

The spatial distribution and population density of tigers in mountainous terrain of Bhutan

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ABSTRACT

Habitat loss, prey depletion, and direct poaching for the illegal wildlife trade are endangering large carnivores across the globe. Tigers (*Panthera tigris*) have lost 93% of their historical range and are experiencing rapid population declines. A dominant paradigm of current tiger conservation focuses on conservation of 6% of the presently occupied tiger habitat deemed to be tiger source sites. In Bhutan, little was known about tiger distribution or abundance during the time of such classification, and no part of the country was included in the so-called 6% solution. Here we evaluate whether Bhutan is a potential tiger source site by rigorously estimating tiger density and spatial distribution across the country. We used large scale remote-camera trapping across $n = 1129$ sites in 2014–2015 to survey all potential tiger range in Bhutan. We estimated 90 individual tigers (60 females) and a mean density of 0.23 adult tigers per 100 km². Bhutan has significantly higher numbers of tigers than almost all identified source sites in the 6% solution. With low human density and large swaths of forest cover, the landscape of Bhutan and adjacent northeast India is a promising stronghold for tigers and should be prioritized in large-scale conservation efforts.

1. Introduction

Large carnivores are endangered due to habitat loss and fragmentation, prey depletion, and direct poaching for illegal trade and commerce throughout their range (Gittleman et al., 2001; Karanth and Stith, 1999; Ripple et al., 2014; Sharma et al., 2014). Tigers (*Panthera tigris*) are one of the largest apex predators and most endangered big cats in the wild. Tiger numbers have plummeted from as many as 100,000 individuals to around 4000 over the past century (Dinerstein et al., 2007; Seidensticker, 2010), despite decades of conservation efforts and investment.

Tigers are very resilient and can adapt to wide range of climatic conditions, ecosystems, and prey species (Schaller, 1967; Sunquist, 2010). If anthropogenic threats can be minimized, populations of tigers in the wild can rebound (Harihar et al., 2009; Walston et al., 2010b). It was under this premise that the heads of States from 13 tiger range countries endorsed the key element of the St. Petersburg Declaration on Tiger ("Tiger Summit 2010"), held in St. Petersburg, Russia: to double wild tiger numbers by the year 2022 using multi-pronged strategies among different stakeholders and agencies (GTRP, 2010). As a means to

accomplish this goal, Walston et al. (2010a) identified 42 tiger "source sites" (only 6% of the current tiger habitat) thought to contain 70% of the current tiger population; further, Walston et al. (2010a) argued that resources and effort should be directed towards the 6% of current tiger habitat in these 42 source sites.

While this 6% solution may be a pragmatic example of a triage approach for conservation (Bottrill et al., 2008; Wiens et al., 2012), a critical remaining question centers on the potential of the other 94% to contribute to tiger recovery. For example, in areas of Northeastern China not part of the 6% solution source sites, Amur tigers (*P. t. altaica*) are expanding and contributing significantly to tiger recovery (McLaughlin, 2016; Wang et al., 2016; Xiao et al., 2016). China is on track to be perhaps the only country to successfully double tiger numbers, despite being outside of the '6% solution' (Harihar et al., 2018). Importantly, many of the large tracts of tiger habitat omitted from the 6% solution are at risk due to developmental activities such as mining, logging, roads, dams, natural gas, and plantations (Seidensticker, 2015).

In contrast to the 'source site' strategy of Walston et al. (2010a), Wikramanayake et al. (2011) proposed a landscape-level approach to

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double tiger numbers in the wild, arguing that conservation efforts and funding should be distributed to all the Tiger Conservation Landscapes (TCL). The debate between these two ideas is really quite academic. This is because the amount of habitat needed to maintain 75–150 tigers anywhere in tiger range (under the guidelines of Walston et al. 2010) easily become a ‘landscape’ consisting of patches of high quality, perhaps protected areas interspersed with lower quality habitats. There are literally few areas in Asia where a single site could hold 75–150 tigers without an explicit landscape context. There are literally few areas in Asia where a single site could hold 75–150 tigers without an explicit landscape context. Therefore, it is of paramount importance to determine if there are other source sites that were not included by Walston et al. (2010a). The Northern Forest Complex - Namdhapha-Royal Manas (NFC-N-RM) region straddling the border of Myanmar, northeastern India, and Bhutan has the largest intact and contiguous forest cover in the Indian subcontinent (237,820 km²; Sanderson et al., 2010) and is one of the largest TCL. Low human population density and intact forests in NFC-N-RM landscapes offers great potential for Bengal tiger (*P. t. tigris*) conservation, yet little is known about tigers in this TCL (Lynam et al., 2009a; Wang and Macdonald, 2009) and no part of this region has been included within the 6% tiger source sites.

Bhutan falls within the NFC-N-RM and may be more important for tiger conservation than previously appreciated. First, forest cover in Bhutan exceeds 70% with half of the country designated as protected areas. Second, human density is low. Finally, Bhutan is a predominantly Buddhist nation that respects all life forms and has in place conservation-friendly policies and laws (DoFPS, 1995; RGoB, 2008). Bhutan is already recognized as a hotspot for wild felids (Tempa et al., 2013) and may harbor significant tiger populations of its own. Bhutan may also be critical to connect Terai Arc grassland TCLs of India and Nepal to other TCLs in Northeast India and to the Indochina tiger (*P. t. corbetti*) in Southeast Asia.

Here, we describe a national tiger survey to estimate densities across Bhutan for the first time. Our approach is based on state-of-the-art remote camera trap data and spatial capture-recapture models (Efford, 2004; Gardner et al., 2009; Royle et al., 2009b). First, we evaluate whether Bhutan has sufficiently large tiger population sizes to be considered as a tiger source site according to existing tiger conservation policies (Karanth et al., 2010; Walston et al., 2010a). The terms “source” and “sink” have precise definitions in the ecological literature that account for both within population growth rate and per capita contribution of individuals in a population to the greater meta-population (Runge et al., 2006; Griffin and Mills, 2009; Newby et al., 2013). However, current tiger conservation policy (Walston et al., 2010b) defines tiger source sites instead as “those areas embedded within larger landscapes with ‘tiger-permeable habitats’ where tigers are likely to be reproducing above replacement levels and therefore have the potential to repopulate surrounding landscapes”. Specifically, these source sites are defined as having “higher densities of tigers than in the overall landscape within which it is embedded”; exceeding 25 breeding females “alone or combined with other connected source sites”; and being embedded in a larger tiger-permeable landscape with potential to maintain > 50 breeding females.

