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# Multiscale spatially explicit modelling of livestock depredation by reintroduced tiger (*Panthera tigris*) to predict conflict risk probability

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**Abstract**

Understanding the causal factors associated with human/livestock-large carnivore conflict and distribution of conflict risk is key to designing effective preventative and mitigation strategies. Spatial modelling of human-carnivore conflict has recently gained traction, and predictive maps have become a great tool to understand the distribution of present and future conflict risk. However, very few such studies consider scale and use appropriate spatial modelling tools. We aimed to understand the ecological correlates of human-tiger (*Panthera tigris*) conflict, predict livestock predation risk by reintroduced tigers in Panna Tiger Reserve, Central India and understand the prey-predator dynamics behind the conflict. We modelled livestock kill as a function of various tiger relevant ecological variables at multiple scales employing spatially explicit statistical tools. As a first step, we used geostatistical modelling to create raster layers of covariates (prey, cover, human activities), following which we did univariate scaling. We then modelled livestock loss by tiger using a geoadditive model. Employing this model, we predicted and mapped conflict risk probabilities within our study site. It was found that prey and shrub cover both selected at a fine scale, were key ecological determinants of human-tiger conflict. Prey showed an inverse relationship while shrub showed non-linear relationship with livestock predation. Which lead us to conclude that in habitats where optimum ambush cover is available but prey presence is low at fine-scale, carnivores are more likely to depredate domestic livestock since livestock have lost most of their anti-predator behaviours. Livestock kill by tiger is thus a culmination of predator choice and foraging tactics, and prey vulnerability and defence mechanism. The spatially explicit predation risk map produced in this study can guide adequate human-tiger conflict prevention measures.

**Keywords:** human-carnivore conflict, ecological predictors, prey-predator dynamics, geoGAM, domestic livestock, Panna

## 1. Introduction

Human-wildlife conflict, especially by large carnivores, is among the key drivers of local extinction of several species and is also a major cause for local communities turning hostile toward the conservation agenda (Young and Goldman 1944; Seidensticker 1987; Clark et al. 2013; Babrgir et al. 2017; Gross et al. 2021). Revealing the ecological reasoning behind large carnivore attacks on domestic livestock is key to designing effective prevention and mitigation strategies. Studies have linked several ecological factors with human-carnivore conflict (HCC) viz. tree cover, forest area and forest/vegetation types (Amirkhiz et al. 2018; Zarco-González et al. 2018), distance to forest/protected area/reserve (Treves et al. 2011; Broekhuis et al. 2017), wild prey abundance and availability (Cavalcanti et al. 2010; Davie et al. 2014), proximity to predator occupied habitat, predator and cattle density (Silveira et al. 2008; Kissling et al. 2009; Kaartinen et al. 2009), proximity to water (Behdarvand et al. 2014; Abade et al 2014), distance to settlement and road (Mbiba et al. 2018; Amirkhiz et al. 2018), temperature and precipitation (Dar et al. 2009), topography/terrain, elevation and slope (Naha et al. 2018; Chetri et al. 2019), season (Mbiba et al. 2018 ), time (Yirga et al. 2012; Mazzolli et al. 2002), and, predator personality, sex, social status and pack size (Odden et al. 2002; Mattisson et al. 2011). In order to reveal these ecological predictors and understand the distribution of HCC, spatial modelling of conflict or predictive risk modelling has become one of the important tools (Treves et al. 2004; Kissling et al. 2009; Marucco and McIntire 2010; Edge et al. 2011; Zarco-González et al. 2013; Mbiba et al. 2018). Statistical modelling is used to identify the factors related to depredation events, predict its distribution by extrapolating to similar areas, and predict future conflict risk (Treves et al. 2004; Kaartinen et al. 2009; Behdarvand et al. 2014; Rostro-García et al. 2016). The predictive/risk maps assist managers in identifying vulnerable habitats, communities, and species (Treves et al. 2011; Mateo-tomas et al. 2012; Davie et al. 2014; Soh et al. 2014; Broekhuis et al. 2017; Amirkhiz et al. 2018). However, since all the factors associated with HCC are neither linearly related to kill occurrence nor come into play at the same scale, scale must be considered when modelling habitat correlates of HCC.

Most ecological relationships are complex and involve several factors. And because these factors range from macro to microhabitat/environmental covariates, all of them cannot be expected to operate at and influence the relationship at the same scale. Thus, ecological relationships are scale-dependent, such that when examined at different spatio-temporal scales, the relationship and its interpretation are subject to change (Weins et al. 1989; McGarigal et al. 2016). Therefore, when identifying the factors related to a process or phenomenon, they need to be examined at multiple scales to identify the meaningful scale and make ecologically sound inferences (McGarigal et al. 2016). In the absence of such a multiscale approach, misleading conclusions may be drawn.

Even if we are able to identify the causal factors of a problem, we would not know at which level to intervene without understanding the scale at which these causal factors are influencing the problem. In which case, selection of the scale at which the variables are meaningfully correlated with the issue becomes as crucial as the selection of variables themselves (Mateo Sánchez et al. 2013). Thus, coupled with variable selection, scale optimisation should be the first step to predictive modelling.

Multiscale models have been proven to perform better than single-scale models at identifying and predicting relationships between environmental variables and the phenomenon/process under study (Mateo Sánchez et al. 2013; Timm et al. 2016). Thus, multiscale modelling has become an important tool for studying a myriad of ecological and biological processes/problems/groupings, including community ecology (Dray et al. 2012), ecological niche modelling/niche/resource partitioning (Hearn et al. 2018; Khosravi et al. 2019), habitat selection (Mateo Sánchez et al. 2013)/ habitat suitability modelling (Store and Jokimäki 2003; Kittle et al. 2018; Khosravi et al. 2019; Rather et al. 2020), predicting indicator species hotspots (Grand et al. 2004) and predicting carnivore dispersal (Krishnamurthy et al. 2016). Even though HCC often involves different variables and complex interactions, very few studies have tried to examine the factors determining HCC at multiple scales (Wilson et al. 2005; Soh et al. 2014; Miller et al. 2015; Rostro-García et al. 2016; Broekhuis et al. 2017). These studies have found that scale influences livestock predation risk (Davie et al. 2004), with certain habitat factors influencing livestock depredation at a broad scale and others at a fine scale (Miller et al. 2015; Rostro-García et al. 2016; Broekhuis et al. 2017). Upon comparison of multiscale model with a single-scale model, studies have concluded that scale optimisation improves modelling results of livestock predation risk by large carnivores like tiger (*Panthera tigris*) (Rostro-García et al. 2016). However, most studies employ aspatial models to predict predation risk using spatial correlates (Soh et al. 2013; Miller et al. 2015). Since most ecological variables exhibit a certain degree of spatial autocorrelation, it is important to account for the spatial nature of the data (Griffith 1992; Legendre 1993), when modelling predation risk by carnivores. In the absence of which, the 'independence of data points', a common assumption across most statistical models, is violated, leading to unreliable model outcomes (Legendre 1993; Dale and Fortin 2002; Dormann et al. 2007).

