DISTRIBUTION AND HABITAT USE OF TIGERS IN BHUTAN

NATURE CONSERVATION DIVISION

Department of Forests and Park Services

Ministry of Agriculture and Forests

2019

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Royal Government of Bhutan
Ministry of Agriculture and Forests
Department of Forests and Park Services
Thimphu

DIRECTOR

FOREWORD

The Department of Forests and Park Services conducted the National Tiger Survey in 2014 and 2015 which was expansive and yielded huge information on the wide array of wildlife besides tiger. The photographic records of tigers were analyzed using robust analytical method producing the estimates of tiger density and abundance in Bhutan. This information became critical and in concordance to our commitment to the 2010 St. Petersburg Declaration, gave us a platform to understand the status of the tiger in Bhutan.

The first report on the National Tiger Survey produced information on the number of tigers and the total population in Bhutan. This report contains information other than abundances such as distribution, the probability of habitat use and the relationship between environmental or anthropogenic variables and tiger habitat use. This report was also motivated by the need of producing a fine-scale predictive probability map and a distribution map of tigers in Bhutan.

The report will serve as a guiding document for land-use planning and management in Bhutan. It contains information both on the distribution and predictive habitat use. Often, we come across an idiosyncratic field situation where the balance between conservation and development have to be struck. In such cases, the information on the distribution and habitat use of umbrella species such as tiger will guide the placement of infrastructure obviating the jeopardy between conservation and socio-economic development.

I congratulate and thank the Nature Conservation Division for making use of the data and producing additional information on tigers in Bhutan. Further, I also thank the field crews who painstakingly conducted the field survey and collected data during the year 2014 and 2015. I am happy that our effort to protecting expansive forest at the helm of benevolent monarchs is paying dividends as apparent from the tiger distribution map and thus getting a step closer to fulfilling our commitment to double tiger numbers.

Tashi Delek!

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Ministry of Agriculture and Forests
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"Managing Bhutan's Natural Heritage"

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On behalf of the Department of Forests and Park Services, Nature Conservation Division would like to thank the donors: World Bank International Development Association, World Wildlife Fund Bhutan, Bhutan Foundation and Royal Government of Bhutan. The generous funding made the arduous field survey possible and kept the field crew motivated.

We thank Ugyen Wangchuck Institute for Conservation and Environmental Research and all the field offices for their support in course of fieldwork. We are grateful to Professor David Macdonald and Dr. Cedric Tan of Wildlife Conservation Research Unit, University of Oxford for providing feedback and for fruitful discussions. We also convey our gratitude to Mr. Sonam Wangchuk, CEO NRDCL (then CFO, WCD) and Mr. Sangay Dorji, NCD at whose helm the first ever comprehensive National Tiger Survey was a big success.

Finally, we thank all the field crew members who put in their strength and effort to collect and gather data for the first-ever national survey of the tiger which was a grand success of the Department. Not the least, the team members of the first report and analyses are gratefully acknowledged for successful publication of the report 'Counting tigers in Bhutan: Report on the National Tiger Survey of Bhutan 2014-2015' which formed the basis of this report.

Nature Conservation Division, 2019

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Executive Summary

Tigers are the largest extant felid, feared and revered. They have been an integral part of history and culture in Bhutan. The famous Indian saint Guru Padmasambhava (known as Guru Rinpoche in Bhutan) who brought Buddhism to Bhutan is said to have ridden a flying tigress in course of preaching Buddhism and subduing demons in the seventh century. Thus, tiger conservation in Bhutan has a strong religious bond and sentiment.

This report on the status and distribution of tigers in Bhutan is a supplement to the first report published in 2015. This report contains information on the distribution of tigers in Bhutan. It also has a spatial prediction of tiger distribution and habitat use derived from robust occupancy modeling techniques (both under maximum-likelihood and Bayesian frameworks as well as correction of spatial autocorrelation for spatial mapping). Further, the habitat suitability of tigers was assessed in relation to environmental and anthropogenic variables.

Independent observations of 311 tigers were made at 143 camera stations (out of 848 retrieved stations) over a total trap effort of 61476 trap days. The naïve occupancy was 0.169 (the number of camera stations with tiger capture divided by the total number of retrieved camera stations). The estimated occupancy probability is 0.31 (0.16 SD; meaning about 31% of the total geographical area, discounting areas above 4500m and high-density settlement, is a suitable tiger habitat). The protected areas have a higher probability of occupancy than the non-protected areas (Ψ_{PA} = 0.41 (0.14 SD) vs. $\Psi_{non\text{-}PA}$ = 0.25 (0.15 SD). This shows a higher habitat suitability inside protected areas but could change if adequate habitat and prey protection is provided in forested habitat outside the protected regime.

The important determinants of tiger habitat use are protected areas and adequate prey. These variables have a significant influence on the tiger habitat use with small standard errors and non-overlapping credible intervals. The habitat use increased with the increase in large prey abundance and decreased further away from the protected area edge. The protected area also includes the biological corridors which are under the management of territorial divisions. Other variables influencing the habitat use are distance to settlement and distance to the river. The habitat use probability increased farther from the settlement and huge river network. Most huge rivers in Bhutan are concentrated with settlements or are unsuitable for tiger use due to deep gorge or steep outcrops.

The spatial distribution map shows that the central, north-central, south-central, north-east, east and west part of Bhutan is occupied by tigers. It also predicted areas with the high potential of use by tigers which is important for dispersing tigers. The current stronghold of tiger habitat in Bhutan includes Royal Manas National Park, Jigme Singye Wangchuck National Park, Phrumsengla National Park, Jomotshangkha Wildlife Sanctuary, Zhemgang Division, Bumthang Division, Sarpang Division, Wangdue Division and Tsirang Division. The list is not exhaustive and final. We have evidence of tiger capture in Paro, Thimphu, Gedu, Samdrup Jongkhar, Jigme Dorji National Park, Wangchuck Centennial National Park, Sakteng Wildlife Sanctuary, and Phibsoo Wildlife Sanctuary. These areas also show the high potential of tiger habitat use (Appendix and Map plates) and therefore warrants equal protection.

This study assesses for the first time the relationship between tiger habitat use and environmental and anthropogenic variables in Bhutan. The prediction maps further to add on to the importance of having a spatially explicit map. Together these would help in land-use planning, resource management and implementation of conservation activities.

Chapter 1: Introduction

The tiger Panthera tigris is the largest extant felid species, feared and revered for its magnificence yet hunted and poached to the brink of extinction (Karanth, 2001). It is classified as endangered under the International Union for Conservation of Nature Red List of Threatened species and has suffered a collapse of 93% of range and 97% reduction in numbers in the last century (Goodrich et al., 2016; Karanth and Stith, 1999; Dinerstein et al., 2007). Asia's forests are amongst the most fragile and rapid economic development adds on to the immense pressure on consumer demand of wildlife products leading to increasing in the frequency of poaching (Linkie et al., 2018). Additionally, habitat fragmentation, loss of prey, isolation, anthropocentric mortality and genetic and demographic stochasticity as a result of human-induced disturbances add on to the risk of imminent extinction crisis (Smith, 1984; Karanth and Stith, 1996; Woodroffe and Ginsberg, 1998; Miquelle et al., 1999; Dinerstein et al., 2007; Goodrich et al., 2008; Borah et al., 2016; Wikramanayake et al., 2011; Thapa et al., 2017).

A landmark petition was signed by 13 tiger range countries during the 2010 St. Petersburg Declaration in Russia (World Bank, 2011) with the commitment to double tiger numbers by 2022. However, there is a dichotomy in opinions on how best to conserve tigers with the debate over the merits of protecting tigers in potential source sites (Walston te al., 2010) versus the landscape approach connecting source sites through corridors to main maintain contiguity (Wikramanayake et al., 2011). Kenney et al., (1995) further supported by Chapron et al., (2008) suggested that human-induced mortality was the main driver of tiger decline and that a female mortality rate of 15% can be deciding factor for long-term persistence in a landscape. Assessment of environmental variables influencing tiger habitat use or occupancy at the small scale has been conducted (e.g. Karanth et al., 2004) but little is known about the relative importance of environmental, biological and anthropogenic factors to tiger space use on a national scale.

In Bhutan, more than 50% of the total area is gazetted as protected (DoFPS, 2011), and there is a constitutional mandate to maintain 60% forest cover of the total geographical area in perpetuity (RGoB, 2008). This mandate is supported by well-developed forest laws and environmental legislation (RGoB, 1995). Adaptive management is implemented in protected areas to deliver the conservation of tigers and other wildlife. These are amongst the features contributing to Bhutan's fourth-ranked place in a global analysis of megafauna conservation (Lindsey et al., 2017). Although Bhutan's Tiger Action Plan (NCD, 2005) guides the management and conservation of tigers and their prey, a crucial unanswered question in Bhutan, as elsewhere, has been how tigers respond to environmental and anthropogenic variables (Wang et al., 2018). To address this question, this report quantifies the influence of environmental and anthropogenic factors on tiger habitat use and, based on the findings, propose strategic actions for tiger conservation in Bhutan. The findings and proposals have general relevance to tiger conservation throughout their range.

Use of occupancy models in ecology has increased manifold since it was proposed in the early 2000s by MacKenzie and colleagues (MacKenzie et al., 2002). The feat lies in the ability to account for imperfect detection, which in ecology is a form stochasticity and without correcting would lead to bias in occupancy estimates and spurious inferences thereof (MacKenzie et al., 2002, 2006). Failure to account for imperfect detection in occupancy models yields apparent occupancy rather than true occupancy (Kery and Schaub, 2012). For a better understanding of species distribution and their responses to changes in the surrounding (environmental and anthropogenic induced), a prerequisite to effective conservation planning, it is important to explicitly account for stochasticity using appropriate tools (Kery and Schaub, 2012; Kery and Royle, 2016). Spatial autocorrelation in occupancy models has been found to cause in confounding between predictors and latent process thus producing biased estimates (Hughes and Haran, 2013; Johnson et al., 2013). A new approach to occupancy modeling was developed by Johnson et al., (2013) which corrects for autocorrelation in observations and habitat variables and also accounts for imperfect detection. This report used spatial occupancy model accounting for spatial autocorrelation because of the non-independence between camera stations as there were repeated captures of the same tiger at multiple stations and the camera traps were close together as compared to the range of movement (i.e., home range radius; Mike Meredith, personal communication).

Monitoring of the number of tigers, their habitat use, and their prey provides essential information to conservation planners (Nichols and Williams, 2006). Recent advances in species distribution models in ecology provide conservation planners with new insight (Guisan et al. 2013). This report assesses the relationship between factors that influence habitat use of tigers using occupancy models corrected for spatial autocorrelation (Johnson et al., 2013), and predicted its habitat use distribution across Bhutan and for individual protected areas (hereafter PA) and territorial divisions (hereafter TD).

Chapter 2: Methodology

2.1. Study area

Bhutan is a small, landlocked country with a total geographical area of 38,394 km2. Nested in the eastern Himalayas, Bhutan shares international boundaries with the Tibetan Autonomous Region (China) to the north and India to the east, west, and south. Bhutan harbors rich floral and faunal diversity with estimated 5000 vascular plants, 200 mammals, and 700 bird species are reported (DoFPS, 2011). Forest cover constitutes c. 70% of the total geographical area (FRMD, 2017). Broadleaved forests constitute c. 45% and coniferous forests c. 25% of the total forest cover. Additionally, shrubs and alpines scrubs constitute c. 10%, thus taking total green cover to c. 80% (FRMD, 2017). The altitude ranges from less than 100m in the south to more than 7000m in the snow-capped mountains in the north. Four seasons are prominently observed in Bhutan (winter (December to February), spring (March to May), summer (June to August) and autumn (September to November)). The monsoon (rainfall) occurs between July to September and brings precipitation of about less than 100mm in the north to more than 5000mm in the sub-tropical region in the south. As per the recent population survey, the total population of the country is 779,665 (NSB, 2017).