Therefore, we tested whether Bhutan could be considered a source site against these existing tiger conservation policy criteria (Walston et al., 2010b). First, we predicted that Bhutan would have higher densities of tigers than in the overall landscape (NFC-R-NM) within which it is embedded. In practice, the mean population size of the 42 source sites identified by Walston et al. (2010b) was 50 individuals. Thus, we tested whether Bhutan had > 50 adult tigers. Second, we tested whether Bhutan itself and the broader NFC-R-NM tiger conservation landscape would have the potential to maintain > 25 or > 50 breeding females (Walston et al., 2010b, Appendix A). Alternatively, if Bhutan is a sink habitat for tigers, then we would predict tiger populations numbering fewer than 50 individuals, restricted to the low elevation foothills and plains along the Indian border. If this were true,

we would predict a strong negative effect of elevation on tiger density. In this scenario, we would further expect any breeding females in Bhutan would be limited to the low elevation areas adjacent to the Indian border.

Our second overall objective was to test for the effects of human disturbances on tigers in Bhutan in a spatially explicit capture-recapture framework. The prevailing paradigm in tiger-human studies is a negative effect of humans on tigers, mediated by human-caused mortality of tigers through poaching, human-tiger conflict, loss of tiger prey through poaching, and habitat loss (Goodrich et al., 2008; Karanth and Gopal, 2005). In contrast, recent studies from Nepal showed tigers and humans co-existing in a landscape at finer scales (Carter et al., 2013; Kafley et al., 2016). We do not know how human disturbances affect tigers and other wildlife population in Bhutan. Humans are part of Bhutan's protected area systems and unlike many other countries, the Royal Government of Bhutan (RGoB) allow people to reside within national parks and protected areas. We used proximity to human settlement as a measure of human disturbances and tested for its effects on tiger density. We hypothesized that the negative effects of human disturbances on tiger density and distribution will be weaker in Bhutan than elsewhere because of low human density, Buddhist beliefs and a formal governmental sustainable development policy based on Gross National Happiness that explicitly supports biodiversity conservation.

2. Materials and methods

2.1. Study area

Bhutan (38,394 km²) is located in the eastern Himalayas, between China to the north and India to the east, west, and south (Fig. 1a). Elevation rises from as low as 100 m along the southern border with India to > 7500 m in the north, within an aerial distance of 170 km. This extreme altitudinal gradient causes great variation in climatic zones ranging from wet sub-tropical in the south to permanent alpine pastures and glaciers in the north, thus making this landscape a biodiversity hotspot (Myers et al., 2000).

Top predators including tiger, leopard (*Panthera pardus*), snow leopard (*Panthera uncia*) and Asiatic wild dog (*Cuon alpinus*) are supported by diverse prey species that include: guar (*Bos gaurus*), sambar (*Rusa unicorn*), wild pig (*Sus scrofa*), serow (*Carpicornis thar*), Asiatic Water Buffalo (*Bubalus arnee*), barking deer (*Muntiacus muntjak*), goral (*Naemorhedus goral*), blue sheep (*Pseudois nayaur*), takin (*Budorcas taxicolor whitei*), 3 species of langurs, 2 species of macaques, and 3 species of porcupines.

2.2. Camera trap field survey

We randomly overlaid a 5 × 5 km grid cell across the entire country of Bhutan using Arc GIS 10.1 (ESRI, 2014; Fig. 1a). The grid size was chosen based on the minimum territory size (15–20 km²) of female tigers in the Indian subcontinent (Karanth and Sunquist, 2000; Smith et al., 1987). We deployed camera traps in 1129 grid cells, after removing towns, villages, and alpine habitats above 4500 m. If the grid cell falls completely on settlement (either on agriculture crop land or buildings and other infrastructure) those grids were rejected. If the grid cell falls completely on settlement (either on agriculture crop land or buildings and other infrastructure) those grids were rejected. If the grid square has 50% or more of forest land, then those grids were selected as suitable camera trap stations.

Camera trapping for the national tiger survey was carried out for one year from March 2014–March 2015. Camera trapping was divided into two blocks based on field logistics and the monsoon season. We began camera trapping in the southern zone for 5 months and then moved to northern blocks for another 6 months. We monitored camera traps once per month, but weather and logistics prevented monthly monitoring in a few remote and isolated camera sites. We identified