Moreover, most studies on HCC attempt to only map risk and discuss the causal factors. They rarely address the ecology (like prey-predator dynamics) behind how these factors interact to cause conflict (Wilkinson et al. 2020). As there is a dearth of studies examining HCC at multiple scales employing appropriate spatial statistical models; our study aims to identify the ecological determinants of human-tiger conflict (HTC) at suitable scales, predict livestock predation risk by tigers in and around Panna Tiger Reserve, Central India, and reveal the ecology behind livestock depredation by large carnivores in the light of the identified causal factors.

In order to do so, our study addresses three main questions:

1. What are the ecological variables that predict livestock predation by tiger and at which scale?
2. How do these ecological variables explain livestock predation by tigers?
3. How is the livestock predation risk probability by tiger distributed spatially within our study site?

For this purpose, we modelled livestock kill as a function of various tiger relevant ecological variables, viz. prey, cover, water, and anthropogenic disturbance (Miquelle et al. 1999; Karanth and Sunquist 2000; Sunarto et al. 2012), at multiple scales employing spatially explicit Generalized Additive Model (GAM) and mapped conflict risk.

Various statistical tools have been applied to model the relationship between habitat variables and livestock kill, most of the times as presence vs absence (or classification into kill or no kill) using linear parametric models for e.g. discriminant function analysis (Edge et al. 2011; Treves et al. 2004), binary logistic regression or generalized linear model (GLM) with logit link function and binomial error distribution (Broekhuis et al. 2017; Karanth et al. 2013; Kissling et al. 2009; Michalski et al. 2006; Miller et al. 2015; Thorn et al. 2012); or when modelling the frequency of occurrence of kills (count data), then negative binomial distribution (Penteriani et al. 2016) or if kill events are rare, then zero-inflated negative binomial model (Soh et al. 2014) or rare event model in a binary logistic regression (Naha et al. 2018). However, classical statistical tools like parametric models have several assumptions relating to data distribution and linearity, even though most relationships are not linear in the real world and most of the data does not have a Gaussian distribution (Chambers and Dinsmore 2014; Mahmoud 2021). Thus, in recent times, machine learning algorithms are being increasingly used to generate accurate predictions without having to worry about the data distributions, a priori (Kuhn and Johnson 2013). Several studies have employed machine learning algorithms to model conflict/predation risk (Abade et al. 2014; Amirkhiz et al. 2018; Mbiba et al. 2018; Rostro-García et al., 2016). Although machine learning algorithms may perform better than classical statistical models when it comes to giving more accurate predictions, if the purpose is to draw inferences about the relationship between variables, they are not very interpretable (Stewart 2019).

GAM, while retaining the interpretability of GLM has the flexibility of machine learning algorithms, because it does not assume a linear relationship between dependent and independent variables (Hastie and Tibshirani 1990; Larsen 2015). GAM is, as the name suggests, a generalisation of the linear model, in which the linear function of the covariate is replaced with a smooth function (Hastie and Tibshirani 1990). Because of their semiparametric nature, GAMs are much more sensitive to unique data distribution than GLM, allowing for the modelling of nonlinear relationships by deriving predictor functions during model building (Härdle and Turlach 1992; Larsen 2015). At the same time to avoid overfitting, one can control the smoothness or 'wiggliness' of the predictor function (Larsen 2015). Despite their versatility, GAM has not been explored as much as linear or machine learning models to understand the relationship between livestock depredation by carnivores and their ecology/environmental factors (Kaartinen et al. 2009; Miller et al. 2015; Rostro-García et al. 2016; Broekhuis et al. 2017; Struebig et al. 2018). Therefore, we have carried out multivariate multiscale predictive modelling to identify the ecological factors linked to livestock depredation by tiger, employing geoGAM, and discussed how these factors might be linked to prey-predator dynamics.

## 2. Materials and Methods

**2.1. Study area:** Panna Tiger Reserve (24°16′N to 24°42′N and 79°29′E to 80°16′E), covering an area of 1598.10 km² is situated in the state of Madhya Pradesh in central India. The Critical Tiger Habitat (CTH), or core of the reserve comprises Panna National Park and Gangau Wildlife Sanctuary, covering an area of 576.13 $km^2$ (Madhya Pradesh Forest Department 2007). The buffer covers an area of about 1,021.97 $km^2$ (Madhya Pradesh Forest Department 2012). The reserve lies in Vindhyan hills, its altitude ranging between 330 and 540 m a.s.l. (Chawdhry 1996; Rodgers et al. 2002). It has an average annual humidity of 86%, and temperature ranges from 5 to 45°C. Both monsoon (July-September) and winter (November-February) are short, thus, the climate is mostly hot and dry (Chawdhry 1996; Gopal et al. 2010). Ken a major tributary of the river Yamuna, cuts through the reserve, flowing from South to North. The major forest type is dry deciduous forest with teak (*Tectona grandis*) as the most dominant flora (Meher-Homji 1990). Apart from tigers, the major faunal community comprises of carnivores, viz. leopard (*Panthera pardus*), striped hyena (*Hyaena hyaena*), wild dog (*Cuon alpinus*), golden jackal (*Canis aureus*), Bengal fox (*Vulpes bengalensis*), jungle cat (*Felis chaus*), and sloth bear (*Melursus ursinus*); herbivores, viz. sambar (*Cervus duvauceli*), chital (*Axis axis*), nilgai (*Boselaphus tragocamelus*), chinkara (*Gazella bennetti*), chousingha or four-horned antelope (*Tetraceros quadricornis*) and wild pig (*Sus scrofa*); and primates, viz. hanuman or common langur (*Semnopithecus entellus*) and rhesus macaque (*Macaca mullata*) (Gopal et al. 2010). There are four villages within the national park area, however, there are seven villages in sanctuary area and 49 villages in the buffer of the reserve. Many of the communities living in these villages are dependent on the reserve for fuelwood, fodder and NTFPs (Malviya et al. 2022). The current study focussed on the CTH and two kilometres of natural buffer around it (Figure 1).

