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Estimating Wild Tiger (*Panthera tigris* Linnaeus) Abundance and Density using a Spatially-explicit Capture-recapture Model in Jigme Dorji National Park, Bhutan

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Abstract

Wild tiger populations have rapidly declined in most of the range countries, and there is an urgent need to reliably estimate their numbers for effective management. The use of remotely-triggered camera traps has proven to be an efficient method to sample populations of highly elusive animals such as tigers. In addition, the spatially-explicit capture-recapture (SECR) models are the latest developments in estimation methods to reliably estimate animal density and abundance. Therefore, the objectives of this study were to reliably estimate the density and abundance of tigers and to study their distribution in Bhutan's Jigme Dorji National Park (JDNP) using the latest sampling and estimation methods. During 7,462 trap-days with 41 camera traps functionally stationed for 6 months in approximately 656 km^2 of highly probable areas of tiger occurrence in JDNP, 80 photographs of tigers (48 right flanks and 32 left flanks) were obtained. Analysis of all left flank pictures yielded seven unique tiger individuals. The SECR model, using an R programme package "SPACECAP" which uses Bayesian framework for inference, estimated the tiger abundance of 19 (*SE* = ± 6, 95% CI of 9 to 29 individuals) and the density of 3.7 (*SE* = ± 1.1, 95% CI of 1.8 to 5.8 individuals) per 100 km^2. Photographic recaptures and the SECR model yielded the highest tiger density occurring in the south-central region of the park. Using the model estimates, we determined that JDNP can support a maximum of 59 tigers. We posit JDNP as an important tiger conservation area in the upper Himalayan region of Bhutan.

Key words: Abundance, Bhutan, camera trapping, density, spatially-explicit capture-recapture, suitability, tiger

Introduction

Wild tiger (*Panthera tigris* Linnaeus) populations, estimated to have numbered near 100,000 individuals in the early twentieth century, are now diminished to a mere 3,500 (Wikramanayake *et al*., 2011) spread across 13 countries: Bhutan, India, Nepal, China, Russia, Bangladesh, Thailand, Vietnam, Malaysia, Indonesia, Laos, Cambodia, and Myanmar. In most of these countries, tigers face continuous pressure from poaching, retaliation by humans, and habitat fragmentation and degradation. Indeed, it has been noted that the twenty-first century holds a grim future for Asia's largest and most charismatic cat species (Dinerstein *et al*., 2007).

In the face of such rapid population decline and mounting threats, evidence is building that Bhutan could be one of the few strongholds left for tiger populations in the wild. Since the first camera trap study in Bhutan by Wang and Macdonald (2009), photographic evidence has been steadily accumulating to verify the occurrence of tigers in many parts of the country. This is not surprising given the vast tracts of contiguous and relatively undisturbed habitat provided by approximately 70.46% forest cover (NSSC and PPD, 2011) associated with a very low human population density of 19.1 persons per km^2 (NSB, 2013). In addition, tigers benefit from strong political support for habitat conservation from the Royal Government of Bhutan, which has dedicated half of the country to a network of protected areas and biological corridors for wildlife (MOAF, 2010).

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To date, six tiger surveys have been carried out in Bhutan, with three at the national level and three at the level of individual parks, to estimate the number and density of tigers in the country. These surveys have employed different methods at varying scales, yielding different population estimates. Dorji and Santiapillai (1989) estimated 150 to 250 individuals in the country using mostly local community interviews and a few track surveys along transects. Later, McDougal and Tshering (1998) surveyed nationwide for tiger sign along human trails, and estimated 115 to 150 individuals which include the cubs and sub-adults. Wang and Macdonald (2009) used camera trap surveys and analysed the data using the programme CAPTURE (Rexstad and Burnham, 1991) to estimate a tiger population of eight individuals in Jigme Singye Wangchuck National Park (JSWNP). Similarly, in similar study using the same survey method and analysis programme, Tempa *et al*. (2011) estimated 10 individuals in half of Royal Manas National Park (RMNP).

These earlier studies provided important contributions to tiger conservation in Bhutan, but there is a strong need to explore the latest refinements in survey and data analysis methods (Karanth *et al*., 2011) in our continued efforts to improve estimates of tiger abundance and density in Bhutan. The use of remotely-triggered camera traps, first used in India by Karanth (1995) for tigers, has proven to be an efficient method to non-invasively detect animal presence, and to estimate the population of highly elusive animals (Karanth and Nichols, 2010). Since then, deriving reliable estimates of population abundance and density have attracted much attention, and analytical techniques have advanced with improvements in camera trap models, GIS technology, and statistical inferences. In due course of time, researchers have critiqued estimations of animal densities from camera trap studies (Foster and Harmsen, 2012), and have recommended additional use of spatially-explicit capture-recapture (SECR) models (Efford, 2004; Borchers and Efford, 2008; Royle *et al*., 2009) as an alternative approach.

The incorporation of spatial distribution and patterns of the camera trap data would eliminate the challenges of estimating effective sample area in conventional capture-recapture models. Such an approach is promising (Karanth *et al*., 2011) because it formalises a linkage between effective sample area and capture history by a statistical model, instead of using *ad hoc* or heuristic methods as in traditional models (Royle and Gardner, 2011). Based on the work of Royle *et al*. (2009), Singh *et al*. (2010) developed the package SPACECAP, a SECR model based in R programming (R Core Team 2014), which not only uses photographic images and capture history, but also uses trap location data to address issues related to individual heterogeneity in estimating capture probabilities. Therefore, the objectives of this study were to reliably estimate the density and abundance of tigers and to study their distribution in Jigme Dorji National Park (JDNP) using camera traps and a SECR model.