2.2. Camera trap survey

The nationwide national tiger survey was conducted between March 2014 and March 2015 in two blocks, north, and south. The country was gridded with 1522 square cells of the size of 25 km2 to help guide placement of camera traps (Fig. 1). A total of 1129 camera stations (north = 681 and south = 448) were established discounting major settlement, huge river network, and areas above 4500m because these areas did not report any tiger evidence during the preliminary reconnaissance survey and the likelihood of capture was minimum. This grid size represents a little larger than average home range size of female tigers in India (Karanth et al., 2002). In each station, paired non-baited cameras facing each other and separated by 5m distance were placed at 45cm above ground to capture the left and right flanks of tigers. Five camera models were used during the survey (viz. BushnellTM, CuddeBackTM, HCO-ScountGuardTM, ReconyxTM, and U-WayTM). At every 30th day, monitoring was carried out to change batteries, clear bushes, replace memory cards and retrieve data. A minimum distance of 2km between camera stations was maintained in the context of impassable rivers and steep terrain. For logistical convenience, the country was divided into three regions (eastern, central and western) and three different teams deployed camera traps in those regions. In the south, camera traps were deployed for 141 days between March 2014 and June 2014 and in the north for 157 days between October 2014 and March 2015.

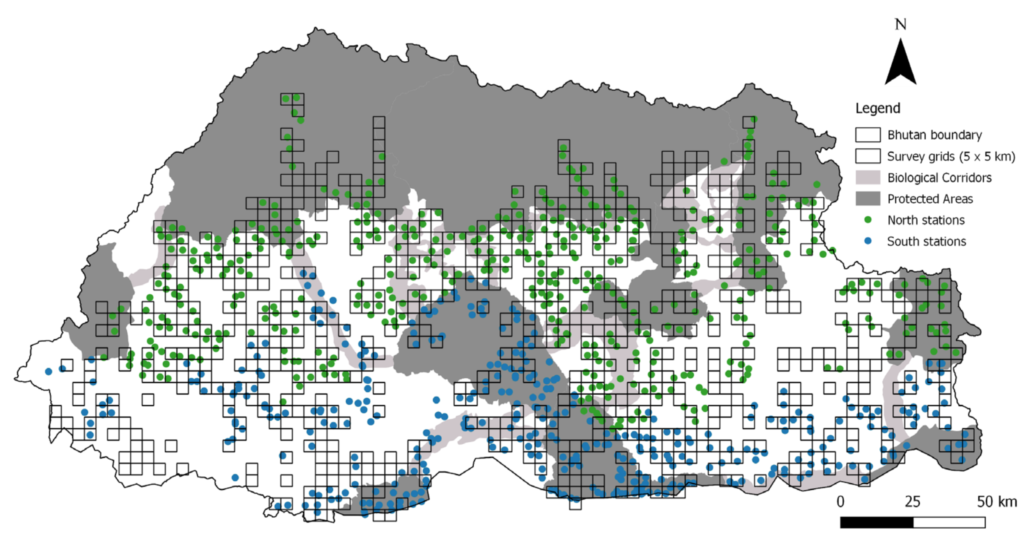

Figure 1: Survey design and grids for the National Tiger Survey 2014-15.

2.3. Environmental and anthropogenic covariates

Site covariates at the landscape-scale were selected based on a priori knowledge and previous studies on tigers (Karanth et al., 2004; Carroll and Miquelle, 2006; Karanth et al., 2011; Sunarto et al., 2012; Harihar and Pandav, 2012; Thapa and Kelly, 2017). The site covariates were classed into anthropogenic and environmental categories. The hypothesis was that the probability of occupancy of tigers may be influenced by these variables at varying degrees at each site (i.e. camera station). Environmental variables included in the modeling were relative abundance of large prey species (PREY; sambar deer Rusa unicolor, wild boar Sus scrofa), forest cover (Global Forest Change (GFC) at different thresholds, (Hansen et al., 2013) and Vegetation Continuous Field (VCF; DiMiceli et al., 2011), distance to river (DRIV), slope (SLO), elevation (ELE) and distance to protected area (DPA). A 30-m resolution GFC layer for the year 2014 (coinciding with the year of camera trapping exercise) was used to test for the effect of forest cover on occupancy probability. We have the liberty to define the percentage of tree cover to be considered as a forest with GFC layer and for our analysis, we tested four thresholds of 30%, 50%, 75% and 90% independently on occupancy probability. These thresholds were tested to avoid subjective selection of forest cover because during the camera trapping exercise, forest cover data was not collected uniformly. Further, the effect of a 250-m resolution VCF forest cover data on occupancy was also tested but was highly correlated with GFCs and did not perform better than GFCs in the univariate modeling. The anthropogenic variables included distance to settlement (DSET), distance to the logged forest (DLOG) and distance to road (DROAD). All the site covariates values were continuous variables generated using the Euclidean distance tool in ArcGIS 10.2 (ESRI, 2010) at 90m resolution. Each covariate value was the mean of pixel values (raster cells) within varying buffer distances (500m, 1km, 2km, 3km, and 5km) of each camera station (radii around camera station). These radii were chosen to represent average site characteristics surrounding each camera station. The covariates were rasterized to the resolution of 90m and distance metrics were generated using Euclidean distance tool in ArcGIS (ESRI, 2011). Territorial divisions are management areas outside PAs where timber extraction and other developmental activities are not restricted as compared to PAs.

2.4. Detection covariates

Imperfect detection is an inherent problem in ecological studies where animals present is not always detected (MacKenzie et al., 2002) and direct inference on occurrence from the observational data is not feasible (Royle and Dorazio, 2006). Failure to account for imperfect detection (or false absence) in occupancy models may result in spurious estimates (MacKenzie et al., 2002, 2006) and will underestimate occupancy when $p < 1$ (Kéry and Schaub, 2012) which is common for low density carnivores such as tigers (Lynam et al., 2009). This analysis assumed that the observation process was imperfect owing to the fact that different camera models (CAM) have different operative capabilities and resistance to environmental stochasticity thus producing nuances in capture success. Because the cameras were installed by different teams (TEAM), it was assumed that the variability in detection processes that may arise due to the difference in skills in handling camera traps and choices of spots to establish stations based on field experiences (effectiveness of camera placement). Not all the cameras at all stations were functional for the entire study period. Some were lost to animal vandalism while others were lost to theft and mechanical malfunction. Thus, detection was modeled as a function of the number of active camera trap days (EFFORT).

2.5. Occupancy modelling framework

Detection/non-detection data for each camera station was binned into 7-day, 10-day, 12-day, and 15-day per sampling occasion survey replicates (x replicates per site) instead of using per day occasion. This was further tested to select the best sampling occasion (supporting information). Collapsing 120 days into different sampling occasions helped to reduce the number of zeros and improved detection probability. It is important in occupancy modelling that we consider population closure or the constant state of occurrence (i.e. there is no death, birth, immigration or emigration) during the study period and no false identifications are made for the focal species (i.e. no false positives) (MacKenzie et al., 2002, 2006; Kéry and Schaub, 2012). This assumption was accounted in our study by taking only first 120 days of capture period for each camera stations for analysis and animal identification was authenticated using the camera trap images. Since the data came from two different years (March – June 2014 and October 2014 – March 2015), the occupancy probability is interpreted as the proportion of area used by tigers (Wang et al., 2018) because tigers might have moved in and out of the sampling sites thus violating the geographic closure assumption which is typical of occupancy models (MacKenzie et al., 2002).

Occupancy models are hierarchical in nature in the sense that there are two processes we need to estimate (i.e. ecological/unobserved and observation processes; MacKenzie et al., 2002, 2006; Royle and Dorazio, 2008). The ecological process is the state of occurrence and observation process is the actual observation we make (Kéry and Schaub, 2012). We modelled the true occurrence of the tiger (z_i) as a latent, partially observable state variable, such that $z_i = 1$ if a tiger was captured at site i in at least one of the two camera traps during the sampling occasion j and is zero ($z_i = 0$) otherwise. We describe this ecological process underlying the true pattern of occurrence as a Bernoulli random variable with a parameter ψ_i, the probability of occupancy at a camera station i and the likelihood of occurrence was defined as $z_i \sim \text{Bernoulli}(\psi_i)$. Occupancy models can be extended to accommodate the effect of measured covariates and deterministic and/or stochastic mechanisms in order to improve inferences on occurrence and site use probability (MacKenzie et al., 2002, 2006; Kéry and Schaub, 2012).

Prior to modelling, all continuous site covariates were standardized by subtracting the individual value by its arithmetic mean and dividing this value by the standard deviation to facilitate model convergence and reduce computational runtime (centered and scaled to have a zero mean and unit standard deviation). Categorical covariates such as camera models and survey teams were converted into integers for analytical convenience. Test for collinearity was performed using Pearson's correlation and any pair-wise combination of $|r| \geq 0.6$ was considered strongly correlated. We retained only one covariate from the correlated pairs whose performance in the univariate occupancy models was better (low AICc) than others for the multivariate modelling.

The two-staged process to multivariate modelling under a maximum likelihood framework was adopted. First, the detection probability was modelled, keeping occupancy constant, using the detection covariates. After fixing detection probability with best detection covariates, occupancy was modelled using all possible combination of uncorrelated variables in an additive manner (no interaction terms were tested). Single-season, single species occupancy models (MacKenzie et al., 2002, 2006) were constructed using the package "unmarked" (Fiske and Chandler, 2011) to estimate maximum likelihood probability of habitat use while accounting for imperfect detection in R (R Core Team, 2018). Model comparison for models with uncorrelated variables was made using the package "AICcmodavg" (Mazerolle, 2015). We considered models within delta AICc score of 2 to be most supported by the data (Burnham and Anderson, 2003).

To assess the magnitude and direction of covariates on the tiger habitat use, the best model from the maximum likelihood estimates was fitted under the Bayesian framework in the software JAGS v 4.3.0 (Just Another Gibbs Sampler; Plummer, 2013) called through R (R Core Team, 2018) using the package 'jagsUI' (Kellner, 2015). The priors used for the intercepts and parameters were weakly informative vague priors so as to not to constrain the posterior estimates. The model was fitted using Markov Chain Monte Carlo (MCMC) simulations to estimate the posterior distributions. The posterior distributions of the parameters were generated by running three parallel MCMC chains of 30000 iterations each, setting the number of adaptations to 10000 (Meredith, 2016), discarding first 10000 as a burn-in and thinning the chains by one. The model convergence was assessed using the R-hat statistics (i.e. all values were < 1.1; Gelmen and Hill, 2006). Further, trace plots were also used for the visual examination of chain convergence (i.e. convergence would yield plots with 'grassy' appearance; Kery and Royle, 2016). Only those covariates whose 95% CRI (Bayesian credible interval) did not include zero was considered significant to tiger habitat use (Kery and Schaub, 2012).

For predictive mapping, the covariates in models within delta AICc 2 score from the maximum likelihood analysis was tested for spatial autocorrelation using the package "stocc" (Johnson, 2015). Spatial autocorrelation was corrected under the hierarchical Bayesian framework with the inclusion of the spatial parameter. This framework employs restricted spatial regression (RSR) approach to estimate occupancy probability and uses probit link formulation which is computationally efficient (Johnson et al., 2013). To detect the spatial correlation between neighbouring sample locations, we set the distance threshold to 8 km based on the average home range size of female tigers and spatial distribution of camera stations assuming that captures of tigers in camera traps within this distance exhibit spatial autocorrelation (Karanth et al., 2002). A gamma prior ($\tau \sim 0.5, 0.0005$) distribution was specified for the spatial component following Johnson et al., (2013). The moran.cut for the spatial model was 10% of the number of sites (Hughes and Haran, 2013). Moran.cut parameter in the model controls the number of spatial components used and can be interpreted equivalent to the correlation coefficient for the correlation in the site use (Johnson et al., 2013). Gibbs sampler for the spatial occupancy model was allowed to stabilize after 70000 iterations and discarding 10000 iterations as burn-in. Non-spatial model in the Bayesian framework with the same number of iterations, thinning and burn was run and the model fit was assessed using posterior predictive loss criterion (PPLC) between the spatial and non-spatial model (Johnson et al., 2013). Chain convergence was visually inspected from the trace plots. We used the parameter estimates from spatial occupancy model for predicting tiger habitat use and distribution across Bhutan.