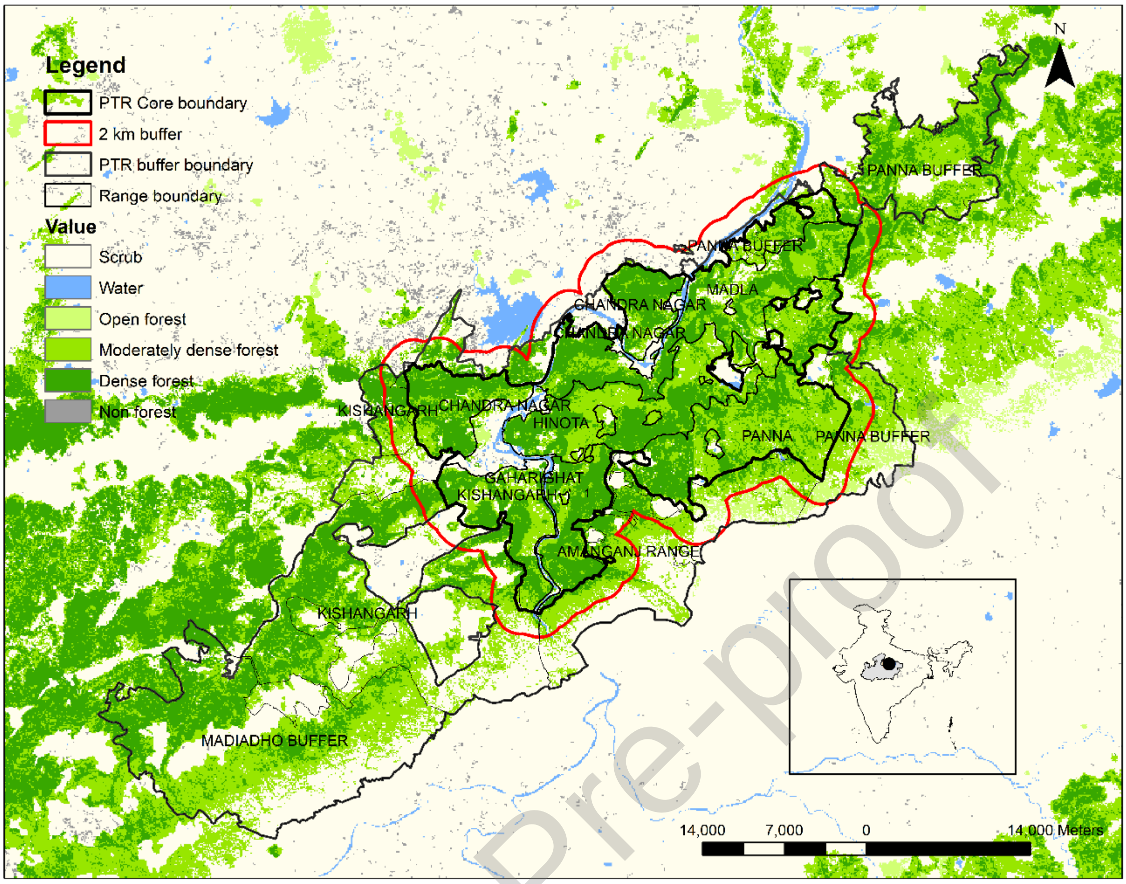


**Fig. 1**. Map depicting the study site i.e., Core area of Panna Tiger Reserve and 2 km natural buffer around it

The original tiger population in Panna was lost due to poaching and as a population recovery measure, tigers were reintroduced from neighbouring reserves in 2009 (Sarkar et al. 2016). Since then, the tiger population in Panna has increased exponentially from seven founders to more than 60 individuals in 2020 (Sharma and Jarande 2020).

**2.2. Livestock kill quantification and kill site location:** In India, forest department of the state compensates livestock depredation by wild carnivores. The owner of the livestock has to inform the local forest guard and file an application. After the site visit and getting the kill verified by a veterinarian, the forest guard then files an official report and confirms the validity of the claim, upon which the compensation is paid to the victim by the department. We collected livestock compensation records from Panna Tiger Reserve management to understand the intensity of HTC within the reserve. But the compensation data was not geotagged, hence we also obtained the livestock kill data (that has GPS locations), which is collected by tiger monitoring teams in the reserve, for the period 2009-2016. Since in case of Panna, there are several feral cattle, and no distinction is made between feral and domestic cattle in the kill records, we matched kill and compensation data to obtain reliable locations for domestic livestock kill within the reserve. We thus matched 156 locations for the period 2011-2016. For predation risk probability modelling, we treated livestock kill data as presence and generated equal number of random pseudo-absence points using the 'create random points' tool in ArcGIS 10.4 (ESRI 2016a) within the study site (discarding the absence points falling within a buffer of 42m around each presence point). We used livestock kill data for the period 2011-2015 for training the model and 2016 data for testing the model.

**2.3. Measuring ecological variables:** We considered a total of 27 variables for ecological driver modelling, which can be grouped under the following heads:

***2.3.1. Prey:*** To understand the distribution of prey species, we carried out line transect surveys. We surveyed a total of 41 line transects each up to 2 km in length, during winter 2012-13 and 2013-14. All the line transects were walked in a replicate of three. We then combined the data for both years. The prey species recorded were sambar, chital, wild pig, nilgai, chinkara, chousingha, hanuman langur, hare, peacock and livestock (cattle and buffalo). We calculated encounter rates (total no./transect length) of all prey (wild and livestock), wild prey, and livestockfor each transect.