Materials and Method

Study area

JDNP, measuring approximately 4,316 km^2, is the second largest and the oldest of the 10 protected areas in Bhutan (Figure 1). Reflecting the breadth of major climatic conditions, five major habitat types (warm broadleaved forest, cool broadleaved forest, mixed-coniferous forest, sub-alpine forests, and alpine meadows) constitute the park's landscape, all distributed along an elevation gradient, extending from 1,600 to 7,100 m. The park has been described as a conservation jewel, endowed with more than 40 species of mammals, 328 birds, 5 reptiles, 39 butterflies, and 1,450 vascular plants. Many globally-endangered species of mammals, such as tiger, snow leopard (*Panthera uncia* Schreber), dhole (*Cuon alpinus* Pallas), musk deer (*Moschus chrysogaster* Hodgson), and birds such as the critically endangered white-bellied heron (*Ardea insignis* Hume) find safe sanctuary in the park. In addition, approximately 300 species of medicinal plants grow in the park's alpine meadows and screes (Thinley *et al*., 2015).

Study design and selection of camera trap locations

Based on an ecology-based niche model of suitable areas for tigers, which is developed in GIS (Geographic Information System) using the input layers of prey distribution, vegetation cover, road, human settlement, and elevation (Thinley, 2008), the entire park was divided into likely and unlikely areas for tigers, with likely areas encompassing approximately 1,620 km^2 (Figure 1). Using an area close to the smallest reported tiger home range size of 15 km^2 (Karanth *et al*., 2011), a grid of 4 x 4 km cell size was overlaid on the map of probable tiger areas.

Within the entire designated tiger area, a reconnaissance survey was conducted by well-trained park rangers and their support staff across all grid cells. In each designated grid cell, all identifiable human and animal trails were traversed to search for direct evidence of tiger presence, such as scat, tracks, scratch marks, rubbings, scent marks, carcasses, and sightings. Additionally, reports of

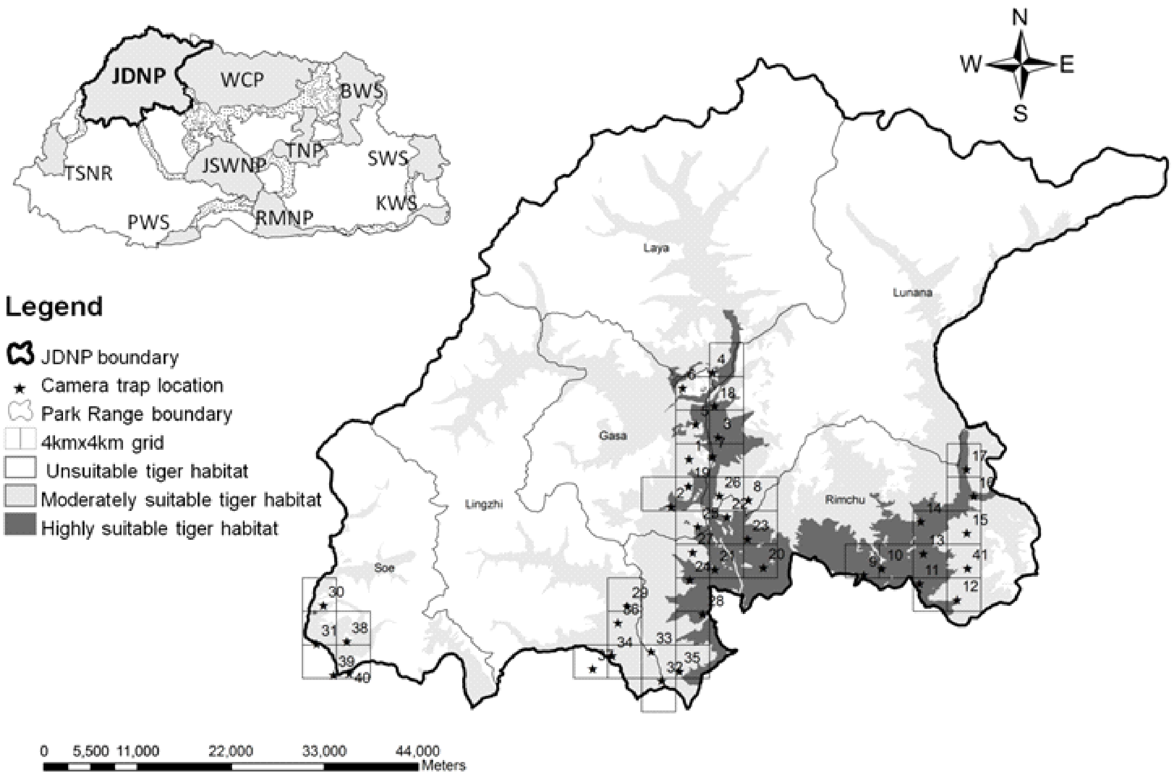

Figure 1. Location of the study area, showing camera traps with ID number, and suitable and unsuitable areas for tigers in JDNP. The inset shows the map of protected areas (grey areas) and biological corridors (dotted lines) in Bhutan

livestock killed by tigers, and local people's knowledge, also were recorded to help identify areas with the highest probability of tiger occurrence. Based on this preliminary survey, finally, 31 grid cells containing areas with the most evidence were identified for stationing camera traps (Figure 1). An additional 10 grid cells in the southeastern region of the park were added to the study to check if there was any tiger there, because tiger presence was expected in that region of the park due to presence of highly suitable habitat (Thinley, 2008).