Chapter 3: Results

In total, 311 independent observations of tigers were made at 143 stations (out of 848 stations) over a total trap effort of 61476 trap days. The naïve habitat use was 0.169 (i.e. detections in camera stations divided by the total number of camera stations). The number of trap days per camera station ranged from 1 to 120 days. From the correlated forest cover variables, univariate models revealed that GFC at 30% threshold within 3km buffer distance of camera station (spatial scale) performed better and was thus retained for further analyses.

The best detection model included camera and team covariates (Table 1 and 3). The detection probability varied between teams and camera models (Table 3). The occupancy covariates within delta AICc 2 score included in the final model were forest cover at 30% threshold at the spatial scale of 3km (GFC30), distance to river at the spatial scale of 5km (DRIV), distance to settlement at the spatial scale of 5km (DSET), distance to protected area at the spatial scale of 5km (DPA), elevation at the spatial scale of 2km (ELE) and large prey abundance (PREY; Table 2). The goodness-of-fit test of this multivariate model showed no evidence of overdispersion (c-hat = 0.68, p-value = 0.56). When analysed in the Bayesian framework for spatial prediction, the spatial model was a better fit than the non-spatial model (PPLCspatial = 420.77 vs PPLCnonspatial = 453.27). This shows that a random spatial effect contributed to the model uncertainty. The spatial variance parameter was not far from zero (posterior 95% credible interval of 0.03 – 0.13) thus implying that spatial effect contributed to habitat use variability.

Table 1: Detection probability models p(.).

Model	AICc	ΔAICc	AICc Wt	-2LogLik	K
CAMERA + TEAM	1691.22	0	0.65	-841.59	4
CAMERA + TEAM + EFFORT	1692.94	1.72	0.28	-841.44	5
Null	1714.96	23.74	1	-855.47	2

Covariates are different camera models (CAMERA), different survey teams (TEAM) and total number of active camera-trap days (EFFORT). AICc, Akaike information criterion corrected for small sample size; ΔAICc, relative difference between AICc of subsequent models compared to the top model; AICcWt, AICc weight and K, number of parameters. Occupancy was held constant ψ(.).

The results for the best model fitted under Bayesian framework are showed that increase in large prey abundance had a strong positive influence on tiger habitat use (β = 0.49) while the habitat use probability decreased sharply with increasing distance from protected areas (β = -0.72). These effects were highly significant based on the 95% credible interval (CRI) (zero excluded; Table 3). Tiger habitat use increased with increase in distance from the river (β = 0.13) and increase in distance from settlement (β = 0.18), however, the effects were not very strong because the 95% CRI overlapped zero.

The spatial habitat use model showed a positive relationship with increased forest cover, farther distances from the settlement and increased elevation (Table 4). However, the effects were not strong with credible intervals overlapping zero (Table 4). The mean habitat use probability (Ψ) from the spatial model estimated at 0.31 (0.16 SD). The probability of habitat use was higher in the PAs than TDs (Ψ_{PA} = 0.41 (0.14 SD) vs. Ψ_{TD} = 0.25 (0.15 SD)). The habitat use probability for individual PAs and TDs are given in the annexure.

Table 2: Multivariate model selection of tiger habitat use probability in Bhutan.

Model	AICc	ΔAICc	AICc Wt	-2LogLik	K
PREY + DPA + DRIV + DSET	1638.8	0	0.3	-810.29	9
GFC + PREY + DPA + DRIV + DSET	1639.17	0.37	0.25	-809.46	10
GFC + PREY + DPA + DRIV + DSET + ELE	1639.52	0.72	0.21	-808.6	11
PREY + DPA + DRIV	1640.51	1.7	0.13	-812.17	8
PREY + DPA + DRIV + DSET + ELE	1640.68	1.87	0.12	-810.21	10
Null	1714.96	23.74	0	-855.47	2

Models strongly supported by the data (ΔAICc < 2) are shown in comparison to null model. Site covariates tested were prey abundance (PREY), distance from protected area (DPA), distance from river (DRIV), distance from settlement (DSET), forest cover at 30% threshold (GFC), elevation (ELE), slope (SLO), distance from logged forest (DLOG) and number of staff per km2 (STA). Detection model included significant covariates, p(CAMERA + TEAM). Null model = p(.) ψ(.).

Table 3: Parameter estimates of tiger habitat use and detection probabilities generated by hierarchical Bayesian models. The camera model HCO was fixed as reference because of highest number and survey team Central was fixed as reference due to highest number of camera stations fixed by Central team. Figures in bold indicate the non-overlapping on zero in 95% CRI.

Model	Covariate	Mean	SD	95% CRI		Rhat
				2.5%	97.5%	
Occupancy	Intercept	-0.86	0.15	-1.15	-0.55	1
	Prey	0.49	0.20	0.16	0.92	1
	Distance from protected area	-0.72	0.18	-1.09	-0.40	1
	Distance to river	0.13	0.11	-0.08	0.34	1
	Distance to settlement	0.18	0.13	-0.06	0.45	1
Detection	Intercept	-1.25	0.21	-1.66	-0.85	1
	Bushnell	0.36	0.30	-0.23	0.94	1
	Cuddeback	-0.77	0.32	-1.41	-0.14	1
	Panthera	-1.69	1.39	-4.92	0.56	1
	Reconyx	-0.21	0.26	-0.73	0.31	1
	Uway	-0.10	0.25	-0.60	0.39	1
	Eastern	-3.20	0.57	-4.44	-2.19	1
	Western	0.27	0.25	-0.23	0.76	1

Table 4: Parameter estimates (mean beta coefficients), standard deviation (SD) and 95% credible intervals (CRI) from spatial occupancy model for the tiger habitat use in Bhutan. These estimates were used for prediction mapping which correct for residual spatial autocorrelation. Figures in bold indicates that 95% CRI excludes zero.

Model	Covariate	Optimal scale (km)	Mean	SD	CRI	
					2.50%	97.50%
Detection	Intercept	-	-0.97	0.14	-1.24	-0.69
	Camera	-	-0.008	0.03	-0.06	0.05
	Team	-	0.12	0.06	-0.003	0.25
Habitat use	Intercept	-	-2.21	0.83	-3.88	-0.6
	Distance from protected area	5	-0.5	0.15	-0.82	-0.22
	Prey	-	0.43	0.17	0.15	0.8
	Distance to river	5	0.28	0.1	0.08	0.5
	Forest cover (GFC30)	3	1.03	0.95	-0.83	2.92
	Distance to settlement	5	0.2	0.11	-0.02	0.44
	Elevation	2	0.13	0.14	-0.13	0.4

The highest probabilities of occupancy were observed in Royal Manas National Park (Ψ=0.43 (0.14 SD)) and Jigme Singye Wangchuck National Park (Ψ=0.40 (0.20 SD)). The medium probabilities of occupancy were observed in Phrumsengla National Park, Jomotshangkha Wildlife Sanctuary, Phibsoo Wildlife Sanctuary, Bumthang Division, Sarpang Division, Samdrup Jongkhar Division, Tsirang Division, Wangdue Division and Zhemgang Division (Table A1 & A2). The lowest were observed in Bumdeling Wildlife Sanctuary, Jigme Dorji National Park, Jigme Khesar Strict Nature Reserve, Sakteng Wildlife Sanctuary, Wangchuck Centennial National Park, Dagana Division, Gedu Division, Mongar Division, Paro Division, Pemagatshel Division, Samtse Division, Thimphu Division and Trashigang Division (Table A1 & A2).

Chapter 4: Discussion

The best model for tiger habitat use when analyzed under Bayesian framework has two important covariates showing strong relationship: relative abundance of large prey and distance from protected area. Higher use probability is expected for areas with higher abundance of prey. The tigers preferred habitat inside protected area than outside showing decrease in use probability for the habitat farther away from protected area edge.

The spatial model for predicting tiger habitat use included the covariates; forest cover, distance to the settlement, distance to river and distance to the protected area. However, only three covariates had a significant association with habitat use. Of these, large prey abundance and distance to rivers were positively correlated with habitat use whilst distance to protected areas was negatively correlated with habitat use. Put simply, higher predictions of habitat use by tigers were shown in areas with abundant prey and farther away from a river, and this expectation was further increased when it is closer to protection (Fig. 3). The estimated habitat use was higher (almost the double) than naïve occupancy, emphasizing the importance of accounting for imperfect detection. The probability of detection differed between camera models. It also differed between teams, seemingly due to variation in field knowledge and experience.

As expected, tiger habitat use showed a positive association with large prey abundance. Tigers are known to be ecologically resilient species given adequate prey, space, and protection from poaching (Karanth et al., 2004; Chapron et al., 2008; Wikramnayake et al., 2011). Prey decline has been identified as the main factor causing tiger numbers to dwindle elsewhere (Hayward et al., 2007; Miquelle et al., 1996). Threats to prey include hunting, habitat fragmentation and competitive exclusion from grazing (Fleischner, 1994; Karanth, 2001; San Miguel-Ayanz et al., 2010; Wang et al., 2018). Therefore, we agree with and Karanth et al., (2004) Chapron et al., (2008) that protection of the tiger's prey is a prerequisite to sustaining tiger and prey numbers.

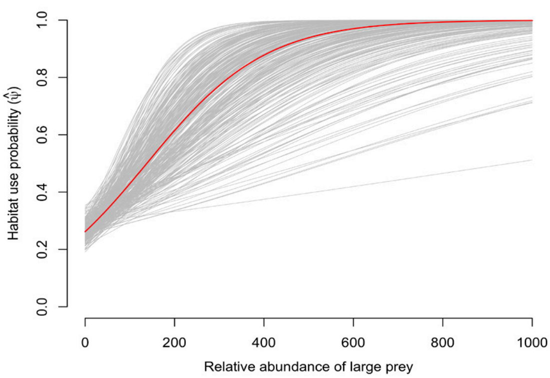

Figure 2: Relationship of tiger habitat use with large prey abundance. Posterior mean is represented by the red line and the gray lines represent the 95% Bayesian credible intervals from 300 random posterior samples.

Tiger habitat use decreased farther away from a protected area. This supports the proposition that protected areas, with their greater protection and law enforcement, are cornerstones of biodiversity conservation (Mace, 2014; Watson et al., 2016). In Bhutan, settlement density is comparatively low inside PAs and it is relatively easy to manage and implement integrated conservation and development programs. Bhutan is working on expanding the PA network to include more wild areas for conservation in spite of rapid socioeconomic development. This involves the usage of the forest natural resources and the development of co-benefit schemes such as carbon payments and ecosystem services (Wikramnayake et al., 2011; Joshi et al., 2013; Watson et al., 2014). 'Bhutan for Life' (BFL), initiated by the Royal Government of Bhutan, is one such financing mechanism for sustainable protected area management (RGoB, 2017). This approach requires adaptive management and accountability amongst relevant stakeholders (Harihar et al., 2017) and is intended to underpin wildlife conservation and natural resource management policy in Bhutan.

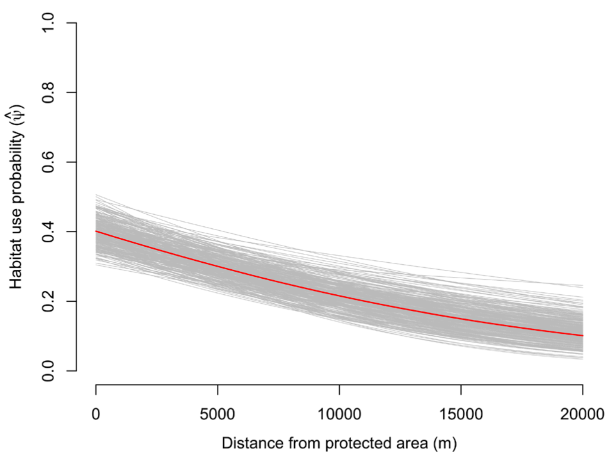

Figure 3: Relationship of tiger habitat use with distance from protected area. Posterior mean is represented by the red line and the gray lines represent the 95% Bayesian credible intervals from 300 random posterior samples.