***2.3.2. Vegetation cover:*** We quantified vegetation indices, viz. canopy cover and shrub abundance in 15m circular plots laid at every 400 m on the line transects during winter 2012-13 (Jhala et al. 2009). We laid a total of 234 circular plots. Within the plots, we made ocular estimations of canopy cover (0-100%) and scored shrub cover according to its abundance (0-4). The same team of two people carried out all the vegetation related estimations to avoid interobserver bias.

For further understanding the vegetation cover of the tiger reserve, we downloaded LANDSAT 8 (OLI/TIRS) scenes for the reserve from USGS website (https://earthexplorer.usgs.gov/) for April 2013 (LANDSAT SCENE ID = LC81440432013119LGN01; Download date = 20 April 2015) and November 2013 (LANDSAT SCENE ID = LC81440432013327LGN01; Download date = 15 December 2020). We calculated Normalized Difference Vegetation Index (NDVI) (Rouse et al. 1974) using these scenes. NDVI uses the property of plants to absorb red spectral band and highly reflect near infrared, to give an index of biomass or density of vegetation for a given area. The values range from -1 to +1, near zero values indicate barren soil, 0.2 to 0.3 correspond to grasslands and values between 0.4 to 0.8 correspond to dense vegetation. We calculated NDVI employing Raster Calculator in ArcGIS 10.1 (ESRI 2012) by the formula:

NDVI = (Near Infrared - Red)/ (Near Infrared + Red).

***2.3.3. Water:*** Using the same LANDSAT scenes as used for calculating NDVI, we calculated Normalized Difference Water Index (NDWI) (McFeeters 1996). NDWI uses green and near infrared bands to show presence of water bodies, because water absorbs light in visible to infrared electromagnetic spectrum. NDWI was calculated using Raster Calculator in ArcGIS 10.1 (ESRI 2012), by the formula:

NDWI = (Green-Near Infrared)/ (Green+Near Infrared).

Additionally, we obtained drainage and water source data from the forest department and created Euclidean distance raster using 'Euclidean Distance' tool in the Spatial Analyst toolbox in ArcGIS 10.4 (ESRI 2016a). We also created Euclidean distance rasters for Ken River and its tributaries, and water sources tagged perennial.

***2.3.4. Topography****:* We downloaded ASTER Global Digital Elevation Model (DEM) data from USGS Global Visualization Viewer website. We used 'Slope' tool in the Spatial Analyst toolbox to calculate slope from DEM layers in ArcGIS 10.1 (ESRI 2012). Additionally, we calculated topographic ruggedness index or terrain ruggedness index (TRI) that measures elevation difference between a cell and mean of its eight neighbouring cells (Riley et al. 1999) using raster calculator in ArcGIS 10.1 (ESRI 2012), by the formula (Cooley 2016):

TRI = SquareRoot (Abs((Square("3x3max")-Square ("3x3min")))).

***2.3.5. Land Use Land Cover and forest contiguity:*** We procured Land Use Land Cover (LULC) prepared by Forest Survey of India (FSI) for the entire country at 98m resolution for the year 2009 (FSI 2009). We studied landscape characteristics and patterns, particularly habitat connectivity, using multiple indices in program FRAGSTATS (ver. 4.2). We ran FRAGSTAT analysis using the FSI LULC and calculated three class-level metrics: Patch Density (PD) (number of patches per hectare), Large Patch Index (LPI) (percentage of total landscape area comprised by the largest patch), and Clumpiness Index (CLUMPY) (a measure of fragmentation). LPI is a simple measure of dominance. And CLUMPY that ranges from -1 (patch type is maximally disaggregated) to 1 (patch type is maximally clumped) provides an index of fragmentation of the focal class that is not affected by changes in class area (McGarigal 2015).

***2.3.6. Disturbance:*** We also quantified anthropogenic disturbance indices in the circular plots (as discussed earlier under section 2.3.2.). In each plot, we counted all the lopped (only branches were cut) and cut (cut to stump) trees. We deployed camera traps (Cuddeback Attack pairs) in 109 locations in 2x2 km grids within the national park area, in the winter of 2013-14. Cameras were set to function 24x7 and delay between 2 consecutive captures was kept 15 seconds. We then manually counted the number of tigers, livestock, humans, and vehicles captured in each camera trap and calculated encounter rates (total no. of captures/total trap nights).

We also obtained village and road location data from the forest department and calculated Euclidean distance rasters. Additionally, we downloaded human footprint data from Socio Economic Data and Application Centre (SEDAC) website for the year 2009 (Sanderson et al. 2002; Venter et al. 2018). We also downloaded population census data for the year 2011 from SEDAC (Balk et al. 2020).

**2.4. Geostatistical modelling to create rasters:** We interpolated canopy cover, prey, human, livestock, and vehicle encounter rates, and cutting and lopping intensity rates, to create rasters using the Geostatistical wizard in ArcGIS 10.4 (Cressie 2015; ESRI 2016a). For this purpose, we considered four interpolation tools: Inverse Distance Weighing, Simple Kriging (SK), Ordinary Kriging (OK), and Empirical Bayesian Kriging (EBK). We used statistical measures of correctness (mean prediction error, root-mean-square error, standardized root-mean-square error, average standard error) to compare the kriging algorithms. We selected the model that had the smallest root-mean-squared prediction error (RMSE), standardized mean nearest to zero, the average standard error nearest the root-mean-squared prediction error, and the standardized root-mean-squared prediction error nearest to 1 (ESRI 2016b) (Table A.1).

**2.5. Scale and variable selection:** To construct a multiscale model, we resampled each of the variables (except for human footprint (which was available at ~1 km resolution)) at five scales: 30m (the highest resolution available), 50m (mean drag distance for tiger kill (Karanth and Sunquist 2000)), 100m (midpoint between fine and coarse resolution), 350m (maximum kill drag distance (Karanth and Sunquist 2000)), 1200m (coarsest resolution used by us and at which most global environmental data is available). LULC (available at 98m) could only be resampled at coarse scale (100-1200m). Thus, in total, we had 118 variables. We then extracted all the variables for each of the presence/absence points using the Spatial Analyst toolbox of ArcGIS 10.4 (ESRI 2016a).