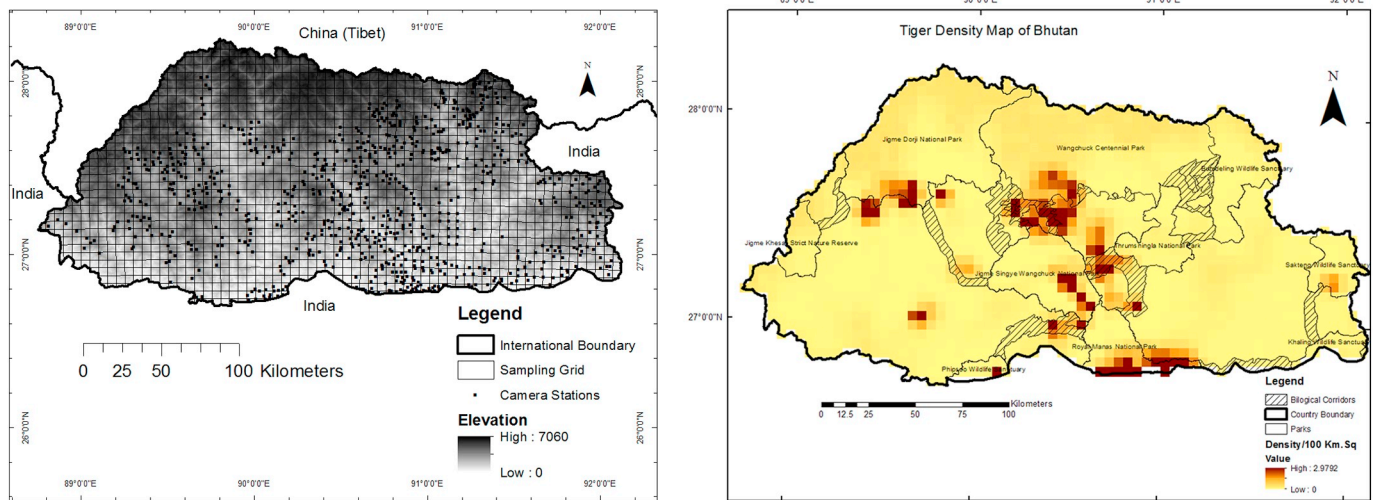


Fig. 1. a: Map of Bhutan showing 5 × 5 km survey grid with elevation. Each black dot represents one camera station, the darker color of elevation gradient represents high elevation in meters.

b: Bengal tiger (*Panthera tigris tigris*) density map from the best Bayesian spatial capture-recapture model ($D + \sigma_{\text{sex}}$) in Bhutan, Years 2014–2015. The darker colors represent higher density (per 100 km²). Protected areas and biological corridors overlaid to show where tigers are distributed.

each individual tiger manually based on stripe patterns on flanks (Karanth, 1995; Schaller, 1967) and gave unique identifiers according to their sex. We defined 7 trap nights as one sampling occasion, which should balance bias and precision for our spatially-explicit capture recapture parameter estimates (Goldberg et al., 2015).

2.3. Spatially-explicit capture recapture modeling

Spatially-explicit capture recapture (hereafter referred to as SECR; Efford, 2004; Royle and Young, 2008) explicitly models the spatial relationships between an individual animal's movements and the detection device to estimate capture probabilities. SECR models assume that each individual has a home range with activity center s_i around which animals move to meet resource needs. Thus the number of individual animals in the population (N) exposed to sampling is deduced by summing up the number of home range centers s_i . The home range centers are unobserved locations, $s_i = s_1, s_2, s_3, \dots, s_N$, where s_i is the home range center of tiger i (i.e., its Cartesian coordinates in 2-dimensional space (s_{1i}, s_{2i})) assumed to be distributed uniformly over some region S Eq. (1).

$$s_i \sim \text{Uniform}(S) \quad (1)$$

These activity centers represent the outcome of a point process of the state space S (Gopalaswamy et al., 2012; Royle et al., 2011b). Density is then derived as $D = N/\text{area}(S)$, where N is model estimated abundance and $\text{area}(S)$ is the known area of the prescribed state-space (Royle et al., 2013).

We developed trap specific encounter histories y_{ijk} for individual $i = 1, 2, \dots, n$, in trap $j = 1, 2, \dots, J$; sampling period $= 1, 2, \dots, K$, where $y_{ijk} = 1$ if individual i was captured at camera location j during sampling occasion k (or 0 if the individual tiger was not captured at that time and place). We allowed individuals to be captured at multiple camera locations during the same sampling period, but considered multiple captures of an individual in a particular trap during the same sampling interval as a single capture. We followed the model formulation of the observation process used by Gardner et al. (2010) and Russell et al. (2012) that describes the encounter probabilities of individual i at trap j during occasion k as a function to distance between individual activity center (i) and trap location (j) as in Eq. (2):

$$\text{Pr}(y_{ijk} = 1) = 1 - \exp(-\lambda_0 g_{ij}) \quad (2)$$

where λ_0 is the baseline detection probability given that the camera

trap is located exactly at the center of home range of an individual tiger, $g_{ij} = \exp\left(-\frac{d_{ij}^2}{\sigma^2}\right)$, where d_{ij} is the Euclidian distance between individual's activity center s_i and trap location x_j and σ is a scaling parameter. This distance function is adopted from the theory of distance sampling (Buckland et al., 2005). As in Russell et al. (2012), and Proffitt et al. (2015) we included sex as covariate for the detection function Eq. (3):

$$\log(\lambda_{0,jk}) = \lambda_0 + \beta_{\text{sex}_i} \quad (3)$$

We also modelled sex and distance as the interactive effects on detection probability as in Proffitt et al. (2015). From Royle et al. (2013) and Proffitt et al. (2015), we modelled elevation and proximity to human settlement as covariates on density. Although we use two covariates for our models, the current version of SCRbayes can handle only one covariate at a time, therefore, our covariate model is as follows Eq. (4):

$$\log(\mu(s, \beta)) = \beta_0 + \beta_v C_v(s) \quad (4)$$

where $\mu(s, \beta)$ is a function that returns the expected density of activity center at location s for the given covariate value at s and β_v is the parameter estimate (regression coefficient) for covariate $C_v(s)$. Elevation data for each state space for our models were extracted from raster of Digital Elevation Model (DEM-30 × 30) map of Bhutan in R using the package raster. The nearest distance for the state space from the village/settlement was calculated in ArcGIS 10.2.2 (ESRI-2015) based on the nationwide housing and population census of Bhutan for 2005 (RGoB, 2006).

We fit 11 models to the data to quantify the effect of different covariates on density estimates, facilitating our examination of hypotheses regarding the effects of human development and terrain on tiger density. For example, if Bhutan was not a tiger source site, and tiger density was only high along the southern Indian border, then we predicted that elevation would strongly influence tiger density. Furthermore, if humans exerted a negative effect on tiger density, then we also predicted a negative effect of human activity on tiger density. We further tested for sex-specific differences on the baseline detection function (λ_0) and scale parameter of the activity center (σ) (see Table A.1 for description of models).

