology* **83**, 2248–2255.
- Marchini, S. & Macdonald, D.W. (2012). Predicting ranchers' intention to kill jaguars: case studies in Amazonia and Pantanal. *Biol. Cons.* **147**, 213–221.
- McCarthy, J.F. (2000). 'Wild Logging': The rise and fall of logging networks and biodiversity conservation projects on Sumatra's rainforest frontier. Bogor, Indonesia: CIFOR.
- McKay, J.E., St. John, F.A., Harihar, A., Martyr, D., Leader-Williams, N., Milliyawati, B., Agustin, I. & Anggriawan, Y. (2018). Tolerating tigers: gaining local and spiritual perspectives on human-tiger interactions in Sumatra through rural community interviews. *PLoS ONE* **13**, e0201447.
- Michalski, F., Boulhosa, R.L.P., Faria, A. & Peres, C.A. (2006). Human-wildlife conflicts in a fragmented Amazonian forest landscape: determinants of large felid depredation on livestock. *Anim. Conserv.* **9**, 179–188.
- MoEF. (2018). Rekalkulasi penutupan lahan Indonesia tahun 2017. Indonesian Ministry of Environmental and Forestry. Retrieved from <http://webgis.menlhk.go.id>.
- MoEF. (2019). Daerah Aliran Sungai. Webgis Kementerian Lingkungan Hidup dan Kehutanan (KLHK). Retrieved from <http://webgis.menlhk.go.id:8080/kemenhut/index.php/id/fitur/unduh>
- Nyhus, P.J. & Tilson, R. (2004). Characterizing human-tiger conflict in Sumatra, Indonesia: implications for conservation. *Oryx* **38**, 68–74.
- Pusparini, W., Batubara, T., Surahmat, F., Sugiharti, T., Muslich, M., Amama, F., Marthy, W. & Andayani, N. (2017). A pathway to recovery: the critically endangered sumatran tiger *panthera tigris sumatrae* in an 'in danger' UNESCO World Heritage Site. *Oryx*, 1–10.
- R Core Team. (2017). A language and environment for statistical computing. Vienna, Austria. <https://www.r-project.org/>.
- Ripple, W.J., Estes, J.A., Beschta, R.L., Wilmers, C.C., Ritchie, E.G., Hebblewhite, M., Berger, J., Elmhagen, B., Letnic, M., Nelson, M.P. & Schmitz, O.J. (2014). Status and ecological effects of the world's largest carnivores. *Science* **343**, 1241484.
- Robinson, T.P., Wint, G.R.W., Conchedda, G., Van Boeckel, T.P., Ercoli, V., Palamara, E., Cinardi, G., D'Aiotti, L., Hay, S.I. & Gilbert, M. (2014). Mapping the global distribution of livestock. *PLoS ONE* **9**, e96084.
- Soofi, M., Ghoddousi, A., Zeppenfeld, T., Shokri, S., Soufi, M., Egli, L., Jafari, A., Ahmadvour, M., Qashqaei, A., Ghadirian, T. & Filla, M. (2019). Assessing the relationship between illegal hunting of ungulates, wild prey occurrence and livestock depredation rate by large carnivores. *J. Appl. Ecol.* **56**, 365–374.
- St. John, F.A.V., Linkie, M., Martyr, D.J., Milliyawati, B., McKay, J.E., Mangunjaya, F.M., Leader-Williams, N. & Struebig, M.J. (2018). Intention to kill: tolerance and illegal persecution of Sumatran tigers and sympatric species. *Conserv. Lett.* **11**, e12451.
- Struebig, M.J., Linkie, M., Deere, N.J., Martyr, D.J., Milliyawati, B., Faulkner, S.C., Le Comber, S.C., Mangunjaya, F.M., Leader-Williams, N., McKay, J.E. & John, F.A. (2018). Addressing human-tiger conflict using socio-ecological information on tolerance and risk. *Nat. Commun.* **9**, 3455.
- Walston, J., Robinson, J.G., Bennett, E.L., Breitenmoser, U., da Fonseca, G.A.B., Goodrich, J., Gumal, M., Hunter, L., Johnson, A., Karanth, K.U. & Leader-Williams, N. (2010). Bringing the tiger back from the brink—The six percent solution. *PLoS Biol* **8**, e1000485.
- WCS. (2018). Wildlife Response Unit - Wildlife Conservation Society. Unpublished raw data.
- WCS. (2019). SMART Patrols - Wildlife Conservation Society. Unpublished raw data.
- Wibisono, H.T., Linkie, M., Guillera-Aroita, G., Smith, J.A., Pusparini, W., Baroto, P. & Brickle, N. (2011). Population status of a cryptic top predator: an island-wide assessment of tigers in Sumatran rainforests. *PLoS ONE* **6**, e25931.

## Supporting information

Additional supporting information may be found online in the Supporting Information section at the end of the article.

**Table S1.** Environmental variables used to model the distribution of key tiger prey (sambar deer and wild boar) in Leuser Ecosystem from occupancy survey conducted from 2007–2009



**Table S2.** Correlation matrix of variables used in the tiger prey distribution model (TRI=Terrain Ruggedness Index; Rivdist=distance to river; Fordist=distance to forest edge; Prop Forest=Proportion of forest; NDVI=normalized differenced vegetation index)

**Table S3.** Model selection results for tiger prey (sambar deer and wild boar) occupancy in the Leuser Ecosystem (showing only the first 10 models). We considered the best model with the one that have lowest AIC and used to construct the spatially-explicit final wild prey model. The results found that the occupancy is negatively influenced by elevation and positively influenced by proportion of forest and NDVI. Detection probability is negatively influenced by distance to river and positively by distance to forest.

**Table S4.** Correlation matrix of variables used to model the occurrence of HTC in the Leuser Ecosystem (Livestock=Livestock density; Prey=Habitat use of prey; Vildist=distance to village; Defdist=distance to recent deforestation occurring from 2000-2018)

**Table S5.** Estimated coefficients, standard errors and P-values for Resource Selection Function models of human-tiger conflict in the Leuser Landscape using the full data set and a 5 fold cross-validation technique

**Figure S1.** Covariates used to model the occurrence of HTC in the Leuser Ecosystem. All covariates were scaled using z-transformation