For scale and feature selection, firstly, we ran univariate logistic regressions, after performing Box-Tidwell procedure to test for logistic regression’s linearity assumption, i.e., logit transformation of the dependent variable and continuous independent variables have a linear relationship (Hosmer et al. 2013; Shin and Ying 1994). Secondly, we ran univariate GAMs to understand how much r square/deviance was explained by each of the predictors at each of the scales. We selected the scales at which the variables were best explaining the response (livestock kill presence/absence). Additionally, we employed Information Value and Weight of evidence for feature selection (Good and Osteyee 1974). We studied the results of univariate GAM and Information value to select the explanatory variables at appropriate scales. We then checked the data for multicollinearity and spatial autocorrelation. To check for multicollinearity among the selected variables, we ran appropriate tests of association (for continuous vs continuous and continuous vs ordinal variables, Kendall's tau b; for categorical vs continuous variables, logistic regression; and for categorical vs categorical variables, Cramer's V). Among the correlated variables, we included those variables in the model that better explained the response. For example, all prey (wild prey plus livestock) was highly correlated to wild prey encounter rate ($r=0.812$). Between the two, we selected all prey encounter rate since it was explaining higher deviance of the dependent variable in univariate GAM. Similarly, NDVI and NDWI were moderately correlated ($r=0.636$); we selected NDVI since it was explaining higher deviance.

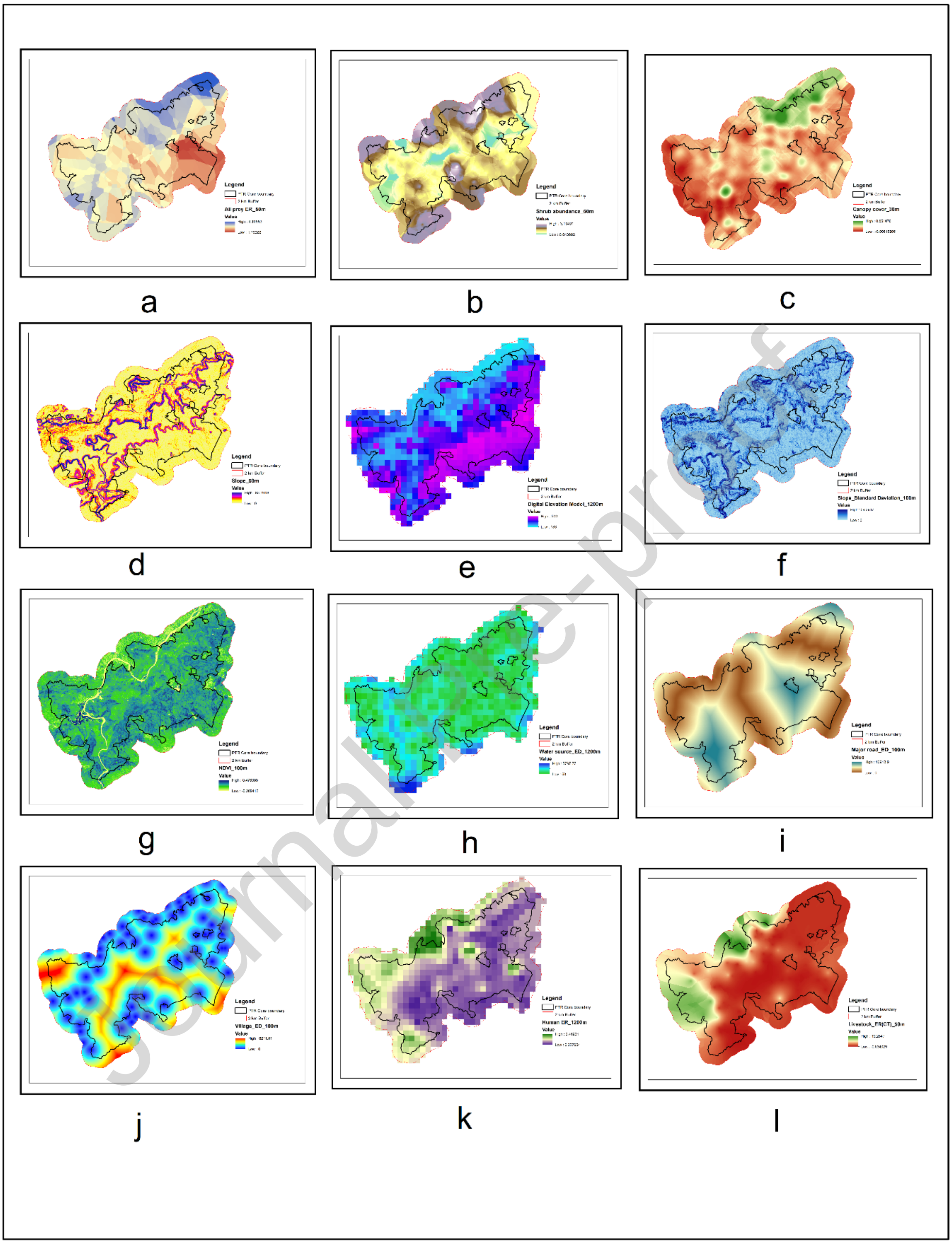


**Fig. 2**. Interpolated layers of variables included in the global model for livestock depredation by tiger, at selected scales: a) All prey encounter rate (50m), b) shrub abundance (50m), c) canopy cover (30m), d) slope (50m), e) elevation (1200m), f) slope deviation (100m), g) NDVI (100m), h) distance to water hole (1200m), i)

distance to road (100m), j) distance to village (100m), k) human encounter rate (1200m), l) livestock encounter rate (ct) (50m)

So, after variable selection, the global model consisted of the following 12 variables at these scales: All prey encounter rate (50m), slope (50m), elevation (1200m), slope deviation (100m), NDVI (100m), shrub abundance (50m), canopy cover (30m), distance to water (1200m), livestock encounter rate (camera trap) (50m), human encounter rate (1200m), distance to road (100m), distance to village (100m) (Figure 2).