Installation and monitoring of camera traps

We used only one camera per station, unlike Karanth (1995) and Tempa *et al*. (2011), primarily because of the limited number of cameras. Such a design had the added value of allowing us to cover more areas (Foster and Harmsen, 2012). One camera trap was stationed within each of 41 selected grid cells that altogether encompassed approximately 656 km^2. Because tigers were known to often use human trails (Smith *et al*., 1989), in each grid cell, a camera was placed in the most probable location for spotting tigers, as determined by the presence of narrow trails, few or no alternate trails, or the junctions of several trails. Also, areas with high density of prey signs were chosen for stationing camera traps, because tiger densities were reported to be higher in areas with high prey densities (Karanth *et al*., 2004b). Cameras were placed on a tree or a pole, at a minimum height of 1 m above ground, to capture the flank of a tiger, a leopard (*Panthera pardus* Linnaeus), or other similar-sized wild predators.

We used CuddebackTM camera traps with infrared sensors, but without flash (Capture IR model, Non Typical Inc., Wisconsin, USA), to avoid detection by humans, to avoid frightening the animals, and to ensure minimal or no influence of the camera on avoidance of the trap site by the target species. No cameras were lost to thieves, nor damaged by wild animals during the entire study.

Cameras were regularly checked every two weeks as part of the monthly work plan at each ranger station, and the monitoring was incorporated into periodic anti-poaching patrols. During each camera check, battery level and remaining memory capacity were monitored, overhanging leaves and branches obstructing views between the animal pathway and the cameras were removed, and displaced cameras were repositioned. The camera-traps were maintained for six months from 1 September, 2011 to 29 February, 2012.

We used two weeks (15 days) as a monitoring interval for several reasons. First, shorter intervals and more frequent visits to the trap stations would likely reduce the frequency of tiger sightings, as they instinctively avoid encounters with humans (Karanth *et al*., 2011). More extended intervals were not feasible, because the batteries lasted for an average of 20 days, and the vegetation around the camera stations grew fast in warm broadleaved forests, and could quickly obscure the camera lens if not cleared. Thus, a two-week interval was a good compromise between too short and too long duration.

We could have baited the traps to increase visitation rates near the trap stations and possibly increase capture-recapture probabilities (Thorn *et al*., 2009; Karanth *et al*., 2011). However, baits were not used in this study for ethical and religious reasons.

Data organisation

After each monitoring period, the park rangers organised the images by camera trap identification (ID) and monitoring period. Images were submitted every month to the park head office where the research ranger consolidated the image data by ranger station in a central database. All tiger images were classified by camera ID, monitoring period, and ranger station. They were then organised into two folders (one designated for left flank images and one for right flank images), because we could not ascertain if both flank images belonged to a specific individual tiger due to the long time gap between successive tiger images. For mark-recapture estimation, we considered a two-week monitoring period as a unique sampling occasion, and this minimum period was appropriate because no individuals were captured in two or more different stations within this same sampling period which otherwise would have resulted in information loss.

Identification of tiger individuals

Tigers possess uniquely identifiable stripe patterns (Karanth, 1995; Reddy and Aravind, 2012), which allowed us to distinguish individual tigers from others (Hiby *et al*., 2009) and identify them in subsequent sampling occasions and at different camera trap locations (Nichols, 1992). Further, it has been shown that estimation of abundance is possible with single-flank photographs (Wang and Macdonald, 2009; Karanth *et al*., 2011; Foster and Harmsen, 2012). In our study, we used left flank images for identification of individuals and their recaptures in various stations and sampling occasion, because there were more colored and clearer pictures of left flanks for identification of individuals. Individual tigers were identified from uniquely distinguishing characteristics – unique stripe patterns on head, neck, shoulder, flank, rump, and tails, and scars or other distinguishing characters like body size and sex – discernible from the camera trap images. Because subjective identification of individuals can significantly bias estimates of abundance and density (Mendoza *et al*., 2011), additional and independent assessments were sought on the distinctiveness of individual tigers from several field staff and tiger experts. Photographs of individual tigers were assigned a unique identification number and capture histories were constructed for each individual tiger.

Data analysis

We used the package “SPACECAP”, developed by Singh *et al*. (2010) based on Bayesian spatially-explicit models (Royle *et al*., 2009), in R 3.0.2 (R Core Team 2014) to analyse the capture-recapture data derived from tiger images. Following the instructions in the package information, we organised the data into three input files. The first input file contained capture details of tigers by location of camera traps, animal ID, and sampling occasion to account for individuals trapped at more than one camera location, and on more than one sampling occasion. The second input file contained location information in the form of Universal Transverse Mercator (UTM) coordinates for the camera traps by sampling occasion. This file also included details about the duration when specific cameras were operational at a particular site. The third input file contained the partial home range centres in UTM coordinates of the 4 x 4 km grid centres derived from the minimum-area rectangle and its buffer of 12 km width containing the trap array created in ArcGIS 9.3 (Environmental Systems Research Institute, Inc., California, USA). In this file, suitability of each grid centre for tigers was determined from the map of tiger suitability areas designed by Thinley (2008).