2.4. Bayesian analysis by MCMC

The main advantage of Bayesian approaches is that posterior

inferences are valid at any sample size, often a necessity for ecological studies of rare and elusive species such as tigers (Royle et al., 2013). Bayesian approaches to SECR analyses use data augmentation (Royle and Dorazio, 2008) to estimate tiger densities, following recent large carnivore and tiger studies (Goldberg et al., 2015; Xiao et al., 2016). Data augmentation is done by adding large number of undetected individuals, each having all zero encounter histories, say $M-n$ where M is pseudo-individuals and n is number of captured individuals. It is assumed that the actual population size (N) is a subset of M (Royle and Young, 2008). We chose a uniform prior distribution from $[0, M]$ on population size. The super population (M) and population size (N) is related by parameter ψ . ψ is the probability that an individual from M is a member of the population, N , exposed to sampling by the trap array. We choose $M (=200)$ sufficiently large so as not to truncate the upper limit of the estimated population size, N .

We fit our models using Markov chain Monte Carlo (MCMC) methods in R (R Development Core Team, 2016), using the *SCRbayes* package (available at: <https://sites.google.com/site/spatialcapturecapture/scr-bayes-r-package>). We masked our state-space with elevation > 4500 m as non-tiger habitat (Fig. 1a) based on data on the highest distributional record in our data for tiger elevation (see Discussion). We also used 5 km grid to discretize our statespace of potential tiger activity centers. We ran models for 50,000 iterations, discarded the first 20,000 iterations as burn-in and further thinned the chain by skipping every other iteration to reduce autocorrelation, leaving 15,000 iterations in our posterior sample. We assessed the convergence of the MCMC samples using the diagnostic tests in coda package in R (Plummer et al., 2006) and by examining trace plots and histograms for each parameter. From these converged samples, we computed the mean, median and 95% credibility intervals for the model parameters for each model. We determined significance based upon 95% credible intervals that did not overlap zero. We further explored Bayesian based model selection and goodness of fit tests (see Appendix B). To compare the results from our Bayesian models to that of maximum likelihood based SECR models, we also fit these models using the *secr* R package (Efford, 2015, see Appendix C).

3. Results

3.1. Camera trapping

Of the 1129 total camera stations deployed across Bhutan, 834 yielded data for our analysis. From these 834 camera stations, we captured 1406 photo images and 138 videos of tigers during the entire survey period (March 2014 to March 2015). We used 1231 images and 138 videos to develop encounter data files (Royle et al., 2013). The first phase of the survey (March 2014 to July 2015) in the southern block resulted in 712 images and 25 videos of tigers from 78 of the 448 camera stations from 22 sampling occasions (7 trap nights per occasion). In the northern block (October 2015 to March 2015), 82 out of 681 camera stations captured 694 images and 113 videos of tigers from 32 sampling occasions. Therefore, our dataset yielded 54 sampling occasions, 317 independent events, and 66 individual tigers. The detailed encounter histories are provided as a supplementary (Table A.2).

Of 66 individual tiger captures, 10 individuals were captured only once, 15 individuals twice, 12 individuals 3 times, 6 individuals 4 times and 1 individual 21 times (Table A.3). The details of individuals captured at individual camera traps are: 27 individuals were captured at only 1 camera location, 13 individuals at only 2 camera locations, while 1 individual was captured at as many as 11 camera stations (Table A.3). Raw female detections are in Table A.2 and females with cubs in Fig. 2. We plotted the centroid point for each individual from the raw capture data to visualize and cross-check our data (Fig. A.1).

3.2. Bayesian results and model selection

The fit statistics and Bayesian P value for our model was 1 indicating lack of goodness of fit, though Bayesian P values are prone to falsely concluding a lack of fit (Conn et al., 2018; Royle et al., 2013). To evaluate if this lack of model fit was due to the large area of the state space, we subset the data for Jigme Singye Wangchuck National Park (JSWNP), and re-ran the models using same formulation and assumptions. The goodness of fit test resulted in Bayesian p -value of 0.53 for this subset of data indicating that our models were adequate in high density areas, suggesting GOF test failed in the wider study area because of areas of low tiger densities. Thus, following Proffitt et al. (2015), we compared expected number of captures to the actual number of captures as another form of testing for goodness of fit test. Using this method, our expected captured numbers were 64–81 (Table 1) very similar to our observed number of captured individuals, $n = 66$, confirming the adequacy of model goodness of fit. Based on these two additional tests, despite the overall failure of the GOF test, we assumed that our top model(s) adequately described the combination of the underlying point process and capture of individuals. Based on this, we selected 3 top models along with basic models (distance only) to compare the posterior estimates of density and abundance N (Table 1).

Following Royle et al.'s (2013) hypothesis testing methods for SECR model selection (see Appendix B), our top model was Model 3 ($D + \sigma_{\text{sex}}$): Effect of sex on the scale parameter (σ) of the activity center (Table 1). Based on our top model, the estimated tiger population size (N) was 91 individual tigers with 60 adult females and a density of 0.24 tigers/100 km² (Table 1). The posterior estimated density map showed tigers are distributed across Bhutan, both in protected areas and biological corridors and also outside of protected areas at elevations up to 4500 m (Fig. 1b). The overall tiger density for the whole study area was low, but certain areas (e.g. JSWNP, Trongsa, and Royal Manas National Park [RMNP]) had densities up to 3 tigers per 100 km². Elevation and distance from the human settlement without other covariates (sex and σ_{sex}) had no significant effect on tiger density (Table A.4). Elevation with σ_{sex} as covariate showed weak negative effect and distance from the human settlement with σ_{sex} as covariate showed weak positive effect on the density (Table A.4). Overall, these results imply no effect of elevation and distance from human settlements on tiger density; this rejects both hypotheses that the higher density of tigers only occurred in the lower elevations and that humans had a negative effect on tiger density in Bhutan.

In our other top models, the scale parameter (σ) (the rate at which encounter probability of tiger decreases as distances between camera traps and home range center increases) showed a positive effect of being male. Our top model estimated σ of 5.20 km for female, versus than 6.30 km for male (Table 2, Fig. 3). The baseline detection (probability of detection if camera trap is located exactly at come activity center) was not significantly different between male and females (Table A.4). The baseline detection probability λ_0 of tigers from our top model per session was 0.025. We also estimated home range size using a basic Minimum Convex Polygon (MCP) for those individuals that were capture from more than 3 camera station (Fig. 2). The mean MCP home range size of males was 169.4 km² (Range 17.3 – 547.8) and females, it was 70 km² (7.4 – 199.2).

3.3. Maximum likelihood based SECR estimates of density and abundance

For the maximum likelihood based SECR approach (Borchers and Efford, 2008), we followed AIC model selection methods (Burnham and Anderson, 2002) (Table A.5). The density estimates of 0.23 (95% CI 0.19–0.31) tigers per 100 km² and N of 88 individuals (95% CI 79–106) from MLE-based *secr* (Table 3) were very similar to results from *SCRbayes*. The estimated scale parameter σ for female tigers was 4.92 km and that of males was 6.01 km (Table 3), similar to results from Bayesian-based models. Unlike Bayesian based models, however, sex

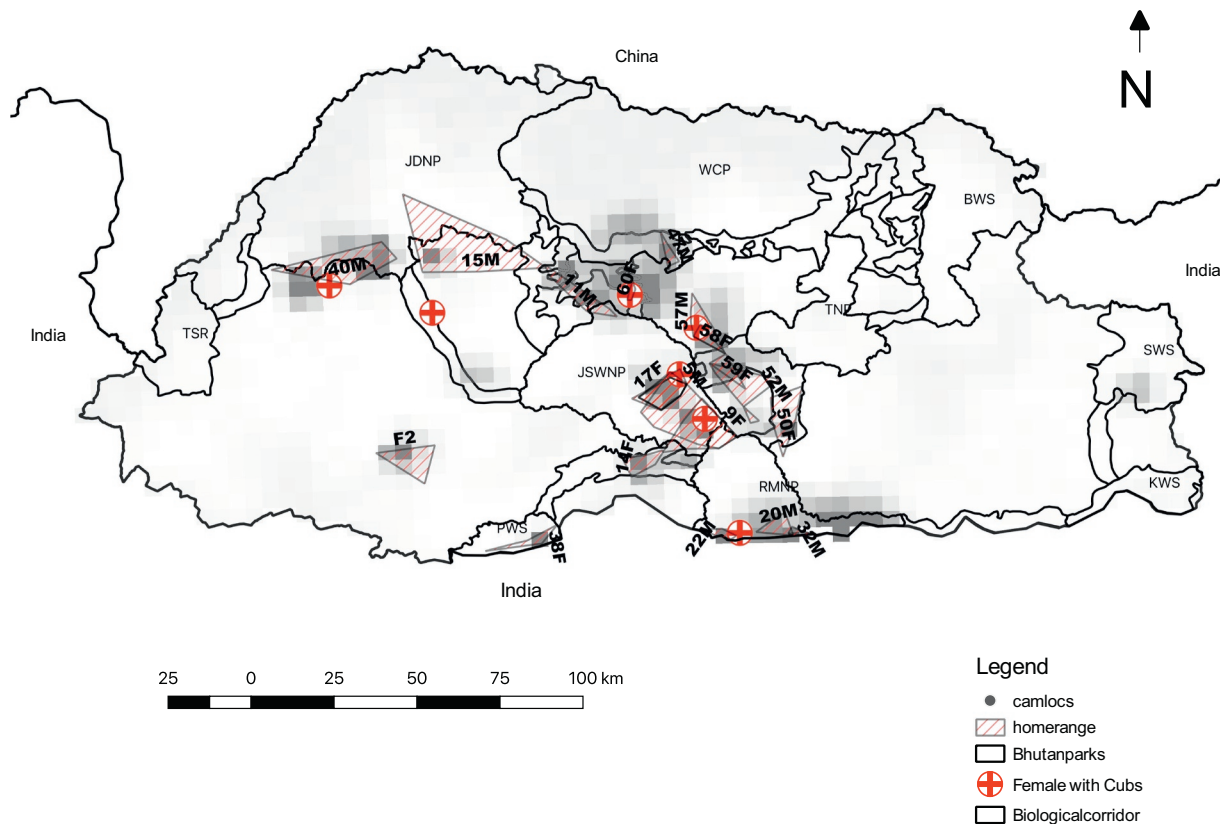


Fig. 2. Location of each home range calculated from MCP for Bengal tigers (*Panthera tigris tigris*) captured at > 3 camera stations in Bhutan, year 2014–2015. The numbers represent the individual ID and the letter M/F represent male/female. The red cross represents camera locations where females with cubs were captured. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

Table 1

Median posterior abundance and density estimates with 95% credible intervals from Bayesian spatially explicit capture recapture models for Bengal tigers (*Panthera tigris tigris*) in Bhutan, years 2014–2015. N is the number of tigers estimated by each model, and density is the number of tigers per 100 km². GOF (P-value) is the Bayesian *p*-value for fit statistics and E(N_{cap}) is the expected number of captures. D is the basic model with detection as the function of distance between activity center and camera location.

Models	N		Density		GOF (P-value)	E(N _{cap})
	Median	95% CI	Median	95% CI		
D + σ_{sex}	91.00	81–105.00	0.24	0.20–0.27	1	64–81
D + σ_{sex} + human	92	81–107.53	0.24	0.21–0.28	1	64–85
D + σ_{sex} + Ele	89.00	79–102.00	0.23	0.20–0.26	1	66–87
D	89.00	80–103.00	0.23	0.21–0.27	1	67–85

Table 2

Median posterior parameter estimates from Bayesian spatially explicit capture recapture models for Bengal tigers (*Panthera tigris tigris*) in Bhutan, years 2014–2015. σ is the scalar parameter, λ_0 is the base line detection probability, ψ is the data augmentation parameters, β is the coefficient of elevation and human settlement. The values in the parenthesis represent 95% credible interval.

Models	σ_{Female}	σ_{Male}	λ_0	ψ_{Female}	ψ_{Male}	β
D + σ_{sex}	1.04 (0.96–1.13)	1.26 (1.25–1.37)	0.025 (0.020–0.031)	0.332 (0.268–0.410)	0.448 (0.323–0.573)	
D + σ_{sex} + Human	1.04 (0.96–1.22)	1.25 (1.15–1.37)	0.016 (0.0147–0.020)	0.350 (0.279–0.426)	0.457 (0.334–0.598)	6.5E ⁻⁰⁶ (6.51E ⁻⁰⁶ –6.53E ⁻⁰⁶)
D + σ_{sex} + Ele	1.04 (0.96–1.13)	1.26 (1.15–1.38)	0.016 (0.014–0.019)	0.334 (0.268–0.411)		–1.14E ⁻⁰⁴ (–1.65E ⁻⁰⁴ –1.11E ⁻⁰⁴)
D	1.14 (1.07–1.22)		0.016 (0.014–0.019)	0.338 (0.269–0.413)		

had a significant effect on both baseline detection and scale parameter. The baseline detection g_0 (analogues to λ_0 of SCRbays) for males was 0.024 and 0.039 for females (Table 3). This means female tigers had higher baseline detection probabilities than male tigers. Despite this minor discrepancy in baseline detection rates, our MLE secr results similarly showed that elevation and human disturbances had no effect on tiger density.

4. Discussion

We rigorously estimated tiger density and population size in the first country-wide survey across the rugged terrain of Bhutan. This study firmly establishes Bhutan as an important tiger source with tigers distributed throughout the country (not just along the Indian border). We also found tiger density was not negatively affected by human settlements, suggesting the potential for minimal tiger-human conflict in Bhutan, at least compared to other tiger range countries. Although our

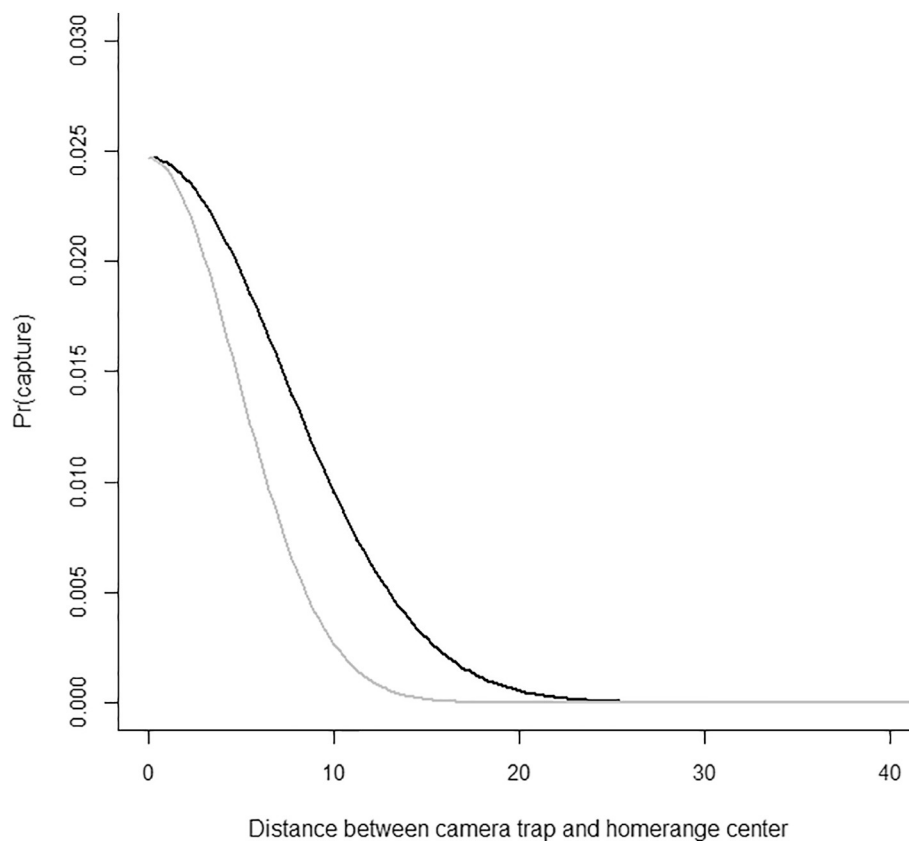


Fig. 3. The detection probability (encounter probability) of male (black line) and female (grey line) tigers as a function of distance (km) from the home ranger center based on the Bayesian SECR model ($D + \sigma_{\text{sex}}$).

discussion will focus only on the Bayesian-based posterior parameter estimates from (Royle 2013), our maximum likelihood based estimates were similar (Tables 2 & 3).

Our current tiger number estimate of 91 individuals with 60 adult females in one connected landscape is relatively large, and substantially larger than the mean tiger population size of 54 across the sources identified in the “6% solution” paradigm (Walston et al., 2010a). There are more tigers in Bhutan than almost all other tiger source populations listed by Walston et al. (2010b). Although our tiger density estimate across all of Bhutan was relatively low at 0.24 tigers per 100km² (Table 2), the country includes areas where tigers do not occur (Fig. 1a). So, for the country-wide effective sampling area of 31,500 km², our estimated tiger density estimate is ecologically reasonable.

However, our results also showed where tigers are concentrated, with protected areas such as JSWNP, RMNP, and Jigme Dorji National Park (JDNP) having as many as 2–3 tigers per 100 km² (Fig. 1b). These density estimates are comparable to tiger density estimates from some protected areas designated as tiger source sites in India such as Tadoba,

Bhadra, and Kalakad-Mundanthurai (Karanth et al., 2004; Ramesh et al., 2012). Further, our density estimate for these three national parks were much higher than other south Asian countries such as Malaysia (Kawanishi and Sunquist, 2004), Sumatra (O'Brien et al., 2003; Wibisono et al., 2009), Lao PDR (Johnson et al., 2006), and Myanmar (Lynam et al., 2009a, 2009b) that also are formally designated as tiger source sites. Within Bhutan, therefore, these three national parks likely anchor the nation's tiger population.

Our study follows up on previous estimates within Bhutan. For example, Wang and MacDonald (2009) reported tiger density of 0.4–0.5 tigers per 100 km² from a portion of JSWNP, slightly higher than the tiger density that we estimate for the whole country, but much lower than our estimated 2 tigers 100 km² for all of JSWNP (Fig. 1b). Our estimate of 18 individual tigers was also higher than the 8 individual tigers estimated by Wang and Macdonald (2009) in the same study area. We believe these differences do not reflect a doubling of tiger densities between the earlier Wang and MacDonald (2009) study and ours. Instead, we believe it more likely that small differences in the study area placement within different portions of JSWNP, camera

Table 3

Parameter estimates from Maximum Likelihood based SECR method for Bengal tiger (*Panthera tigris tigris*) for Bhutan, Year 2014–2015 from top three models using half hazard detection model. Values in the parenthesis represent 95% confidence interval.

Models	σ		g_0		Density	N
	Male	Female	Male	Female		
Model 10:	6.42	4.60	0.024	0.039	0.24	92
D~Ele, $g_0 \sim \text{sex}$, $\sigma \sim \text{sex}$	(6.01–6.87)	(4.30–4.92)	(0.021–0.029)	(0.030–0.048)	(0.19–0.31)	(81–109)
Model 8:	6.39	4.70	0.024	0.039	0.23	92
D~Human, $g_0 \sim \text{sex}$, $\sigma \sim \text{sex}$	(5.72–7.15)	(4.29–5.03)	(0.019–0.031)	(0.032–0.047)	(0.19–0.31)	(81–109)
Model 11:	6.34	4.58	0.024	0.040	0.24	92
D~Ele + Human, $g_0 \sim \text{sex}$, $\sigma \sim \text{sex}$	(5.68–7.08)	(4.24–5.00)	(0.019–0.032)	(0.033–0.05)	(0.19–0.31)	(81–109)

trapping methods, and differences between the earlier non-spatial, and our spatially-explicit methods resulted in these differences. Such inconsistencies between non-spatial and spatial capture-recapture methods have been noted in other species, such as for Grizzly bears (*Ursus arctos*) in Alberta (Boulanger et al., 2018; Morehouse and Boyce, 2016). Reconciling potential methodological differences would require a joint analysis framework with the original datasets of the two studies, which is often challenging (e.g., Morehouse et al. 2016, Boulanger et al., 2018). Nevertheless, future studies will be able to use our nationwide survey as a baseline against which to gauge future trends in tiger populations.

We also confirmed biologically expected patterns in differential spatial range use by male and female tigers, similar to previous tiger SECR studies (Fig. 3). Females had higher baseline detection rates compared to males, probably because male tigers had larger home ranges than females, as suggested in conventional radio-telemetry (Seidensticker, 1976; Sunquist, 1981) and recent spatial capture studies (Royle et al., 2009a). As a territorial animal, male tigers spent more time marking and moving along the fringes of their home range thereby reducing their baseline encounter at the center of their home range. Our baseline detection rate λ_0 is similar and comparable to estimates from Bengal tiger studies in South India (Royle et al. 2009a, Kalle et al. 2011, Gopalaswamy et al. 2012, Ramesh et al. 2012).

For a country-wide landscape with an elevation gradient spanning from 100 to 4500 m across a straight-line distance of 170 km, we expected elevation to have strong influence on tiger density. This would have been especially true if Bhutan's tiger population acted as a landscape-wide sink, distributed only along the southern Indian border. Surprisingly our results suggest otherwise, with no discernible effect of elevation on tiger density. Most ecological studies on Bengal tigers (*Panthera tigris tigris*) were done in the plains of India and Nepal (Karanth and Sunquist, 2000; Schaller, 1967; Seidensticker, 1996), suggesting the Bengal tiger inhabited the plains, and not mountainous landscapes (Kafley et al., 2016; Thapa and Kelly, 2016). And other mountainous landscapes in Asia have often been reported to have lower tiger densities (e.g., Myanmar, Lynam et al. 2009). In the absence of systematic studies in mountains, the occurrence of tigers at higher elevations has been dismissed as representing transient or old males from the plains. Thus, mountainous regions have been given little priority for the conservation of tigers in the region. Bhutanese people, however, have always had local knowledge that tigers occupy the mountains. Our results here confirm that elevation is not a strong deterrent for tigers in Bhutan, as we found tigers distributed from 100 m in the southern foothills up to the Himalayan mountain tops as high as 4400 m above sea level (Fig. 1b). A recent camera trapping exercise in Dibang Wildlife Sanctuary in Arunachal Pradesh also showed that tigers can occur in high altitudes up to 3600 m (Adhikarimayum and Gopi, 2018). Our long camera trapping periods had resulted in failure of our closure test, indicating that we had violated population closure assumptions (Kendall et al., 1997; White, 1982). However, for a country-wide surveys like in our study, it is challenging to complete surveys in all areas within short survey period to address closure assumptions (Karanth and Nichols, 2002). While, the closed population assumption is important, but other studies in large carnivores had shown that an extended study periods also have advantages such as an increased number of detections (du Preez et al., 2014; Jędrzejewski et al., 2017). For example, better detectability of all sex/age groups would allow estimating population breeding structure and would broaden the applicability of camera trapping to an array of other ecological and conservation questions (Jędrzejewski et al., 2017). In future, we are going to examine open SECR models in Bhutan especially in our long term study sites in JDNF-JSWNP-RMNP.

More importantly, tigers in Bhutan not only occupied mountainous landscapes, but also reproduced across elevations. We found that 6 out of 7 adult female tigresses captured in our camera traps with cubs were above 2500 m above sea level (Fig. 2). Abundant large bodied prey

species are a prerequisite for tigers to breed, and marginal small size prey such as *Muntjac* cannot sustain breeding females (Karanth et al., 2004). While prey such as gaur are concentrated and limited in the lower foothills, we were occasionally able to document them at altitudes above 4000 m (Tempa, 2017). Another primary prey species, wild pigs, (Hayward et al., 2012; Reddy et al., 2004), were very abundant and widely distributed across Bhutan (Tempa, 2017; Wangchuk et al., 2004). We collected about 60 samples of likely tiger scats and 80% of those scats samples contained pig hair (T. Tempa, unpublished data). These observations confirm the crucial role of wild suids to tiger distribution and reproduction found across their range (Hayward et al., 2012; Petrunenko et al., 2016; Gu et al., 2018). Thus, wild pigs could be a key prey species of tigers, and support breeding females even at high elevations. One plausible reason for such large number of wild pigs in mountains is that the cloud forests of the montane ecosystem are always moist and contain preferred pig foods, such as roots, acorns, insects and grubs, year-round (Tempa, 2017). Crops like potatoes, corn, rice and wheat also supplement wild pig diets.

Tempa (2017) modelled the abundance of wild pigs and other ungulates throughout Bhutan using the same camera trapping data used here, and found no strong signature of human disturbance on tiger prey. Indeed, many ungulate species were positively associated with cattle grazing, suggesting a potential indirect positive effect on tiger prey. This is consistent with the positive effects of traditional swidden agricultural practices which Bhutanese farmers traditionally use to enhance cattle grazing, and may indirectly benefit wild ungulates (Siebert and Belsky, 2014). Collectively, these assemblages of prey support breeding tigers at higher altitudes than previously recognized in the tiger conservation community.

As for the question of whether Bhutan should be considered a "tiger source site" as defined in the tiger conservation literature, we find strong evidence that Bhutan fulfills almost all the criteria of source sites and contained more tigers than most of 42 existing tiger source sites (Karanth et al., 2013; Walston et al., 2010b). We also clearly found evidence of 6-7 breeding tigresses distributed widely through Bhutan, and greater than > 50 female tigers. Even if we just considered the 3 core protected national parks (JSWNP, RMNP and JDNF) and corridors linking them, these 3 parks had 60–70 tigers, in the upper quartile of tiger source sites reported by Walston et al. (2010b). Furthermore, the presence of breeding tigers at high elevations and their spatial distribution across altitudinal gradients both imply that Bhutan is not dependent on tiger immigration from India to sustain populations. Therefore, we conclude that Bhutan is a source site for tigers in the region and deserving of landscape-level conservation priority (Sanderson et al., 2010; Wikramanayake et al., 2011). Our results further emphasize the importance of the entire Northern Forest Complex - Namdhapha -Royal Manas (NFC-NRM), straddling the border of Myanmar, northeastern India, and Bhutan, to global tiger conservation.

Proximity to human settlement is a standard surrogate for human disturbance to wildlife in most human-wildlife conflict studies (Singh et al., 2010; Burton et al., 2012; Kafley et al., 2016; Barber-Meyer et al., 2013), leading us to predict that distance to human settlement would have strong negative effects on tiger density. However, contrary to these predictions, and to earlier studies from other tiger habitats (Barber-Meyer et al., 2013; Kerley et al., 2002; Linkie et al., 2006), we did not find strong negative influence of humans on tiger density. Our finding of no significant relationship between distance of human settlement and tiger density in Bhutan is consistent with findings from Nepal (Carter et al., 2012; Kafley et al., 2016). Likewise, our results correspond to local knowledge that livestock depredation hotspots occur even in villages and settlement areas in and outside of protected areas (Rostro-García et al., 2016; Sangay and Vernes, 2008). However, it is important to note that using human settlement as a surrogate for human disturbance is very different in Bhutan as compared to rest of the world. Bhutan has the lowest human density (17 people per km²) in the region (World Bank, 2015), and 70% of country is under forest

cover. Also, most Bhutanese are Buddhist with a strong aversion towards killing other life forms, and hunting wildlife is still taboo and rare. Overall tigers are known to tolerate human presence if enough prey and cover exists and they are not poached (Sunquist et al., 1999). Tigers respond positively to removal of human pressure (Harihar et al., 2009). It appears that as a country, Bhutan currently has attributes that support tigers as well as people.

5. Conclusion: conservation implication for regional tiger conservation

We develop the first scientifically rigorous estimate of tiger density for the country of Bhutan, including its extensive mountainous landscapes. Although the lack of comparable earlier density studies prohibits conclusions about current tiger population trends, this study will form the basis for future monitoring of tiger population dynamics in Bhutan. The most important conservation impact of this study is the finding that Bhutan should be included in any discussion of important tiger conservation areas (Walston et al., 2010b). Bhutanese tigers can both reinvigorate the whole NFC-N-RMNP TCL and provide critical linkages between Terai-Arc landscape and Indochinese tigers in Myanmar and further east. JSWNP and RMNP together with Indian Manas tiger reserve comprise the most important and largest protected area network in south Asia and can support large numbers of tigers (Ranganathan et al., 2008). Mountains are equally important for tigers in Bhutan, particularly cloud forests that support large populations of wild pigs and other prey for tigers. A mosaic of mountains, valleys and pasture lands are critical for tigers in Bhutan. Due to the strong commitment and visionary leadership towards conservation of the Bhutanese government, as well as the unwavering Buddhists beliefs of most Bhutanese, humans and tigers co-exist together in Bhutan. This delicate balance needs to be maintained and nurtured. To ensure the persistence of tigers and other wildlife in this *tigerscape*, we must be mindful that future changes do not undermine the conservation status of tigers in Bhutan.

Acknowledgments

The whole Department of Forests and Park Services (DoFPS) was behind Nation-wide tiger survey and many individuals participated in many ways. We would like to thank all field staff under DoFPS who participated in the nationwide tiger survey. We would also like to thank Ugyen Tenzin (from UWICE), Sangay Dorji (NCD), Dorji Duba (from JSWNP), Tshering (JSWNP), Letro (JSWNP), Dew Badhur Kumar (RMNP), and Mr. Tashi Dendup (UWICER) for their hard work and dedication in setting camera traps and getting camera traps data. We had the opportunity to work with some truly exceptional leaders within the Ministry of Agriculture and Forests. We thank His Excellency Lyonpo Yeshe Dorji, the former Agriculture and Forests Minister, His Excellency Lyonpo Yeshe Penjor, the current Agriculture and Forests Minister, Dasho Rinzin Dorji, Honorable Secretary, Dasho Chenchu Norbu, former Director General of Department of Forests and Park Services (DoFPS), Mr. Phento Tshering, former Director of DoFPS, and Mr. Lobzang Dorji, the current Director of DoFPS for their support and guidance and support. We would also like to thank Bhutan Foundation, Jigme Singye Wangchuck Research and Training Fund at UWICE, WWF, WCS, National Geographic Society (Waitt Grants), and Karuna Foundation for their generous funding support.

Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.biocon.2019.07.037>.

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