We checked spatial autocorrelation in these variables using Moran's I statistic using ArcGIS 10.4, and it was found that spatial autocorrelation was present in many variables (Getis 2007; Moran 1950).

**2.6. Spatial GAM:** We used GAM to model livestock kill locations as a function of various tiger relevant ecological factors (Wood 2017). To account for the spatial autocorrelation in the data, we constructed spatial GAM model using geoGAM package in R ver. 3.6.3. (Nussbaum and Papritz 2017). It's a procedure to build a parsimonious model based on gradient boosting, smoothing splines and a smooth spatial surface to account for the spatial structure. The GAM for spatial data or geoadditive model in its full generality is represented by

$$\mathrm{g}\left(\mu\left(\mathrm{x}(\mathrm{s})\right)\right) = \nu + \mathrm{f}\left(\mathrm{x}(\mathrm{s})\right) =$$

$$\nu + \sum_{u} f_{j_u}(x_{j_u}(\mathrm{s})) + \sum_{v} f_{j_v}(x_{j_v}(\mathrm{s})) \,.\, f_{k_v}(x_{k_v}(\mathrm{s}))$$

$$+ \sum_{w} f_{s_w}(\mathrm{s}).\, f_{j_w}(x_{j_w}(\mathrm{s})) + f_s(\mathrm{s})$$

Where, $f_s(\mathrm{s})$ is a smooth function of spatial coordinates, which accounts for residual autocorrelation (Nussbaum and Papritz 2017).

Since the response variable, in this case, is binary, Bernoulli distribution is assumed, and logit link used

$$\mathrm{g}\left(\mu\left(\mathrm{x}(\mathrm{s})\right)\right) = \log\left(\frac{\mu\left(\mathrm{x}(\mathrm{s})\right)}{1 - \mu\left(\mathrm{x}(\mathrm{s})\right)}\right)$$

where,

$$\mu\big(x(s)\big) = \text{Prob}[Y(s) = 1|\, x(s)] = \frac{\exp(\nu + f(x(s)))}{1+\exp(\nu + f(x(s)))}$$

For building parsimonious model geoGAM automatically selects factors, covariates and spatial effects using componentwise gradient boosting, following which model is further reduced using cross validation (Nussbaum and Papritz 2017).

The geoaddttive model was run on training dataset (n=144) and the final model so selected was run on test data (n=62), to get model performance measures, area under the curve (AUC) and true skill statistic. We performed all the analyses using R Statistical Software (v3.6.3; R Core Team 2020).

**2.7. Risk map:** We created a raster with 42m cell size (average of kill drag distance for tiger as reported by literature (Karanth and Sunquist 2000; Miller et al. 2015)) and masked it to the reserve boundary using ArcGIS 10.4 (ESRI 2016a). We then converted it into points and, for each of these points, extracted the values for all the explanatory variables using the Spatial Analyst toolbox of ArcGIS 10.4 (ESRI 2016a). We then ran the final selected model on this data in R to predict predation risk probability for each point and converted the points back to raster. Finally, we assigned risk predictions as the value of the raster to create HTC risk map using ArcGIS 10.4 (ESRI 2016a).

## 3. Results

The variables selected to be included in the final geoGAM model were all prey encounter rate (50m), elevation (1200m), NDVI (100m), shrub abundance (50m), and human encounter rate (1200m). Among these smooth terms, all prey encounter rate and shrub abundance were significant at $\alpha$=0.05 level (Table 1).

**Table 1:** Approximate significance of smooth terms of final geoGAM model predicting livestock predation by tiger

| Smooth terms | Effective degree of freedom (edf) | Ref. df | Chi. sq | p-value |
|---|---|---|---|---|
| **s(prey encounter rate at 50 m)** | 3.17 | 3.85 | 16.65 | 0.002 |
| **s(shrub abundance at 50 m)** | 3.23 | 3.97 | 10.95 | 0.025 |
| **s(human encounter rate at 1200 m)** | 3.26 | 4.02 | 6.46 | 0.170 |

| | | | | |
|---|---|---|---|---|
| **s(NDVI at 100 m)** | 3.18 | 3.95 | 5.72 | 0.190 |
| **s(elevation at 1200m)** | 3.41 | 4.13 | 9.37 | 0.089 |

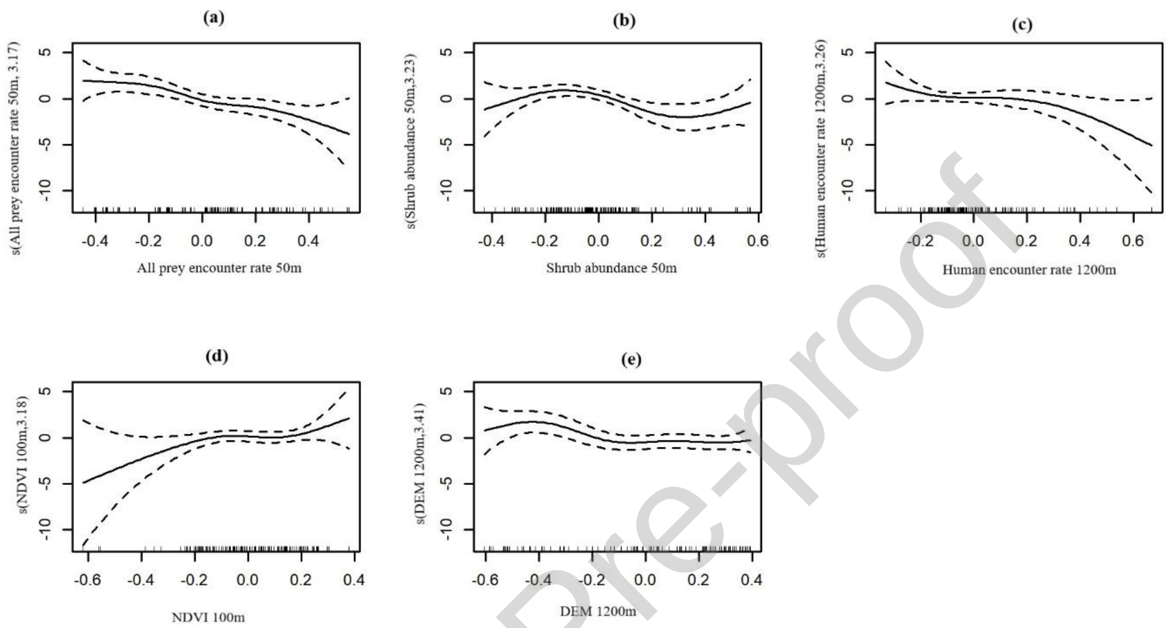


**Fig. 3.** Partial effect plots for livestock kill by tiger in Panna Tiger Reserve: a) all prey encounter rate (50m), b) shrub abundance (50m), c) human encounter rate (1200m), d) NDVI (100m), e) elevation (1200m). The dashed line represents 95% confidence interval, and the lines on x axis represent the frequency of data.