Counter-intuitively, the tiger habitat use increased farther away from rivers. The river covariate used in the analysis was dominated by large river systems, most of which are dammed and tapped for hydroelectricity. Carnivores elsewhere have been shown to avoid such systems with heavy human activity (Seidensticker et al., 1999; Sunarto et al., 2012; Tan et al., 2017; Penjor et al., 2018). Generally, tigers are considered water-loving animals and spend most of their time close to small streams and rivers during hot, sunny days (Karanth, 2001). The avoidance of large, heavily managed rivers revealed by our analysis may also reflect the avoidance of settlement which is concentrated along the rivers in Bhutan. This was further supported by the relationship between habitat use and distance to settlement which shows that the probability of habitat use increased as the cameras were placed farther away from the settlement (Fig. 4). Tigers tend to avoid human interface and this easily explains that given adequate habitat, tigers would not come in conflict with humans. A similar finding was reported by Sunarto et al., (2002) where human-disturbance related variables negatively affected tiger habitat use. It is evident from the finding that when we have adequate forested habitat, tigers selected such habitats and remained away from the settlement. Our findings are further corroborated by the fact that this trend is not only at the local scale but at the landscape and or regional scale because the camera trapping survey in 2014-15 spanned the whole of the country.

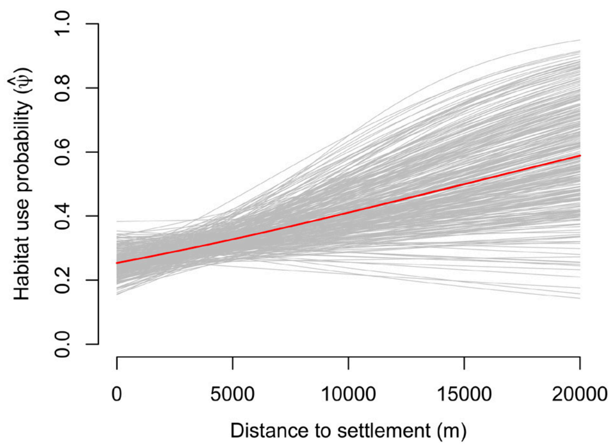

Figure 4: Relationship of tiger habitat use with distance to settlement. Posterior mean is represented by the red line and the gray lines represent the 95% Bayesian credible intervals from 300 random posterior samples.

4.1. Study limitations

In the absence of local home range data for tigers in Bhutan, the grid spacing of 25km2 based on the female home range in the plains of India (Karanth et al., 2002; Simcharoen et al., 2014; DoFPS, 2015; Tempa 2017). Insofar, this extrapolations between nations is inappropriate, there is therefore the risk of having more than one camera station within one tiger's home range leading to our estimates being more reflective of habitat use (proportion of area used at some point in time by a species) than of occupancy (proportion of area occupied by a species; MacKenzie and Royle, 2005; MacKenzie et al., 2002; 2006). Another limitation is that the covariates were derived from GIS-based data and not primary field data. The PPLC analysis favored the spatial model over the nonspatial one, but the performance of PPLC for hierarchical models has not been fully explored (Broms et al., 2014). Considering that PPLC does not indicate model fit, it is recommended the readers interpret the results with caution (Broms et al., 2014).

4.2. Methodological considerations

Further, the models highlight the need to account for spatial autocorrelation and imperfect detection, both of which are important in ecological studies to improve the predictive ability of the model. Finally, the effect of covariates at different spatial scales was tested. Apart from identifying correct factors, it is important to analyse scale effects in species-habitat relationship to have right understanding of the interaction between the species and considered parameters (McGarigal et al., 2016).

4.3. Management implications

The results show that tiger conservation in Bhutan is contingent on three factors: availability of large-bodied prey, protection of habitats, and increasing distance from huge rivers. Protected areas where the tiger was not captured during the survey nonetheless had a high probability of use (e.g. Jigme Khesar Strict Nature Reserve and Phrumsengla National Park). Tigers had been found in these parks previously. There are to possibilities two this: i.e. the tigers may be locally extinct from these two parks but have a high potential of recolonization and the survey may simply have missed them. Thus, future surveys should delve deeper into such observations. However, during the wildlife monitoring program, the tigers were captured in camera traps in the three parks across the country (Bumdeling Wildlife Sanctuary, Jigme Khesar Strict Nature Reserve, Phrumsengla National Park) after the survey. This shows that the survey duration was inadequate to capture all the tigers that were either transient or dispersing individuals in these parks. Tigers have relatively longer lifespan compared to other small felids and hence deploying camera traps longer than four months may not violate the closure assumption. For instance, it was observed that a camera trap installed in the Nganglam region of southern Bhutan did not capture tiger image during the survey period, but when the camera trap was left for longer duration on the same spot the tiger was captured (in the month of November, 2014 five months after the survey period). Such observations are important findings to guide future surveys.

Although some areas had high tiger captures, the probability of occupancy was low. For example, Paro Division, Thimphu Division and Jigme Dorji National Park had good number of tiger captures but the probability of occupancy was low. The reason could be attributed to low number of tigers (only dominant and territorial individuals) and unsuitable alpine and rocky outcrops. These habitats are suited for alpine dwelling species like snow leopards. Tigers on the other hand would require cover for hunting and concealing their kill.

This report can be supplemented with the National Tiger Survey Report 2014-2015 to guide in managing important tiger areas. We define important tiger areas as those areas which have high tiger density and high habitat use probability (refer NCD, 2015 or Figure 5 to see the areas of high tiger density).

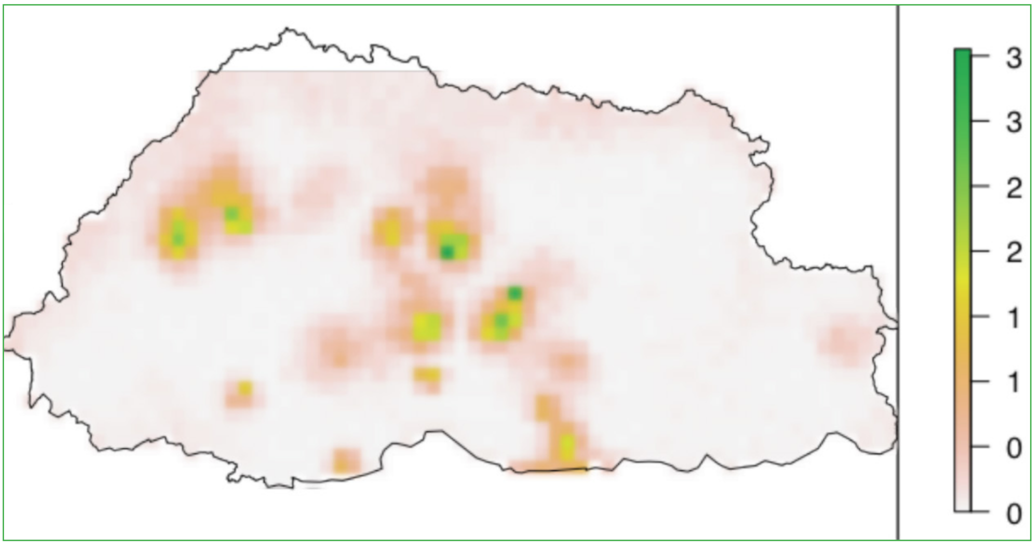

Figure 5: Density map of tiger in Bhutan (NCD, 2015)

In conclusion, the findings from this report indicate that Bhutan's policy of maintaining large protected landscapes connected via corridors is paying dividends, but in order to fulfill its capacity, more funding might be needed. The mountainous terrain requires copious 'boots on the ground' for effective patrolling to detect illegal activities and poaching. Protected areas such as Royal Manas National Park, Jigme Singye Wangchuck National Park, Jigme Dorji National Park and Phibsoo Wildlife Sanctuary and non-protected areas such as Sarpang, Tsirang, Zhemgang, Thimphu, Paro and Trongsa districts which have high tiger records require rigorous protection and are pivotal for long-term tiger conservation in Bhutan. The findings on the probability of habitat use by tigers can inform conservation planning, and the maps can be used to identify and designate areas of high tiger use and guide future land-use and management (Fig. 6). It is recommended that such findings may be used to guide the development and implementation of conservation action plans.

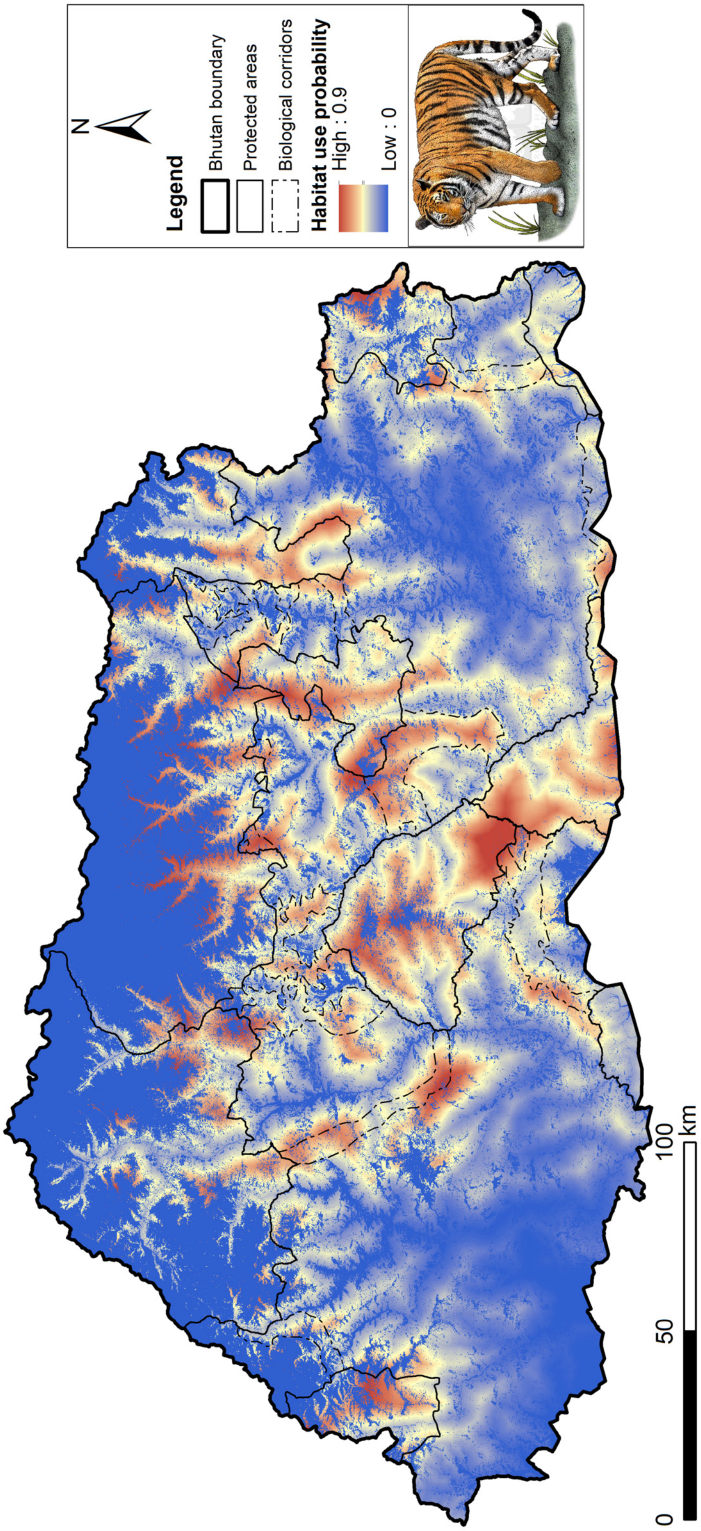

Figure 6: Landscape scale habitat use probability of tigers in Bhutan.

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Annexure

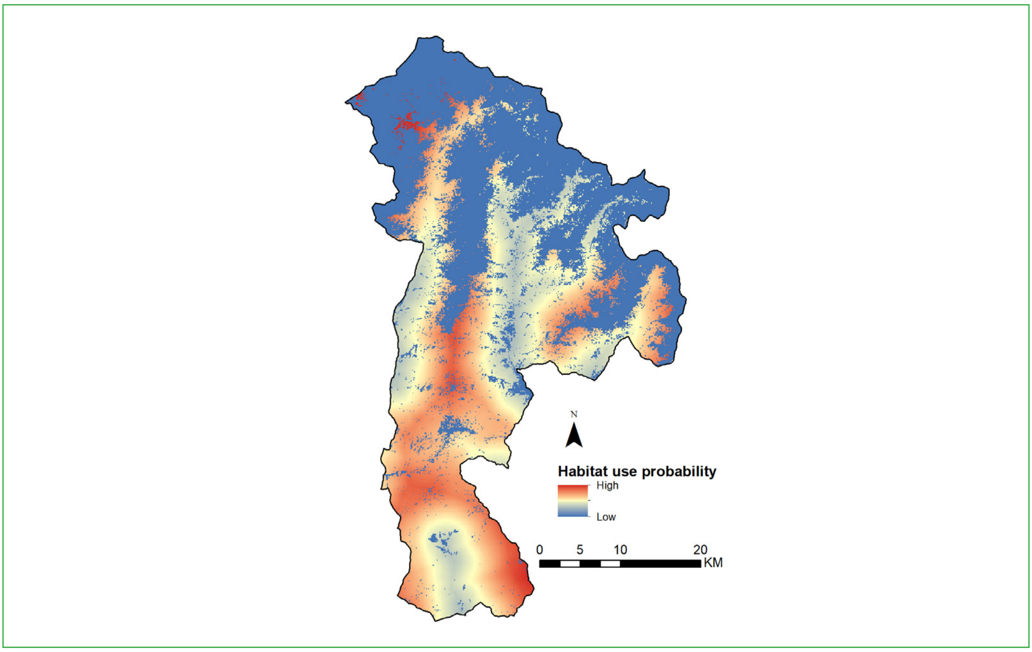
Table A1: *Mean (SD) habitat use probability of tiger in Protected Area.*

Protected area	Mean	SD
Bumdeling Wildlife Sanctuary	0.23	0.22
Jigme Dorji National Park	0.12	0.19
Jigme Khesar Strict Nature Reserve	0.27	0.25
Jigme Singye Wangchuck National Park	0.4	0.2
Jomotshangkha Wildlife Sanctuary	0.27	0.12
Phrumsengla National Park	0.39	0.18
Royal Manas National Park	0.43	0.14
Sakteng Wildlife Sanctuary	0.26	0.2
Wangchuck Centennial National Park	0.15	0.23
Phibsoo Wildlife Sanctuary	0.24	0.09

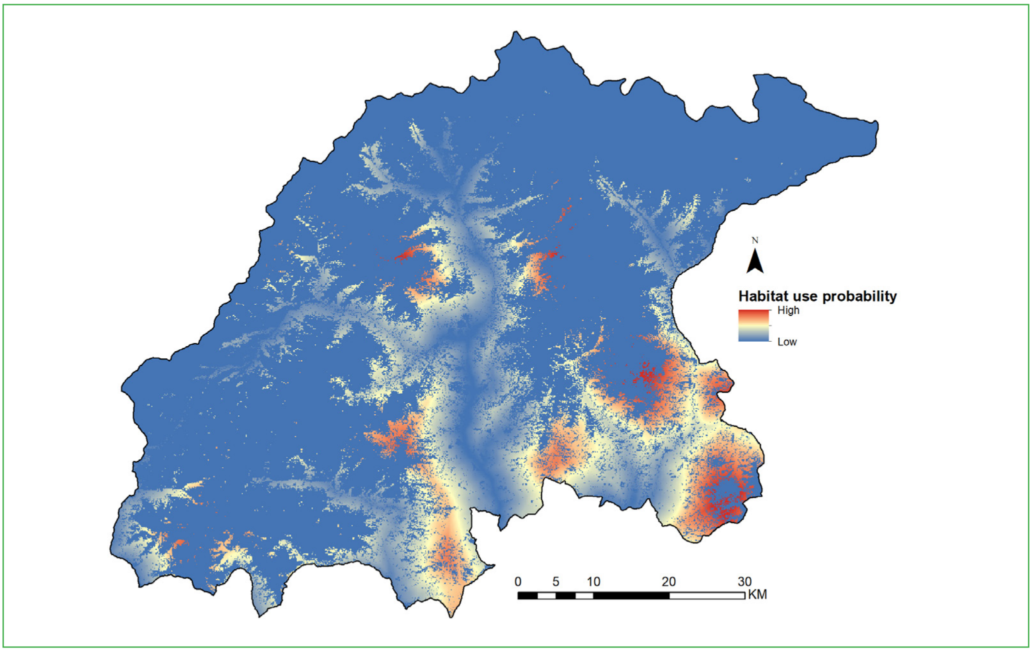
Table A2: *Mean (SD) habitat use probability of tiger in Territorial Division.*

Territorial Division	Mean	SD
Bumthang Division	0.3	0.2
Dagana Division	0.19	0.14
Gedu Division	0.07	0.06
Mongar Division	0.2	0.16
Paro Division	0.15	0.14
Pemagatshel Division	0.17	0.13
Samtse Division	0.07	0.07
Sarpang Division	0.28	0.17
Samdrup Jongkhar Division	0.2	0.11
Thimphu Division	0.17	0.16
Trashigang Division	0.18	0.15
Tsirang Division	0.26	0.16
Wangdue Division	0.28	0.19
Zhemgang Division	0.3	0.15

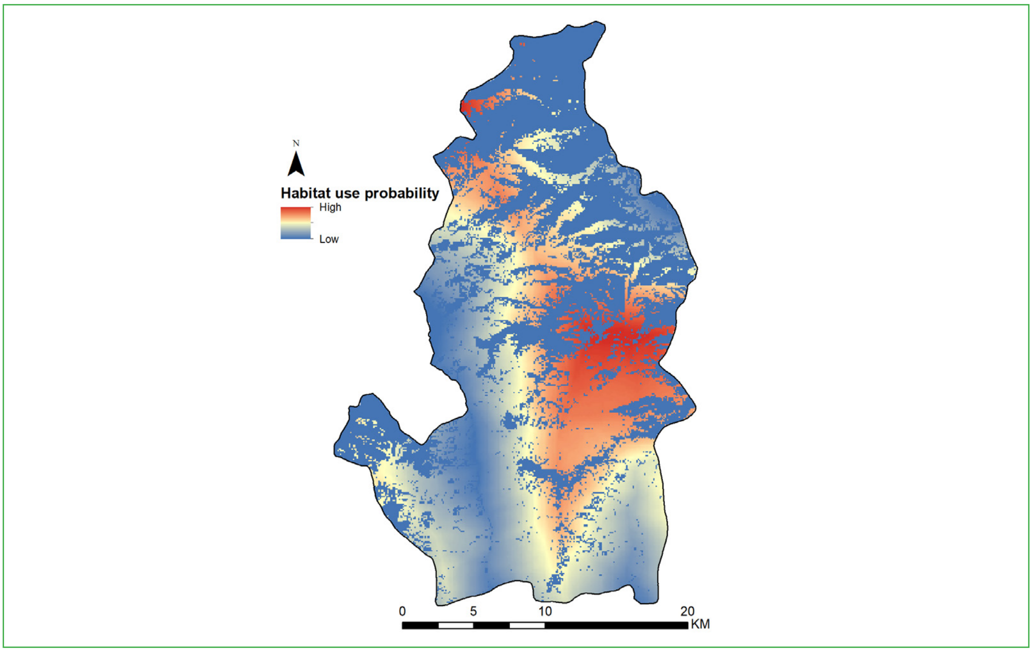
Map plates showing habitat use probability (suitability) of tiger in Protected Areas and Territorial Divisions.



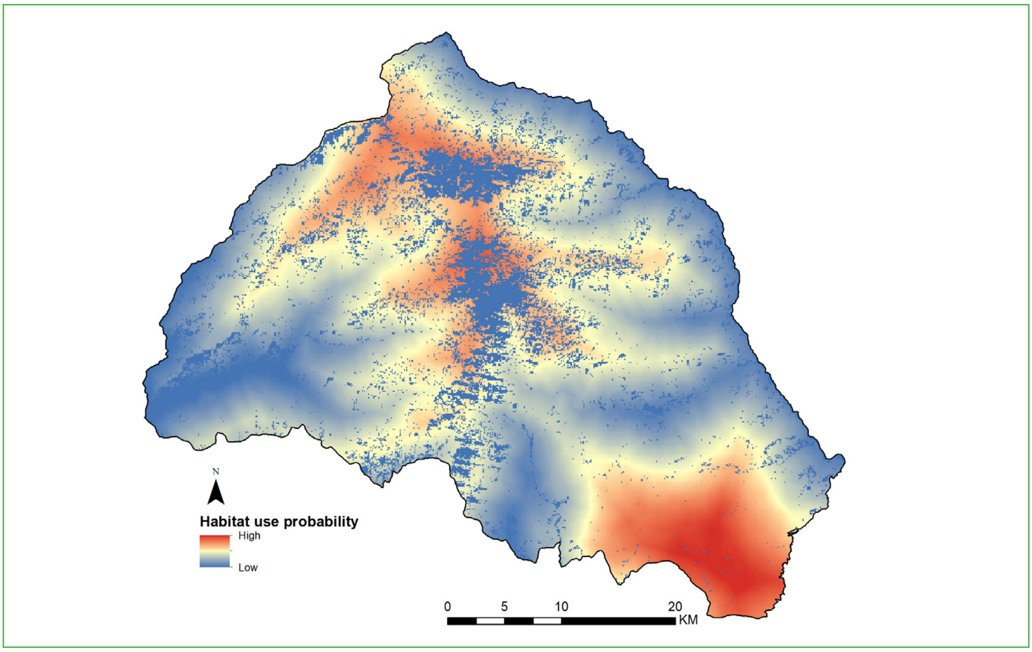
Map 1: Predicted habitat use probability of tiger in Bumdeling Wildlife Sanctuary



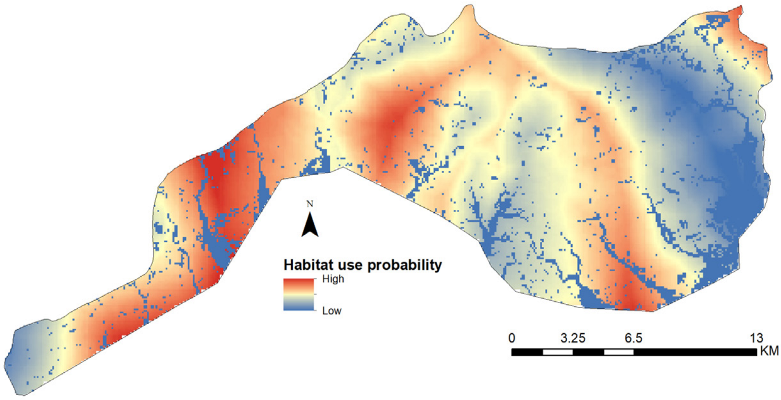
Map 2: Predicted habitat use probability of tiger in Jigme Dorji National Park



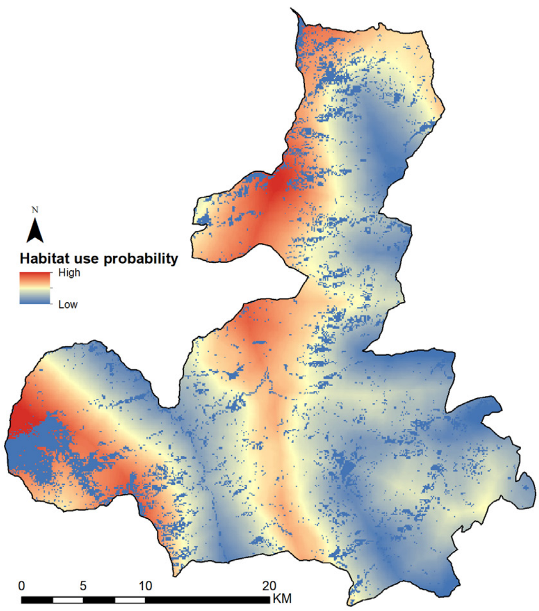
Map 3: Predicted habitat use probability of tiger in Jigme Khesar Strict Nature Reserve



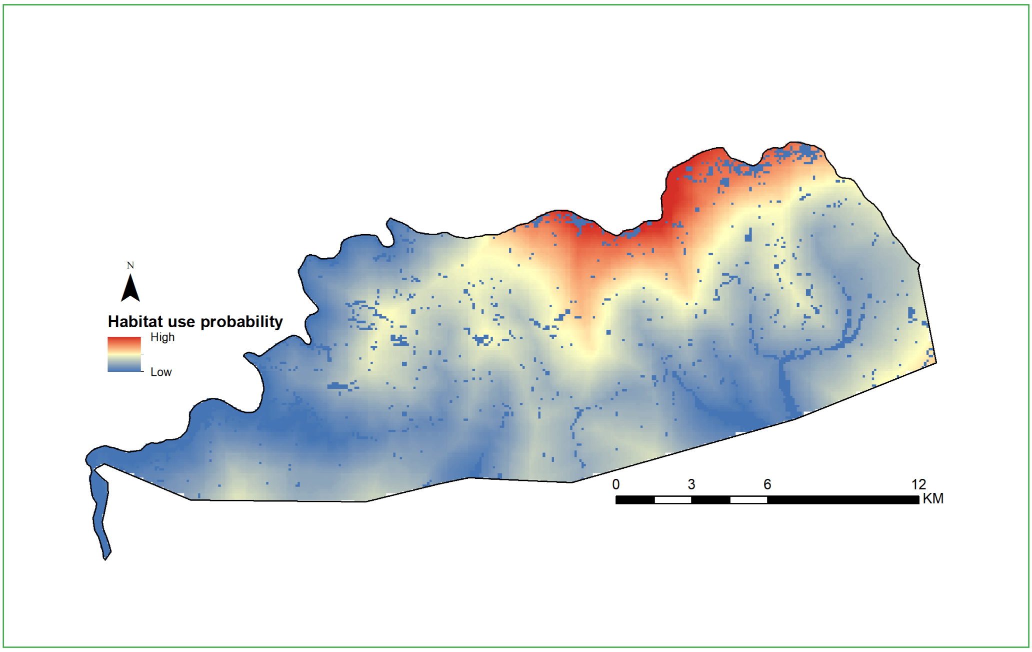
Map 4: Predicted habitat use probability of tiger in Jigme Singye Wangchuck National Park



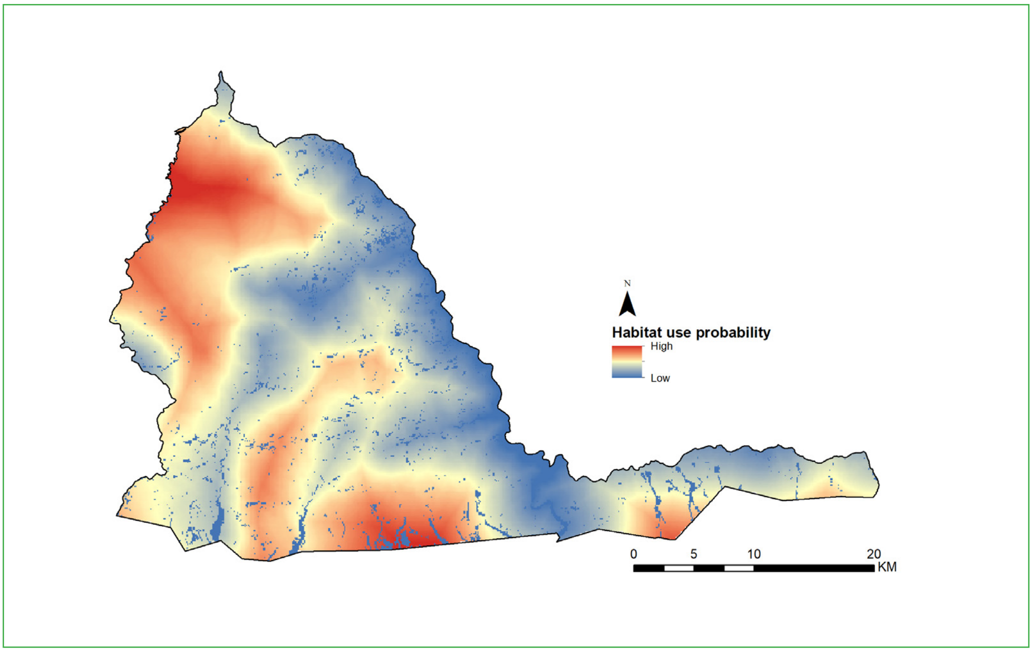
Map 5: Predicted habitat use probability of tiger in Jomotshangkha Wildlife Sanctuary



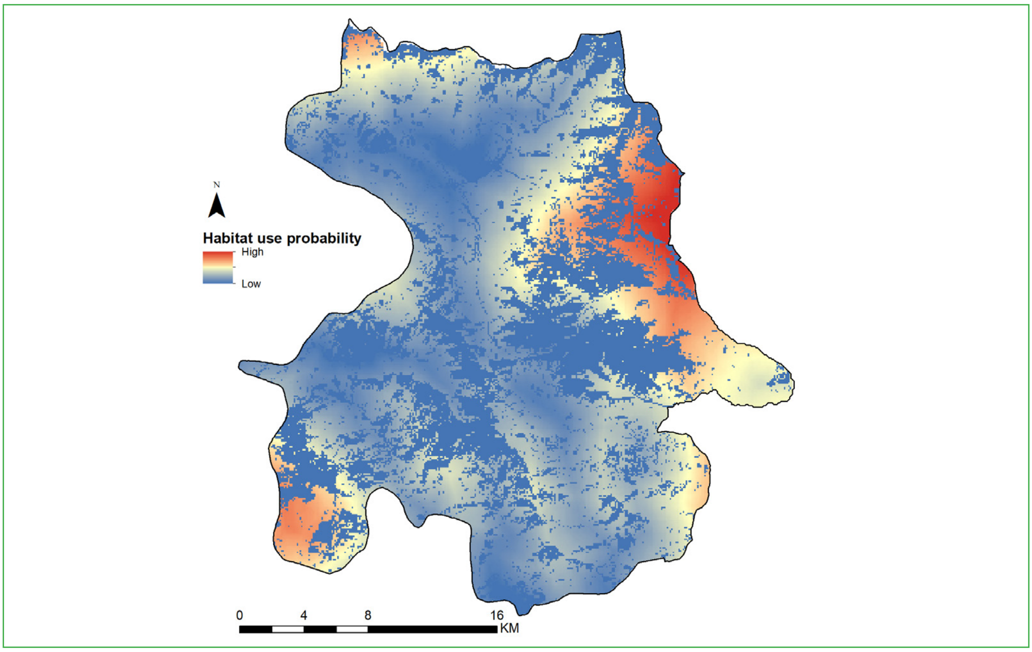
Map 6: Predicted habitat use probability of tiger in Phrumsengla National Park



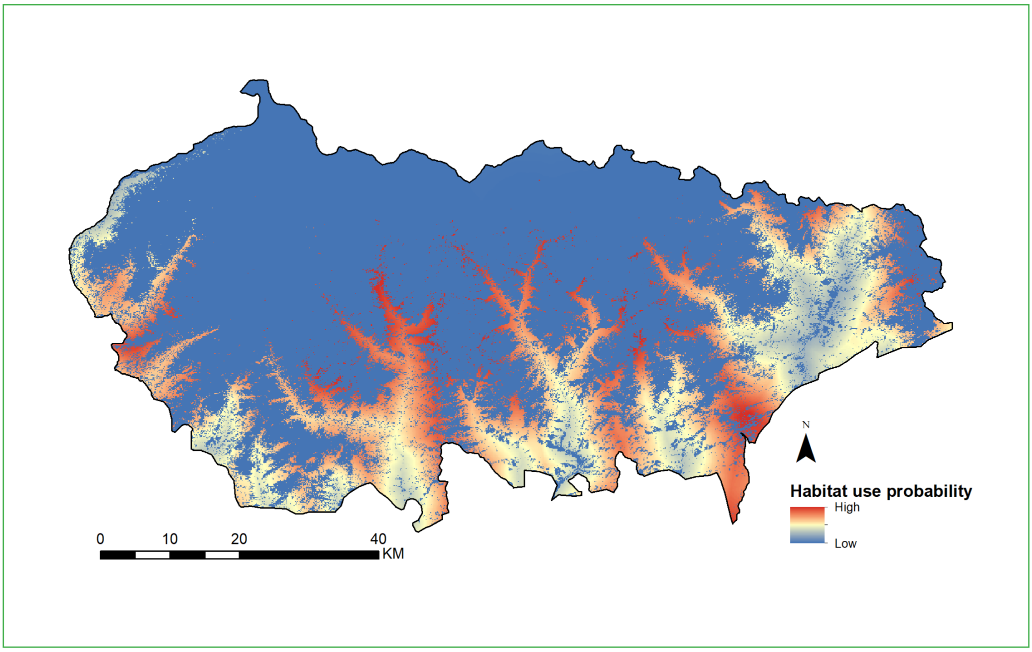
Map 7: Predicted habitat use probability of tiger in Phibsoo Wildlife Sanctuary



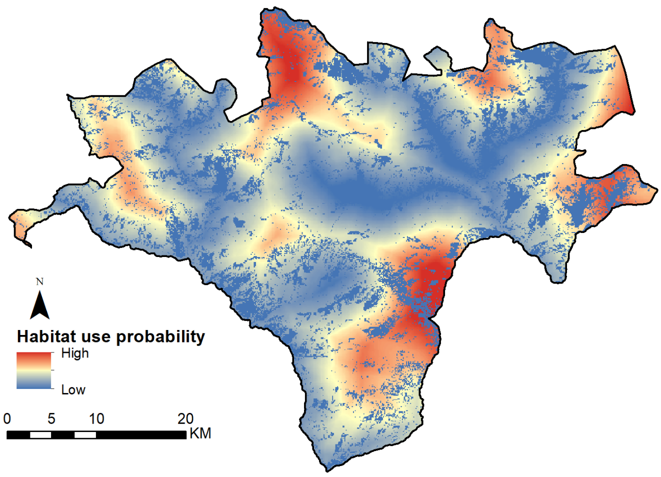
Map 8: Predicted habitat use probability of tiger in Royal Manas National Park



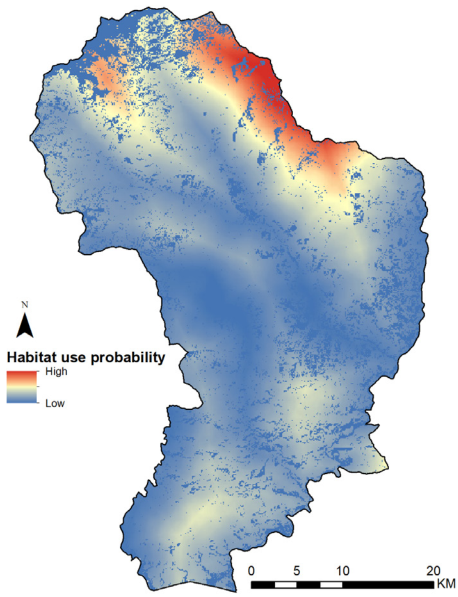
Map 9: Predicted habitat use probability of tiger in Sakteng Wildlife Sanctuary



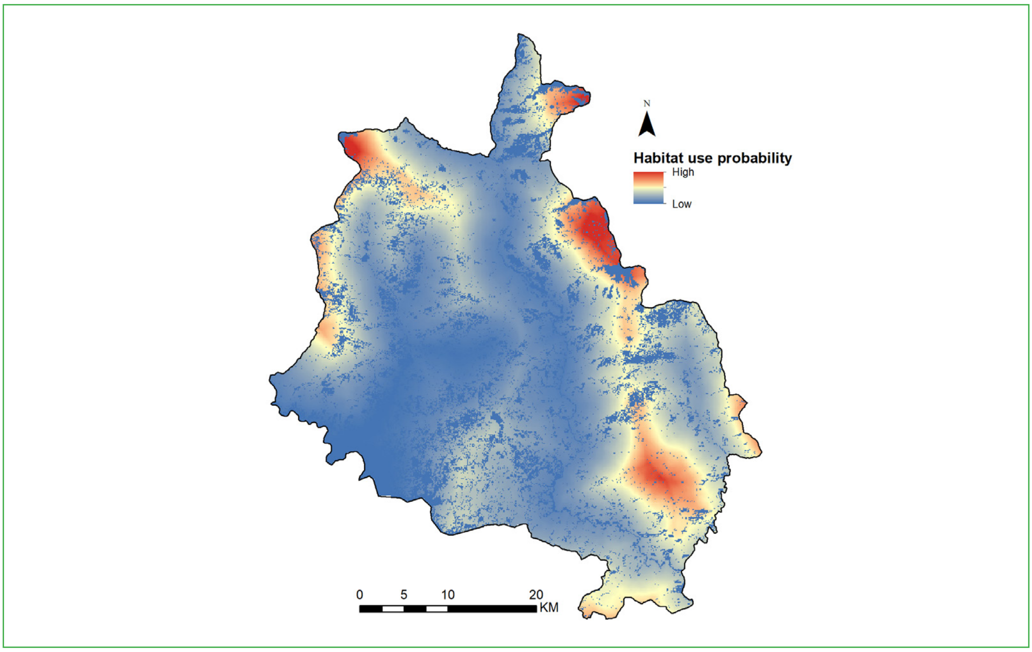
Map 10: Habitat use probability of tiger in Wangchuck Centennial National Park



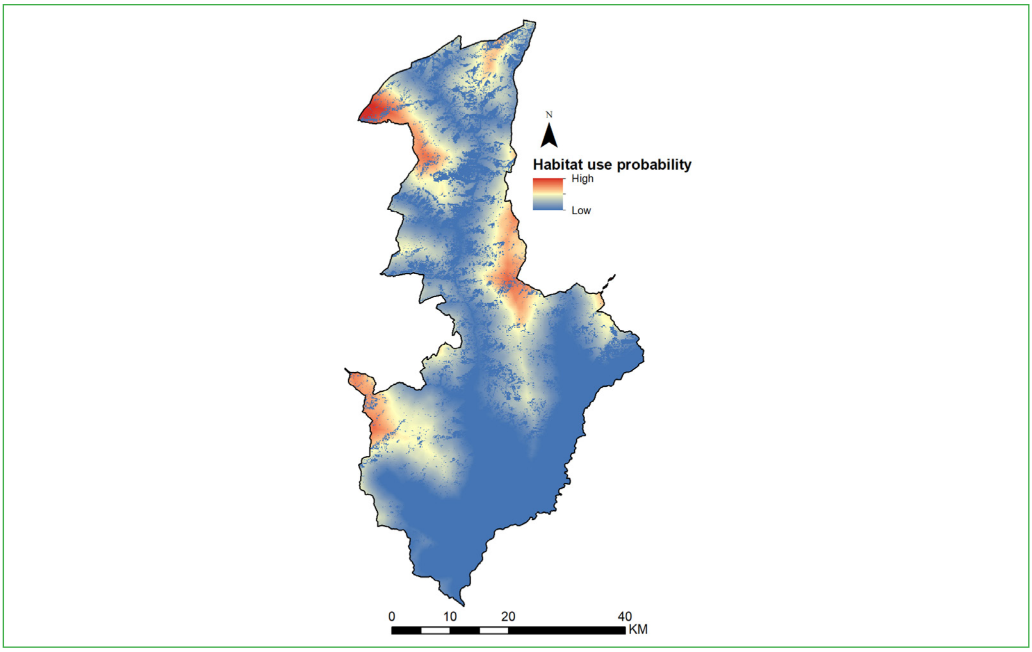
Map 11: Predicted habitat use probability of tiger in Bumthang Division



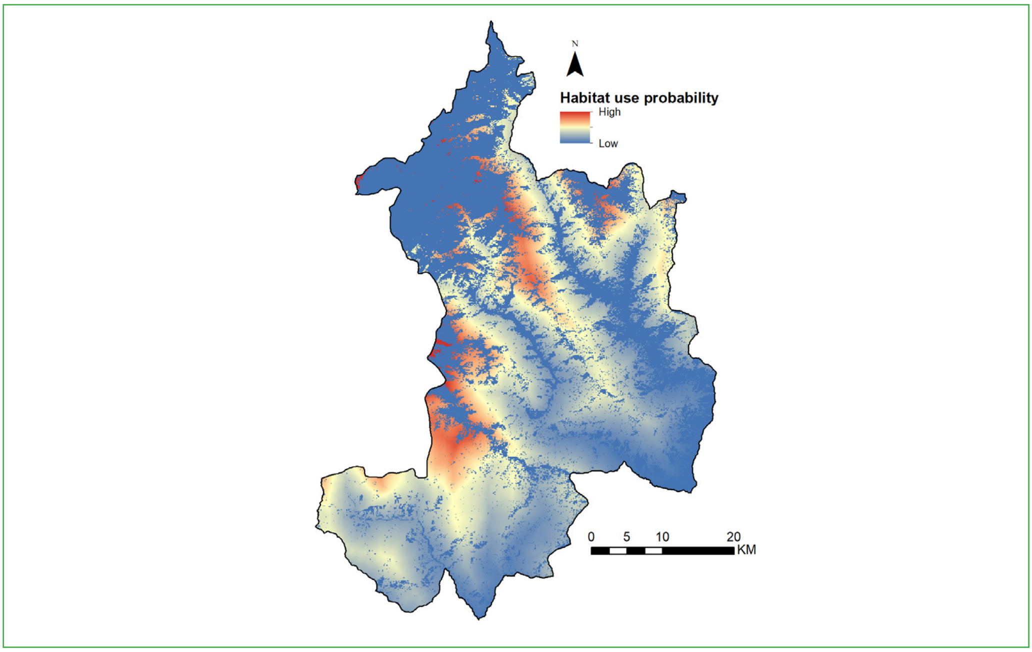
Map 12: Predicted habitat use probability of tiger in Dagana Division



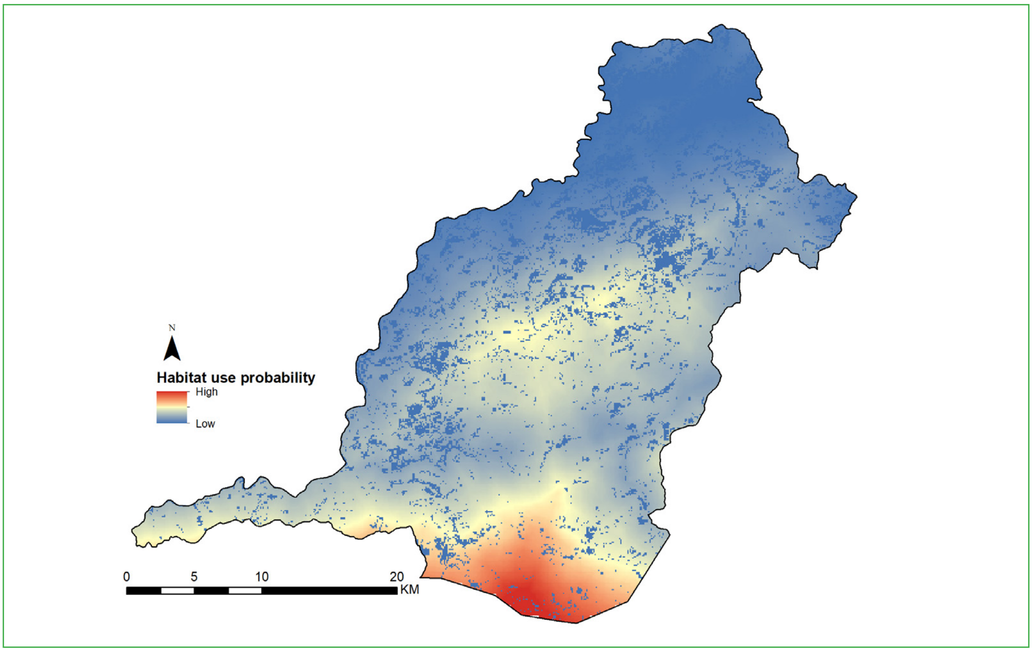
Map 13: Predicted habitat use probability of tiger in Gedu Division



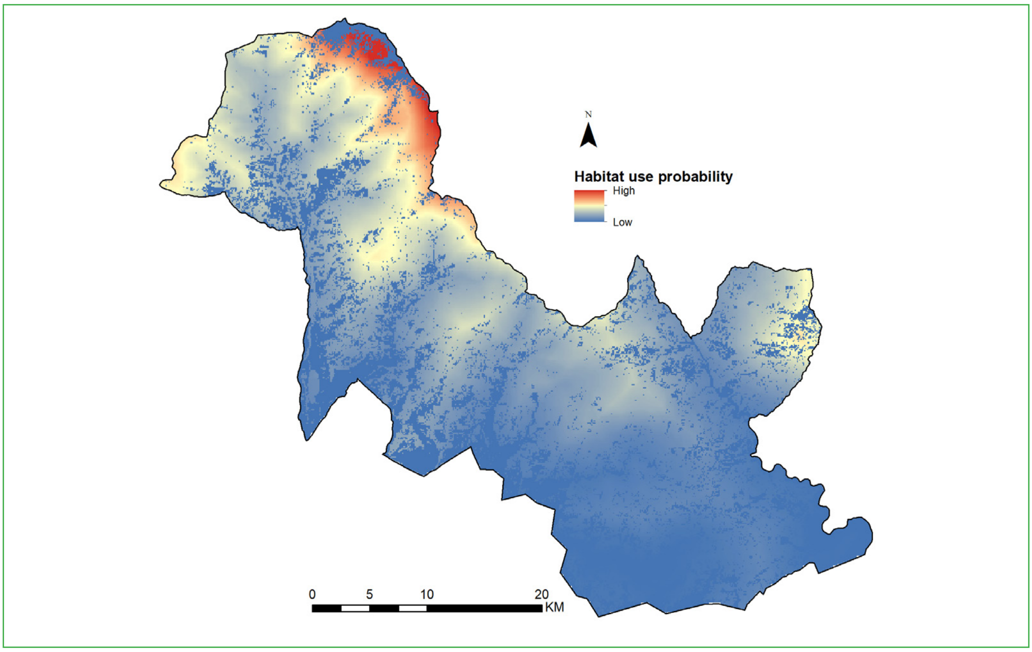
Map 14: Predicted habitat use probability of tiger in Mongar Division



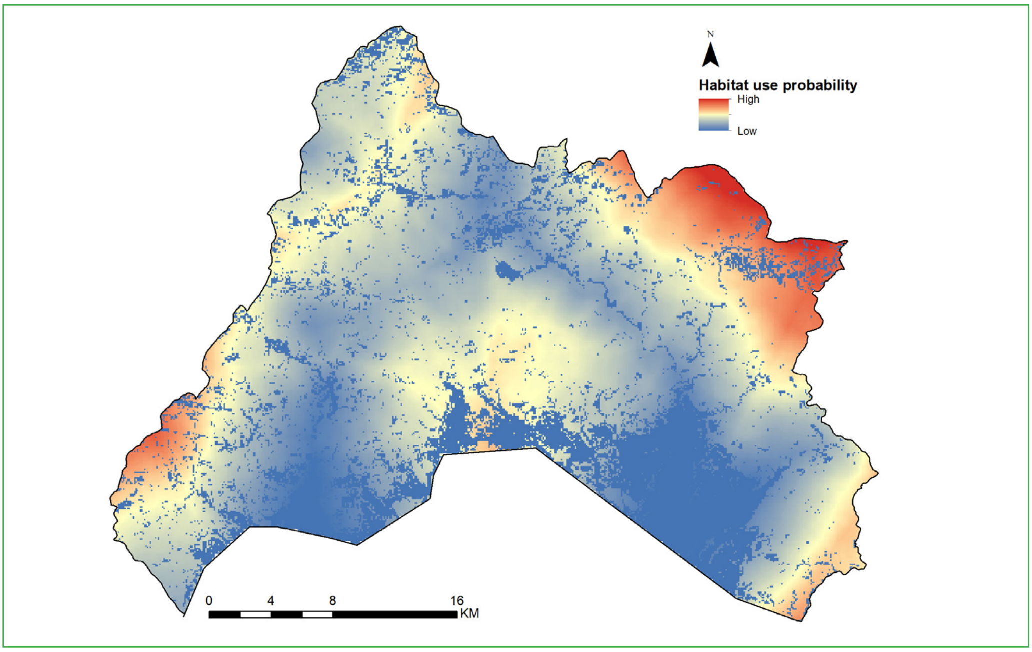
Map 15: Predicted habitat use probability of tiger in Paro Division



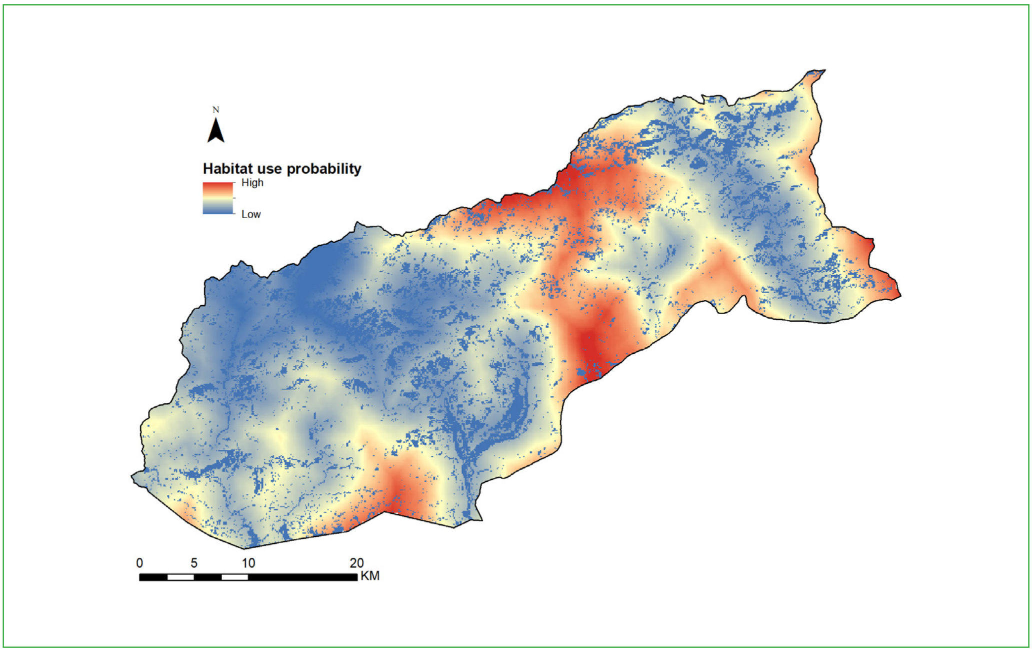
Map 16: Predicted habitat use probability of tiger in Pemagatshel Division



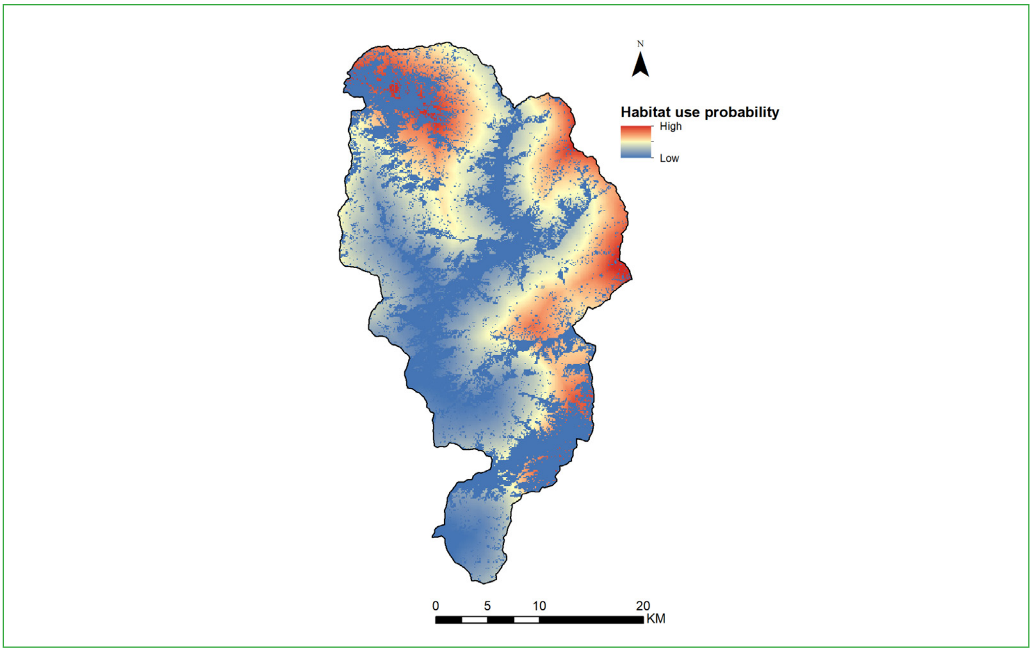
Map 17: Predicted habitat use probability of tiger in Samtse Division



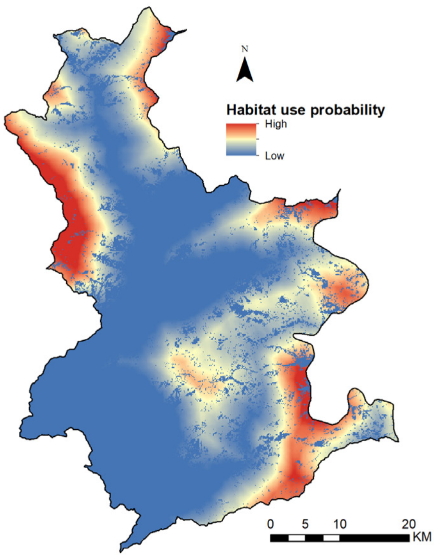
Map 18: Predicted habitat use probability of tiger in Sarpang Division



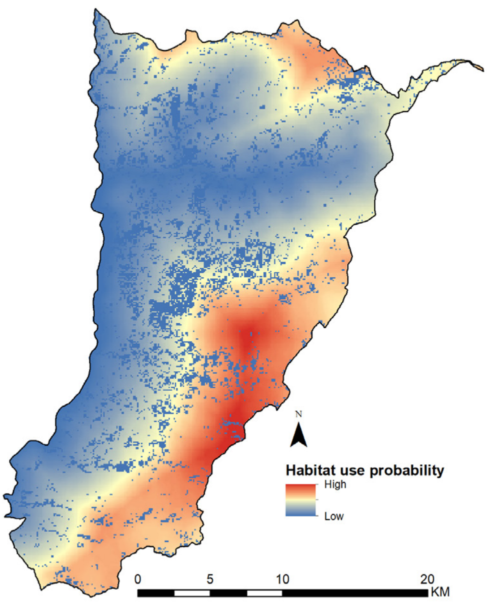
Map 19: Predicted habitat use probability of tiger in Samdrup Jongkhar Division



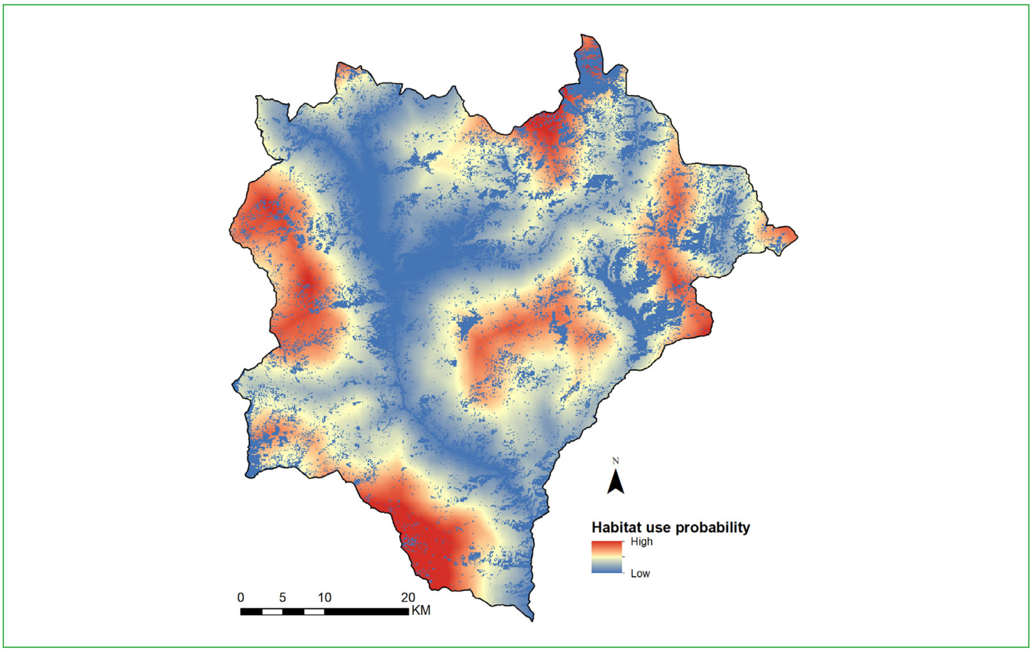
Map 20: Predicted habitat use probability of tiger in Thimphu Division



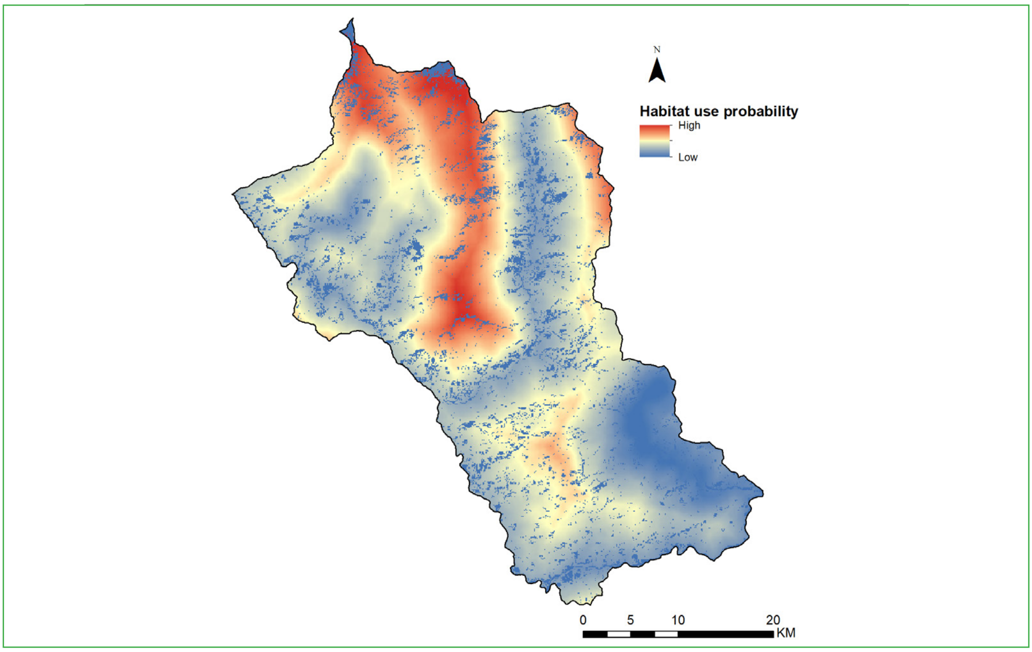
Map 21: Predicted habitat use probability of tiger in Trashigang Division



Map 22: Predicted habitat use probability of tiger in Tsirang Division



Map 23: Predicted habitat use probability of tiger in Wangdue Division



Map 24: Predicted habitat use probability of tiger in Zhemgang Division

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