Results and Discussion

Photographic capture-recapture of individuals

A sampling effort of 7,462 trap days, using 41 camera traps stationed for 6 months, yielded 80 photographs of tigers, including 48 images of right flanks and 32 of left flanks. Through extensive scrutiny and a series of separate identification processes of all left flank images, at least seven distinct tigers were observed in the park. For the most part, we could not determine the sex and age of these individuals, because only a few images clearly showed the tail portions and canines. We also did not see any images of tiger cubs or lactating females.

Out of 41 camera traps, tiger images were obtained from only 18 stations. Three individual tigers (JDNP-1, 5, and 6) were captured on three different cameras.

All seven individuals were captured on at least three different cameras. All these indicate potential range overlap among the individual tigers (Figure 2).

A single individual tiger (JDNP-6) was photographed eight times, accounting for 20% of total captures, and this was the tiger recorded most often. The least recorded tiger (JDNP-7) was photographed three times, comprising 7% of total captures.

Abundance and density estimates

We constructed a capture history for the six-month sampling period covering September, 2011 through February, 2012, which included 12 separate two-week sampling occasions (Table 1). In this study, we assumed population closure (Otis *et al*., 1978), which was supported by a lack of evidence of tiger poaching, deaths, and cub births (as there was no images of cubs throughout the sampling period).

Using the capture histories and a posterior model fit with half-normal detection function, the estimated number of tigers in JDNP was 19 (*SE*= ± 6, 95% CI of 9 to 29 individuals). This was a plausible estimate judging from the observed pattern of new tigers photographed in sampling occasions 1,2,4, and 9 (Table 1, Figure 3). From the SPACECAP model estimates, the tiger density in JDNP was calculated to be 3.7 (*SE* = ± 1.1, 95% CI of 1.8 to 5.8 individuals) per 100 km^2.

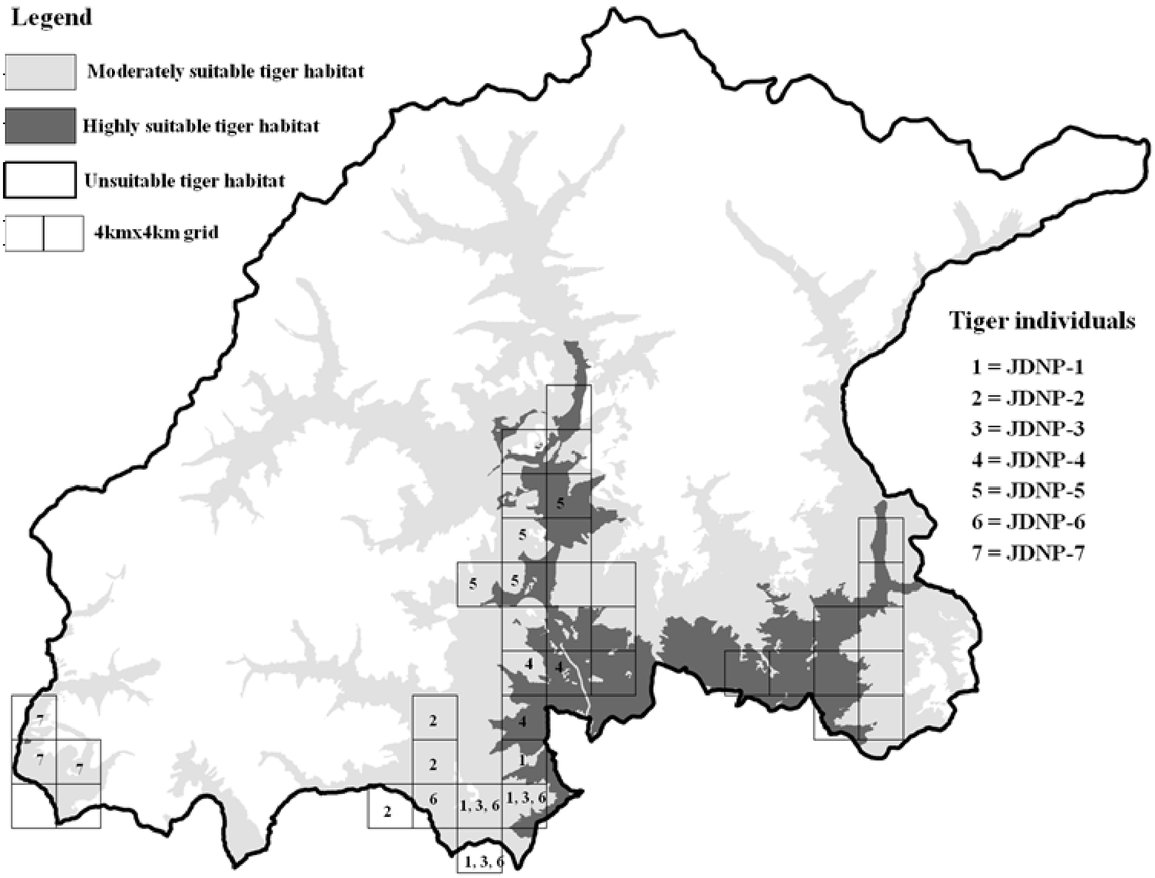

Figure 2. Distribution of tigers in JDNP as per captures on camera traps stationed in the park

The model fitted the data well, with a Bayesian *p*-value of 0.4, based on individual encounters (probability of observed dataset > simulated dataset). Values close to 0.5 would indicate adequate description of the data by the model, whereas values close to 0 or 1 would imply lack of fit (Royle *et al*., 2009).