The effective degree of freedom (edf) is higher than 3 for most of the smooth terms, indicating that the wiggliness is high and relationships are nonlinear (Table 1). Even more is revealed by examining the partial effect plots of smooth terms, also called rug plots. A partial effect plot shows the effect of an explanatory variable on the response variable after accounting for the effects of all the other variables included in the model. Upon examining the partial effect plot for all prey encounter rate, we found that it has an inverse relationship with log odds of livestock kill i.e., the odds of livestock kill by tiger are higher when prey is low (Figure 3 a). In case of shrub abundance, we observed a unique trend, log odds of livestock kill increase with shrub abundance but only till it reaches a certain mark, after which increase in shrub abundance seems to reduce the odds of livestock kill (Figure 3 b). NDVI, human encounter rate and elevation, as also indicated by their chi-square p values, do not seem to have a significant relationship with the odds of livestock kill (Figure 3 c, d, e).

The deviance explained by the model was 44.4%, and AUC of the model was 0.91. When run on the test dataset, the model accuracy was calculated to be 0.65 (Table 2), and AUC was found to be 0.70, indicating that the model had fair amount of prediction capability.

**Table 2:** True skill statistic of final geoGAM model predicting livestock predation by tiger (run on test dataset)

| Statistic | Value |
|---|---|
| **Accuracy** | 0.65 |
| **95% CI** | 0.52-0.77 |
| **Kappa** | 0.30 |
| **Sensitivity** | 0.61 |
| **Specificity** | 0.69 |
| **Positive Predicted Value** | 0.66 |
| **Negative Predicted Value** | 0.65 |
| **Prevalence** | 0.49 |
| **Detection Rate** | 0.30 |
| **Detection Prevalence** | 0.46 |
| **Balanced Accuracy** | 0.65 |

## 4. Discussion

Spatial modelling of HCC has enabled conservationists to visualise where the risk of conflict is high and requires mitigation (Kaartinen et al. 2009; Treves et al. 2011; Zarco-González et al. 2013; Amirkhiz et al. 2018; Broekhuis et al. 2017). Potential habitat/environmental factors identified as drivers of conflict risk can help reduce conflict potential, and design targeted mitigation measures (Behdarvand et al. 2014). However, spatial modelling should consider scale/resolution of the data and spatial autocorrelation. In the absence of which, model results can be unreliable leading to inaccurate identification of HCC drivers and the resultant conflict risk.

Habitat factors that structure the carnivore use of an area are likely to dictate livestock kill by the carnivore and, thereby, HCC. Preferred habitat parameters for tiger have been identified mainly as high prey density, forest contiguity, thick understory, proximity to water, and low human disturbance (Miquelle et al. 1999; Karanth and Sunquist 2000; Sunarto et al. 2012). Among these, past studies have linked HTC with tree cover, elevation/altitude, slope, aspect, proximity to reserve forest, proximity to water, distance to village, distance to road, and density of livestock, settlements, and roads (Li et al. 2009; Ahmed et al. 2012; Soh et al. 2014; Miller et al. 2015; Rostro-García et al. 2016; Struebig et al. 2018; Ramesh et al. 2020). Our spatial modelling revealed that the potential ecological drivers of livestock depredation by tigers in Panna Tiger Reserve were prey, and shrub, at a fine scale, i.e., 50m which is the mean drag distance of kill by tigers in tropical landscapes (Karanth and Sunquist 2000). Miller et al. (2015), while studying livestock predation risk by tigers in India, also found that the fine-scale model (20m) performed the best (among the three spatial scales viz. 20m, 100m, and 200m at which they measured vegetation structure). They concluded that fine spatial grain risk models are more accurate in predicting human-carnivore conflict. And although Rostro-García et al. (2016) while examining livestock depredation by tiger and leopard in Bhutan tested all their variables at five scales, and found that vegetation cover was more influential at a broader scale (2000m), they concluded that scale optimization improves modelling results with multiscale model performing better than single-scale model. Albeit our modelling results also reveal that both the predictors were operating at a fine scale. It should be emphasised that since we tested each variable at multiple scales, our multiscale model is more reliable than the single scale models or models that did not consider scale, employed by past studies on HTC (Li et al. 2009; Ahmed et al. 2012; Soh et al. 2014; Struebig et al. 2018; Ramesh et al. 2020).

Our model suggests that when prey encounter is low at fine scale (50m), i.e., tiger encounters less prey, it is more likely to predate upon domestic livestock. Low availability of prey has been linked with livestock depredation by carnivores, including tiger (Fritts et al. 2003; Bhattarai and Fischer 2014; Burgas et al. 2014; Khorozyan et al. 2015). Moreover, vulnerability of prey influences predator choice (Greene 1986; Onkonburi, and Formanowicz' Jr 1997; Provost et al. 2006; Cresswell et al. 2010). Predators are known to select a kill that is easier to catch (Mueller 1977; Lang and Gsödl 2001; Weise et al. 2020). Livestock, having lost most of their anti-predator behaviour during the domestication process are vulnerable to becoming easy prey for predators in the absence of human herders (Linnell et al. 1999; Laporte et al. 2010; Flörcke and Grandin 2013; Weise et al. 2020). Thus, in predator-occupied habitats where there is low availability of wild prey if the optimal foraging theory (large prey, high in abundance, easy to catch) is applied (Emlen 1966; MacArthur and Pianka 1966; Werner and Hall 1974), the tiger kills what it can with least effort i.e., livestock.