Identifying 7 distinct individuals, our study estimated 19 tigers in JDNP. Using an estimated density of 3.7 individuals per 100 km^2 and the total potential tiger area of 1,620 km^2, JDNP could support up to 59 tigers. Comparing our estimate to other studies in the country, Tempa *et al*. (2011) estimated 10 individuals (*SE* = ± 2.78) with a density of 4.9 tigers per 100 km^2 in approximately 50% of RMNP. However, these estimates may increase if the entire park area is studied. In addition, our estimates of abundance and density in JDNP were higher than those reported by Wang and Macdonald (2009) in JSWNP, where they estimated only 8 tigers (*SE* = ± 2.12) with a density of 0.52 per 100 km^2 using camera trap survey but using the programme CAPTURE.

Table 1. Capture history for tigers in JDNP from 41 functional camera traps

Individual ID	Sampling occasions											
	1	2	3	4	5	6	7	8	9	10	11	12
JDNP-1	0	0	0	**1**	1	1	0	0	1	1	1	0
JDNP-2	0	**1**	0	1	0	1	0	0	1	0	0	1
JDNP-3	0	0	0	**1**	0	1	1	0	1	0	0	1
JDNP-4	0	**1**	0	1	1	0	1	1	0	1	1	0
JDNP-5	0	**1**	1	1	1	0	1	0	0	1	1	1
JDNP-6	**1**	1	0	0	1	1	0	0	1	0	1	1
JDNP-7	0	0	0	0	0	0	0	0	**1**	1	1	0

Note: New tigers encountered in a sampling occasion are highlighted in bold

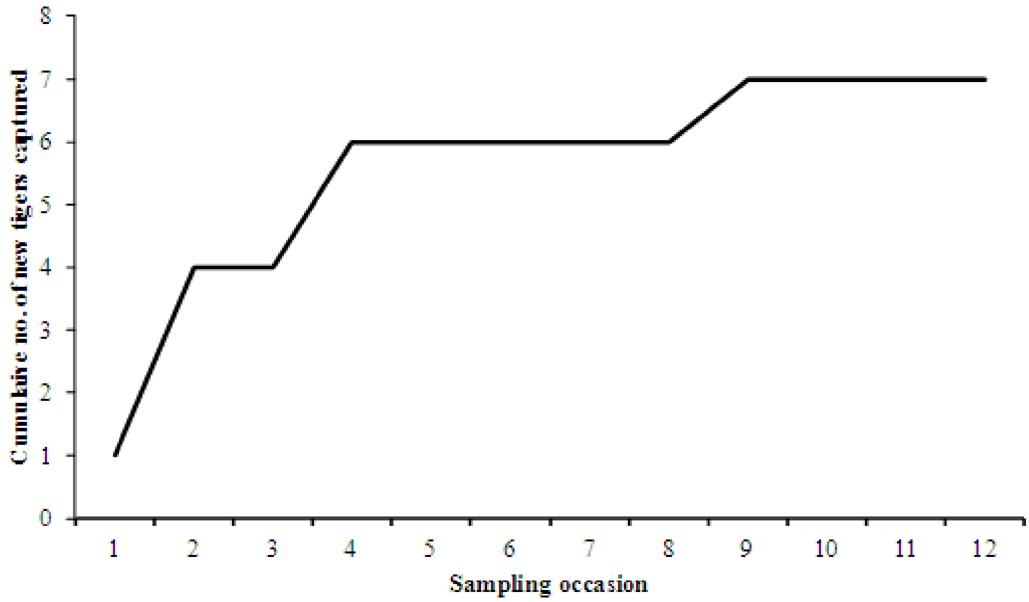

Figure 3. Cumulative number of new tiger individuals captured in camera traps within successive sampling occasions

In addition, our estimated tiger density in JDNP was similarly much higher than estimates of 0.5 adult tigers per 100 km^2 reported for the Inner Himalayan ranges (McDougal and Tshering, 1998). Regionally, our estimate of tiger abundance is comparatively lower than those estimated in many other national parks in India (Karanth *et al*., 2004a; Gopalaswamy *et al*., 2012).

Tiger distribution and management implications

According to the model-estimated distribution, most tigers in JDNP were confined to its south-central region (Figure 4). Specifying the locations, tigers were distributed among the areas of Domenday, Dolamkencho, Drololum, Charilum, Pelgiri, Zatola, and Dochupangkha, which had four different individuals (JDNP-1, 2, 3, and 6; Figure 2). One tiger (JDNP-5) ranged along Yamipangkha, Phuntshogang, Jabesa, Gezatop, and Gangchenzoekha, and another tiger (JDNP-4) confined itself to Tshechudrag, Khailotop, Nangsigoenpa, and Drochukhatop. These areas, together measuring about 608 km^2, formed a continuous prime habitat for tigers with a high density of wild prey and domestic cattle (Thinley, 2008). These areas were also least impacted by human activities, except for the occasional release of domestic cattle. Most tigers, six of seven recognised from camera trap photographs, were captured within this habitat continuum.

Similarly, a lone tiger (JDNP-7), residing in Shana and Namchakha areas which are located in the southwestern part of the park, was captured in three of four camera traps. This region of the park includes about 92 km^2 of prime habitat with adequate wild prey and domestic cattle available. This tiger also seemed to be moving along the corridor connecting JDNP and Jigme Khesar Strict Nature Reserve (JKSNR) located in the western most Bhutan, and it is probable that it came from the south-central part of the park due to connectivity of habitats along the park's southwestern border (Figure 2).

Surprisingly, not a single tiger image was captured from any of the 10 cameras stationed in the southeastern region of the park, where the habitat appeared equally good as in the other two regions where tigers were observed. Many pictures of sambar (*Rusa unicolor* Kerr), Himalayan serow (*Capricornis thar* Hodgson), and barking deer (*Muntiacus muntjak* Zimmermann) were captured by this group of cameras, indicating at least adequate presence of prey for tigers. Casual interviews with the local residents supported our finding, indicating that no tigers had been sighted in the area during the past two years. The possibility that there was not a single tiger residing in 920 km^2 of highly suitable habitat in the southeastern part of the park (Figure 2) suggested possible poaching and/or disturbance caused by locals or people from other communities, as evidenced by several pictures of men with bows and arrows captured on two camera traps. The absence of tigers in this region of the park, where habitats were suitable, prey density was high, and potential for tiger occupancy was high, evokes a sense of urgency for park management to take over the administrative rights from the nearby territorial forest division. Patrolling and anti-poaching activities should be intensified in this region to encourage re-colonisation by tigers.

Tigers were observed on cameras from elevations of 2,208 to 4,105 m above sea level. Five individual tigers were photographed in three camera traps that were stationed above 4,000 m: camera trap 33 stationed at 4,045 m photographed tiger JDNP-1, 3, and 6; camera trap 29 at 4,100 m captured JDNP-2; and camera trap 31 at 4,105 m captured JDNP-7 (Figure 2). Thus, our study provides empirical evidence of tiger's frequent use of habitats above 4,000 meters, probably attracted by free-ranging yaks in those areas.

The resulting pattern of the estimated posterior density from the SPACECAP model's point process (Figure 4) assigned the highest tiger density to the south-central and southwestern zones of the park, ranging from 2-8 tigers per 100 km^2. Hence, these areas were classified as tiger hotspots in the park. This finding shows that tigers in JDNP were not evenly distributed; instead, there was a clustering in south-central and southwestern areas of the park, where livestock densities were high (Leki, personal comm.). Indeed, the park rangers in these areas registered several complaints of livestock depredation by tigers. For instance, tiger JDNP-5 was captured in a camera trap set up at Damji Village in Gasa Dzongkhag (administrative district) in May 2010 after it had reportedly killed a bull. Notably, tigers in Lingzhi Range seemed to attack domestic yaks (*Bos grunniens grunniens* Linnaeus) at high elevations based on reports of increasing yak losses submitted by individuals in the communities of Naro geog (administrative block). So far, park management

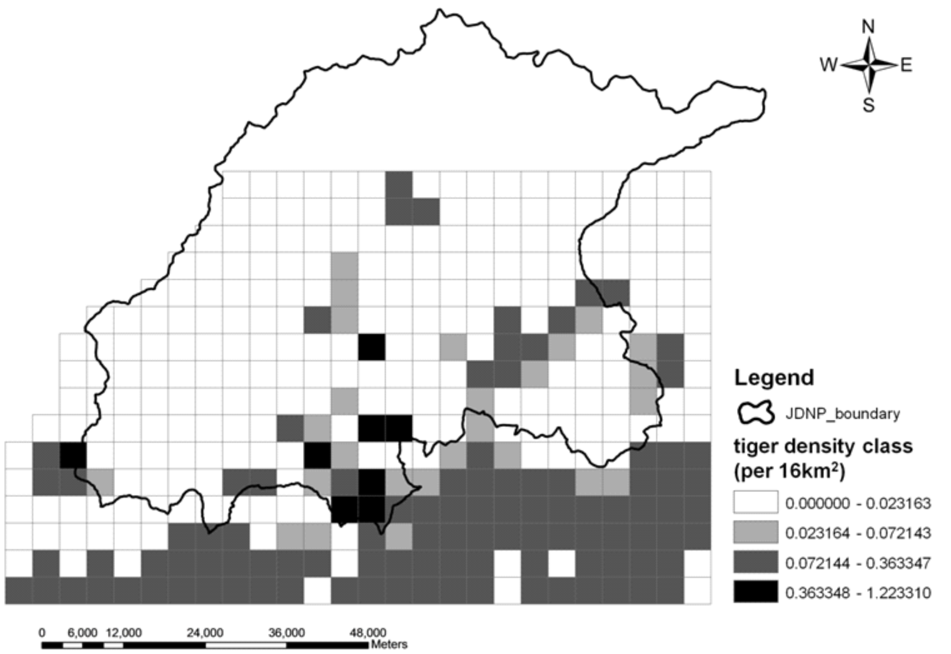

Figure 4. Estimated posterior density of tigers in JDNP's tiger state-space predicted by SPACECAP model in R and projected using ArcGIS. Light grey areas represent low density and darker areas represent high density of tigers

has not received any reports of retaliatory killings of tigers by local yak herders or farmers, indicating a possible tolerance for the tigers. However, these two tiger hotspots should be patrolled regularly for any signs of poaching and retaliatory killing by farmers.

Applicability of SECR model in Bhutan

Despite the limitations imposed by the rugged terrain in Bhutan, we were able to successfully apply the spatially-explicit capture-recapture model using only single-flank images to estimate the abundance and density of tigers in JDNP. Due to differences in topography between our study area and that of Royle *et al*. (2009) and Karanth (1995), our study was limited to only one camera per location to construct capture histories, and to estimate density and abundance. Nevertheless, using an approach similar to that of Wang and Macdonald (2009), we were able to identify 7 individual tigers, and estimate between 9 to 29 tigers for the entire park.

Generally, tigers in the mountainous regions of Bhutan occur at low densities (Wang and Macdonald, 2009) which inevitably necessitate a prolonged trapping effort. Karanth *et al*. (2011) recommended a shorter sampling period, not exceeding 60 days, but in our study we have found that more tigers were captured even after 60 days. Even Kawanishi and Sunquist (2004) and Simcharoen *et al*. (2007) sampled for more than 11 months and successfully applied closed population models. Therefore, our sampling period fixed at six months with a total effort of 7,462 trap-days was valid, while still not violating assumptions of demographic closure for our model. Judging from the recapture rates of individuals at the same cameras, the two-week monitoring interval did not appear to disrupt the tiger's daily activities and visitation.

Conclusion

We posit JDNP as one of the important areas for conservation of the globally-endangered tigers in Bhutan. Although only one third of the park is suitable for tigers, we estimated between 9 to 29 tigers in the park, an abundance range which is very high in relation to the proportion of available habitats. We recommend that the park management conduct periodic camera trapping exercises to monitor tiger populations, and to enhance patrolling programmes in the southwestern region of the park to enable recovery of tiger population in that region.

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References

Borchers, D.L. and Efford, M.G. (2008). Spatially explicit maximum likelihood methods for capture-recapture studies. *Biometrics,* 64: 377-385. doi: 10.1111/j.1541-0420.2007.00927.x

Dinerstein, E., Loucks, C., Wikramanayake, E., Ginsberg, J., Sanderson, E., Seidensticker, J., Forrest, J., Bryja, G., Heydlauff, A., Klenzendorf, S., Leimgruber, P., Mills, J., O'Brien, T.G., Shrestha, M., Simons, R. and Songer, M. (2007). The fate of wild tigers. *Bioscience,* 57: 508-514. doi: http://dx.doi.org/10.1641/B570608

Dorji, D.P. and Santiapillai, C. (1989). The status, distribution and conservation of the tiger *Panthera tigris* in Bhutan. *Biological Conservation,* 48: 311-319.

Efford, M. (2004). Density estimation in live-trapping studies. *Oikos,* 106: 598-610.

Foster, R.J. and Harmsen, B.J. (2012). A critique of density estimation from camera trap data. *Journal of Wildlife Management,* 76: 224-236. doi: 10.1002/jwmg.275

Gopalaswamy, A.M., Royle, J.A., Delampady, M., Nichols, J.D., Karanth, K.U. and Macdonald, D.W. (2012). Density estimation in tiger populations: combining information for strong inference. *Ecology,* 93: 1741-1751.

Hiby, L., Lovell, P., Patil, N., Kumar, N.S., Gopalaswamy, A.M., and Karanth, K.U. (2009). A tiger cannot change its stripes: using a three-dimensional model to match images of living tigers and tiger skins. *Biology Letters,* 5: 383-386. doi: 10.1098/rsbl.2009.0028

Karanth, K.U. (1995). Estimating tiger *Panthera tigris* populations from camera trap data using capture-recapture models. *Biological Conservation,* 71: 333-338.

Karanth, K.U., Chundawat, R.S., Nichol, J.D. and Kumar, N.S. (2004a). Estimation of tiger densities in the tropical dry forests of Panna, Central India, using photographic capture-recapture sampling. *Animal Conservation,* 7: 285-290. doi: 10.1017/S1367943004001477

Karanth, K.U. and Nichols, J.D. (2010). *Non-invasive survey methods for assessing tiger populations.* Pages 241-261 in R. Tilson, and P. J. Nyphus, editors. Tigers of the World: The Science, Politics, and Conservation of *Panthera tigris*. Academic Press, New York, United States.

Karanth, K.U., Nichols, J.D. and Kumar, N.S. (2011). *Estimating tiger abundance from camera trap data: Field surveys and analytical issues.* Pages 97-117 in A. F. O'Connell, J. D. Nichols, and K. U. Karanth, editors. Camera Traps in Animal Ecology: Methods and Analyses. Springer, New York, United States.

Karanth, K.U., Nichols, J.D., Kumar, N.S., Link, W.A. and Hines, J.E. (2004b). Tigers and their prey: predicting carnivore densities from prey abundance. *Proceedings of the National Academy of Sciences of the United States of America,* 101: 4854-4858. doi: www.pnas.org_cgi_doi_10.1073_pnas.0306210101

Kawanishi, K. and Sunquist, M.E. (2004). Conservation status of tigers in a primary rainforest of Peninsular Malaysia. *Biological Conservation,* 120: 329–344. doi: 10.1016/j.biocon.2004.03.005

McDougal, C.W. and Tshering, K. (1998). *Tiger conservation strategy for the Kingdom of Bhutan.* Nature Conservation Division, Department of Forests, Thimphu, Bhutan.

Mendoza, E., Martineau, P.R., Brenner, E. and Dirzo, R. (2011). A novel method to improve individual animal identification based on camera trapping data. *Journal of Wildlife Management,* 75: 973–979. doi: 10.1002/jwmg.120

MOAF. (2010). *National forest policy of Bhutan 2010*. Kuensel Corporation Limited, Thimphu, Bhutan.

NSB (National Statistics Bureau). (2013). *Bhutan at a Glance.* National Statistics Bureau, Thimphu, Bhutan.

NSSC and PPD. (2011). *Bhutan Land Cover Assessment 2010*. National Soil Service Centre, Department of Agriculture, MoAF, Thimphu, Bhutan.

Nichols, J.D. (1992). Capture-recapture models: using marked animals to study population dynamics. *BioScience,* 42: 94-102.

Otis, D.L., Burnham, K.P., White, G.C. and Anderson, D.R. (1978). Statistical inference from capture data on closed animal populations. *Wildlife Monographs,* 62: 3-135.

R Core Team. (2014). *R: A language and environment for statistical computing*. R Foundation for Statistical Computing, Vienna, Austria.

Reddy, K.P.K. and Aravind, R. (2012). *Segmentation of camera trap tiger images based on texture and color features.* Pages 1-5. National Conference on Communications (NCC), 2012, India.

Rexstad, E. and Burnham, K.P. (1991). *Users guide for interactive program CAPTURE.* Cooperative Fish and Wildlife Research Unit, Colorado State University, Fort Collins, United States.

Royle, A.J. and Gardner, B. (2011). *Hierarchical Spatial Capture–Recapture Models for Estimating Density from Trapping Arrays.* Pages 163-190 in A. F. O'Connell, J.D. Nichols, and K.U. Karanth, editors. Camera Traps in Animal Ecology: Methods and Analyses. Springer, New York, United States.

Royle, J.A., Karanth, K.U., Gopalaswamy, A.M. and Kumar, N.S. (2009). Bayesian inference in camera trapping studies for a class of spatial capture-recapture models. *Ecology,* 90: 3233-3244.

Simcharoen, S., Pattanavibool, A., Karanth, K.U., Nichols, J.D. and Kumar, N.S. (2007). How many tigers *Panthera tigris* are there in Huai Kha Khaeng Wildlife Sanctuary, Thailand? An estimate using photographic capture-recapture sampling. *Oryx,* 41: 447–453. doi: 10.1017/S0030605307414107

Singh, P., Gopalaswamy, A.M., Royle, A.J., Kumar, N.S. and Karanth, K.U. (2010). *SPACECAP: A program to estimate animal abundance and density using Bayesian spatially-explicit capture-recapture models.* Wildlife Conservation Society-India Program, Center for Wildlife Studies, Bangalore, India.

Smith, J.L.D., Mcdougal, C., and Miquelle, D. (1989). Scent marking in free-ranging tigers, *Panthera tigris*. *Animal Behaviour,* 37: 1-10.

Tempa, T., Norbu, N., Dhendup, P. and Nidup, T. (2011). *Results from a camera trapping exercise for estimating tiger populations size in the lower foothills of Royal Manas National Park.* Kuensel Corporation, Thimphu, Bhutan.

Thinley, P. (2008). *Design and application of a new conservation paradigm to tiger conservation in Bhutan.* Natural Resources. Cornell University, Ithaca, New York, United States.

Thinley, P. (2010). Technical comments on the design and designation of biological corridors in Bhutan: global to national perspectives. *Journal of Renewable Natural Resources of Bhutan,* 5: 90-105.

Thinley, P., Tharchen, L. and Dorji, R. (2015). *Conservation management plan of Jigme Dorji National Park for the period January 2015 - December 2019: Biodiveristy conservation in pursuit of Gross National Happiness*. Department of Forests and Park Services, Kuensel Corporation Ltd., Thimphu, Bhutan.

Thorn, M., Scott, D.M., Green, M., Bateman, P.W. and Cameron, E.Z. (2009). Estimating brown hyaena occupancy using baited camera traps. *South African Journal of Wildlife Research*, 39: 1-10. doi: http://dx.doi.org/10.3957/056.039.0101

Wang, S.W., and Macdonald, D.W. (2009). The use of camera traps for estimating tiger and leopard populations in the high altitude mountains of Bhutan. *Biological Conservation,* 142: 606-613. doi: 10.1016/j.biocon.2008.11.023

Wikramanayake, E., Dinerstein, E., Seidensticker, J., Lumpkin, S., Pandav, B., Shrestha, M., Mishra, H., Ballou, J., Johnsingh, A.J.T., Chestin, I., Sunarto, S., Thinley, P., Thapa, K., Jiang, G.S., Elagupillay, S., Kafley, H., Pradhan, N.M.B., Jigme, K., Teak, S., Cutter, P., Aziz, M.A. and Than, U. (2011). A landscape-based conservation strategy to double the wild tiger population. *Conservation Letters,* 4: 219-227. doi: 10.1111/j.1755-263X.2010.00162.x