Shrub abundance, the second explanatory variable (also selected at 50m scale), seems to have a unique relationship with livestock kill, increase in shrub abundance increases the odds of livestock kill up to a certain point after which increase in shrub abundance decreases the odds of livestock kill. Although it is difficult to explain such a complex relationship, it can be examined in the light of predation technique of tigers. Tiger is an ambush predator therefore, in areas where there is very low cover, it might be very difficult to make a kill, but in areas where cover is high, the chances of success may improve (Greene 1986; Murray et al. 1995; Karanth and Sunquist 2000; Sunquist 2010). Studies on tiger and other carnivores have also found that livestock predation risk was higher in habitats with high shrub density because it provides cover for these predators (Davie et al. 2014; Miller et al. 2015). However, if the cover is too dense, grazers like livestock are also less likely to venture into such patches because they would be devoid of grasses. Thus, making the relationship curve between livestock kill and shrub cover, bell-shaped. Livestock kill by tiger is thus a culmination of predator choice and foraging tactics, and prey vulnerability and defence mechanism.

Therefore, from studying the ecological drivers of HTC in Panna Tiger Reserve, we inferred that in a predator-occupied habitat if prey availability is low at fine scale, domestic livestock availability is high, and ambush cover is available, the odds of a predator depredating livestock become high.

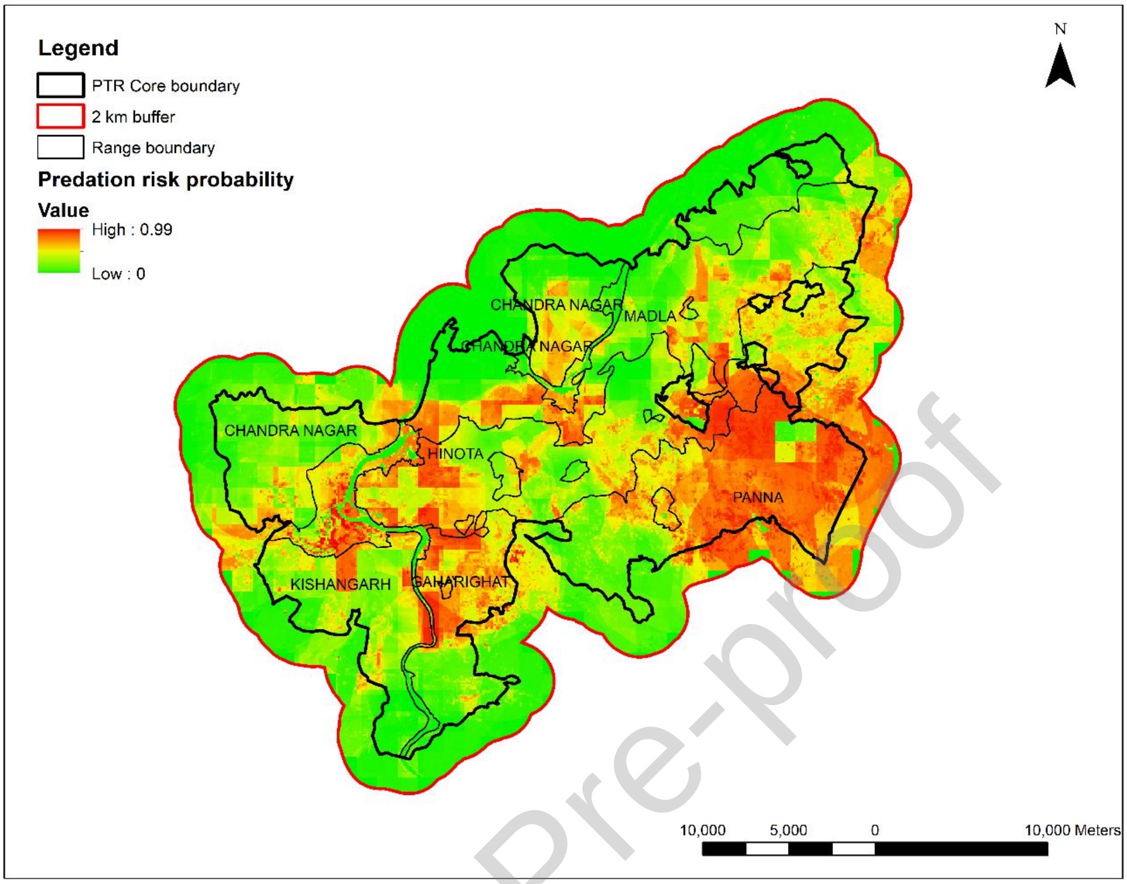


**Fig. 4.** Risk map depicting probability of livestock kill by tiger in Panna Tiger Reserve predicted employing geoGAM model

The risk map produced using spatial modelling shows that domestic livestock predation risk is higher in the south eastern part of the tiger reserve encompassing Panna Range and parts of Gahrighat Range (Figure 4). Preventative measures like fencing, viz. biofencing or electric/solar fencing (Distefano 2005; Sapkota et al. 2014), increased protection through livestock entry point monitoring and patrolling (Pettigrew et al. 2012), change in livestock husbandry and dependence, or village resettlement (Treves and Karanth 2003), education and awareness (Consorte-McCrea et al. 2017), should be focussed on the high-risk areas and villages in the proximity of these areas.

## 5. Conclusion

Ecological drivers of HCC are complex and scale dependent. The likelihood of conflict is high in a large carnivore habitat that has low prey encounter and an influx of domestic livestock. In case of Panna, we suggest that mitigation efforts should be focussed on the administrative units flagged as high risk by our study.

Furthermore, a detailed study should be conducted to understand the lower availability of wild prey and higher availability of livestock in certain parts of the reserve, based on which prey augmentation should be considered where required and deemed feasible.

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**Statements & Declarations**

**Data Availability Statement:** The datasets generated and/or analysed during the current study are available on public data repository figshare and can be accessed using the following link: https://figshare.com/s/a9cc82045fd2960f7c9d.

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**Declaration of interests**

☒The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

☐The authors declare the following financial interests/personal relationships which may be considered as potential competing interests: