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THE ECOLOGY OF MONTANE BENGAL TIGERS (Panthera tigris tigris) IN THE HIMALAYAN KINGDOM OF BHUTAN

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THE ECOLOGY OF MONTANE BENGAL TIGERS (*Panthera tigris tigris*) IN THE

HIMALAYAN KINGDOM OF BHUTAN

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The ecology of montane Bengal tigers (*Panthera tigris tigris*) in the Himalayan kingdom of Bhutan

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ABSTRACT

Large carnivores are endangered across the globe. Loss of habitat and habitat fragmentation, prey depletion, and direct poaching for the illegal wildlife trade are the major causes driving them towards extinction. Although tigers (*Panthera tigris*) once roamed across Asia, they are now restricted to 7 % of their historical range and experiencing rapid population declines. This warrants a concerted, multipronged strategy that will halt further declines of tigers in the wild. One approach put forth by some scientists is to focus conservation on 6% of the presently occupied tiger habitat identified as tiger sources sites. Other scientists argued for a broader strategy to enhance tiger populations outside of tiger sources sites. Bhutan, for example, was not included in this 6% solution. Here we evaluate whether Bhutan is a potential tiger source site using spatially-explicit mark recapture models to estimate tiger density and spatial distribution in Bhutan. We used large scale remote-camera trapping across n=1,129 sites in 2014 – 2015 to survey all potential tiger range in Bhutan. We estimated 90 (95% CI 80 – 103) individual tigers with 45 females (95% CI 49 – 80) and with a mean density of 0.23 (0.21 – 0.27) adult tigers per 100 km^2. Thus, Bhutan has significantly higher numbers of tigers than almost all identified source sites (mean=54) in the 6% solution. We used N-mixture models to estimate spatial distribution and relative abundance of primary prey species of tigers in Bhutan, and the effects of anthropogenic disturbance on tigers and their prey. Gaur (*Bos gaurus*) and sambar (*Rusa unicolor*) are concentrated in the southern part of Bhutan and were strong determinants of tiger occupancy. Wild pigs (*Sus scrofa*) and muntjac (*Muntiacus muntjak*) are wildly distributed across Bhutan, but did not affect tiger occupancy. In contrast to many other tiger ranges, anthropogenic disturbance did not show consistent negative impacts on tigers and their prey. We show how important the landscape of Bhutan and adjacent northeast India is to regional tiger conservation. With low human density and large swaths of forest cover, this landscape is a promising stronghold for tigers in future.

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ཨོཾ་མ་ཎི་པདྨེ་ཧཱུྃ།(“*Om Mani Pedme Hung*”) salutation to Avalokiteśvara**,** the embodiment of the compassion of all the Buddhas**.** I take this opportunity to pay my homage and gratitude to His Majesty the fifth King of Bhutan, for awarding me the most prestigious fellowship to study Wildlife Biology at the University of Montana. It was here, at the University of Montana that I met many wonderful souls that I decided to continue and complete my PhD.

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Chapter 1: Dissertation overview and introduction

Habitat loss, prey depletion and poaching are the major causes of population declines for large carnivores in the wild (Karanth and Gopal 2005, Seidensticker 2010, Ripple et al. 2014). The most difficult task for conservation agencies is to maintain viable populations of large carnivores that require large and intact habitats (Ray et al. 2005). Because these large carnivores are rare, elusive, and wide ranging, they are difficult to conserve as well as study and manage. As apex predators, large carnivores also generate fear and hatred in humans often resulting from human-carnivore conflicts, but they are also charismatic and iconic for which they are respected by other segments of society (Clucas et al. 2008, Ripple et al. 2014). Thus, they are both persecuted as well as revered as guardians of the wild (Seidensticker 1996, Nyhus and Tilson 2010).

Tigers (*Panthera tigris*) are one of the largest and the most endangered large carnivores on the planet (Goodrich et al. 2015). They are often used as a flagship and umbrella species for conservation of Asian landscapes (Wikramanayake et al. 1998, Barua 2011). Tigers once roamed in most of Asia's wild lands. Historically there were around 100,000 tigers at the turn of last century, but today their numbers have plummeted below 3,200 and they occupy mere a 7% of their historical range (Dinerstein et al. 2007). There were as many as 10,000 tigers in the wild when the species was declared as endangered in 1969 by the International Union for Conservation of Nature and Natural Resources (IUCN) (Nyhus and Tilson 2010). However even after five decades of conservation efforts, the status of the tiger has not changed and its number in the wild continues to fall. There is no other species in Asia that has received the attention of both scientists and conservationists like the tiger (Seidensticker 2010). The future of this charismatic predator is however, not yet secured.

The 13 tiger range countries that harbor the last remaining tiger populations in the wild are also amongst the most densely populated by humans. The paradox of conserving wildlands and large carnivores while at the same time improving human welfare has generated much debate. Many tiger range countries are geared towards human welfare and socio-economic development, and are experiencing profound economic growth fueled by open markets and globalization. In light of this, conservationists and practitioners have identified 76 Tiger Conservation Landscapes (TCLs) to prioritize and reinforce tiger conservation efforts in these 13 tiger range countries (Dinerstein et al. 2007, Sanderson et al. 2010) (Figure 1). A Tiger Conservation Landscape is "a block or cluster of blocks of 'potential effective habitat' within 4 km of each other, meeting a minimum, habitat-specific size threshold, where tigers have been confirmed to occur during the last 10 years and are not known to have been extirpated since the last observation" (Sanderson et al. 2010). However, only 21 % of the existing 76 TCLs are under some form of protected areas (PAs) and enormous pressure persists for exploitation of natural resources such as gas, oil and timber in the TCLs and PAs (Forrest et al. 2011) as well as new threats such as infrastructure development (Seidensticker 2015). Although habitat loss will continue to be the major threat for tiger survival, increasing poaching activities in the protected area also pose a serious threat to tiger populations (Wright 2010, Sharma et al. 2014). The insatiable market for tiger parts in China coupled with culture of Southeast Asia and North Eastern India to eat anything that moves is a sad reality that creates "empty forests" in these regions, reducing tigers indirectly (Redford 1992, Datta et al. 2008, Harrison 2011, Velho et al. 2012).

There are a few encouraging stories from well-protected and regularly monitored tiger populations in the national parks. In Nagarhole and Bandipur in India, Chitwan in Nepal and the

Russian Far East and Northeastern China, provide a ray of hope that tiger can come back if a conducive environment is provided (Karanth et al. 2006, Seidensticker et al. 2010, Wang et al. 2016, Xiao et al. 2016). Against all odds, these areas offer some hope that conservation of tigers can be guaranteed into the future with political will and commitment from local and international conservations agencies. The global tiger recovery program that was endorsed in the St. Petersburg Declaration on Tiger Conservation at the International Tiger Forum ('Tiger Summit'), held in St. Petersburg, Russia, on November 21–24, 2010 has one of its goals to double wild tiger numbers by year 2022 (GTRP 2011). One proposal put forth is conservation of only 6% of the tiger habitat considered as "source sites", known as the "6% solution" (Walston et al. 2010b). "Tiger source sites" are defined as an area 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 (Karanth et al. 2010; Walston et al. 2010). This is slightly different from the ecological definition of "source" and "sink" in ecological literature (Runge et al. 2006, Mills 2012). Others have proposed landscape-level conservation (Sanderson et al. 2010, Wikramanayake et al. 2011) to achieve the goal of doubling tiger numbers. In contrast to the 6% strategy, landscape-level conservation would protect large tracks of tiger habitat areas left out under the 6% solution.

A pressing question is how much tiger habitat of conservation value might be lost in the 94% of tiger habitat not included in the 6 % solution. One tiger conservation landscape not included in the 6% solution is the Northern Forest Complex - Namdhapha -Royal Manas that straddles the border of northeastern India, Bhutan and Myanmar (Figure 1). This region has the largest intact and contiguous forest cover on the Indian subcontinent (237,820 km^2; Sanderson et al. 2010), and is the largest TCL outside of the Russian Far East. The low human population density and intact forests in these landscapes offer great potential for Bengal tiger (*P. t tigris*) conservation (Ranganathan et al. 2008) . Our recent preliminary result from Royal Manas National Park and Jigme Singye Wangchuck National Park in the Bhutan portion of the NFC-N-RM indicates that Bhutan has healthy population densities of tigers equal or greater than other Indian populations (Tempa et al. 2011, Tempa et al. 2013). One of the goals of my Dissertation is to expand these previous preliminary studies to the entire country of Bhutan. Moreover, the Indian Manas Tiger Reserve is recovering after huge setbacks due to militant insurgents from the late 1980s to the early 2000s (Goswami and Ganesh 2011, Soud et al. 2013, Goswami and Ganesh 2014). Thus, the NFC-N-RM region seems likely to harbor large numbers of tigers in one large, connected landscape, and should be considered in global tiger conservation strategies. In addition to potentially harboring significant tiger populations of its own, Bhutan may also be important in connecting the Terai Arc grassland of India and Nepal TCL's to other TCLs in Northeast India and indeed to Indochinese tiger (*P. t. corbetti)* populations in Southeast Asia along the foothills of Himalaya. Connectivity along the Indian portion of this TCL has largely been severed by dense settlement and agriculture, but most of the forest in the Bhutan and NFC-N-RM is still intact and in many parts pristine, possibly providing safe corridors for tigers to disperse and move between these TLCs (Sharma et al. 2011). Thus, Bhutan may form a linkage for connectivity and gene flow between Bengal tiger populations in the Indian subcontinent and Indochinese tigers.

Bhutan is a global biodiversity hotspot for wild felids (Tempa et al. 2013) where tiger conservation would benefit many other species. It is perhaps one of the few landscapes where snow leopard (*Panthera uncia*) and tigers co-exist together in one landscape. Buddhist beliefs and their ethos that respects all life forms have contributed to tiger and their prey species to co-exist alongside humans and livestock (*sensu* Li et al. 2014). Bengal Tigers are known to occur in Bhutan from sub-tropical jungles near the Indian plains to above tree line on the Tibetan border (Dorji and Santiapillai 1989). However, Bhutanese society is undergoing changes in recent times as Bhutan has become a constitutional democracy in 2008 with increasing economic development as with other nations in the region. In pursuit of economic development, forests are increasingly cleared for roads, hydroelectric dams, power transmission lines, mines and commercial logging. Over the last 5 years alone, 3 mega hydro-power dams were constructed in prime tiger habitat with growing evidence of the biodiversity threats of hydropower growing through the Himalaya (Pandit and Grumbine 2012). While the proponents of these economic development projects claim that habitat disturbances will be temporary, the scale of development is unprecedented in scale and intensity through Bhutan's history. Moreover, there have been no consistent efforts to evaluate cumulative effects of development at the country scale in Bhutan (Kennedy 2002) Therefore, in light of all these changes, it is imperative to know how these changes will affect tigers and their prey (ungulates), how those populations will respond to such changes, and what promise Bhutan holds for the conservation of tigers in the region. Thus, the most important task is to determine abundance and distribution of tigers and their prey in Bhutan.

Abundance and spatial distribution of any wildlife species is the foundation of ecology and conservation (Williams et al. 2002, Mills 2012). Since Aldo Leopold's "game census" in his book Game Management (1933), wildlife scientists have produced a large body of literature on statistical methods that deal with estimation of animal abundance in their natural habitats (Seber 1982, Williams et al. 2002, Lancia et al. 2006). One of the workhorses of modern population estimation are Capture-Mark-Recapture (CMR) methods that account for the fact that all animals cannot be captured or seen, so that detection probability must be estimated. Critical to the estimation of detection probability and abundance with the CMR methods is that different individuals must be distinctly identified. Unfortunately, classic CMR approaches are of little or no use for large carnivores because they are difficult to capture and mark in sufficient numbers for rigorous population estimates. Thus, early common methods for population estimates of large carnivores like tigers were though track counts also known widely as “pug mark census” in the Indian subcontinent (Panwar 1979, Hayward et al. 2002). The pugmark censuses were used as the standard monitoring method for Bengal tigers in the Indian subcontinent as recently as the early 2000s, despite its lacks of statistical rigor and high error rates (Karanth 1995, Karanth and Nichols 2010), Therefore, there has been a growing need for rigorous approaches to estimate tiger abundance and population trend.

Major breakthroughs in the last two decades have revolutionized our ability to non-invasively identify individuals using remote camera traps and estimate abundance with rigorous CMR methods (Karanth and Nichols 1995, O’Connell et al. 2010, Mills et al. 2013). Ecologists started using remote cameras to estimate abundance for species that were individually recognizable (e.g., spots, stripes, marked with tags) using CMR (Karanth 1995, O'Connell et al. 2010, Kelly et al. 2012). Remote camera trapping was first used in in 1877 (Guggisberg 1977) to photograph animals for aesthetic reasons, but has been increasingly used in wildlife biology. Camera trapping has a long history in wildlife biology, it was only in the 1990s that this method was used to estimate the abundance of tigers (Karanth 1995). Since then, camera trapping has been used extensively for estimating abundance and distribution of many felids, including ocelots *Leopardus pardalis* (Dillon and Kelly 2008); jaguars *Panthera onca* (Soisalo and Cavalcanti 2006); common leopards *P. pardus* (Goldberg et al. 2015); tigers (Karanth 1995); and snow leopards *P. uncia* (Jackson et al. 2006). This technique is well suited for animals like many felids that are marked with distinct coat patterns that make them individually recognizable in photographs. Camera traps are perhaps the most efficient, effective, and widely used method of estimating abundance of rare and elusive species (O'Connell et al. 2010). This method is now being widely adopted in different mountainous landscapes (Myanmar, Lynam et al. 2009; Thailand, Simcharoen et al. 2007; Bhutan, Wang and Macdonald 2009, Tempa et.al 2013, Goldberg et al. 2014; China, Xiao et al. 2016, Wang et al. 2016).

A second major recent advance in the field of capture-recapture studies, especially relevant for large carnivores, is the formal treatment of space in the estimation of the area occupied. Earlier capture-recapture methods often made ad-hoc assumptions about the area occupied by the population, or used the mean maximum distance moved (MMDM) to buffer spatial locations of captures to estimate the area, and hence, density of a species (Karanth and Nichols 1998, Williams et al. 2002). Recently spatially explicit capture–recapture models have been widely used to estimate density and abundance of wildlife (Efford 2004, Gardner et al. 2009, Royle et al. 2009b, Gopalaswamy et al. 2012, Goldberg et al. 2015, Proffitt et al. 2015). The most important feature of SECR models is the ability to formally link individual activity centers to encounters of individuals to estimate the spatial distribution of both observed and unobserved individuals (Efford 2004, Royle and Young 2008). This relationship is the reason why SECR models have become the most prominent and widely used method for density and abundance estimation of wildlife populations (Royle et al. 2011, Russell et al. 2012, Goldberg et al. 2015, Proffitt et al. 2015, Xiao et al. 2016). In contrast to the conventional methods where densities of animals were estimated by adding an ad-hoc buffer width around the study areas, spatially explicit capture–recapture (SECR) models are statistically more rigorous and density estimates from these models are more reliable.

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 (Kerley et al. 2002, Karanth and Gopal 2005, Dinerstein et al. 2007). A study from Nepal on the contrary showed tiger and human co-existing in a landscape at finer scales (Carter et al. 2012, 2013, Kafley et al. 2016). These studies, particularly Carter et al. (2012) drew criticisms from scientists and conservationists alike (Goswami et al. 2013, Harihar et al. 2013). In Bhutan, it is not known how human disturbances affect tigers and other wildlife population in Bhutan, but the aforementioned unique Bhutanese Buddhist culture may be more compatible with coexistence with large carnivores such as tigers because of the lack of a hunting culture, reverence for all life, and reverence especially for tigers.

Building on these themes, in my Dissertation I seek to test the overall hypothesis that Bhutan is functioning as a tiger source site in the NFC-R-NM forest complex in Northeastern India and Bhutan. To do this, I first estimate tiger spatial distribution and occurrence in Bhutan, and then second, estimate the factors affecting tiger occupancy and distribution including biotic (e.g., primary prey) and anthropogenic effects. Therefore, for my Dissertation I used camera trap data to address the two following questions:

1. What is the spatial distribution and population density of tigers in mountainous terrain in Bhutan? (Chapter 2)
2. What is the relative abundance of important prey species and how does prey abundance and human activity influence tiger occupancy (Chapter 3)?

Addressing these two key questions will form the basis of the first scientifically rigorous conservation management action plan (Chapter 4) for tigers and other wildlife species for Bhutan. Importantly, genetic techniques can also be used to non-invasively sample carnivores

(Kelly et al. 2012, Mills et al. 2013). Although original plans were to include scat genotyping in this dissertation, my sample size was too small for a useful analysis. In contrast, my initial plans to focus camera trapping on just the RMNP and JSWNP were expanded to a country-wide scale through the National Tiger Survey (see next paragraph).

In Chapter 2, I used both Bayesian and likelihood-based SCER models to estimate the tiger density and spatial distribution of tigers to address two questions. The first is whether Bhutan is a putative tiger "source site" or not. The second is how human disturbances affect tiger abundance and density. For this, I took advantage of my collaboration in the National Tiger Census of 2014 to estimate the tiger density and distribution for Bhutan. This monumental task was carried out to commemorate the 60th Birth Anniversary of our 4th King and to pay our respect for His Majesty's visionary leadership and stewardship in the field of environmental conservation. My original study area was supposed to be only in Jigme Singye Wangchuck National Park (JSWNP), Royal Manas National Park (RMNP) and part of Zhamgang Division, but then I was asked to join the national tiger survey and collaborate with the entire team. This is how my study area expanded to the whole of Bhutan. As one of the core members of the national tiger survey team, I participated from the inception in developing plans, study design, field logistics and the final phase of data analysis and report writing, besides carrying out field work and training crew members in JSWNP and RMNP. One third of the tigers indentified came from this study area. The crew members from these areas were then sent to other areas to further train other field staff and crew members who had little or no experiences with camera trapping. Setting up of 1,129 camera stations took almost one year for our brave field crew to cover the whole country. The whole Department of Forests and Park Services was behind this important task and many individuals participated in many ways. Regional coordinators for the East, Central and Western region along with focal persons from each division and park did a remarkable job in coordinating and carrying out fieldwork. The national coordinator for the national tiger survey put in a tremendous effort to raise funds for equipment, logistics and fieldwork. The funding for this survey came from World Wildlife Fund, Bhutan Foundation, and World Bank (as International Development Association -IDA credit).

In Chapter 3, I use camera trap data from the nationwide tiger survey to estimate the abundance of important prey species for tigers in Bhutan and to quantify how abundance of prey and human disturbances influence tiger occupancy. Using an N-mixture model (Royle 2004), I test which covariates affect relative abundance of prey; 1) human disturbances: number of human at each trap location, settlement densities (number of houses at 500m, 1km, 2 km, 3km, and 4km radii), distance from the nearest settlement, and number of cattle per camera station; 2) abiotic covariates: average slope (at 5m. 10m, 20m, 50m, 100m, 500m, 1 km, 2 km) and elevation; and 3) forest types at different radii (50m, 100m, 500m, 1km). I used prey abundance as covariate for a tiger occupancy model and estimate the occupancy of tigers for the whole country of Bhutan.

In Chapter 4, I synthesize the results from Chapter 2 and Chapter 3 to develop the first scientifically rigorous, proposed conservation plan for tiger population management in Bhutan. The tiger conservation action plan for Bhutan expired in 2015, and the government is looking to develop new action plans for tiger conservation in Bhutan. This chapter will be critical in developing the tiger action plan for Bhutan for the next 10 years.

These chapters represent contributions from many colleagues and each chapter includes a tentative listing of co-authors. Also, I use “we” instead of “I” to embrace the collaborative nature of these chapters.

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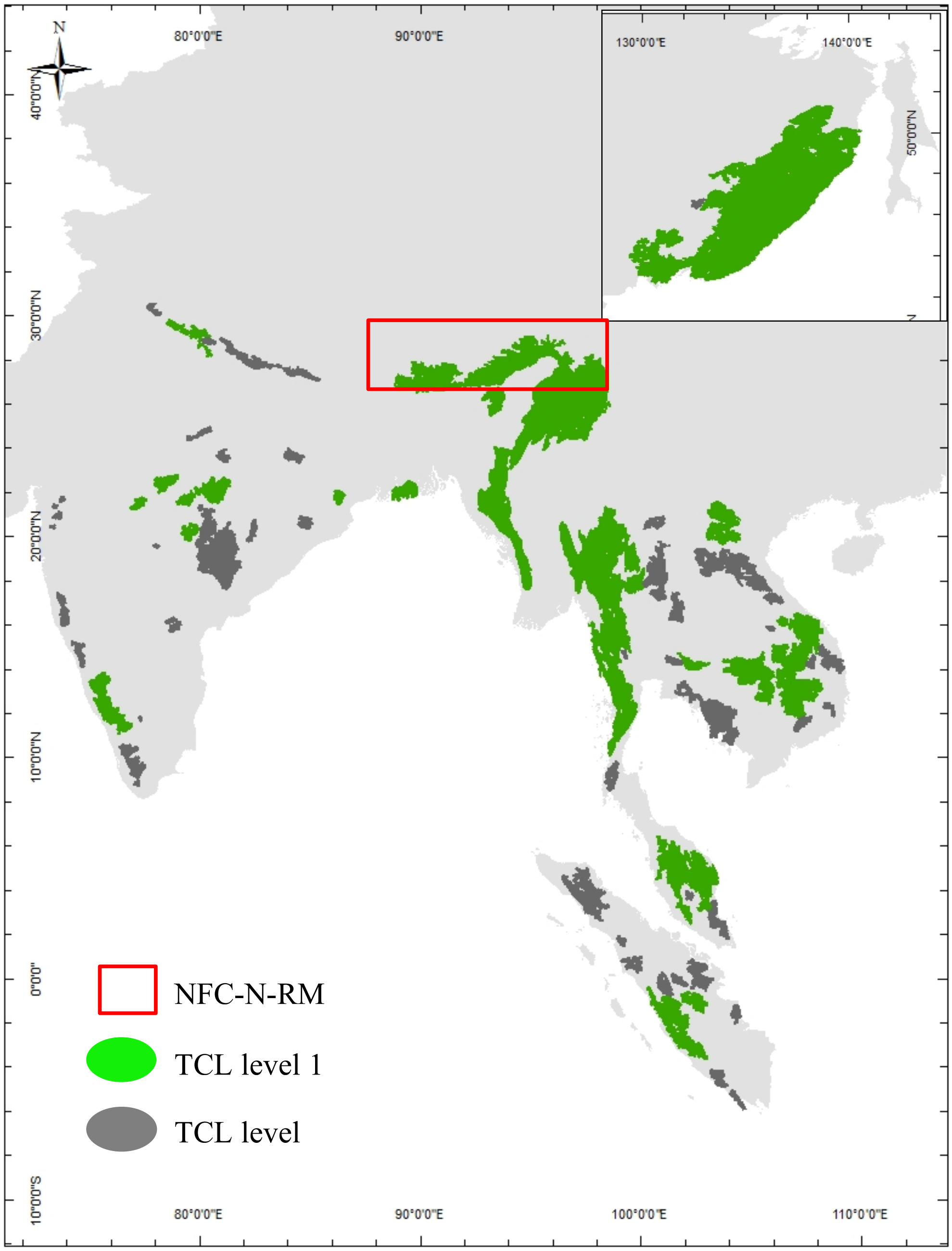

Figure 1- 1: Map of Tiger Conservation Landscapes in the 13 tiger range countries. The red rectangle on the map represents the location of Northern Forest Complex- Namdhapha-Royal Manas tiger conservation landscapes. Light green represent priority level 1 Tiger Conservation Landscape (TCL) and grey level 2-4 TCL (Source: Sanderson et al. 2010).

Chapter 2: Spatial distribution and population density of tigers in mountainous terrain in Bhutan

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INTRODUCTION

As apex predators, large carnivores play an important role in ecosystems and provide important ecosystem services (Ripple et al. 2014, Newsome and Ripple 2015). However, throughout their range these apex predators are in peril and their populations in the wild continue to decline due to habitat loss and fragmentation, prey depletion and direct poaching for illegal trade and commerce (Ripple et al. 2014, Ripple et al. 2016). Tigers (*Panthera tigris*) are one of the largest apex predators and one of the most endangered big cats in the wild. Poaching, prey depletion and habitat loss have decimated tiger populations in the wild and today they occupy a mere 7 percent of their historical range (Dinerstein et al. 2007, Seidensticker 2010). Tiger numbers have plummeted from as many as 100,000 individuals to 3,200 over a period of a hundred years (Dinerstein et al. 2007). Tiger populations in the wild continue to fall even after 6 decades of conservation efforts and investment (Seidensticker 2010).

Tigers are very resilient and can adapt to wide range of climatic conditions, ecosystems, and prey species (Schaller 1964, Sunquist 1997). If not for its resiliency and adaptability, this species may have long gone extinct in the wild given the intensity of poaching, habitat loss and the fact that it shares the most densely human populated landscape on the face of this planet. Scientists have shown that tigers can tolerate some level of human-induced mortality as long as there is sufficient habitat and large ungulate prey (Karanth and Smith 1999). If the anthropogenic threats can be reversed and halted, populations of tigers in the wild could rebound (Harihar et al. 2009, Walston et al. 2010b, Wikramanayake et al. 2011). It was under this premise that the heads of States from 13 tiger range countries endorsed the St. Petersburg Declaration on Tiger Conservation at the International Tiger Forum ('Tiger Summit'), held in St. Petersburg, Russia, on November 21–24, 2010 to double wild tiger numbers by year 2022 (GTRP 2011). There was an unprecedented commitment and political will from these tiger range countries to revive the dwindling tiger population in the wild. Attendees set a goal to double the tiger population by 2022.

Doubling tiger numbers in the wild in 12 years is by no means an easy feat. It will require multi-pronged strategies among different stakeholders and agencies. This would also mean a huge increase in resources, manpower on the ground and securing habitat for tigers. In light of this, Watson et al. (2010b) identified 42 tiger "source sites" (only 6% of the current tiger habitat) thought to contain 70% of the current tiger population and argued that resources and effort should be directed towards these 42 source sites rather than thinly spreading limited resources across to all tiger conservation landscapes. This 6% solution sounds like a pragmatic example of a triage approach for conservation where conservation efforts are strategically allocated to the most viable populations (Bottrill et al. 2008, Wiens et al. 2012). However, most of these tiger source sites have existing high tiger density and to double their number without expanding or restoring adjacent tiger habitat will be very difficult. Another important issue is that many large tracts of tiger habitat are left out under 6% solutions, and are at particular risk of loss due to development such as mining, logging, roads, dams, natural gas, and plantations (Seidensticker 2016). The best example comes from Northeastern China (not part of the 6% solution source sites), where tigers are expanding and offer the best chance perhaps at doubling a countries tiger population by 2022, thereby underpinning the importance of other tiger habitat besides Walston's (2010b) source sites (Wang et al. 2016, Xioa et al. 2016, McLaughlin 2016). In contrast to the "source sites" strategy of Walston et al. (2010b), Wikramanayake et al. (2011) proposed a landscape-level approach as a more realistic and easy way to double tiger numbers in the wild. In this approach, Wikramanayake et al. (2011) argue that conservation effort and funds should be distributed to all the Tiger Conservation Landscapes (TCL) defined as "block of potential effective habitat within 4km of each other, meeting a minimum, habitat-specific size threshold, where tigers haven been confirmed to occur during the last 10 years and are not known to have been extirpated since the last observation" (Sanderson et al. 2010). There are currently defined 72 such sites (Sanderson et al. 2010). With sufficient conservation funding, we should by all means protect and focus on all these landscapes, but unfortunately conservation dollars are hard to come by and some level of triage will be inevitable. But this brief review highlights some weaknesses in the 6% solution; thus, there is a need to use quantitative data to identify other areas harboring important tiger populations in the wild.

Bhutan is an example of a tiger conservation area that failed to make the list of tiger source sites, although it is one of the top 20 priority TLC (Sanderson et al 2010). Bhutan together with Northern Forest Complex - Namdhapha -Royal Manas (NFC-N-RM) straddling the border of Myanmar, northeastern India, has the largest intact and contiguous forest cover in the Indian subcontinent (Figure 1-1, 237,820 km^2; Sanderson et al. 2010) and is the largest TCL outside of the Russian Far East. The low human population density and intact forests in NFCNRM landscapes offer great potential for Bengal tiger (*P. t tigris*) conservation. Yet little is known about tigers in this TCL. The general view of tiger researchers for many years was that tigers do not really occur at high elevations of Bhutan (Vernes and Rajaratnam 2012) and that Bhutan was only sink habitat for India. Most of the tiger ecology and spatial distribution studies were conducted in plains of India, Nepal, Russian Far East (Karanth 2004, Seidensticker 2010,(Miquelle et al. 2015). Very few studies of tiger ecology and spatial distribution have been conducted in Mountainous terrain in southeast Asia. Those that did report the density of tigers are reported to be very low (Lynam et al. 2009), indirectly supporting the assumption of low tiger densities in mountainous countries. In Bhutan, only one study on tigers was done in one of the parks (JSWNP) and the density reported from that study was very low (Wang and Macdonald 2009). However, Bhutan may be more important for tiger conservation than previously thought or reported. Forest cover in Bhutan is more than 70%, 50% of the country is designated as protected, and it has a unique Bhutanese-Buddhist culture that may be more tolerant of wildlife, has a low density of people, and conservation-friendly policies and laws are in place (FNCA 1995, Constitution 2008, FNCR 2013). All these have contributed towards preserving tigers and other wildlife habitats. Bhutan is a hotspot for wild felid diversity and may harbor significant tiger populations of its own (Tempa et al. 2013). Bhutan may provide critical connectivity between the Terai Arc grassland of India and Nepal TCL's and other TCLs in Northeast India and to the Indochina tiger (*P. t. corbetti)* in Southeast Asia. (Sharma et al. 2011).

Here, we used remote camera trap data to estimate the density of tigers in the entire country of Bhutan using spatial capture-recapture models (Efford 2004, Gardner et al. 2009, Royle et al. 2009b). First, we test the overall hypothesis that Bhutan contains a sufficiently large tiger population to be considered as a tiger source site (Karanth et al. 2010a, Walston et al. 2010b). In ecological literature, “source” and “sink” have precise definitions 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, Mills 2012, Newby et al. 2013). However, tiger conservation policy (Karanth et al. 2010a, Walston et al. 2010b) has defined tiger source site 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”. Therefore, to be consistent with tiger policy criteria, we would consider Bhutan as a source site if it fulfilled Karanth et al. (2010a)’s criteria for tiger source sites.We predicted that Bhutan would have higher densities of tigers than in the overall landscape (NFC-R-NM) within which it is embedded. Although no threshold number of tigers is given in existing TCL’s for demographic viability, the mean population size from the 42 source sites identified by Walston et al. (2010b) was 50 individuals. Thus, we tested whether Bhutan had > 50 adult tigers. The second criteria suggested by Karanth et al. (2010a) is that we would find evidence of current tiger reproduction in Bhutan itself and that within the NFC-R-NM tiger conservation landscape, there would be the potential to maintain > 25 to > 50 Breeding females. We predict that Bhutan will have evidence of tiger breeding, and breeding tigers will not just be distributed along the low elevation Indian border. Karanth et al. (2010a) suggest that there should be supportive policies and legal frameworks for the conservation of tigers in source sites. Here, we focus on the demographic criteria of tigers in Bhutan but focus on policy support in Chapter 4.

Alternatively, if Bhutan is sink habitat for tigers, then Bhutan could have tigers, but they could be distributed only along the Indian borders as they spill over from parks in India. If this were true, we would predict a strong negative effect of elevation on tiger density. Under the sink hypothesis, we would expect tiger densities to be higher in the lower elevations of the country, but not just along the Indian border, as deeply incised river valleys penetrate far north into the country. In addition, we estimate home range size (e.g., activity center area) based on sigma to validate our density and abundance estimation (Royle et al. 2013). A comparable home range would reassure us that our estimates of abundance and density are reasonable. Finally, we account for sex-specific differences in male and female home range size in our spatially explicit capture recapture model, expecting that, like elsewhere (Goodrich et al. 2010), males will have much larger home range sizes than females.

Our second overall objective was to we test for the effects of human disturbance on tigers in Bhutan. The prevailing paradigm in tiger-human studies is a negative effect of humans on tigers, mediated by human-caused mortality through poaching, human-tiger conflict, loss of tiger prey through poaching, and habitat loss (Kerley et al. 2002, Karanth and Gopal 2005, Dinerstein et al. 2007). In contrast, recent study from Nepal showed tigers and humans co-existing in a landscape at finer scales (Carter et al. 2012, 2013, Kafley et al. 2016). These studies, particularly Carter et al. (2012) drew criticism from scientists and conservations alike (Goswami et al. 2013, Harihar et al. 2013). In Bhutan, we do not know how human disturbance affect tigers and other wildlife population in Bhutan. Humans are part the protected area systems and unlike in many other countries, the Royal Government of Bhutan (RGoB) allows people to reside within the national parks and protected areas. This proximity heightens human-wildlife interactions often leading to conflicts in protected areas (Wang et al. 2006, Wang and Macdonald 2006, Barber-Meyer et al. 2013). We used proximity to human settlement as a measure of human disturbance to test its effects on tiger density. We hypothesize that the negative effects of human disturbance on tiger density and distribution will be weaker in Bhutan than elsewhere because of low human density and the unique Bhutanese-Buddhist culture that may have higher tolerance for wildlife (*sensu* Li et al. 2014).

MATERIALS AND METHODS

Study Area

Bhutan (38,394 km^2) is located in the biodiversity hotspot of eastern Himalayas, landlocked between the Tibet Autonomous Region of China to the north and India to the east, west, and south (Figure 2-1). It lies between latitudes 26°N and 29°N, and longitudes 88°E and 93°E. Elevation ranges from as low as 200 m in the southern foothills to more than 7500 m in the north within an aerial distance of 170km. This extreme altitudinal gradient causes great variation in temperature and rainfall, creating different climatic zones ranging from wet sub-tropical in the south to permanent alpine pastures and glaciers in the north. This great geographical diversity combined with equally diverse climate conditions contributes to Bhutan's outstanding range of biodiversity and ecosystems.

Bhutan has more than 70% of country under forest cover and more than 50% of the total geographic area under protection in the forms of national parks and biological corridors. The top predators like tiger, leopard, snow leopard, and Asiatic wild dog (*Coun alpinus*) roam these areas supported by diverse prey species including guar (*Bos gaurus*), sambar (*Rusa unicolor*), 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. Bhutan is also home to many other endangered wildlife species including Indian one-horned rhinoceroses (*Rhinoceros unicornis*), elephants (*Elephas maximus*), Asiatic water buffalos, wild dogs, golden langurs (*Trachypithecus geei*), musk deer (*Moschus chrysogaster*), red panda (*Ailurus fulgens*), and hispid hares (*Caprolagus hispidus*) and critically endangered species like pigmy hogs (*Porcula salvania*) and Chinese pangolin (*Manis pentadactyla*)

Camera Trap Field Survey

We randomly laid a 5x5km grid cell across the entire country using Arc GIS 10.1 (ESRI 2014; Figure 2-1). The grid size of 5x5 km was chosen based on the minimum territorial size of female tigers in the Indian subcontinent (15-20 km^2; Karanth and Smith 2000, Sunquist 2010). Earlier works (Wang and Macdonald 2009, Tempa et al. 2011) indicated that the territory size of female tigers in Bhutan is at the larger end of the range in the subcontinent. A cell size of 5x5 km should meet density-sampling protocols of having a minimum of 2 to 3 camera stations in one home range of a tiger (Karanth and Nichols 2002). We selected 1,522 grid cells, after screening out town and cities, villages and other unlikely habitat of tigers above 4500 m elevations. We then opportunistically selected camera stations within each 5x5 km grid cell to maximize the capture of tigers based on sign and tracks. For example, we emphasized roads and trails because like most felids, tigers are known to travel non-randomly along preferred trails (Karanth et al. 2002, Kelly et al. 2013). Minimum distance between two-camera stations was 2 km to avoid clustering of cameras in one area.

We deployed two sets of cameras at each camera station. Cameras were set 6-7 meters away from each other at a height of 45 cm from the ground on each side of a trail or road in order to photograph both flanks of the tiger (tigers have different pelage patterns on different flanks; Karanth and Nichols 2002). We used five different models of camera trap, *viz*., Bushnell, CuddeBack, HCO-ScoutGuard, Reconyx (HC500 Hyperfire), and U-way. All models used passive infrared systems (triggered by body heat as the animal passes in front of the sensor into the camera). We made sure that cameras were positioned in such a way that two cameras were not in the same line of view to avoid the flash of one disturbing pictures on the other camera. We gave each camera trap a unique camera number and marked all the locations with Global Positioning System (GPS). We further recorded other metadata such as habitat type, ground cover, canopy cover and height, and signs of prey and other carnivores.

Camera trapping for the national tiger survey was carried out for a period of one year from March, 2014 – March 2015 across tiger range in Bhutan. For effective coverage, the camera trapping was divided into two phases based on field logistics and the monsoon season (which affected the southern zone in summer). We began our camera trapping in the southern zone for 5 months and then moved to northern blocks and set there for another 6 months. We attempted to monitor camera traps once every month, but weather and logistics prevented monthly monitoring in a few remote and isolated camera sites. At each monitoring session, we downloaded all the pictures directly from SD cards to computers. Photos were segregated into different species and renamed accordingly to dates using the program Renamer (Sanderson and Harris 2013) to construct individual capture histories. For tigers, we further identified each individual manually based on stripe patterns on flanks, head, tail, and limbs (Karanth, 1995, Schaller, 1967) and gave each a unique identification number. We could usually identify sex based on presence or absence of scrotum from multiple pictures and because male tigers have a very prominent protrusion from their testicles. We grouped tigers into two age categories, adults independent of their mothers and cubs dependent on their mothers (always recorded with their mothers). We aggregated the daily sampling occasions into a single weekly sampling occasion (our primary sampling occasion is equal to 7 trap nights). Goldberg et al. (2015) tested the effect of the duration of sampling occasions on the parameter estimates in SECR for common leopards on RMNP, Bhutan, and found no significant evidence to suggest that it affects parameter estimates. Kelly et al. (2012) suggested that grouping sampling occasion into fewer sampling occasion increase the recapture rates and thereby increase the detection probability in capture recapture studies, thus providing better estimate of abundance.

Spatially-Explicit Capture Recapture Modeling

The traditional mark-capture-recapture approach for closed population provides a reliable estimate of the abundance of animals exposed to sampling, but density estimates are based on ad-hoc methods of adding varying buffers around the study area. By contrast, spatially-explicit capture recapture (hereafter referred to as SECR) explicitly models spatial organization of individual animals and the encounter devices (Efford 2004, Borchers and Efford 2008, Royle and Young 2008, Royle et al. 2009b, Royle et al. 2011). SECR models are based on the assumption that each individual animal in a population has a home range with activity center s_i around which animals roam and move to meet their daily resource needs. This is particularly relevant to carnivore populations, and especially tigers, which are strongly territorial and maintain exclusive home ranges (Sunquist and Sunquist 2002, Goodrich et al 2015). Thus the number of individual animals in the population (N) exposed to sampling is estimated by summing up the number of home range centers s_i. The home 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*.

$$s_i \sim \text{Uniform S} \qquad \text{Equation 2.1}$$

SECR models regard these activity centers as the outcome of a point process of the state space *S* (Gopalaswamy et al. 2012, Royle et al. 2013). Density is then derived as D = N/area(S), where N is the parameter of the model and 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 ,.....n;*, in trap *j=1,2,....J*; sampling period=*1,2,...K*. We allowed individuals to be captured at multiple camera locations for the same sampling period, but multiple captures of an individual in a single location during the same sampling interval was considred 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 as function to distance between individual activity centers and trap as:

$$\Pr(y_{ijk} = 1) = 1 - \exp(-\lambda_0 g_{ij}) \qquad \text{Equation 2.2}$$

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, $g_{ij} = \exp(-d_{ij}^2/\sigma^2)$, 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 (Gardner et al. 2010). This distance function is adopted from the theory of distance sampling (Buckland et al. 2001, Borchers and Efford 2008). As in Gardner et al. (2010) and Russell et.(2012), and Proffitt et al. (2015) we included sex as covariate for the detection function:

$$\log(\lambda_{0,jk}) = \lambda_0 + \beta \text{sex}_i \qquad \text{Equation 2.3}$$

We also modelled sex and distance as interactive effects on detection probability (Proffitt et al. 2015). From Royle et al. (2013) and Proffitt el al. (2015) we modelled elevation and distance to the human settlement as covariates to test their effects on density. The current version of SCRbayes can handle only one covariate at a time, therefore, our covariate model is as follows:

$$\log(\mu(s, \beta)) = \beta_0 + \beta_v C_v(s) \qquad \text{Equation 2.4}$$

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-30x30) map of Bhutan in R (R Core Team 2016) 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 that has the location of each household in Bhutan (RGoB 2006).

We fit 11 models to the data to see the effect of covariates on density estimates using both Bayesian based (Royle et al. 2009a, Gopalaswamy et al. 2012, Royle et al. 2013) and likelihood (Efford 2004, Borchers and Efford 2008) based SECR methods. The main advantages of Bayesian approaches are that the posterior inferences are valid to any sample size and this becomes very important particularly for ecological studies of rare and elusive species such as tigers were samples sizes are often very small (Royle et al. 2013). However, running large MCMC chains takes a long time and required high performance computing. The model selection framework under Bayesian based SECR and goodness of fit test also does not have strong theoretical basis (Royle et al. 2013). Likelihood base SECR models on the other hand are computationally easier and much faster. Model selection can be done under conventional AIC methods, but for small sample size, estimates can be heavily biased.

Our 11 models were: (1) Model 1(D): basic model with no effect of covariate, detection as the function of distance between activity center and camera location; (2) Model 2 (D+sex): Effect of sex on the baseline detection (λ_0); 3) Model 3: Effect of sex on both baseline detection and the scale of the activity distribution (σ) sex+ σ_{sex}; 4) Model 4: Effect of sex + elevation ; 5) σ_{sex} +Elevation; 6)Elevation; 7) Model 7: sex+ σ_{sex}+Elevation; 8) sex+σ_{sex} + settlement; 9)sex+ settlement; 10) Model 10: σ_{sex} + settlement; 11) Model 11: Effect of settlement (human). Finally, to obtain an estimate of the number of adult females, we also conducted a separate estimate of just the number of adult females with the top-ranked model, but considering only 1 sex (female).

Bayesian Analysis by MCMC

Bayesian approaches to SECR analyses use data augmentation (Royle et al. 2007, Royle and Dorazio 2008, Gardner et al. 2010) to estimate tiger densities, following many recent large carnivore and tiger studies (Royle et al. 2009a, Gopalaswamy et al. 2012, Sollmann et al. 2013, Goldberg et al. 2015, Proffitt et al. 2015, Xiao et al. 2016). Data augmentation is done by adding a large number of undetected individuals, each having all zero encounter histories, say M-n where M is the total number of individuals and n is the number of observed individuals (Royle and Dorazio 2008). It is assumed that this list of M pseudo-individuals includes the actual N individuals in the population as a subset of M. We chose a uniform prior distribution from [0, M] on population size. The super population (M) and population size (N) are related by parameter ψ. ψ is the probability that an individual on the list of size M is a member of the population of size N that was exposed to sampling by the trap array (Royle and Young 2008). We choose M (=200) sufficiently large as not to truncate the upper limit of the number of augmented animals.

We fit our models using Markov chain Monte Carlo (MCMC) methods in R (R Development Core 2016), using the *SCRbayes* package (available at: https://sites.google.com/site/spatialcapturerecapture/scrbayes-r-package; 2–A File). We masked our statespace with elevations more than 4500 meters masked as non-tiger habitat (Figure 2–1) based on data on the highest distributional record in our data for tiger observation (see Discussion). We also used 5 km as spacing for our statespace. 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 the 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 details of Bayesian-based model selection and goodness of fit test, see Appendix (Text 2–B).

We estimated the approximate tiger home range (i.e., activity center area) during our sampling period (i.e., not an annual home range) using a bivariate normal (Gaussian) probability density function model for encounter probability as described by Royle et al. (2013) to validate our density and abundance estimation (For detail Appendix 2–B). We acknowledge that secr models don't really estimate home range size in a comparable way to, for example, radio telemetry. But because so little is known about tiger spatial ecology in Bhutan, and because comparable home range estimates would reassure us that our estimates of abundance and density are reasonable, we compared estimates from our secr models to minimum convex polygon (MCP) home ranges on individual tigers with > 3 locations (Mohr 1947).

Maximum-likelihood based SECR

To compare the results from our Bayesian models to that of maximum likelihood based SECR models (Efford 2004; Borchers & Efford 2008), we ran 11 models using the R package *secr* (Efford 2015) for our data set based on a half-normal detection function and a Binomial encounter process. Maximum likelihood method applies integrated likelihood analysis to estimate density and related parameters in a state space within a trapping array (Efford 2004; Borchers & Efford 2008). We used Akaike information criterion (AIC) method to compare these models (Burnham and Anderson 2002).

RESULTS

Camera trapping

Based on 1,522 total camera stations deployed across Bhutan, we captured a total of 1,406 photo images and 138 videos of tigers during the entire survey period (March 2014 to March 2015). We used 1,231 images and 138 videos to develop encounter records (Royle et al. 2013), (Table 1, see also Appendix Table 1S). 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. 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 62 individual tigers.

Of 62 individual tiger captures, 10 individuals were captured only once, 15 individuals were captured twice, 12 individuals captured 3 times, 6 individuals were captured 4 times and so on while 1 individual was captured 21 times (Table 2–2a). The details of individuals captured at individual camera traps are: 27 individuals were captured at only 1 camera location, 13 individuals were captured at only 2 camera locations, while 1 individual was captured at as many as 11 camera stations (Table 2–2b). We also captured 7 females with their cubs at multiple camera locations. The detail encounter histories are provided as an Appendix (Table 2–B1). We plotted the centroid point for each individual from the raw capture data to visualize and cross-check our data (Figure 2–2).

Bayesian Results and Model Selection

Our top model was model D + Sex: Effect of sex on the baseline detection (λ_0), indicating that male and females had different baseline detection. From this model, we estimated the tiger population size (N) of 90 individuals and a density 0.23/100 km^2 across all of Bhutan (Table 2-3). Tigers were distributed across Bhutan, not only in the southern boundary with India, nor just in protected areas and biological corridors, but outside of protected areas too, as well as across elevations up to 4500m (Figure 2-3). The overall density for the whole study area was low, but showed areas like JSWNP, Trongsa, and RMNP had high density as many as 3/100km^2 (see Discussion). Using this top model, focusing only on adult females, we estimated 45 (95% Bayesian Credibility Interval, CI 38 – 60) females in Bhutan.

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 sex, with a 95% credible interval that did not overlap zero. Our top model estimated σ of 4.75km (95% CI: 4.3 – 5.1 km) for females and 5.75km (95% CI: 5.45 – 7.25) for males (Table 2.4, Figure 2-D1). The baseline detection (probability of detection if camera trap is located exactly at come range center) was not different between male and females, with a 95% credible interval overlapped with zero (Table 2-C1). The baseline detection probability of tigers, $\lambda_{0,}$ from our top model was 0.025 per session (95% CI: 0.020 – 0.031). The data augmentation parameters ψ, the probability that the augmented data belongs to N for a female was 0.34 and 0.45 for male, however, the 95% CI overlap for male and female suggests the difference was not significant (Table 2-4). Elevation and distance from the human settlement had no effect on tiger density.

The fit statistics Bayesian P value for our model was 1 indicating lack of goodness of fit. To evaluate if this lack of fit was due to a large area of the state space, we subset the data just for

JSWNP, and re-ran the models using the 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 that indeed a failure of the GOF statistic in the wider study area was potentially being driven by areas of low tiger densities. For our smaller data set, the power to reject the null that "data do not fit the model" was also lower. On the other hand, for the large data set, the power to reject the null increases and our failure of GOF test could simply be because our large sample sizes. Evaluating GOF for secr models is an active area of current research, and experts advise that the failure of GOF test for large data is not a serious problem and recommended other qualitative measures to judge model fit (Gelman et al. 1992, Royle et al. 2013, Kery and Royle 2015). Following Proffitt et al. (2015), we compared the expected number of captures to the actual number of capture as another form of evaluating goodness of fit. Using this method, our expected captured numbers were 65 – 81 (Table 2-3) very similar to our observed number of captured individuals, *n*= 62, confirming the adequacy of model goodness of fit. Moreover, our home range estimates obtained by secr were similar to previously published estimates of home range (see below), offering another indirect form of model goodness of fit. Based on these two additional tests, despite the overall failure of the GOF, 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 2-3).

Maximum likelihood based SECR estimates of density and abundance

The density estimate of 0.23 (95% Confidence Interval 0.19–0.31) tigers per 100 km^2 and N of 88 individuals (95% CI 79–106) from MLE-based *secr* was very similar to results from SCRbayes. The scale parameter σ (the rate at which detection probability decreases) for female tigers was 4.92 km and for males, it was 6.01 km (Table 2-5) similar to results from our Bayesian-based models. Unlike the Bayesian based models, sex had a significant effect on both base line detection and the scale parameter. The baseline detection g_0 (analogues to λ_0 of SCRbayes) for a male is 0.024 and 0.039 for female (Table 2-5). This means female tigers have higher base line detection than male tigers. Our results showed that elevation and human disturbances have not effect on tiger density. For the MLE based SECR approach, we followed AIC model selection method (Burnham and Anderson 2002) (Table 2-3). Using this top model, focusing only on adult females, we estimated 60 (95% CI 49 – 80) females in Bhutan using maximum likelihood.

Home Range Sizes

The home range size calculated following Royle et al. (2013) formulation using sigma under the assumption of a bivariate normal home range size gave us 450 km^2 for females and 675 km^2 for males. 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. The mean MCP home range size of males was 169.4 km^2 (Range 17.3 – 547.8) and females, it was 70 km^2 (7.4 – 199.2) (Table 2-6; Appendix 2-B Figure B1. We did not include 1 female and 1 male that had an MCP of just 3.7 km^2 and 9.8 km^2, respectively, as outliers because we knew that these individuals were transboundary and their range extended into India across Bhutan borders.

DISCUSSION

We successfully used both Bayesian based and MLE-based SECR models to estimate tiger density and population size for tigers in Bhutan. Our posterior parameter estimates from the *SCRbayes* package (Royle 2015) and Maximum Likelihood based *scer* package (Efford 2015) gave very similar estimates. The top models from these two approaches gave same estimates of density (D) and abundance (N), while g_0/λ_0 and σ slightly vary, but not significantly (Table 2-3). The similar parameter estimates from these top models from these two approaches support our argument that the model formulations and assumption in our models are adequate. Our current tiger number estimate of 90 individuals (95% CI: 80 –103) with 60 (95% CI: 49–80) is relatively large in one connected landscapes, substantively larger than the mean tiger population size from 42 source sites (Fig.2–4). Only a few designated sources sites (Corbett and Nagarahole/Bandipur/ Mudumula in India , Sundarbans in Bangladesh, Chitwan/Persa in Nepal, and Huai Kha Khaeng in Thailand) have tigers numbers more than our estimated population size from Bhutan (Walston et al. 2010b). Our tiger density estimate across Bhutan was 0.23 tigers per 100km^2 (Table 2–3) and is fairly low compared to tiger density estimates from deciduous habitats in the Indian sub-continent India (Karanth et al. 2004). This estimate is low when compared with the tiger density in similar habitats in the region, but it is probably an artifact of including the whole country in the state space that includes areas where tigers do not occur (Figure 2-1). We had to cover the whole area of Bhutan with exception of grid cells higher than 4500 meters irrespective of whether tigers are there or not as part of national tiger survey for whole country. So, for the whole country of effective sampling area of 31,500 km^2, this tiger density estimate is realistic and ecologically reasonable.

Our results however showed where tigers are concentrated and pointed out that protected areas such as JSWNP, RMNP, JDNP have as many any 2–3 tigers per 100 km^2 (Figure 2-3). The density estimate of 2–3 tigers/100 km^2 in JSWNP, RMNP and JDNP from our study is comparable to tiger density estimates from some of the protected area in India like Tadoba, Bhadra, and Kalakad-Mundanthurai (Karanth et al. 2004, Ramesh et al. 2012), which have been designated as tiger source sites (Walston et al. 2010b). Our density estimate for JSWNP, JDNP and RMNP 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. 2009) that had been designated as tiger source sites. Our work confirms that non tiger source sites can have globally significant tiger populations.

Wang and MacDonald (2009) reported tiger density of 0.4 – 0.5 tigers per 100 km^2 from JSWNP for the year 2006, slightly higher than the tiger density that we estimated for the whole country, but much lower than our current density estimate for JSWNP (Figure 2-4). Our density estimate of 2 tigers per 100 km^2 (95% CI 2 – 3 tigers 100 km^2) in just our JSWNP data subset was four times more than 0.50 tigers per 100 km^2 reported by Wang and Macdonald (2009; Appendix Table S4). Our estimate of 18 (95% CI 13–27) individual tigers was also significantly higher than that of 8 (95 % CI 6–10) individual tigers estimated by Wang and Macdonald (2009). Since, Wang and Macdonald (2009) used program CAPTURE to estimate N, we also used program CAPTURE (Otis et al. 1978) to estimate our abundance and detection probability to compare our results. Our estimates of abundance 13 (95 % CI 10–18) from program CAPTURE were much higher than Wang and Macdonald (2009; 95 % CI 6–10). Thus, the difference between Wang and MacDonald (2009) and our results were not just because of methodology (i.e., secr vs. non-spatial mark recapture). Nonetheless, there were other methodological differences between the studies; the number of camera trap sites in our study area was lower (60 camera station) than 81 camera stations of Wang and Macdonald (2009); our effort of 9729 trap nights was almost double (Table 2–C3); our study duration was also more than double Wang and MacDonald (2009, 50 days versus our estimate of 91 days); and we used 2 camera's per site instead of only 1 camera, which required Wang and MacDonald to only estimate N using photos of the left flank of tigers. Thus, these other methodological factors may influenced reliability of the Wang and MacDonald (2009) estimate. Assuming accuracy of the Wang and Macdonald (2009) estimate from 2006, tiger density in JSWNP may have increased over the past decade. Alternatively, the higher camera trapping effort, longer duration, and use of twin camera's to capture both sides of the tiger in our study may provide more reliable estimates. For elusive and rare carnivores, increasing the sampling duration increases the detectability of females and cubs and makes the density estimates more robust (Jedzrejewski et al. 2016). Likewise, Augustine et al.(2016) showed using two camera traps reduces the bias and improves the precision of density estimates.

The recent population estimates in Bhutan in the national tiger report of 103 tigers (95% CI 79 – 126, Thinley et al. 2015), based on the same study design, were slightly higher than our median estimate of abundance of 90 tigers (95% CI 80 – 103). However, the 95% CI's overlap with each other and the two estimates are therefore not statistically different. One reason for the difference is that 4 individual tigers were misclassified in Thinley et al. (2015) as unique individuals, but during our analyses, we recognized this minor mistake and reclassified these 4 individuals. Thus, our estimates were based on 62, and not 66, captured individuals as reported by Thinley et al. (2015). Regardless, the overlapping estimates from this study and the previously published tiger report (Thinley et al. 2015) suggest estimates do not differ for any biological or ecological reason. Regardless, the challenges in comparing population estimates using different methods over time highlights the importance of considering sampling design in developing a monitoring protocol for tigers in Bhutan (see Chapter 4).

The scaler parameter on detection probability (σ) for male was 7.25 km and for female it was 4.75 km. This means the rate of detection probability decreases much faster for females as camera traps are move further from home range center (Appendix Figure 2–E1). This is expected as male and female tigers have different movement pattern and home range sizes (Smith et al. 1987, Karanth and Sunquist 2000, Simcharoen et al. 2014). Our scaler parameter on detection probability (σ) was larger than 2–3km reported from India (Royle et al. 2009a, Kalle et al. 2011, Gopalaswamy et al. 2012, Ramesh et al. 2012), but is similar to estimates from Thailand and northeast China (Duangchantrasiri et al. 2016, Xiao et al. 2016). Our home range size estimates based on sigma of 450 km^2 for female and 675 km^2 for male tigers are likely biased high (see Royle et al. 2013 for discussion). In comparison, our minimum convex polygon estimates for individuals with > 3 locations were smaller than our sigma-based activity center. Our mean MCP home range size of 70 km^2 for female and 169 km^2 for male was comparable is home range size from tigers in Thailand (Simcharoen et al. 2014), but larger than estimates from Indian, Nepal, and Bangladesh (Smith et al. 1987, Karanth and Sunquist 2000, Barlow et al. 2011) and smaller than Russian Far East (Goodrich et al. 2010, Xiao et al. 2016). That our estimates are between India and Russian home range estimates is also consistent with what we know about tiger home range ecology across their distribution. Future studies using telemetry can correct and calibrate our results, but at least from the perspective of evaluating model fit, our estimates of home range from activity center based on the sigma parameter are believable in the context of previous estimates from the tiger literature.

The baseline detection for male and female was same; sex had no effect (95%CI of coefficient of sex as covariate overlap with zero) on it. However, sex did show a negative effect on baseline detection λ_0, when we included effect of sex on scaler parameter on detection probability (σ) in our model. Females have higher baseline detection compared to males, probably because male tigers have larger home ranges than females. 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 landscape that has an elevation gradient from 150 meters to 7500 meters within an aerial distance of 180 km, we expected elevation to have a strong influence on tiger density. Surprisingly our results suggest otherwise. Tigers are very resilient and can adapt to wide range of climatic conditions from tropical evergreen forests and swamps to cold tundra climatic conditions in the Russian Far East. (Schaller 1967, Sunquist et al. 1999). Most of the ecological studies on Bengal tigers were done in the plains of India and Nepal (Sunquist 1981, Smith et al. 1998, Karanth et al. 2004). In the scientific world mountains were not considered as a tiger source habitat and yet, not much is known about tiger use of mountainous environments, as tigers were traditionally believed to be inhabitants of the plains (Kafley et al. 2016, Thapa and Kelly 2016), and most tiger studies have been focused in non-mountainous systems. In the absence of systematic studies in these mountains, the occurrence of tigers at higher elevations were dismissed as transient or old males from the plains and therefore accorded little priority for the conservation of tigers in the region. In contrast, Bhutanese local traditional knowledge has had a long record of knowledge that tigers occupy high elevation mountains and not only valley bottom (Dorji and Santiapillai 1989, Vernes and Rajaratnam 2012). Our results showed that elevation is not necessarily a strong deterrent for tiger in Bhutan.

We have confirmed that tigers in Bhutan are distributed all the way from elevation of 150 meters in the southern foothills up to the Himalayan Mountain tops as high as 4400 meters above sea level (Figure 2–3). Not only do tigers occur across elevations, but we also report 45 (38-60) female tigers as well, providing clear evidence of the reproductive potential of mountain systems for tigers. For example, of the 7 female tigresses captured with cubs, 6 were above 2500 meters. Abundant large bodied prey are prerequisite for tigers to sustain and breed, and marginal small size prey such as *Muntajc* cannot sustained breeding females (O'Brien et al. 2003, Karanth et al. 2004). While prey such as gaur are concentrated, and limited in the lower foothills, we were occasionally able to camera trap them at altitude above 4000 meters. Wild pigs on the other hand are very abundant and widely distributed across Bhutan (Wangchuk 2004). Although wild pigs are notorious pests for farmers in Bhutan, they do support tigers. Wild pigs are preferred prey species for tigers (Reddy et al. 2004, Lynam et al. 2009, Hayward et al. 2012). We collected about 60 samples of likely tiger scats and 80 percent of those scats samples contained pig hair. Thus, pigs could be the principle prey species of tigers and support breeding females even at very high elevation. To see as many as 30–40 pigs in one group at on camera station was not uncommon in our study area. One plausible reason for such large number of pigs in these landscapes is that the cloud forests of the montane ecosystem are always moist throughout the year and contain preferred pig food such as roots, acorns, insects and grubs. Crops like potatoes, corns, paddy and wheat also supplement their food supply. Other prey species such as sambar, serow, and barking deer are widely distributed and common in most part of Bhutan. These assemblages of prey base support breeding tigers at the higher altitude that has not been known in the tiger conservation world before.

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 fulfill almost all of the policy-relevant criteria of source sites (Table 2–5) and contain many more tigers than most of 42 existing tiger source sites (Figure 4–4, Walston et al. 2010b, Karanth et al. 2013). We report a median of 45 adult female tigers in Bhutan, making it one of the largest source sites for breeding females. While we observed a minimum 7 females traveling with dependent cubs on our surveys, the number of actual breeding females is certainly much higher because of low detection of cubs during their first 6–12 months of life when they do not travel with their mother regularly (Karanth and Nichols 2002). Nonetheless, the presence of breeding tigers at high elevation, the high number of female tigers, and their wide spatial distribution throughout altitudinal gradient all support the alternative hypothesis that Bhutan is an important source site for tigers in the regions and landscaped level focused of the existing tiger conservation landscapes is warranted (Sanderson et al. 2010, Wikramanayake et al. 2011).

Our second question regarding the effect of human settlement on tiger density led us to predict that distance to human settlement (as a surrogate of human disturbance) will have strong negative effects. 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). In this study, we did not find any strong negative influence of humans on tiger density. Only one model with sex covariate for baseline detection showed very weak negative affect of distance from human settlement on tiger density. This is in contrast to earlier studies from other tiger habitats (Kerley et al. 2002, Linkie et al. 2006, Karanth et al. 2010b, Barber-Meyer et al. 2013). This anomaly is not only for Bhutan, Carter et al. (2013) published controversial paper that showed tiger and humans co-existing at fine scale level from Nepal. The weak relationship between distance of human settlement and tiger density in in our study area is consistent with the findings of Carter et al. (2013) and Kafley et al. (2016). Likewise, our results correspond to local knowledge that livestock depredation occurs even in villages and settlement areas across in and outside of protected areas (Sangay and Vernes 2008, Rostro-García et al. 2016). The patterns that we observed from our study and livestock predation studies by tigers from Bhutan suggest that humans in Bhutan are not a deterrent to tigers per se. However, it is important to note that human settlement as a surrogate to human disturbance is very different in Bhutan compared to rest of tiger range. Bhutan is a very different landscape, has the lowest human density 17 people per km^2 in the region (World Bank 2015), and 70 percent of country is under forest cover. Also, most Bhutanese practice the unique Bhutanese Buddhist culture, and have an aversion towards killing other life forms and hunting wildlife is taboo and rare. Although preliminary, we observed that large body ungulates and tigers were scarce in and around non-Buddhists settlements, in spite of these areas being ecologically more productive and suitable for large ungulates like gaur, sambar and wildlife pigs, and we observed snares and traps in these areas (T. Tempa, *personal observation*). Overall tigers are known to tolerate human presences if enough prey and cover exists as long as they are not prosecuted and poached (Sunquist et al. 1999) and tigers respond positively to removal of human pressure (Harihar et al. 2009, Harihar et al. 2014). Further, longterm studies have shown that the tiger densities in well protected areas that limits extractive human use have three to five times more than those poorly protected areas that have high human uses (Karanth et al. 2011, Barber-Meyer et al. 2013, Karanth et al. 2013). It appears that as a country, Bhutan currently has these attributes that support tigers as well as people.

CONCLUSION: CONSERVATION IMPLICATION FOR REGIONAL TIGER CONSERVATION

We successfully conducted the first scientifically rigorous estimate of tiger density for the country of Bhutan, including its extensive mountainous landscapes. This study will form the basis for future monitoring of tiger populations in Bhutan. Without comparable earlier studies, we cannot compare and draw any conclusion about the tiger population trend for the whole country. The most important conservation impact of this study is we are able to show that Bhutan should be included in any discussion of important tiger conservation areas (Walston et al. 2010b) that support large tiger numbers. Bhutan tigers can not only reinvigorate the whole NFC-N-RMNP, but may also provide critical linkages between Terai-Arc landscape and Indo-Chinese tigers in Myanmar and further east. JSWNP and RMNP together with Indian Manas tiger reserve is the most important and largest protected area network in south Asia and can support as many as 526 tigers (Ranganathan et al. 2008). Mountains are equally important for tigers in Bhutan.

Humans and tigers have historically co-existed together in Bhutan, but this is a delicate balance that needs to be maintained and natured. This has come with the strong commitment and visionary leadership towards conservation and unique Bhutanese-Buddhist culture. As we venture in this 21st-century with a new parliamentary democracy and market economy, we are witnessing unprecedented changes in terms of developmental activities as well as people's beliefs and lifestyle. To ensure the persistence of tigers and others wildlife, we must be mindful that these changes do not undermine Bhutan's potential to continue to be a tiger source site.

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Table 2-1: A part of encounter data file for Bayesian spatially explicit capture recapture models for Bengal tigers (*Panthera tigris tigris*) in Bhutan, years 2014 -2015. Session indicates survey session, Individual ID is the ID of individual tigers, Trap ID represent the trap location where individual tigers were captured, occasion is the sampling occasion.

Session	Individual ID	Trap ID	Occasion
1	1	593	44
1	2	233	4
1	2	233	5
1	2	233	6
1	2	234	8
1	2	234	10
1	2	234	11
1	2	796	43
1	3	707	50
1	3	707	53
1	3	708	47
1	3	708	50
1	4	705	44
1	4	713	44

Table 2-2: Summary of capture histories. a) Number of time individuals was captured. b) Number of individuals caught in unique spatial trap locations.

	a) Number of Individuals	Number of times captured
	10	1
	15	2
	12	3
	6	4
	5	5
	1	6
	4	7
	3	8
	2	9
	1	10
	1	11
	1	12
	1	13
	1	14
	1	16
	1	19
	1	21
Total	62	317

b) Number of traps	Number of Individuals
1	27
2	13
3	5
4	4
5	7
6	6
7	1
8	1
9	1
11	1

Table 2-3: Median posterior abundance and density estimates with 95% credible interval from Bayesian spatially explicit capture recapture models for Bengal tigers (Panthera tigris tigris) in Bhutan, years 2014 -2015. N is the number of tiger estimated by each model, and density of tigers per 100 sq.km. GOF(P-value) is the Bayesian p-value for fit statistics and $E(N_{cap})$ is the expected number of capture. Model D: basic model (no effect of covariate, detection as the function of distance between activity center and camera location), model $\mathbf{D} + \boldsymbol{\sigma}_{\boldsymbol{sex}}$: Effect of sex on the scaler parameter σ, model D+sex: Effect of sex on the baseline detection ($\boldsymbol{\lambda}_{\mathbf{0}}$), and model Sex + Human: Effect of sex on the baseline detection ($\boldsymbol{\lambda}_{\mathbf{0}}$) and effect of human settelement

Models	N		Density		GOF (P-value)	$E(N_{cap})$
	Median	95% CI	Median	95% CI		
$\mathrm{D} + \sigma_{sex}$	90.00	80-103.00	0.23	0.21-0.27	1	65-81
D + Sex	89.00	78-101.53	0.23	0.20-0.26	1	64-85
Sex + Human	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 2-4: 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 scaler 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	1.14 (1.07–1.22)		0.016 (0.014–0.019)	0.34 (0.27–0.41)		
D + σ_{sex}	0.94 (0.86–1.02)	1.45 (1.29–1.63)	0.025 (0.020–0.031)	0.34 (0.27–0.41)	0.45 (0.33–0.57)	
D + σ_{sex}+Ele	1.04 (0.96–1.13)	1.26 (1.15-1.38)	0.016 (0.014–0.019)	0.33 (0.27–0.41)		-0.00011 (-0.00017 – -0.00011)
D+sex+Human	1.14 (1.07–1.22)		0.017 (0.014–0.020)	0.34 (0.27–0.41)	0.46 (0.33–0.59)	-0.000053 (-0.00007 – -0.000053)

Table 2-5: The lists of creteria fulfilled by Bhutan to be designated as tiger source sites.

Karanth et al. (2010a) creteria for source sites	Bhutan's status	Remarks
1. Higher densities of tigers than in the overall landscape within which it is embedded	Yes	RMNP, JSWNP and JDNP have higer tiger densities as high as 3 tigers/100 km^2
2. Some evidence of current tiger reproduction	Yes	60 females of which 7 females captured in camera traps with 2-3 cubs
3. Has the potential to maintain a demographically viable cluster of >25 breeding females, alone or combined with other connected source sites in the same landscape. (Although no threshold number is given for demographic viability, the mean population size from the 42 source sites is 50 individuals).	Yes	Population size of 90 with 60 of them females from this study is more than mean population size of 50 individuals from the 42 source sites
4. Is embedded within a larger tiger-permeable landscape which has the overall potential to maintain > 50 breeding females	Yes	Bhutan is part of the largest tiger conservation landscape NFC-N-RMNP
5. A genuine government/social commitment to preventing further human in-migration and/or infrastructure development	Yes	Forests and Nature Conservation Acts
6. Existing wildlife protection capacity or at least political commitments to establish such capacity in the very near future	Yes	Forests and Nature Conservation Acts
7. A legal framework in place or being developed for the prevention of poaching or hunting of tigers and their prey.	Yes	Forests and Nature Conservation Acts

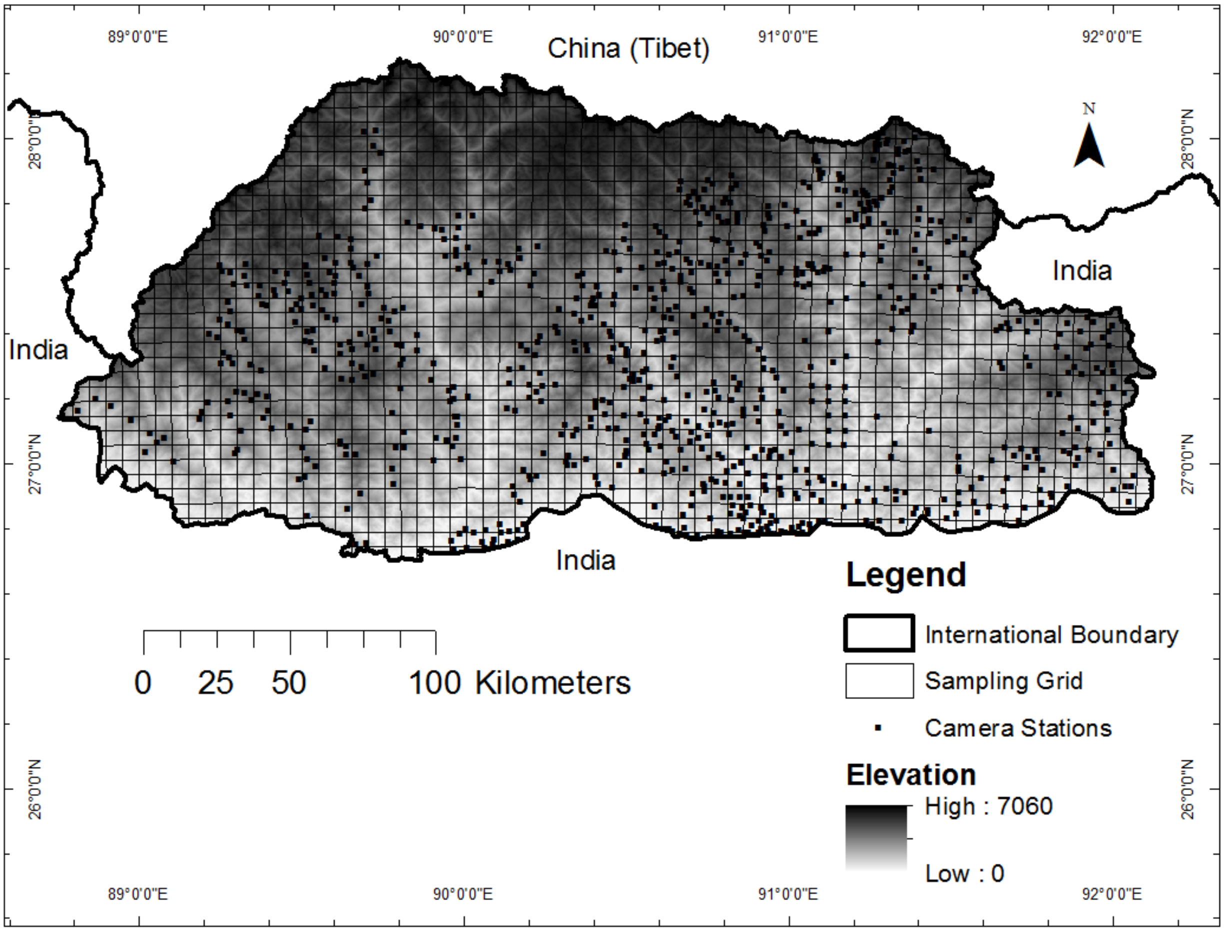

Figure 2- 1: Map of Bhutan showing 5x5 km survey grid with human settlement and elevational gradient. Each black dot represents one household, the darker color of elevation gradient represents high elevation in meters.

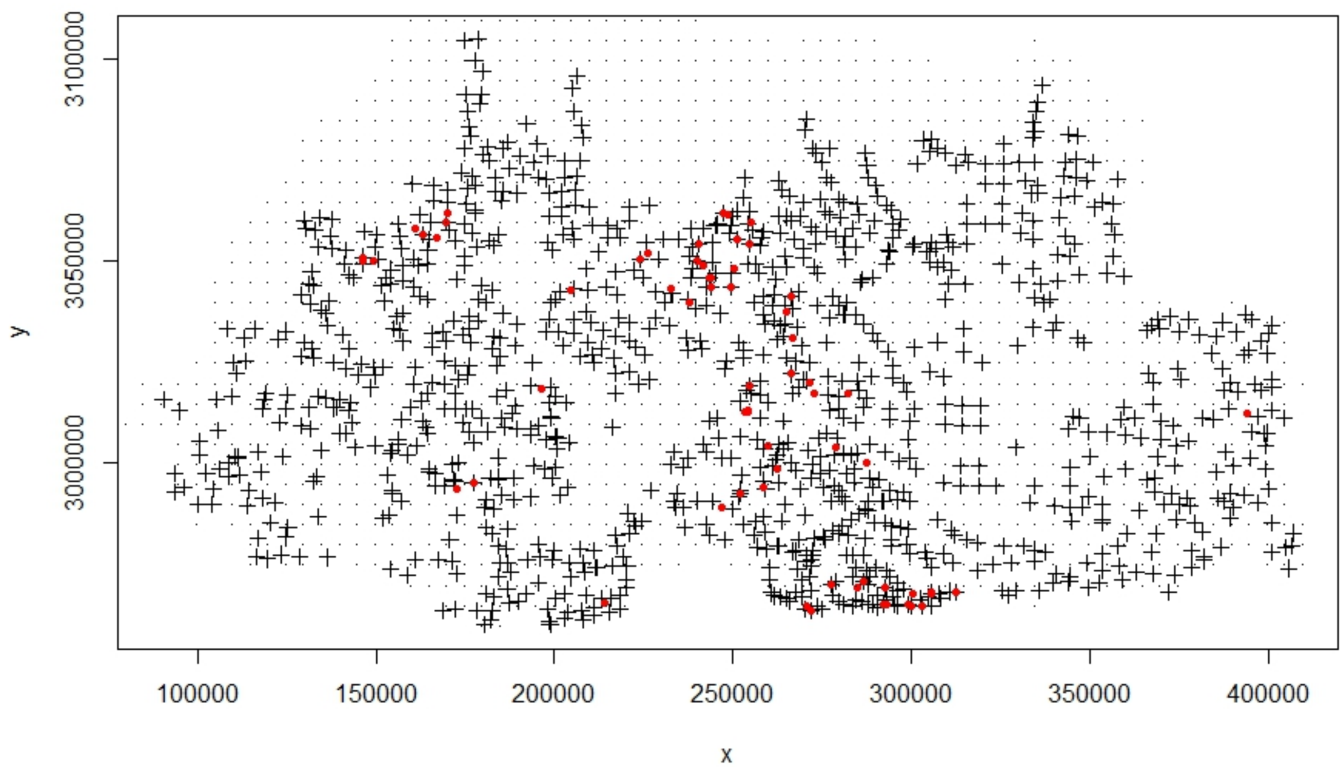

Figure 2-2: Spatial distribution of raw capture records. The red dots are the center points for individual capture based on the raw data. (+) are camera locations, the small black dots (.) are statespace.

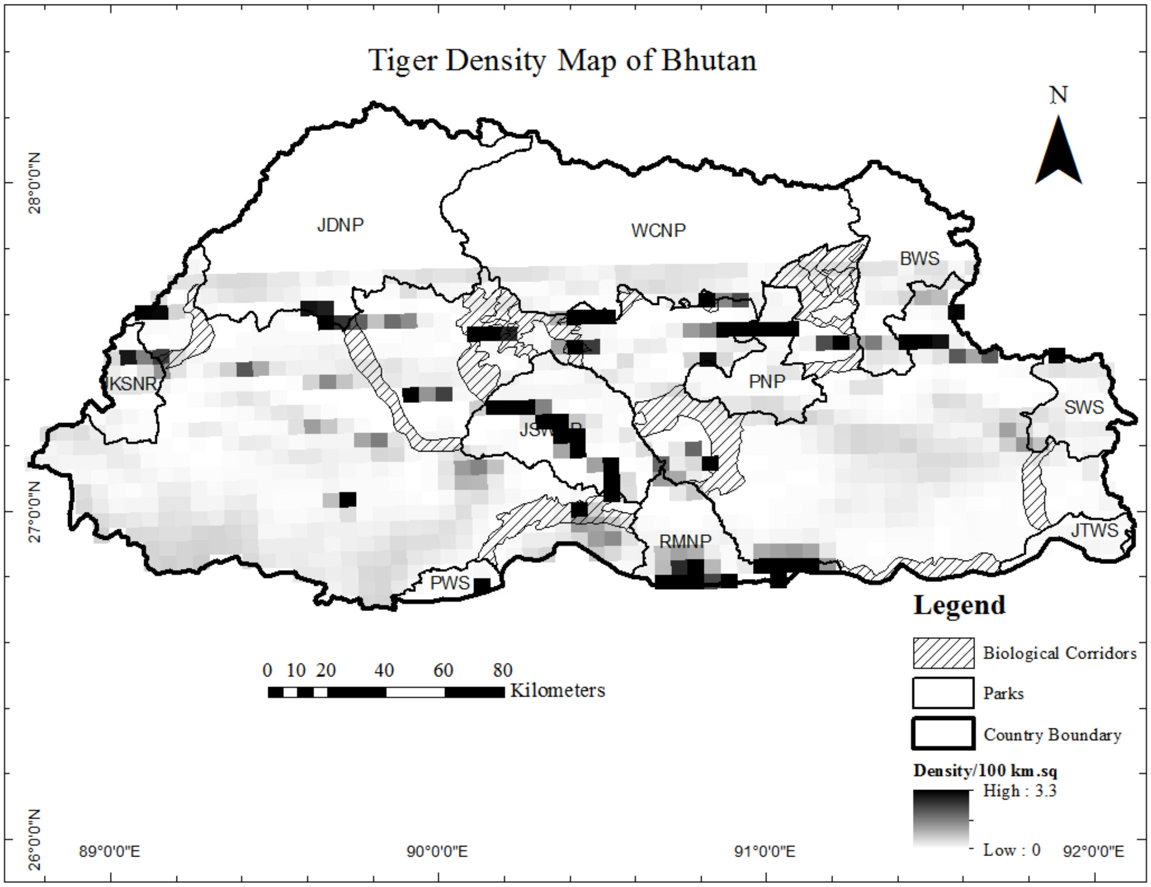

Figure 2- 3: Bengal tiger (*Panthera tigris tigris*) density map from the best Bayesian spatial capture-recapture model (distance + sigma-sex) in Bhutan, Years 2014- 2015. The darker colors represent higher density (per 100 km^2). Protected areas and biological corridors overlaid to show where tigers are distributed.

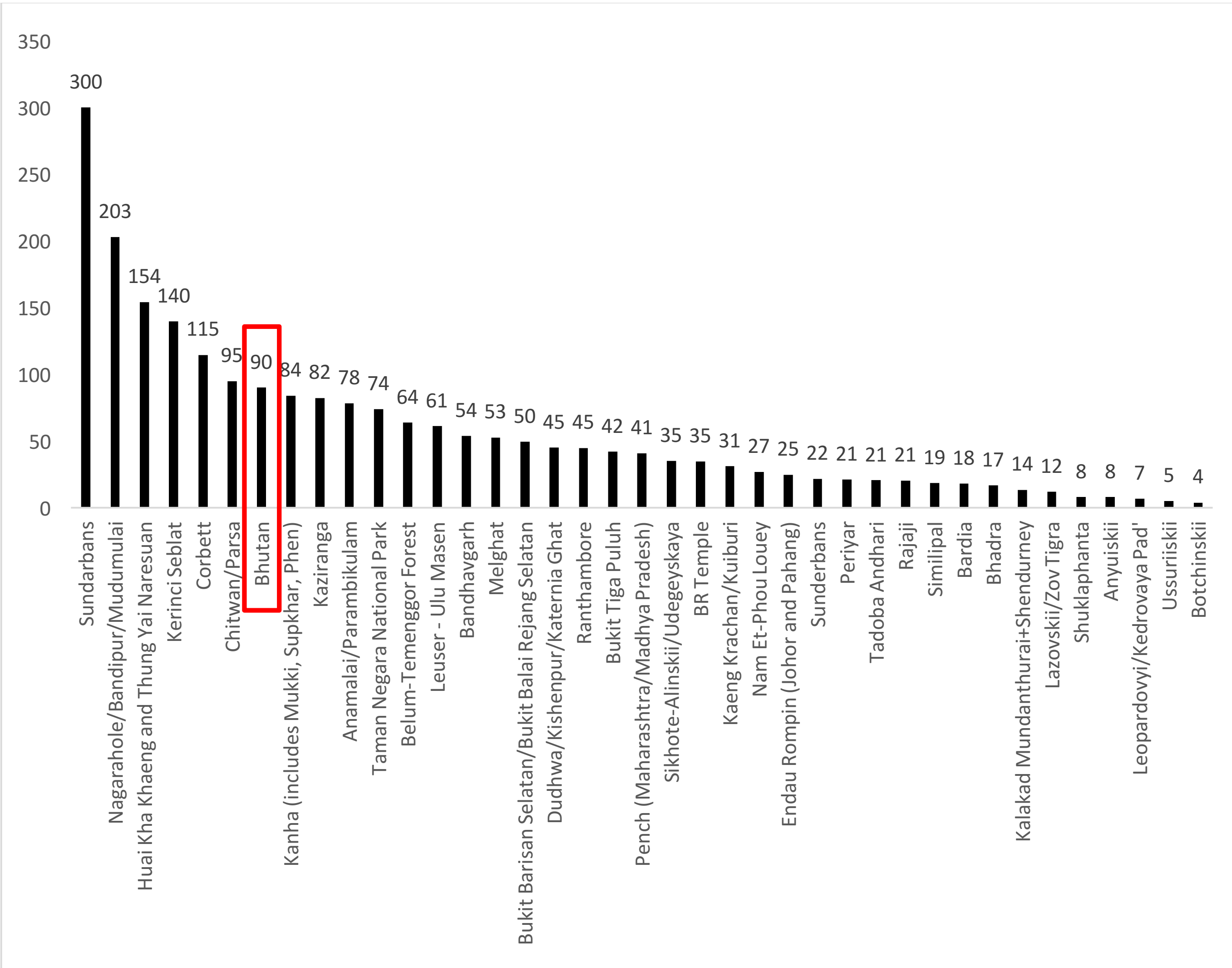

Figure 2- 4: Plot of tiger population in each 42 identified tiger source sites (Walston et al. 2010).

The red rectangle shows Bhutan's tiger population estimates from our study, year 2014-2015.

APPENDIX 2-A: Goodness-of-fit and Model Selection for Bayesian SECR Models

Bayesian model selection is complicated and there is no one best universal approach unlike the apparent simplicity of likelihood-based AIC. Royle et al. (2013) suggested 4 methods for Bayesian models: *viz* 1) hypothesis testing approach; 2) calculation of posterior model probabilities; 3) Deviance Information Criteria (DIC); 4) Logical arguments - for example something like sex specificity of certain parameters if we expect differences (home range sizes), it is better to leave extra parameter in the model if it make biological sense (Royle et al. 2013). Although we have used Bayes factor for model section of our earlier study for common leopard in Bhutan for the Bayesian bases SECR models (Goldberg et al. 2015), we were unable to use this approach due to large state space for our current study (i.e., the entire country). The large state space meant we had points in our statespace where captures had a very small likelihood and were effectively zeros '0's. These '0's create problems for any likelihood-based model selection approach, such as BIC, likelihood ratio test or Bayes Factors. As a result, we used hypothesis testing approach by examining the posterior significance of the parameters in each model and their 95% credible interval. This approached has been used to select competing models in earlier Bayesian based SECR models(Russell et al. 2012, Proffitt et al. 2015).

For the goodness-of-fit for our models, we followed Royle et al. (2011), Russell et al. (2012), and Proffitt et al.(2015) to separately test goodness-of-fit for the encounter process and underlying spatial point process. To evaluate the encounter process, we computed a discrepancy measure for the trap specific individual encounter frequencies to compare posterior samples and new realizations of the data set generated from the posterior distribution. We used the Freeman-Tukey statistic (Freeman and Tukey 1950) to calculate a Bayesian *P*-value as:

$$D = \sum_{i=1}^{N} (\sqrt{n}_i - \sqrt{e_i})^2 \qquad \text{Equation} \quad 2.5$$

where n_i is the (observed or simulated) encounter frequency for individual i conditional on s_i (the activity center) and e_i is the expected value under the model. The Bayesian P-value is the proportion of times D(obs) > D(posterior).

To evaluate the uniformity and independent assumption for the activity centers, we computed a Bayesian *P*-value based on the statistic $I=(G-1) \times s^2/\bar{n}$, where G is the total number of grid cells, and $\bar{n}$ and s^2 are the mean and variance of the number of activity centers per grid cell (Royle et al. 2013). We calculated I using posterior realizations of the point process and compared to the value of I obtained by simulations under complete spatial randomness. We did not apply the point-process GOF test to models with the RSF covariate on the distribution of activity centers, because we would not expect activity centers to be independently and uniformly distributed across space for these models.

Following Proffitt et al. (2015), we also compared the observed and expected number of individuals captured for each model to holistically examine both the point-process and detection process. We calculated the expected number of individuals captured with

$$E(n_{cap}) = \sum_{s} E_{s_i} \times n_{s_i}$$

where E_{s_i} is the exposure probability of an individual with an activity center at s_i and n_{s_i} is the number of activity centers estimated at s_i. By computing these values for each MCMC iteration, we constructed a 95% confidence interval for the number of individuals captured given the complete process described by the model. An observed number of captures that fell outside this range would indicate poor model fit.

APPENDIX 2-B: Estimation of Implied Tiger Home Range

Home Range Estimation

We estimated implied tiger home range during our during our period (i.e., not an annual home range) using a bivariate normal (Gaussian) probability density function model for encounter probability as described by Royle et al. (2013). For the bivariate normal (Gaussian) encounter probability model:

$$\mathrm{p}(x, s) = p_0 \exp\left(-\frac{1}{2\sigma^2} \parallel x - s \parallel^2\right)$$

where $\parallel x - s \parallel^2$ has the chi-square distribution with 2 df (Royle et al. 2013), the 95% use area (home range) can be directly computed as: $A = \pi r^2$, where radius *r* is related to estimated *σ* as: $r = \sigma \mathrm{x} \sqrt{5.99}$. The value 5.99 is the *α* chi-square critical value with 2 degrees of freedom. . The quantity $B(\alpha)$ that encloses $(1 - \alpha)$% of all realized distances is $B(\alpha) = \sigma\sqrt{q(\alpha, 2)}$ where $q(\alpha, 2)$ is the *α* chi-square critical value on 2 df. We used *hra* function in the R package SCRbook (Royle et al. 2013; https://sites.google.com/site/spatialcapturerecapture/scrbook-r-package) to calculate 95% home range.

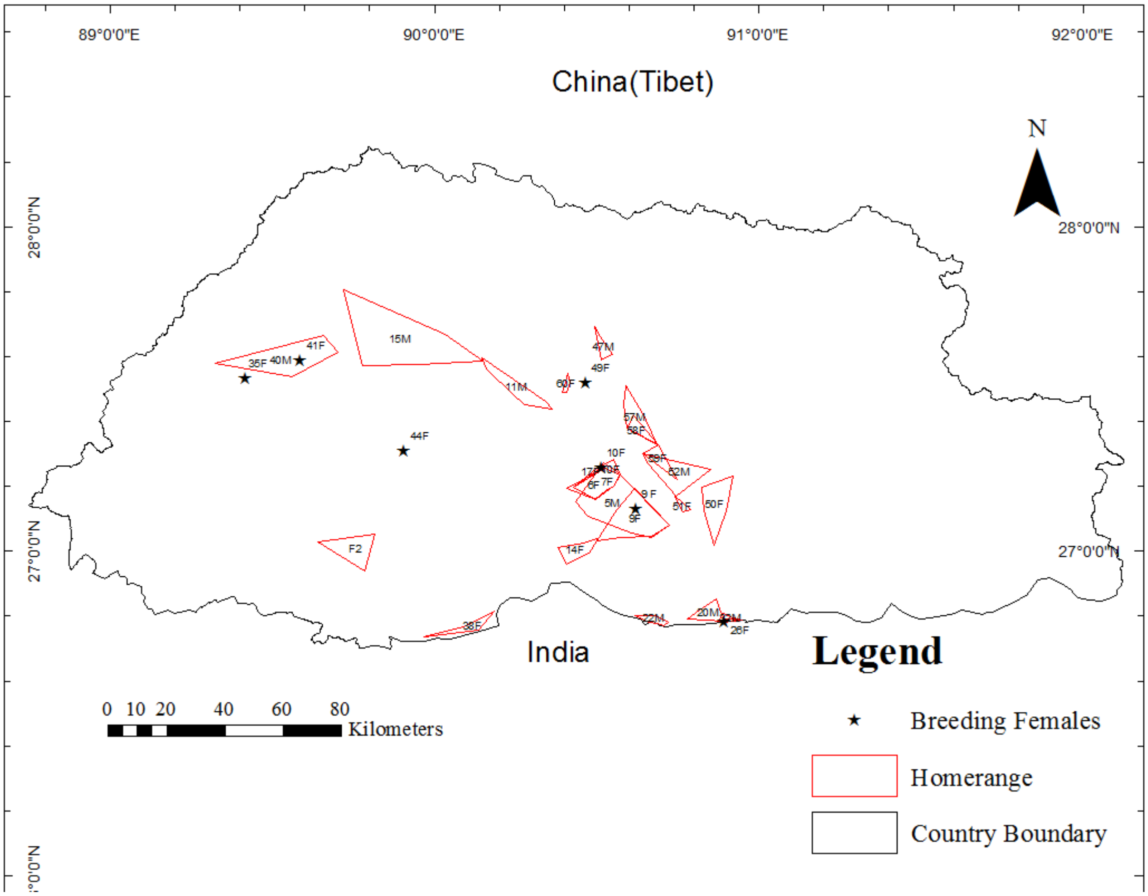

Figure 2-B1: Location of each home range calculated from MCP for Bengal tigers (*Panthera tigris tigris*) captured more than 3 camera stations in Bhutan, year 2014-2015. The numbers represent the individual ID and the letter M/F represent male/female. The black stars represent camera locations where breeding females were captured.

APPENDIX 2-C: Capture history for Bengal tiger (*Panthera tigris tigris*) survey for Bhutan, Year 2014-2015.

Table 2-B1: Capture history for Bengal tiger (*Panthera tigris tigris*) survey for Bhutan, Year 2014-2015.

Session	ID	Trap	occasion	sex
1	1	593	44	1
1	2	233	4	0
1	2	233	5	0
1	2	233	6	0
1	2	234	8	0
1	2	234	10	0
1	2	234	11	0
1	2	235	11	0
1	2	236	22	0
1	2	237	22	0
1	2	795	50	0
1	2	796	43	0
1	3	707	50	1
1	3	707	53	1
1	3	708	47	1
1	3	708	50	1
1	4	705	44	0
1	4	713	44	0
1	5	34	3	1
1	5	35	3	1
1	5	37	2	1
1	5	147	9	1
1	5	154	40	1
1	5	158	31	1
1	5	162	21	1
1	5	350	3	1
1	5	520	24	1
1	6	144	10	0
1	6	151	5	0
1	6	153	8	0
1	6	153	13	0
1	6	158	4	0

1	6	158	5	0
1	6	161	4	0
1	7	144	11	0
1	7	151	5	0
1	7	153	8	0
1	7	153	13	0
1	7	158	4	0
1	7	158	5	0
1	7	161	4	0
1	8	560	52	1
1	8	847	35	1
1	8	565	52	1
1	9	34	3	0
1	9	35	3	0
1	9	37	2	0
1	9	95	26	0
1	9	142	40	0
1	9	142	43	0
1	9	143	1	0
1	9	143	26	0
1	9	146	38	0
1	9	146	39	0
1	9	147	28	0
1	9	147	29	0
1	9	150	45	0
1	9	190	38	0
1	9	190	39	0
1	9	190	40	0
1	9	190	42	0
1	9	190	43	0
1	9	191	10	0
1	9	191	11	0
1	9	191	21	0
1	10	144	7	0
1	10	144	11	0
1	10	144	17	0
1	10	144	47	0
1	10	151	5	0
1	10	151	12	0
1	10	151	38	0
1	10	151	39	0
1	10	153	8	0
1	10	153	13	0

1	10	158	4	0
1	10	158	5	0
1	10	158	42	0
1	10	161	3	0
1	10	161	4	0
1	10	520	2	0
1	10	520	3	0
1	10	520	47	0
1	10	520	48	0
1	11	173	32	1
1	11	174	5	1
1	11	174	26	1
1	11	174	44	1
1	11	579	5	1
1	11	579	7	1
1	11	843	38	1
1	11	848	42	1
1	11	852	43	1
1	12	174	11	1
1	12	174	35	1
1	12	174	52	1
1	12	579	52	1
1	13	147	28	0
1	13	147	29	0
1	13	147	39	0
1	13	192	8	0
1	13	192	11	0
1	14	108	7	0
1	14	117	5	0
1	14	117	16	0
1	14	118	9	0
1	14	192	16	0
1	15	147	28	1
1	15	147	29	1
1	15	724	49	1
1	15	827	34	1
1	15	827	39	1
1	15	827	41	1
1	15	828	32	1
1	15	843	34	1
1	16	192	1	1
1	17	144	10	0
1	17	144	11	0

1	17	151	5	0
1	17	153	8	0
1	17	158	4	0
1	17	158	5	0
1	17	161	4	0
1	17	520	47	0
1	18	160	46	0
1	18	160	54	0
1	19	4	15	1
1	20	1	9	1
1	20	5	11	1
1	20	7	12	1
1	20	9	2	1
1	20	60	8	1
1	21	90	2	0
1	21	90	10	0
1	22	59	4	1
1	22	62	4	1
1	22	72	3	1
1	22	90	3	1
1	22	90	4	1
1	22	90	6	1
1	22	90	15	1
1	22	90	16	1
1	22	91	4	1
1	22	91	5	1
1	22	89	3	1
1	22	89	9	1
1	23	19	2	0
1	23	19	3	0
1	23	19	4	0
1	24	16	5	0
1	25	56	11	1
1	25	56	18	1
1	26	92	1	0
1	26	92	3	0
1	26	92	4	0
1	27	23	2	0
1	27	26	9	0
1	28	28	14	1
1	29	23	4	1
1	29	23	8	1
1	29	23	15	1

1	29	26	1	1
1	29	28	12	1
1	30	27	2	1
1	30	27	14	1
1	31	24	16	1
1	32	1	8	1
1	32	10	14	1
1	32	17	3	1
1	32	17	12	1
1	32	25	1	1
1	32	25	2	1
1	32	25	4	1
1	32	94	10	1
1	33	1	11	0
1	33	1	12	0
1	33	10	2	0
1	33	17	2	0
1	33	25	2	0
1	33	25	3	0
1	33	94	9	0
1	34	19	3	1
1	34	19	4	1
1	34	19	5	1
1	35	649	34	0
1	35	649	48	0
1	35	649	50	0
1	36	649	34	1
1	36	649	41	1
1	36	650	34	1
1	36	650	41	1
1	37	646	34	1
1	37	646	37	1
1	37	646	41	1
1	37	650	37	1
1	38	196	8	0
1	38	202	13	0
1	38	203	2	0
1	38	203	7	0
1	38	203	11	0
1	38	203	13	0
1	38	210	16	0
1	38	210	17	0

1	38	212	2	0
1	38	212	3	0
1	38	212	4	0
1	38	212	9	0
1	38	213	17	0
1	38	213	21	0
1	39	770	49	1
1	39	771	49	1
1	39	771	50	1
1	40	671	32	1
1	40	671	34	1
1	40	672	38	1
1	40	672	47	1
1	40	672	50	1
1	40	672	52	1
1	40	672	54	1
1	40	674	37	1
1	40	675	39	1
1	40	675	41	1
1	40	676	43	1
1	40	676	51	1
1	40	695	44	1
1	40	708	47	1
1	40	708	52	1
1	40	715	47	1
1	41	675	35	0
1	42	707	47	1
1	42	707	49	1
1	42	707	50	1
1	42	707	52	1
1	43	797	43	0
1	43	797	45	0
1	44	348	35	0
1	44	356	35	0
1	45	848	38	1
1	45	848	39	1
1	45	849	40	1
1	46	848	37	0
1	46	848	39	0
1	46	848	42	0
1	47	573	37	1
1	47	575	37	1
1	47	1095	44	1

1	47	1096	45	1
1	48	580	39	0
1	48	581	39	0
1	49	573	50	0
1	49	582	39	0
1	49	582	42	0
1	49	582	44	0
1	49	582	49	0
1	49	582	51	0
1	50	504	17	0
1	50	504	35	0
1	50	516	19	0
1	50	516	23	0
1	50	516	37	0
1	50	517	22	0
1	50	525	51	0
1	51	506	25	0
1	51	507	38	0
1	51	508	37	0
1	52	508	16	1
1	52	528	15	1
1	52	533	42	1
1	52	535	47	1
1	52	535	52	1
1	53	535	39	0
1	53	535	47	0
1	54	529	18	0
1	54	530	23	0
1	55	572	38	1
1	55	572	44	1
1	56	573	36	0
1	56	573	42	0
1	57	543	39	1
1	57	564	48	1
1	57	585	46	1
1	58	543	41	0
1	58	543	48	0
1	58	546	39	0
1	58	547	39	0
1	58	547	40	0
1	58	548	49	0
1	58	550	46	0
1	58	550	55	0

1	58	551	41	0
1	58	551	48	0
1	59	521	28	0
1	59	535	52	0
1	59	543	49	0
1	60	559	41	0
1	60	559	46	0
1	60	559	50	0
1	60	560	50	0
1	60	561	44	0
1	60	561	46	0
1	60	561	47	0
1	60	561	53	0
1	60	562	46	0
1	60	562	47	0
1	60	562	53	0
1	60	567	49	0
1	60	567	50	0
1	61	558	46	0
1	61	558	47	0
1	62	559	51	1
1	63	561	46	0
1	63	561	54	0
1	64	580	40	1
1	65	568	48	0
1	65	568	51	0
1	65	568	54	0
1	66	570	40	0

APENDIX 2-D

Table 2-D1: The posterior parameter estimates from all *SCRbayes* models for Bengal tiger (*Panthera tigris tigris*) survey for Bhutan, year 2014-2015. **σ** is the scaler parameter, λ_0 is the base line detection probability, β is the coefficient of sex and D in the density per 100 km^2 and n is the abundance. The values in the parenthesis represent 95% credible interval.

Models	σ_{female}	σ_{male}	λ_0	N	D	β Sex	β Density
Null	1.14 (1.06–1.22)		0.016 (0.014–0.019)	90 (79–102)	0.23 (0.20–0.26)		
Behavior	1.36 (1.25–1.49)		0.007 (0.005–0.008)	105 (89–124)	0.27 (0.23–0.32)	0.024 (-0.23–0.27)	
Sex+ σ_{sex}	1.03 (0.96–1.13)	1.25 (1.15-1.25)	0.016 (0.014–0.019)	92 (81–106)	0.24 (0.21–0.27)	-0.91 (-1.25–-0.58	
Elevation	1.14 (1.07–1.22)		0.016 (0.014–0.019)	84 (75–95)	0.21 (0.19–0.25)		-0.0003 (-0.0003–-0.0001)
σ_{sex}	0.93 (0.86–1.02)	1.44 (1.29–1.67)	0.24 (0.02–0.03)	90 (80–103)	0.23 (0.20–0.27)		
σ_{sex}+Elevation	1.04 (0.96–1.13)	1.25 (1.15–1.37)	0.016 (0.014–0.019)	89 (79–102	0.22 (0.20–0.25)		,-0.0001 (-0.00015–-0.00005)

Table 2-D2: Comparison of estimates density (D) and population size (N) Wang and Macdonald (2009) and present study in JSWNP

Study	Trap nights	# camera stations	# of unique individuals	D	N	Bayesian P-value
Wang and Macdonald (2009)	4,050	81	6	0.52±0.42	8±2.12	
SCRbayes ($D+\sigma_{sex}$)	9729	60	11	2.09 ±0.49	13±2.9	0.53

APENDIX 2-E

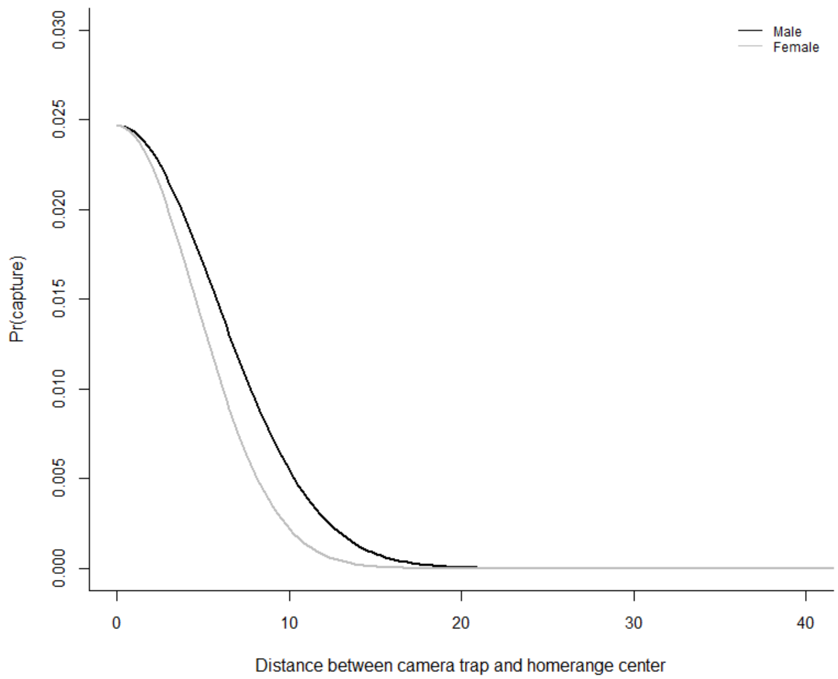

Figure 2-E1. The detection probability (encounter probability) of male (black line) and female (grey line) tigers as a function of distance (km) from the home ranger center based on the Bayesian SECR model (D+ σ_{sex})

Chapter 3: Estimating Tiger-Prey Relationships using N-Mixture Models and Tiger Occupancy in Mountainous Terrain in Bhutan

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INTRODUCTION

Wild ungulates play important roles in ecosystem functioning including seed dispersal (Vellend et al. 2003, Prasad et al. 2006, Stoner et al. 2007), cycling nutrients (Hobbs 1996, McNaughton et al. 1997, Frank and Groffman 1998, Bardgett and Wardle 2003), modifying forests composition and structure (Hobbs 1996, Augustine and McNaughton 1998, Knapp et al. 1999, Augustine and Mcnaughton 2004), and as food for humans (Fa et al. 2003, Hoffman and Wiklund 2006, Ramanzin et al. 2010) (Schaller 1967, Ramakrishnan et al. 1999, Karanth et al. 2004). Ungulates also have important roles as food for carnivores, influencing predator distribution and abundance (Carbone and Gittleman 2002, Karanth et al. 2004, Mitchell and Hebblewhite 2012).

For the endangered tiger (*Panthera tigris*), in addition to direct poaching by humans decline of ungulates prey species is the other major driver of tiger population declines across most tiger range countries (Karanth and Stith 1999, Ramakrishnan 1999, O'Brien et al. 2003, Dinerstein et al. 2007). Indeed, not only tigers are endangered, but many of the prey species of tigers are threatened due to poaching, habitat loss, and competition from livestock, especially in south and southeast Asia (Ripple et al. 2015). For example, two of the three most important principle prey species of Bengal tigers (*P.t. corbetti*) in the Indian subcontinent, gaur (*Bos* *gurus*), sambar deer (*Rusa unicolor*), (Karanth and Sunquist 1995, Hayward et al. 2012), are classified by the IUCN as venerable (IUCN 2016). Other important prey species such as water buffalo (*Bubalus arnee*) and Banteng (*Bos javanicus*) are endangered (IUCN 2016). Therefore, information on density and abundance of these prey species are crucial for the conservation of the predators they support as well as for the prey themselves.

In the Indian subcontinent, the standard method to estimate ungulate densities since the 1970s has been line transects (sometimes, but not always using distance sampling; Seidensticker 1976, Karanth and Nichols 1999, Wegge and Storaas 2009). However, in the rugged and densely forested mountainous landscapes in the Himalayas, where visibility of wildlife is very low, obtaining reliable population abundance of ungulate prey using line transect is infeasible (Jathanna et al. 2003). Indirect methods such as fecal pellet/dung counts as indices of ungulate abundance are also widely used in areas where direct methods are not feasible (Shrestha 2004, Koster and Hart 1988, Plumptre and Harris 1995, Marques et al. 2001, Forsyth et al. 2007, Alves et al. 2013). These methods have been criticized as unreliable by some scientists (Fuller 1991, Barnes 2001, Rönnegård et al. 2008), and fecal pellet/dung counts are not popular among biologists and managers. Line transect have often been used in settings and areas where they are not practical, resulting in extremely variable, impossible and/or otherwise poor ungulate density estimates (Wang and Macdonald 2009, Wang 2010).

Camera trapping methods are now increasingly being used to estimate abundance or relative abundance for species where individuals are not uniquely identifiable like most ungulates (Carbone et al. 2001, Rowcliffe et al. 2008, Curtis et al. 2009). When species, such as tigers, are individually recognizable based on stripes or other pelage patterns, density estimation is straight forward and can take advantage of rich capture-recapture methods (e.g., Karanth et al.

2005). For species that are not individually recognizable, density estimation is not as straight forward. Carbone et al. (2001) reviewed the use of photographic rates from camera trap as indices for animal abundance, and since then many studies have used photographic rates as some measure of index of abundance (O'Brien et al. 2003, Tempa et al. 2013) despite criticisms (Sollmann et al. 2013). Others have used camera trap data to estimate species occupancy in a more statistically robust framework (MacKenzie et al. 2002, MacKenzie 2006, Hines et al. 2010). However, recent statistical advances have enabled researchers to estimate animal abundances from unmarked animals using N-mixture models (Royle 2004, Kéry and Royle 2015). An *N*-mixture model is a hierarchical model that accounts for individual-level detection probabilities from spatially and temporally replicated count data (Royle 2004, Kéry et al. 2005, Fiske and Chandler 2011). Because the key assumption of no false positive errors (i.e., double counting individuals) is likely violated while dealing with camera trap data, N-mixture models may not reliably estimate absolute density (Kery and Royle 2015). Nevertheless, for unmarked animals such as ungulates, N-mixture models may yield a rigorous index of relative abundance for testing hypotheses about tiger density and distribution.

In the absence of poaching by humans, the main factor the determines the health of tiger population is the availability of optimal sized prey species (Ramakrishnan et al. 1999, O'Brien et al. 2003). Tigers have a high habitat association with their primary prey species and the spatial distribution of primary prey will determine the distribution of tigers (Miquelle et al. 1999, Hebblewhite et al. 2014, Kafley et.al 2016). For Bengal tigers in the Indian sub-continent , sambar deer and gaur are the primary prey (Karanth and Sunquist 1995), but Hayward et al. (2012) also showed tiger preferred wild pig more than other prey species. In Bhutan, it is uncertain whether sambar or wild pigs are the most important prey determining the spatial distribution of tigers. The first goal of this chapter is to test which prey species are most important for tigers in the mountainous temperate and subtropical forest of Bhutan. Bhutan is a large and important part of Northern Forest Complex - Namdhapha -Royal Manas (NFC-N-RM) tiger conservation landscapes (TCL) in the eastern Himalayas (Wikramanayake et al.2011). Almost all forest of Bhutan is potential tiger habitat with an estimated 90 individuals (Chapter 2). We used N-mixture models to estimate abundance of five principal prey species of tigers (gaur, sambar, wild pig, serow (*Capricornis thar*) and barking deer (*Muntiacus* muntjak) using camera trap pictures from the nationwide tiger survey data in Bhutan. We predicted relative abundance of primary prey species will have a very strong positive influence on tiger occupancy. Biswas and Sankar (2002) showed that wild pigs, if available, were selected by tiger over other prey species. Previous studies in India showed that often pigs were not the most abundant available prey (Karanth and Sunquist 1992, 1995) and this might have driven prey selection for sambar and gaur. In contrast, pigs are abundant in Bhutan, thus we expect pigs would have the strongest effect on tiger occupancy. Specifically, based on earlier studies on prey selection by Bengal tigers in Bhutan (Wang and Macdonald 2009), we predict sambar and wild pigs would be the primary determinant of tiger spatial distribution in Bhutan. Not much is known about the tiger and their prey in NFC-N-RM although it has the potential to support large number of tiger populations (Ranganathan et al. 2008). In many part of NFC-N-RM, tiger signs and large ungulate prey species are scarce due to indiscriminate poaching by local people (Arunachalam et al. 2004, Data et al. 2008). From our preliminary results, however, Bhutan is one of the largest populations of tiger source sites (Tempa et al. 2013, Chapter 2), and may provide the best chance to understand baseline tiger ecology in this TCL.

Our second overall objective was to test for the effects of human disturbance on tiger prey and tigers in Bhutan. The prevailing paradigm in tiger research is a negative effect of humans mediated by human-caused mortality of tigers, and their prey species, through direct poaching, human-wildlife conflict, and habitat loss (Kerley et al. 2002, Karanth and Gopal 2005, Dinerstein et al. 2007). Tigers and their prey species respond positively to the removal of anthropogenic threats (Harihar et al. 2009, Wegge et al. 2009, Harihar et al. 2014). In contrast, a recent study from Nepal showed tiger and humans co-existing in a landscape at finer scales (Carter et al. 2012, 2013, Kafley et al. 2016). In Bhutan, we do not know how human disturbance affect tigers and their prey species. We predict that because Bhutan is a Buddhist culture that respects all life forms, and because of the largely intact historic landuse patterns that support native biodiversity (Namgyel et al. 2008; Siebert and Belsky 2014), the direct effects of human activities (e.g., no poaching and hunting of ungulate prey) on prey species would be weaker than other tiger range countries (e.g., Suryawanshi et al. 2014), and ungulates would show no negative response to human presence and disturbance. We used the number of households at a different radius from camera station, the number of livestock (mostly cattle and horse, yaks included at high altitude), and the number of people at each camera stations as a measure of human disturbance. We then tested the effect of human disturbance on relative abundance of tiger prey using N-mixture models.

We used the same human disturbance indices to test the impact on tiger occupancy. Similar to our predictions for ungulates, and similar to Carter et al. (2013) and Kafley et al. (2016) for Nepal, we predict that human activity should have no or weak effect on tiger occupancy if Bhutanese-Buddhist culture and historical landuse practices translates to reduced tiger poaching. Alternatively, even if humans in Bhutan do not have direct effects themselves on tigers, humans could have both direct and indirect negative impact on tigers manifested indirectly through the effects of humans on their ungulate prey species. We used proximity to human settlement as a measure of human disturbances and test its effects on tiger density. We hypothesize that the negative effects of human disturbance on tiger density and distribution will be weaker in Bhutan than elsewhere because of low human density, Bhutanese-Buddhist culture (*sensu* Li et al. 2014), and Gross National Happiness (GNH)-based development philosophy.

METHODS

Study Area

Bhutan (38,394 km^2) is located in the globally recognized biodiversity hotspot of eastern Himalayas (Mayer et al. 2000), landlocked between the Tibet Autonomous Region of China to the north and the India to east, west, and south. It lies between latitudes 26°N and 29°N, and longitudes 88°E and 93°E. Elevation rises from as low as 150 m in the southern foothills to more than 7,500 m in the north within an aerial distance of 170km. This extreme altitudinal gradient causes great variation in temperature and rainfall, creating different climatic zones ranging from wet sub-tropical in the south to permanent alpine pastures and glaciers in the north, thus making this landscape a hotspot for wild felid diversity (Tempa et al. 2013). This great geographical diversity combined with equally diverse climate conditions contributes to Bhutan's outstanding range of biodiversity and ecosystems. Bhutan with more than 70% of the country under forest cover and more than 50% of the total geographic area under protected areas in the forms of national parks and biological corridors is a safe haven for wildlife. The top predators like tiger, leopard (*Panthera pardus*), snow leopard (*Panthera uncia*), Tibetan wolf (*Canis lupus chanco*) and Asiatic wild dog (*Coun alpinus)* roam these areas supported by diverse prey species e.g., guar (*Bos gaurus*), sambar (*Rusa unicolor*), wild pig (*Sus scrofa*), serow (*Carpicornis thar*), Asiatic Water Buffalo, muntjac (*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. Bhutan is also home to many endangered wildlife species including tiger, Indian one-horned rhinoceroses (*Rhinoceros unicornis*), elephants (*Elephas maximus*), Asiatic water buffalos, wild dogs, golden langurs (*Trachypithecus geei*), musk deer (*Moschus chrysogaster*), red panda (*Ailurus fulgens*), and hispid hares (*Caprolagus hispidus*) and critically endangered species like pigmy hogs (*Porcula salvania*) and Chinese pangolin (*Manis pentadactyla*).

Camera Trap Design

We randomly laid a 5x5km grid across all of Bhutan using Arc GIS 10.1 (ESRI 2014; Figure 3-1). The grid size of 5x5 km was chosen so that our sampling unit was not too large for smaller prey species (barking deer) or too small for larger prey species (gaur). Similar grid sizes were used in India to estimate forest ungulate and tiger abundances (Gopalaswamy et al. 2012). We selected 1,522 grid cells as potential trap locations, after accounting for town and cities, villages and other unlikely habitats of tigers above 4500 m (see Chapter 2). However, due to remoteness of some camera location, we set remote camera traps in only 834 grid cells. Inside these grid cells, we searched for animal signs and game trails. We opportunistically selected locations along roads and game trails to maximize the capture of tiger and ungulate prey. Setting camera traps along the trails and road is a standard protocol in most carnivore camera trap studies (Karanth and Nichols 2002, O'Connell et al. 2010, Xiao et al. 2016). A minimum distance of at least 2 km between camera stations was maintained to avoid clustering of cameras.

At each camera station, we set two cameras 6-7 meters away from each other at a height of 45 cm from the ground. We used five different models of a camera trap with passive infrared systems (triggered by body heat as the animal passes in front of the sensor into the camera) *viz*., Bushnell, CuddeBack, HCO-ScoutGuard, Reconyx (HC500 Hyperfire), and U- way. We made sure that cameras were positioned in such a way that two cameras are not in the same line of view to avoid the flash of one disturbing picture on the other camera. Each camera trap had a unique camera number and all locations were marked with Global Positioning System (GPS). Further, we recorded metadata such as habitat type, ground cover, canopy cover, and canopy height, signs of prey, and other carnivores were recorded.

Tiger prey surveys using remote camera traps were carried out from May 2014 to May 2015. The camera trapping grid was divided into two phases based on field logistics and the monsoon season (which affected the southern zone in summer). We began our camera trapping in the southern zone for 5 months and then moved to northern blocks and set camera's there for another 6 months. Efforts were made to visit camera traps once per month, but due to weather and season monthly visits were impossible for a few remote and isolated sites. At each camera visit we downloaded all pictures directly from SD cards to computers. Photos were segregated by species using the program Renamer (Sanderson and Harris 2013) to construct detailed species capture histories. We counted the number of individuals (referred here as an event) per sampling occasion. If an animal was captured continuously without time break of 60 seconds, we considered it as a single event. For example, there were 516 photos of one barking deer taken continuously in half an hour, which we defined as a single event. Likewise, if three individual barking deer were photographed simultaneously in one picture, we considered it as three events.

We then summed the number of events (numbers of animal) at each camera station per sampling occasions as the count statistics per station.

N-Mixture modeling

N-mixture models provide a means to estimate abundance from count data that considers imperfect detection (Royle 2004, Denes et al. 2015). An *N*-mixture model is a hierarchical model that accounts for the probability of both abundance and individual-level detection from spatially and temporally replicated count data (Royle 2004, Kéry et al. 2005, Fiske and Chandler 2011). As described in Royle (2004), a count is made for unmarked individuals during sampling occasion j (j=1, . . . , J) at a site i (i = 1, . . . , M). At each site, let N_i, be the unobserved total number of individuals (latent abundance) using a site and define C_{ij} as the number of individuals observed during the jth sampling occasion. Then

State Process: $N_i \sim \text{Poisson}(\lambda_i)$ **Equation** 3.1

Observation Process: $C_{ij} \mid N_i \sim \text{Binomial}(N_i, p_{ij})$ Equation 3.2

where the parameter lambda, λ_i, is the mean number (expected value) of individuals present at the site *i and* p_{ij} is the detection probability. p_{it} is considered as a constant across all sites and through time, thus reducing it to *p*. Following Royle (2004) for the Poisson distribution, analysis is based on the integrated likelihood obtained by marginalizing each N_i from the conditional likelihood (Fiske and Chandler 2011):

$$L(\lambda, p|\{C_{ij}\} = \prod_{i=1}^{M}\left\{\sum_{N_i=\max(C_i)}^{\infty}\left(\prod_{j=1}^{J}\frac{N_{i!}}{(N_i - C_{ij})!}p^{C_{ij}}(1 - p)^{N_i - C_{ij}}\right)\frac{e^{-\lambda}\lambda^{N_i}}{N_{i!}}\right\} \quad \text{Equation } 3.3$$

Where, λ is the mean number (expected value) of individuals present at the site *i and* p is the detection probability, C_{ij} *is count* at site *i* during sampling occasion *j* and N_i is the total number of individuals at site *i.* Covariates can be included at either the state (here, abundance, Eq. 3.1) or detection levels (Eq. 3.2), but abundance is modeled through a log link to enforce its positivity constraint using

$$\log(\lambda_i) = \beta_0 + \sum_k \beta_k x_i \qquad \text{Equation 3.4}$$

where λ_i is the mean abundance at site i for the Poisson distribution, β_0 is the intercept coefficient, the x_i are the predictor variables, and β_k is the predictor coefficient for the kth predictor. In the same way site- and time-specific covariates thought to influence detection probability p can be included using a generalized linear model with the logit link.

$$\log(p_{ij}) = \alpha_0 + \sum_k \alpha_k x_{ij} \qquad \text{Equation 3.5}$$

where p_{ij} is the probability that the individual will be detected at site i at time t, α_0 is the intercept coefficient, the x_i are the predictor variables, and α_k is the predictor coefficient for the kth predictor. If there were M sample units then $\widehat{N} = M\hat{\lambda}$ is an estimate of the total abundance of the sampled area. Finally, if covariates are thought to impact abundance then an estimate of total abundance can be constructed by summing site-specific estimates of each λ_i assuming that the covariates are known (i.e., mapped) over the region of interest.

The N-mixture model assumes no temporary migration in the sites surveyed, the sites are independent of each other and there are no double counts (Kéry and Royle 2015). One of the major caveats of camera trap data in using N-mixture models is the violation of the “no false-positive errors assumption” (i.e. we must not count the same individual multiple times during a single occasion). This assumption is required to describe the binomial observation process in the model (Kéry and Royle 2015). Although N-mixture models have been used successfully to estimate abundances of clouded leopards from camera trap data where such double counts can be avoided (Brodie and Giordano 2013), we use N-mixture models for our tiger prey species to estimate the relative abundance index only instead of a true abundance estimate following Kéry and Royle (2015).

Modeling ungulate detection and abundances

We used the unmarked package in R (Fiske and Chandler 2011) to estimate the relative abundance of 5 ungulate prey species (gaur, sambar deer, wild pigs, and barking deer) known to be the primary prey of tigers in Bhutan (Wang and MacDonald 2009). Following Kéry and Royle (2015) and MacKenzie et al. (2005) we first identified the best detection probability model (Eq. 1) for each species while keeping relative abundance constant without covariates. To achieve this, we evaluated 45 detectability models for each species for five detectability covariates (slopes, trail type, camera type, effort, and time interval). Slope determined the field of view of each camera station, and we predicted that cameras on steep slopes will have a lower field of view than in flat areas and thereby influence the detection of species negatively. We also allowed for time-varying detection probabilities within different time intervals. As the relationship between the time period and detection probability might be linear or variable among different time periods, we treated it as a categorical covariate and a continual covariate both with 10-day, 30-day or 60-day intervals. We then selected the best time-period- specific detection probability models using Akaike information criterion (AIC) to obtain a corresponding time period covariate (Burnham and Anderson, 2002). Once we selected the most supported detection probability model for each ungulate species, we used this detection model as the base for developing the abundance component of the N-mixture model (Eq. 3.2).

For the abundance model, we evaluated the effect of different covariates on our target prey abundance. The environmental covariates that we modeled to estimate ungulate prey species in our study area were human disturbance (number of households, the number of human events per camera station and the number of an event of livestock per camera station), and non-human related covariates (forest type, elevation, and slope). Tigers and their prey species are both affected by covariates at different scales (Miquelle et al. 1996, Rostro-García et al. 2016), therefore we quantified covariates at different spatial scales surrounding each camera location. We used a digital elevation model (DEM, SRTM 90m resolution) to calculate elevation at each camera station, and calculate the slope at 5 meters, 10 meters, 20 meters, 50 meters, 100 meters, 500 meters, 1 km and 2 km radius from camera stations. We used the Bhutan 2010 land cover map (MoAF, 2010) to extract forest types at 500 meters, 1km, and 2km radius from camera stations. For human disturbance, we used population and housing census data (2005) to calculate the number of households (at 500 meters, 1 km, 2km, 3km and 4 km radius of the camera trap), the number of independent events triggered by livestock and human per camera station. We selected the best scale for each of these 3 covariates with the lowest AIC of the corresponding model. All continuous covariates were scaled to have mean = 0 and variance = 1, before carrying out analysis as suggested by Kéry and Royle (2015).

Kery and Royle (2015) note the challenges in selecting the appropriate count distribution for N-mixture models. We ran the global N-mixture models with Poisson, negative binomial, and zero-inflated Poisson distributions for the ungulate count data (Joseph et al., 2009). To determine which count model to choose, we compared these 3 distributions using AIC, root-mean square error (RMSE), visual assessment of spatial residuals of the top model and comparison of observed versus predicted counts (Kery and Royle 2015). Finally, we selected the top model based on AIC (Burnham and Anderson, 2002).

Modeling tiger occupancy

To test how human disturbances, relative abundance of prey species and habitat covariates like elevation, slope and forest cover affect tiger occupancy, we estimated tiger occupancy for each camera station. Unlike SECR density estimates (Royle et al. 2013), which we report in detail in Chapter 2 for this study area, occupancy models can easily handle multiple covariates at a time (MacKenzie 2006), thus making it easier to evaluate the influence of covariates on tiger and their prey species. We used a hierarchical formulation of the single-species occupancy modeling approach described by MacKenzie et al. (2002). Occupancy models assume that site-specific occurrence for species at site (cell) i (i=1,…, M) is an imperfectly observed (latent) random variable, z(i), which is the outcome of a Bernouilli trial:

$$\text{State Process: } z(i) \sim \text{Bern}(\psi_i) \qquad \text{Equation 3.6}$$

where ψ_i is the probability that tiger occurs at cell i, and z(i) = 1 if it does occur and zero if it does not. The observation data, y(i,j), which represent the detection or non-detection of tiger at cell i during the camera trap survey, are conditional upon the true occurrence state, z(i), and are assumed to be Bernouilli random variables if species is present (z(i) = 1) and are fixed zeros if species is absent (i.e., if z(i) = 0, then y(i,j) = 0 with probability 1). This observation model is specified as:

$$\text{Observation Process: } y(i,j) \sim \text{Bern}(p_{ij} \cdot z(i)) \qquad \text{Equation 3.7}$$

where j is independent trials (sampling occasion) and where p_{ij} is the probability of detecting tiger at site i if it is present.

We constructed occupancy data matrix for each camera trap (site) by defining 10 days as one sampling occasion (similar to prey sampling occasions) and established the encounter history at each site *i* using 1 for detected and 0 for undetected. Then we also applied the same two-step approach for building models focusing first on detection, and then, with the best detection model, occupancy (MacKenzie, 2006). We considered similar detection covariates and we used relative abundance of 5 prey species (from the N-mixture models developed above) and human disturbance covariates to test our hypotheses about factors affecting tiger occupancy. All occupancy analysis was conducted in the R package unmarked (Fiske and Chandler, 2011).

The detection covariates included site covariates (trail type, and slope) and the time period as the observation covariate. Similar to the ungulate models, we took a a time period as a categorical covariate and a continual covariate both with 10-day, 30-day or 60-day intervals for univariate models, and then applied AIC to select the appropriate time period covariate for modeling the detection process. The top models for detection probability were identified by ranking AIC.

We used relative abundance of 5 ungulate species, human and cattle as covariates to determined their effect on tiger occupancy. For human and cattle, we measured human presence and cattle grazing frequency by the number of human and cattle presence recorded by our cameras. We also test the effect of environmental covariate (elevation, slope and forest types) on tiger occupancy. The candidate models were built and ranked in order to select the top model. We examined the model fit by goodness-of-fit test with 1, 000 bootstrapping.

RESULTS

Of the 1,129 total camera stations deployed, we use only 834 camera stations as images of prey and other species were delated in the field by field staff. On average, each camera trap functioned for three months with total of 78,830 trap nights (March 2014 to March 2015). We observed 2,891 events of wild pigs, 6,449 events of muntjac, 3,442 events of sambar, 1,644 events of gaur, 857 events of serow, and 456 events of tigers that we used for analysis.

Muntjac

The top detection model for muntjac was simply a function of time-varying detection probabilities during 30-day time periods. In general, detection probability was highest in time periods May, June, and October, and lowest in January, February, and (see Table 3–1 and Appendix 3–F Figure F1). The top model explaining muntjac relative abundance was clearly a function of elevation, forest type at a 1km radius, slope within 2km, settlement density at the radius of 3 km and the presence of livestock (Appendix 3–A Table A1). Muntjac abundance was highest specifically in mixed conifer forests (Appendix3–L Figure L1). Higher elevations had negative effect on muntjac relative abundance, whereas slope had a positive effect (Table 3–1). Settlement density at the radius of 3 km and the presence of livestock also showed positive effects on muntjac relative abundance (Figure 3–2 & Figure 3–3). Model selection was quite certain – only 1 other potential competing model was within 2 deltaAIC, and this model structure was the same except for a marginal (positive) effect of human counts on muntjac abundance (Table 3–1). The goodness of fit tests for muntjac supported Poisson over other count distributions (e.g., negative binomial) based on model fit, graphical assessment of spatial residual plots, RMSE, and predicted versus observations (Appendix 3–G Figure G1 &G2). The estimated measure of over dispersion for muntjac was c-hat = 3.24. Overall, muntjac abundance was predicted to be highest in lower elevation, more southerly regions of Bhutan (Figure 3–4).

Sambar

The top detection model (no other models within 2dAIC, Table 3–1) for sambar was a function of time-varying detection probabilities and trail types. The top model for abundance was a function of elevation, forest type at 1 km radius, slope within 1km radius, settlement density at the radius of 500 m, number of human occurrence, and the presence of livestock (Appendix 3-B Table B1). Sambar abundance was highest mixed conifer followed by broad leaved forests (Appendix 3–L Figure L1). Sambar abundances decreased with increasing elevation, slope, and settlement density (number of houses) at the radius of 500 m (Figure 3–2 & Figure 3–3). The presence of livestock and human however, showed positive effects on relative abundance of sambar (Table 3–2). Overall, sambar abundance was predicted to be highest in lower elevation, more southerly regions of Bhutan (Figure 3–4).

Wild Pig

The best fitting detection probability model for wild pigs varied among 30-day time periods, slope at 5m radius (β= 0.27, SE = 0.13) and trail type ((Table 3–1). The non-human use and high human use trails have high detection, while the very high intensity of human use trails has the lowest detection. Wild pig abundance was a function of elevation, forest type at the radius of 500m, household density at 1 km radius, number of human, and cattle at the camera stations (Appendix 3–C Table C1). The next best model within the range of 2 deltaAIC was the marginal effect of slope at 500m radius (Appendix 3–C Table C1). Wild pig abundance decreased with elevation (β= -0.16, SE = 0.03), house density (β= - 0.30, SE = 0.03), and number of humans per camera station (β= - 0.23, SE = 0.04) (Table 3–2). Cattle had marginal positive effect on wild pig abundance. Wild pig abundance is highest in shrubs and grasslands, followed by conifers and mixed conifer forest types, but lowest in broad leaved forests and others – includes scree, snows, and rock (Appendix 3–L Figure L1). Wild pig abundance was predicted to be highest in lower elevation, in open spaces where shrubs and grasslands dominates throughout Bhutan (Figure 3–4).

Gaur

The top model for gaur detectability was varying time interval (30-day time periods) and correlated trail type. The detections were highest in time interval 5, 6, and 10, and lowest in winter months 1, 12, and 13th time intervals (Appendix 3– F Figure F1). Medium human use trails had the highest detection, while high and very high human use trails had the lowest detection (Table 3–1). The best model of gaur abundance was a function of elevation, forest type at 500m radius, house hold density at 4km radius, number of human and cattle at camera station (Appendix 3– D Table D1). The relative abundances of gaur decreased with the elevation gradient (β= -2.00, SE = 0.05) and presence of cattle (β=-8.66, SE = 0.68). The density of households at 4 km radius also negatively affected gaur abundance (β=-0.22, SE = 0.03). The presence of humans at camera stations had marginal positive effect on gaur relative abundance (β=0.28, SE = 0.01) (see Table 3–1). The broadleaved forest and shrubs and grass lands had the highest abundance, others (includes scree, rock out crops, river beds, and snow cover) and conifer forests has the lowest relative abundance of gaur (Appendix 3–L Figure L1). The overall relative abundance of gaur was predicted to be highest in lower elevation and strictly restricted to more southerly regions of Bhutan (Figure 3–4).

Serow

For serow, the top model for detection probabilities was varying time interval (30-day time periods) and slope at 5m radius and trail type. The detections serow are highest in time periods 4, 9, and 10, but lowest in time period 6 and 7, the peak monsoon period (Appendix 3–F Figure F1). The detection probability increase with increasing slope (β=0.13, SE = 0.04) for serow (Table 3–1). The non-human use trail had the highest detection probability, while the high and very high human used trails had the lowest detection (Table 3–1). The top model for the serow relative abundance was the function of elevation, forest type at the radius of 500 meters, slope at the radius of 2 km, the house hold density at the radius of 4 km human presence, and cattle (Appendix 3–E Table E1). Serow relative abundance increased with the elevation (β=0.35, SE = 0.08) and slope (β=0.42, SE = 0.06). The human (β=0.12, SE = 0.08) and cattle (β=0.16, SE = 0.03) presence also have positive affect, while house hold density(β =-0.21, SE = 0.07) has negative impact on serow relative abundance (Figure 2 &3). The serow was more abundant in the broad leaved forest type and less in grasslands and others (Appendix 3–L Figure L1). The overall relative abundance of serow was predicted to be highest in mountains and higher elevations of Bhutan (Figure 3–4).

Tigers Occupancy

The top detection model for tiger was simply a function of time-varying detection probabilities during 30-day time periods (see Table 3–3). In general, the detections were highest in January, April, and December, and lowest in June and July interval (Appendix 3–F Figure F1). The best model for tiger occupancy was a function of the number of house hold density at a 1km radius from the camera trap, number of cattle at camera stations, and the relative abundance of sambar, gaur, and elevation (Table 3–4, Figure 3–5). The effect of settlement density was weak and not significant (P-value = 0.118). Other competing models within 2 delta AIC contained elevation, gaur, sambar, and number of cattle per camera station (Table 3–4). Tiger occupancy probability showed significant positive correlations to the relative abundance of sambar (β= 0. 51, SE=0.2, P-value = 0.014) and gaur (β= 0.46, SE=0.2, P-value=0.018), and elevation (β=0.41, SE=0.16, P-value =0.015), and the confidence interval for these coefficients did not overlap zero (Table 3–5). The relative abundance of wild pig, muntjac, serow, and the number of humans per camera station were not in the top model. Despite wild pigs being more numerous, sambar and gaur have the strongest effect on tiger occupancy (see discussion). Household density at 1-km radius was in the top model, and showed negative effect on tiger occupancy, but the effect was not significant as the 95% confidence interval as the coefficient overlapped zero (β=-0.26, SE=0.17, P-value =0.13). The number of cattle presence at the camera stations showed significant positive effect on tiger occupancy (β=0.20, SE=0.10, P-value =0.04). Surprisingly, elevation showed positive effects on tiger occupancy (β=0.41, SE=0.16, P-value =0.01).

DISCUSSION

We successfully used N-mixture models (Royle 2004) and occupancy models to estimate relative abundance of tiger prey and occupancy of tigers (MacKenzie et al. 2002) across all of tiger range in the country of Bhutan. We have shown that the camera-trap data can be effectively use for answering important questions on predator and prey associations, human disturbances, and habitat associations. Our first major result was that there was not a strong signature of human disturbance on tiger prey nor tiger occupancy except through the effect of settlement density. Tigers and prey did not show consistent negative responses to other measures of human activity such as cattle grazing nor numbers of humans traveling on tiger trails. Indeed, many ungulate species were positively associated with cattle grazing, suggesting a potential indirect positive effect on tiger prey, and thus tigers. This is consistent with the positive effects of traditional swidden agricultural practices which Bhutanese farmers traditionally used to enhance cattle, and potentially wild ungulate, grazing (Belsky and Siebert 2014). Thus, it seems that tigers avoid occupying areas close to human settlements, but that indirectly, humans may have positive effects on tiger occupancy in Bhutan. Second, we expected that wild pigs and sambar would be the prime determinants of tiger occurrence, but instead found that sambar deer and gaur were the main predictors of tiger occupancy across Bhutan. But supporting our results from Chapter 2, we reported high gaur, sambar and pig densities in central Bhutan and in areas of higher elevations up to 4000m, again confirming the suitability of tiger prey throughout Bhutan.

For our first hypothesis regarding the effects of humans, contrary to our predictions, there was a mixture of positive and negative effects of human disturbances on the relative abundance of tiger prey species in Bhutan. With the exception of muntjac, all tiger prey species were negatively affected by density of settlements (Table 3-2). Wild pigs and Sambar were affected only by the density of settlement at proximity (at the radius of 1 km and 500 m), while gaur and serow on the other hand were affected by household density even at the wider range (4 km radius). In Bhutan, the number of households is closely related to crop land and agriculture fields and settlement, which in turn reduces habitat for tiger prey. As large-bodied mammals are less tolerant to human disturbances (Tania et al., 2009), our results showed guar and were negatively affected by human disturbances. In the Terai of Nepal, both gaur and sambar where negatively affected by human disturbances (Bhattarai and Kindlmann 2013, Thapa and Kelly 2016), however in the Rajaji National Park, India, Harihar et al. (2009) showed that sambar density did not increase with removal of human disturbances. For species like muntjac, we interpret the positive effects of human settlement on their relative abundance because our settlements and agricultures lands are often intermixed by small patch of forests and grazing lands. Muntjac prefers small patches of grassland scattered in dense forests with low vegetation for grazing and uses dense forests as shelter (Teng et al.,2004; Odden and Wegge, 2007). Wegge et al. (2009) found that abundance did not change with improved protection and removal of human disturbances in Bardia National Park, Nepal. Bhattarai and Kindlmann (2011) also found that human disturbances had positive affect on muntjac abundance. Similarly, another small forest ungulate species, the Roe deer (*Capreolus capreolus*), showed positive associations with human agricultural settlements in the range of Amur tigers (*P. t. altaica*) in the Russian Far East (Hebblewhite et al. 2012; 2014, Xiao et al. 2016).

In contrast to the effect of household density, the number of humans counted at the camera stations had no negative impact on all the tiger prey relative abundance, with the exception of wild pigs. Sambar and muntjac do sometimes raid crops but are not major pests, while gaur and serow are not agricultural pests and cause the least problems to Bhutanese farmers (MoAF 2008). As such, farmers trend to tolerate their presence and are not persecuted. Wild pigs on the other hand are a notorious agricultural pest (MoAF 2008) and a nuisance to our farmer, we suspect that pigs are persecuted and harassed by our farmers. That why our pigs are wary of the human presence and thus show negative responses to both human settlements and human activity in general. Similarly, in Nepal, Thapa and Kelly (2016) showed negative effects of humans on wild boar. And in the Russian Far East, Hebblewhite et al. (2014) showed negative effects of agricultural land use and hunting on the occupancy of wild boar, a critical prey species for Amur tigers.

Somewhat paradoxically, the number of cattle counted at camera stations also had positive effects on sambar, pigs, muntjac, and serow relative abundance, but for gaur there was very strong negative relationship with cattle presence. In India, Madhusudan (2004) found that the presence of livestock does not impact the density of wild pigs and sambar, but found to negatively affect gaur abundance similar to our results. Gaur and cattle have similar forage requirements, and high cattle densities exclude Gaur through competitive exclusion (Mishra et.al 2002). Similarly, in Bardia National Park, Nepal, removal of livestock grazing did not resulted in increase in the number of sambar and wild pig. Harihar et al. (2009) also reported that sambar number did not increase even after removing livestock grazing from the Rajaji National Park.

We found that human settlement has strong negative effects on prey relative abundance. This means that prey species avoid human settlement, but other indirect measures of human disturbances did not have negative impact, which suggests that there is little direct hunting and persecution. However, we cannot rule out completely that poaching is non-existent. During field work, we encountered snares and traps mostly for pigs as a retaliatory measure, and in a few incidences signs of deliberate poaching (traps and snare of musk deer, pigs and pheasants, T. Tempa, *unpublished data*). Traditional hunting cultures and bush meat consumption is the main driver of ungulate depletion in the north-east India adjacent and NFC-N-RM (Datta et. al 2008). In contrast, Bhutanese do not have culture of bush meat consumption nor a traditional hunting culture (BAP 2002).   Thus, organized and indiscriminate poaching of wild ungulate poaching does not regularly occur. Therefore, we interpret our results to show no strong direct effects (prey depletion via direct killing) of human disturbance to tigers in Bhutan.

Building on these models of the relative abundance of tiger prey, we found that tiger occupancy in Bhutan was driven by sambar and gaur. In Bhutan, of the 5-prey species, sambar and gaur were the two most important prey that had positive effect on tiger occupancy. The availability of their preferred prey species influence the occurrence of tigers (Karanth et al., 2004; Habblewhite et.al 2014; Steinmetza et.al 2013). Based on previous studies in India, sambar and gaur are the preferred prey species of tigers (Johnsingh, 1992; Karanth and Sunquist, 1995; Karki 2011). In areas where large prey like sambar and gaur are absent, however, wild pigs and muntjack become important for tigers (Biswas and Sankar 2003, Miquelle et al. 2005, Steinmetza et.al 2013). In Bhutan, we expected pigs to be important prey base for tiger as they are most widely distributed and common (Wangchuk 2004), but our results showed wild pigs and muntjac do not influence tiger occupancy. This is consistent with Wang and MacDonald (2009) and Karki (2011) where they found that wild pigs and muntjac were the most common prey, but sambar was the preferred prey species. Tigers in Bhutan prey upon wild pig as evident for scats of tigers (Wang and MacDonald 2009). Sambar and gaur were not as common and widely distributed as pigs, but where they occur, tiger occurs. Thus, we found a strong positive relationship between tiger occupancy and gaur and sambar relative abundances, whereas wild pigs and muntjac do not influence tiger occupancy. Perhaps this might be due to difference in spatial scale of tiger prey selection in the diet and tiger occupancy. Tiger prey selection may not always equal habitat selection (Miquelle et al. 1999). Wild pigs are preferred prey species for tigers (Reddy et al. 2004, Lynam et al. 2009, Hayward et al. 2012), thus pigs should be important for tigers in Bhutan. Further, detail dietary study of tigers is required to understand role of ungulate and their contribution in supporting the tiger population in Bhutan.

In general, we found support for our hypothesis that the effects of humans on tiger occupancy would be weaker than other published studies. Our prediction that human activity in Bhutan will have minimal effects on tiger occupancy if our Bhutanese-Buddhist culture translates to reduced tiger poaching holds true. Human settlement density had weak and non-significant negative effects on tiger occupancy. The weak relationship between settlement and tiger occupancy in our study area was consistent with the findings of Carter et al. (2013), Kafley et al. (2016), and Thapa and Kelly (2017). This is in contrast to earlier studies from other tiger habitats (Kerley et al. 2002, Linkie et al. 2006, Karanth et al. 2010b, Barber-Meyer et al. 2013). Moreover, the number of humans at camera station had no effect on tiger occupancy. The number of humans per camera station was included in the second-best model, but showed a weak negative effect and was not significant as the 95 % confidence interval overlapped with zero. Moreover, considering the effect of livestock, the number of cattle at camera stations had a positive effect on tiger occupancy. This is not surprising given that livestock constituted almost 70% of their diet in JSWNP, one of the important parks for tiger conservation (Wang and Macdonald 2009). Likewise, our results correspond to local knowledge that livestock depredation hotspots occurs even in villages and settlement areas in and outside of protected areas (Sangay and Vernes 2008, Rostro-García et al. 2016). Thus, livestock as supplemental food may directly benefit tiger, especially if there is low human-tiger conflict or retaliatory killing, both of which are rare in Bhutan-Buddhist culture (Sangay and Vernes 2008). The seasonal migratory livestock husbandry in the temperate regions of Bhutan may also help to maintain the pasture and grasslands for wild ungulate, thereby indirectly benefiting tigers. But the positive effect of livestock density on tiger occupancy is in stark contrast to previous studies in the Indian subcontinent and elsewhere that show a pervasive negative effect of livestock presence on tiger occupancy (Wegge et al. 2009, Harihar et al. 2009). However, Jhala et al. (2006) showed that lion densities and pride sizes were larger in areas sympatric with livestock. Similarly, Rominger et al. (2004) show that cattle can subsidize large felid, cougar in North America. For tigers to indirectly benefit from livestock in Bhutan in the future, ensuring that Bhutanese-Buddhist culture continues to tolerate such depredation will be critical.

Despite the evidence for moderated effects of humans on tiger prey abundance and the occupancy of tigers in Bhutan, this does not mean that human activity will necessarily remain beneficial in the future. The relatively high tolerance of Bhutanese for tigers may be changing given dramatic socioeconomic changes in Bhutan, along with traditional landuse practices (Siebert and Belsky 2014). Like many Himalayan countries, Bhutan is experiencing rapid growth of hydroelectric projects (Pandit and Grumbine 2012) and has transitioned from a traditional monarchy to a constitutional democracy. For example, between 2012 and 2016, of the 15 cases of tiger skins and bone sets that has been confiscated by our protection and surveillance unit, at least 4 tigers were killed as part of retaliation by herders and an additional 2 tiger were killed accidentally in the snares meant to trap pigs and others (DoFPS 2017). Human-wildlife conflict in serious concern Bhutan, and is the major threat that can endangered tiger populations in Bhutan (Sangay et al. 2008, Rajaratnam et al. 2016). Unlike in other tiger range countries, there is no deliberate and organized poaching of tigers for illegal trade, but accidental kills of tigers as a result of human wildlife conflict are increasingly being sold in the black markets. This may gradually lead into organized poaching for wildlife trafficking, especially when combined with increasing economic ties through hydroelectric development with neighboring India and China. Moreover, indirect changes to historically beneficial landuse practices such as shifting cultivation which would indirectly enhance forage for tiger prey (as suggested in our results) could also have negative effects on tiger prey, and thus tigers, in the future (Siebert and Belsky 2014).

Given the sharp elevational gradient in Bhutan, a Himalayan country, we found strong effects of elevation on tiger occupancy, but in the opposite direction to what we expected. In our results, tiger occupancy increased at higher elevations in Bhutan. This is counter intuitive as mountains and higher elevation are less productive compared to low lands and valleys (Raich et.al 1997, Girardin et al. 2010). The valley bottoms and lower elevations in the southern Bhutan have higher densities of human settlements and the positive effect of elevation on tiger occupancy could be due to this. In Sumatran, Sunarto et.al (2012) also showed that tiger occupancy had a positive relationship with elevation and posited that human disturbances were concentrated in the low lands so tigers move to higher areas. In Bhutan, tigers occur from the narrow strip of southern foothills to the mountains tops, with higher elevations being the predominant available habitat for tigers.

Comparatively our tiger occupancy estimate is lower than many areas in the Indian sub-continent (Harihar and Pandav 2012 ($\hat{\psi}$= 0.588±0.071 in Western Terai Arc Landscape, India); Kafley et.al 2016 ($\hat{\psi}$=0.73$\pm$0.07 in Chitwan National Park, Nepa); Thapa and Kelly 2017($\hat{\psi}$=0.63 $\pm$0.11 in Churia habitat of Nepal), Carter et al. 2013 ($\hat{\psi}$ =0.82$\pm$0.04 in Chitwan National Park, Nepal)). In comparison to the somewhat higher estimates for tiger occupancy in other studies, our occupancy estimate of $\hat{\psi} = 0.25$(SE = 0.05) is reasonable given our large study area of more than 30,000 km^2, and lower tiger densities (Chapter 2) compared to higher tiger densities in the Indian plains. Most previous studies used smaller, high density and high occupancy study areas rather than a country wide, regional survey.

Finally, occupancy (psi) and abundance (N) have a positive relationship (Nichols and Rolye 2003) that depends on many factors. We feel that the effects of the covariates that drive occupancy in chapter 3 will also drive changes in N from chapter 2. For Amur tiger in North East

China, Xiao et al. (2017) showed a triangular relationship with predicted occupancy probability and estimated density, at 25th, 50th, 75th, 95th percentile according to the quantile regression of density and occupancy. Similarly, Boyce et al. (2016) showed a wedge-shaped (triangular) relationship with the resource selection functions (RSF) and abundance. Thus, to enhance tiger densities in Bhutan, ensuring high relative abundance of sambar and gaur may be the best strategies.

CONCLUSION

We successfully used camera trap data to estimate the relative abundance of principle prey species of tigers and tiger occupancy for the country of Bhutan, including its extensive mountainous landscapes. The Royal Government of Bhutan's pledge to increase tiger number by 20-50% in next 5 years can only be materialized if habitat of main tiger prey species like sambar and gaur are improved and managed properly. Human and human disturbances do not negatively impact tigers in Bhutan as poaching of tiger and their prey are not common, but the fact that cattle are important for tiger as supplementary prey, human-tiger conflicts is a concern that needs to be address for the long-term survival of tigers in Bhutan.

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Table 3- 1: Table of Beta coefficients and standard errors (SE) for detection from the top N-mixture models for 5 ungulate prey species for Tigers in Bhutan, based on country-wide remote camera trapping surveys. N-mixture models were best fit using the Poisson count model. Covariates are 30-day time periods (e.g., 30c1, 2, 3..) corresponding roughly to months from the start (January 2014, time period 1) to January 2015), trail types (intensity of human use, N=no human use, L = low use, M= medium use, VH=very high used), and slope within 5m of the camera trap.

Covariates	Species									
	Muntjac		Wild pig		Sambar		Gaur		Serow	
	β	SE	β	SE	β	SE	β	SE	β	SE
d30c1	-1.91	0.07	-3.09	0.09	-1.70	0.12	-5.48	0.21	-2.99	0.25
d30c2	-2.03	0.06	-2.72	0.08	-1.03	0.11	-4.88	0.18	-2.98	0.25
d30c3	-1.69	0.05	-2.97	0.08	-1.08	0.11	-4.71	0.18	-2.96	0.24
d30c4	-1.53	0.05	-2.96	0.08	-1.02	0.11	-4.86	0.18	-2.81	0.23
d30c5	-1.35	0.05	-2.75	0.08	-1.28	0.11	-3.55	0.18	-3.21	0.24
d30c6	-1.24	0.05	-2.04	0.07	-1.47	0.11	-3.78	0.18	-3.66	0.26
d30c7	-1.58	0.06	-1.83	0.07	-2.01	0.14	-4.01	0.18	-3.59	0.26
d30c8	-2.05	0.08	-2.81	0.08	-2.07	0.15	-5.22	0.21	-3.28	0.26
d30c9	-1.82	0.09	-3.08	0.10	-2.00	0.17	-4.65	0.22	-2.67	0.26
d30c10	-1.2	0.08	-1.78	0.08	-2.22	0.19	-3.76	0.29	-2.55	0.26
d30c11	-1.87	0.09	-2.30	0.08	-2.42	0.19	-4.75	0.42	-2.81	0.27
d30c12	-2.47	0.11	-2.81	0.09	-1.74	0.16	-5.46	0.35	-3.05	0.27

d30c13	-3.1	0.23	-3.31	0.15	-2.36	0.26	-5.73	0.61	-3.94	0.44
Trailtype L			-0.34	0.08	-0.04	0.12	0.89	0.18	0.10	0.24
Trailtype M			-0.44	0.08	0.30	0.11	1.90	0.18	0.04	0.24
Trailtype N			-0.03	0.07	-0.27	0.11	0.19	0.18	0.77	0.22
Trailtype VH			-1.66	0.32	-1.19	0.25	-3.07	0.48	-3.36	0.77
slop5m			0.27	0.01	-0.12	0.03			0.13	0.04

Table 3- 2: Table of Beta coefficients and standard errors (SE) for relative abundance from the top N-mixture models for 5 ungulate prey species for tigers in Bhutan, based on country-wide remote camera trapping surveys. N-mixture models were best fit using the Poisson count model. Covariates are elevation, forest types at 500m radius (BLF= Broad Leaved Forests, Conifers, MCF=mixed conifer forests, Others= Scree, rocks, water bodies, and snow, Sh& Grass= Shrubs and grasslands) , forest type at 1km radius, slope at 1 and 2 km radius, Hhden = house hold density at 500m, 1km, 2km, 3km, and 4km radius, number of cattle, and number of human per camera stations.

Covariates	Species									
	Muntjac		Wild pig		Sambar		Gaur		Serow	
	β	SE	β	SE	β	SE	β	SE	β	SE
Elevation	-0.20	0.03	-0.16	0.03	-0.63	0.05	-2.0	0.1	0.35	0.08
fortype500mBLF			2.28	0.04			-1.4	0.2	0.56	0.10
fortype500mCornifers			2.92	0.06			-11.7	74.8	0.34	0.19
fortype500mMCF			2.75	0.05			-2.3	0.5	0.27	0.14
fortype500mOthers			2.33	0.13			-10.0	13.1	-1.54	0.52
fortype500mSh&grass			3.63	0.06			-1.8	0.7	-0.42	0.29
fortype1kmBLF	1.77	0.04			0.64	0.06				
fortype1kmCornifers	0.54	0.15			-0.60	0.30				
fortype1kmMCF	0.86	0.09			0.95	0.09				
fortype1kmOthers	-1.66	0.71			-11.00	0.54				
fortype1kmSh&grass	0.06	0.29			-0.30	0.40				
Slop1km					-0.31	0.02				
slop2km	0.22	0.02							0.42	0.06
Hhden500m					-0.22	0.05				
hhden1km			-0.3	0.03						
hhden3km	0.07	0.02								
Hhden4km							-0.22	0.03	-0.21	0.07
cattle	0.06	0.02	0.15	0.01	0.08	0.03	-8.56	0.68	0.16	0.03
human	-0.23	0.04	-0.23	0.04	0.29	0.04	0.28	0.01	0.12	0.08

Table 3- 3: Table of model selection results from the top 5 detection models for tiger (*Panthera tigris*) occupancy based on country-wide remote camera trapping surveys. Covariates are 30-day time periods (e.g., 30c-1), effort, and trail type. (Bhutan, 2014-2015).

Models	nPars	AIC	delta	AICwt	Cum.Wt
p(d30c-1)	14	2345.36	0	5.70E-01	0.57
p(d30c-1+effort)	15	2346.68	1.32	3.00E-01	0.87
p(d30c-1+trail)	18	2349.58	4.21	7.00E-02	0.94
p(d30c-1+effort+trail)	19	2349.93	4.57	5.90E-02	1
p(effort)	3	2386.48	41.12	6.80E-10	1

Table 3- 4: Table of model selection results within 2 delta AIC values for tiger (*Panthera tigris*) occupancy based on country-wide remote camera trapping surveys. Covariates are 1km hhden (house hold density), cattle, gaur, sambar, ele (elevation), and pig (Bhutan, 2014-2015).

Models	nPars	AICc	Delta AICc	AICc Wt	Cum. Wt
p(~d30c - 1 ~hhden1km+cattle+gaur+sambar+ele)	19	2316.25	0	0.22	0.22
p(~d30c - 1 ~hhden1km+human+cattle+gaur+sambar+ele)	20	2316.76	0.51	0.17	0.38
p(~d30c - 1 ~cattle+gaur+sambar+ele)	18	2317.14	0.89	0.14	0.52
p(~d30c - 1 ~hhden1km+cattle+gaur+muntjack+sambar+ele)	20	2317.38	1.13	0.12	0.64
p(~d30c - 1 ~hhden1km+human+cattle+gaur+muntjack+sambar+ele)	19	2317.72	1.47	0.10	0.75
p(~d30c - 1 ~human+cattle+gaur+sambar+ele)	21	2317.86	1.61	0.10	0.84
p(~d30c - 1 ~hhden1km+cattle+gaur+sambar+serow+ele)	20	2318.25	2.00	0.08	0.92
p(~d30c – 1 ~hhden1km+cattle+gaur+pig+sambar+ele)	20	2318.25	2.00	0.08	1.00

Table 3- 5: The table of Beta coefficients and standard errors (SE) and p-values from the top tiger (*Panthera tigris*) occupancy model on country-wide remote camera trapping surveys. Covariates are 1km hhden (house hold density), cattle, gaur, sambar, ele (elevation), and pig (Bhutan, 2014-2015).

Covariates	β	SE	z	P(>|z|)
(Intercept)	-1.10	0.12	-9.21	0.00
hhden1km	-0.26	0.17	-1.54	0.12
human	-0.16	0.14	-1.21	0.23
cattle	0.29	0.13	2.15	0.03
gaur	0.47	0.19	2.43	0.02
sambar	0.53	0.20	2.65	0.01
ele	0.41	0.16	2.52	0.01

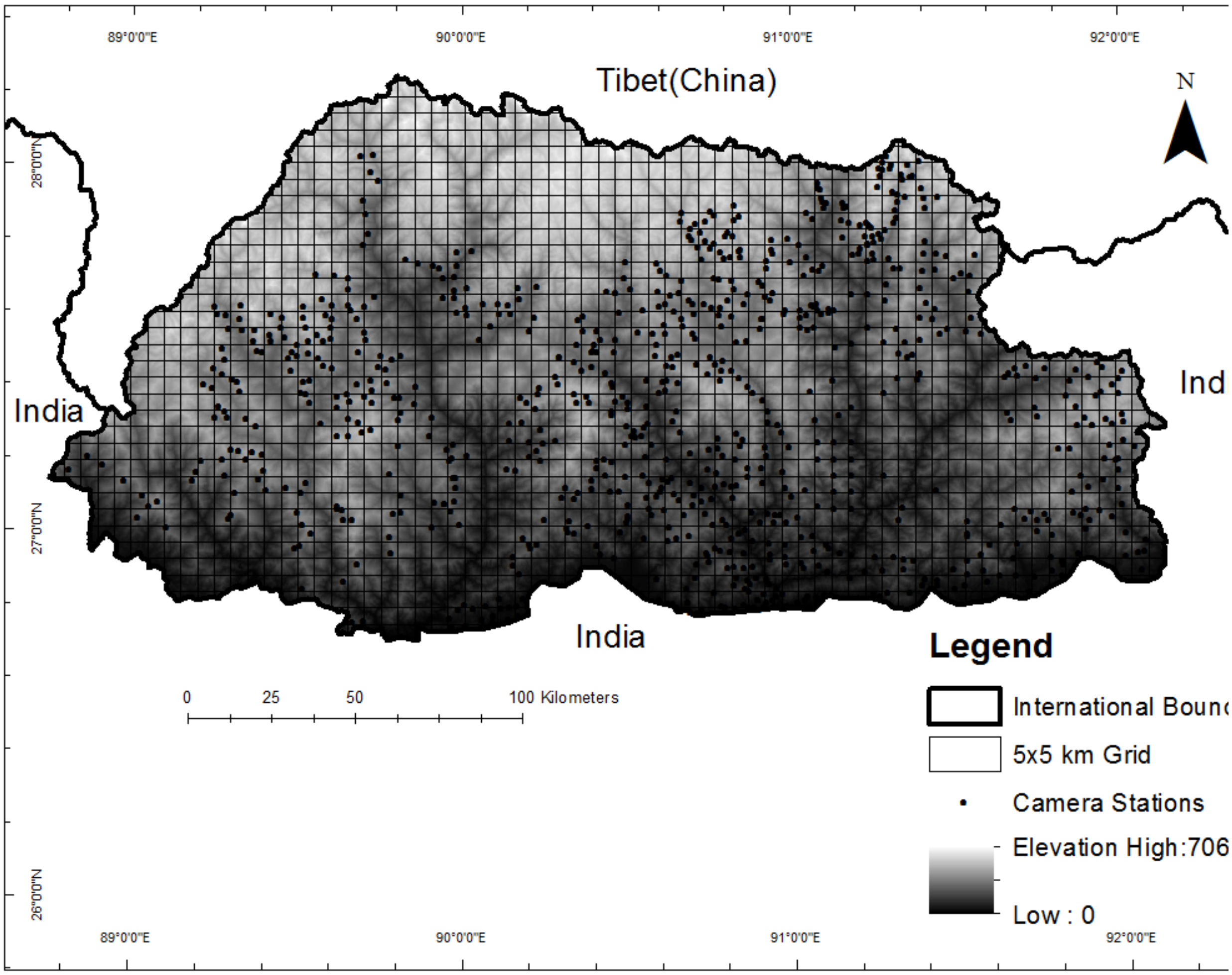


Figure 3-1: Map of Bhutan showing 5x5 km survey grid with human settlement and elevational gradient. Each black dot represents camera station, the darker color of elevation gradient represents low elevation in meters.

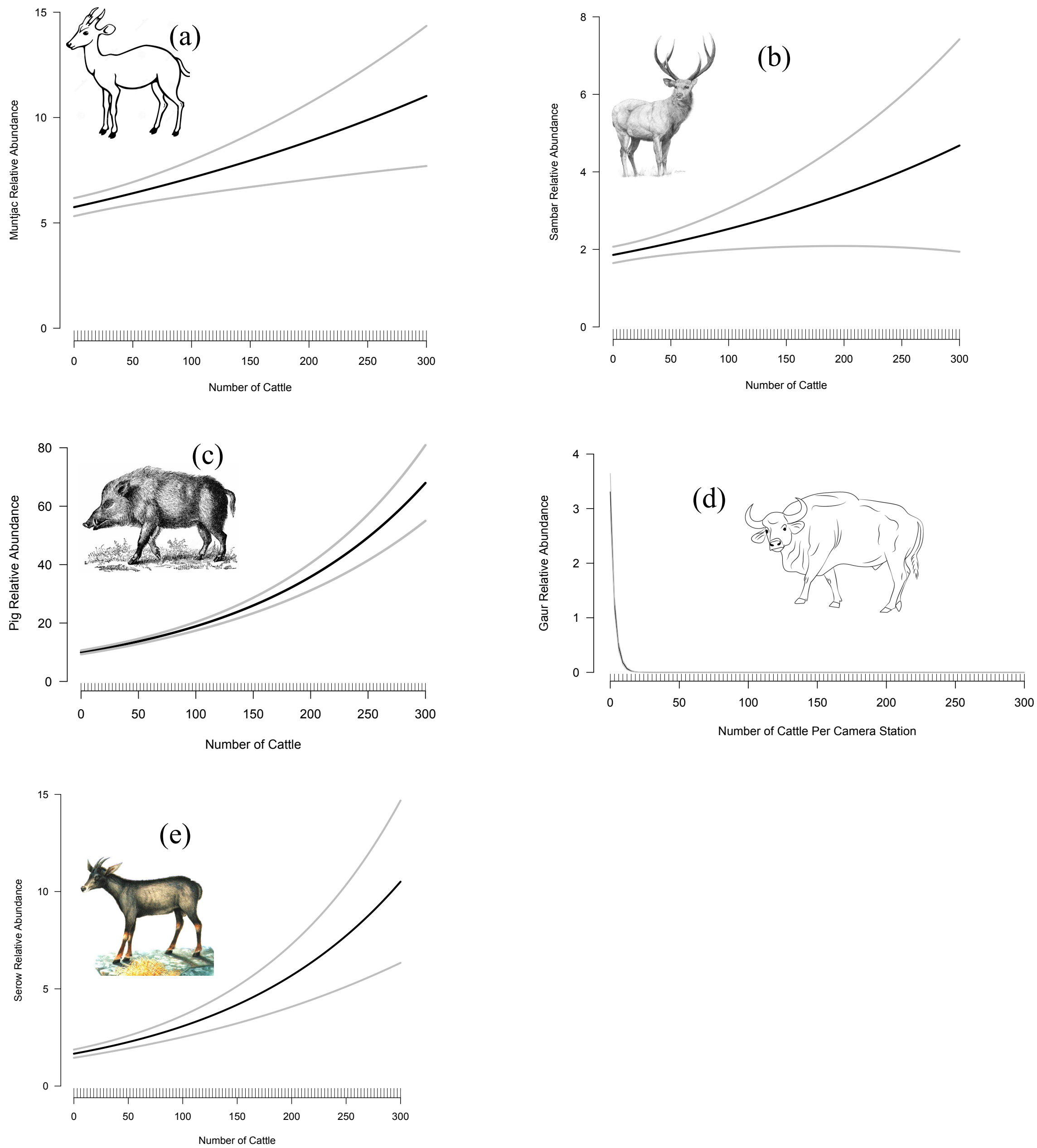


Figure 3-2: Coefficient plots for effects of cattle on the relative abundance of tiger prey species from N-mixture models: (a) Muntjac (*Muntiacus muntjak*), (b) Sambar (*Rusa unicolor*), (c) Wild pig (*Sus scrofa*), (d) Gaur (*Bos gaurus*), and (e) Himalayan serow (*Capricornis thar*) from the best N-mixture models in Bhutan, Years 2014- 2015.

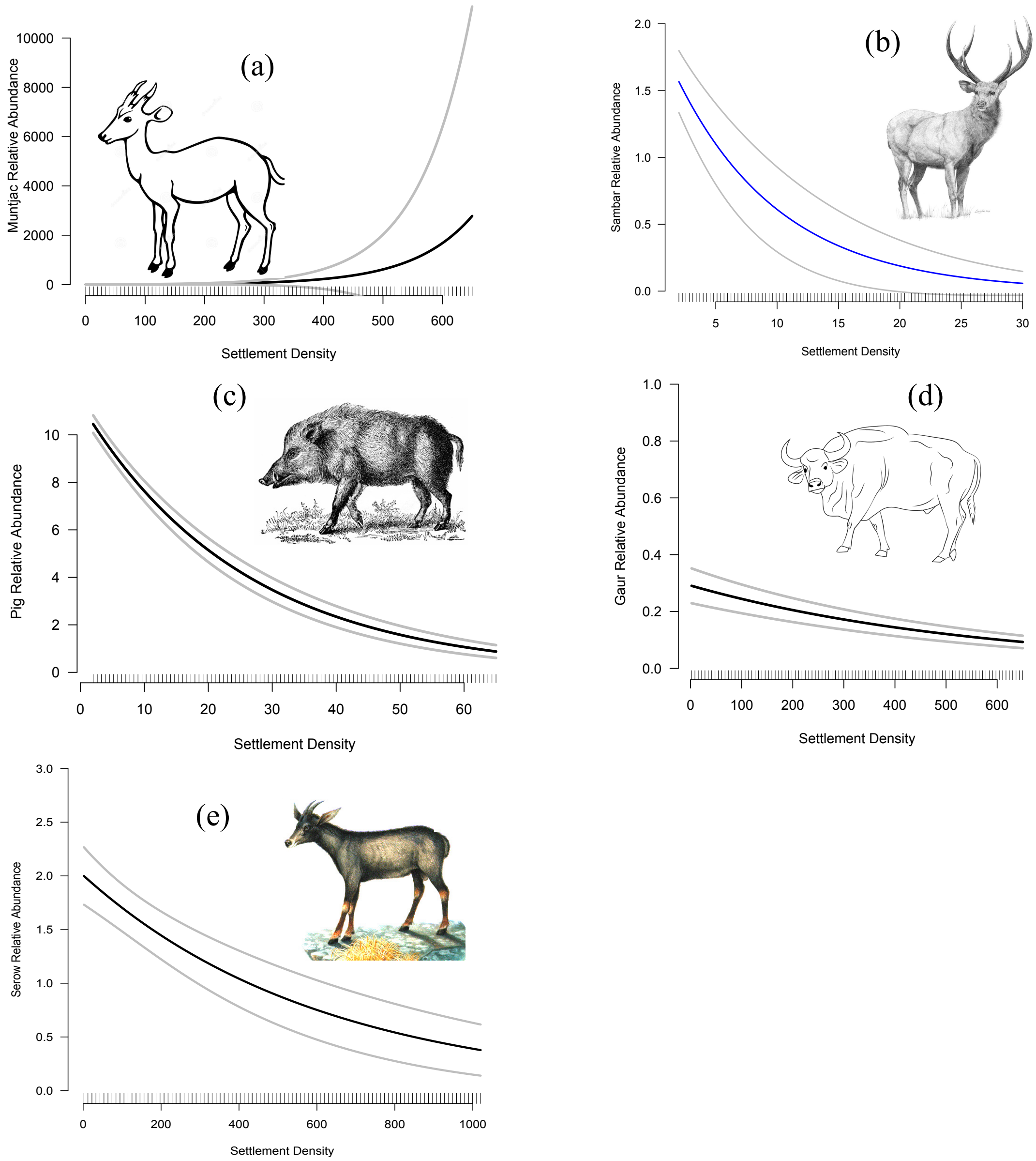


Figure 3- 3: Coefficient plots for effects of the number of houses on the relative abundance of tiger prey species: (a) Muntjac (*Muntiacus muntjak*) at the radius of 3km, (b) Sambar (*Rusa unicolor*) at the radius of 500m, (c) Wild pig (*Sus scrofa*) at 1km, (d) Gaur (*Bos gaurus*) at 4km, and (e) Himalayan serow (*Capricornis thar*) at 4km from the best N-mixture models in Bhutan, Years 2014- 2015. The blue line represents the mean and the gray lines 95% CI.

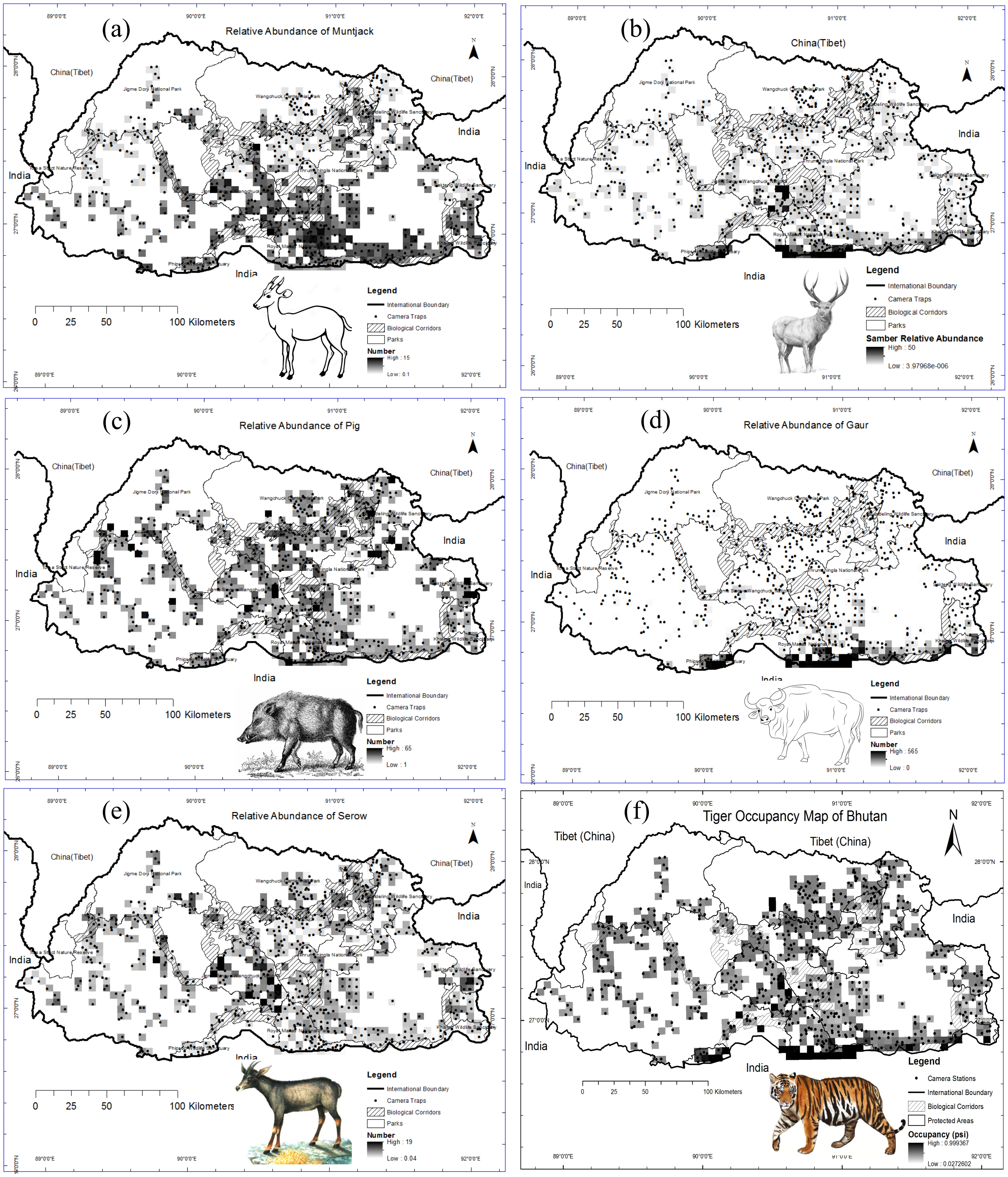


Figure 3- 4: Relative abundance map of tiger prey species: (a) Muntjac (*Muntiacus muntjak*), (b) Sambar (*Rusa unicolor*), (c) Wild pig (*Sus scrofa*), (d) Gaur (*Bos gaurus*), and (e) Himalayan serow (*Capricornis thar*) from the best N-mixture models in Bhutan, Years 2014- 2015. (f) is the

tiger (*Panthera tigris tigris*) occupancy map from the top occupancy model, Years 2014- 2015, Bhutan. The darker colors represent higher relative abundance of the prey species and tiger occupancy (per 25 km^2).

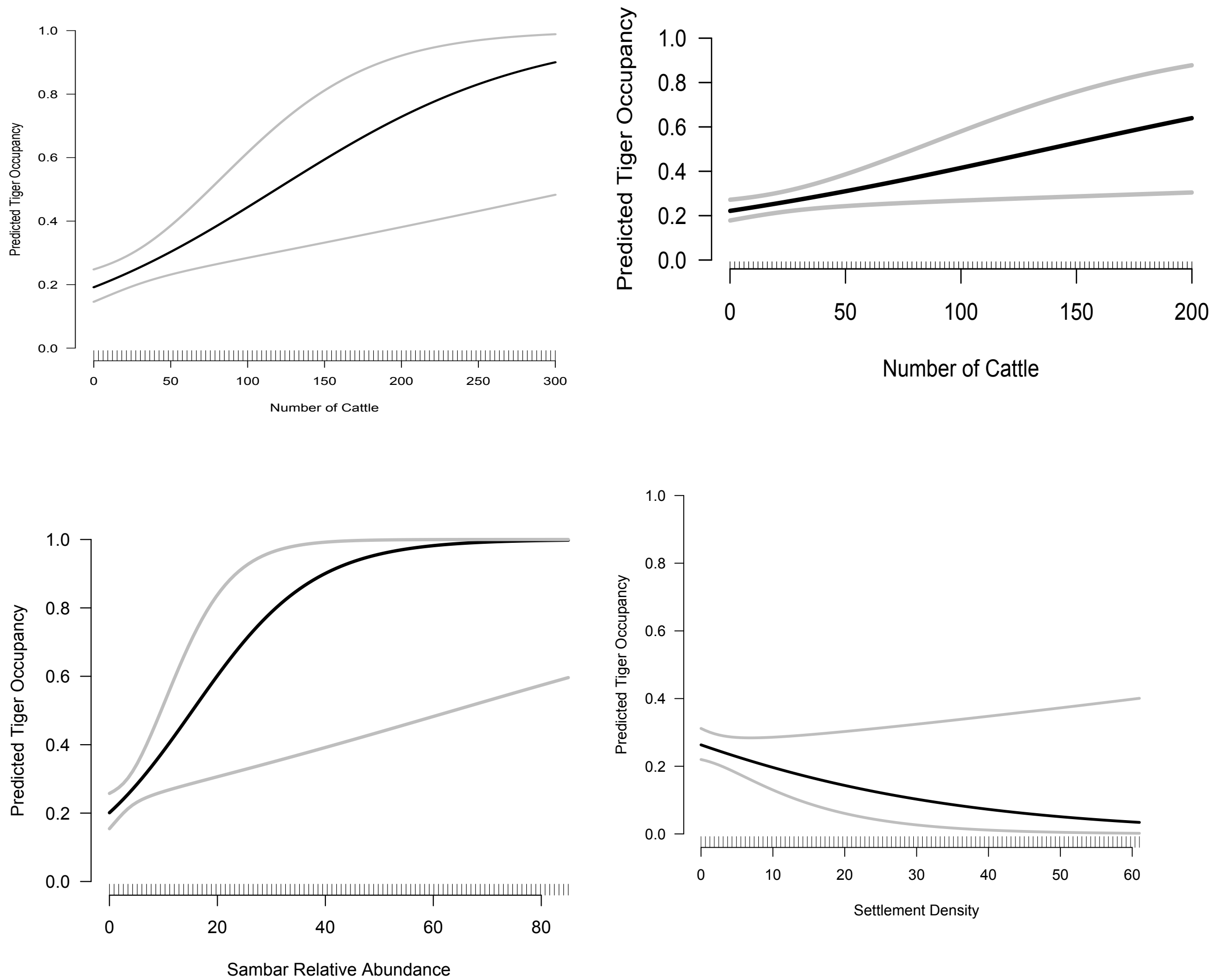


Figure 3- 5: Coefficient plots for Bengal tigers (*Panthera tigris*) from top occupancy models in Bhutan from 2014-2015 showing how tiger occupancy changes as a function of prey relative abundance, as well as human effects.

Appendix 3–A

Appendix 3-Table A1: Table of model selection results for the muntjac (*Muntiacus muntjak*) relative abundance in Bhutan, from the top 4 N-mixture models, based on country-wide remote camera trapping surveys. N-mixture models were best fit using the Poisson count model. Covariates are elevation, forest types at 1km radius (BLF= Broad Leaved Forests, Conifers, MCF=mixed conifer forests, Others= Scree, rocks, water bodies, and snow, Sh& Grass= Shrubs and grasslands), forest type at 1km radius, slope at 2 km radius, hhden = house hold density at 3km radius, number of cattle, and number of human per camera stations.

Models	nPars	AIC	Delta	AICwt	cumWt
(~d30c-1~elev+fortype1km-1+slop2km+hhden3km+cattle)	22	16247.43	0	6.70E-01	0.67
~d30c-1 ~elev+fortype1km-1+slop2km+hhden3km+human+cattle)	23	16249.06	1.63	3.00E-01	0.97
(~d30c-1 ~elev+fortype1km-1+slop2km+hhden3km+human)	22	16254	6.57	2.50E-02	0.99
(~d30c-1~elev+fortype1km-1+slop2km+cattle)	21	16258.01	10.58	3.40E-03	1

Appendix 3–B

Appendix 3-Table B1: Table of model selection results for the wild pig (*Sus scrofa*) relative abundance in Bhutan, from the top 5 N-mixture models, based on country-wide remote camera trapping surveys, Bhutan, 2014-2015. N-mixture models were best fit using the Poisson count model. Covariates are elevation, forest types at 500m radius (BLF= Broad Leaved Forests, Conifers, MCF=mixed conifer forests, Others= Scree, rocks, water bodies, and snow, Sh& Grass= Shrubs and grasslands), forest type at 1km radius, slope at 2 km radius, hhden = house hold density at 1km radius, and number of cattle per camera stations.

Model	nPars	AIC	Delta	AICwt	cumltvWt
(~d30c-1+trailtype-1+slop5m ~ elev+fortype500m-1+hhden1km+human+cattle)	27	33247.7	0	7.10E-01	0.71
(~d30c-1+trailtype-1+slop5m ~ elev+fortype500m-1+slop500m+hhden1km+human+cattle)	28	33249.47	1.77	2.90E-01	1
(~d30c-1+trailtype-1+slop5m ~ fortype500m-1+slop500m+hhden1km+human+cattle)	27	33276.75	29.05	3.50E-07	1
(~d30c-1+trailtype-1+slop5m~ fortype500m-1+hhden1km+human+cattle)	26	33278.91	31.21	1.20E-07	1
(~d30c-1+trailtype-1+slop5m ~elev+fortype500m-1+hhden1km+cattle)	26	33291.15	43.46	2.60E-10	1

Appendix 3–C

Appendix 3—Table C1: Table of model selection results for the Sambar (*Rusa unicolor*) relative abundance in Bhutan, from the top 5 N-mixture models, based on country-wide remote camera trapping surveys, Bhutan, 2014-2015. N-mixture models were best fit using the Poisson count model. Covariates are elevation, forest types at 500m radius (BLF= Broad Leaved Forests, Conifers, MCF=mixed conifer forests, Others= Scree, rocks, water bodies, and snow, Sh& Grass= Shrubs and grasslands), forest type at 1km radius, slope at 2 km radius, hhden = house hold density at 1km radius, and number of cattle per camera stations.

Model	nPars	AIC	Delta	AICwt	cumltvWt
(~d30c-1+trailtype-1+slop5m ~elev+fortype1km-1+slop1km+hhden500m+human+cattle)	28	11231.58	0	9.10E-01	0.91
(~d30c-1+trailtype-1+slop5m ~elev+fortype1km-1+slop1km+hhden500m+human)	27	11236.2	4.61	9.10E-02	1
(~d30c-1+trailtype-1+slop5m ~elev+fortype1km-1+slop1km+human+cattle)	27	11260.45	28.87	4.90E-07	1
(~d30c-1+trailtype-1+slop5m ~elev+fortype1km-1+slop1km+human)	26	11264.74	33.15	5.80E-08	1
(~d30c-1+trailtype-1+slop5m ~elev+fortype1km-1+slop1km+hhden500m+cattle)	27	11284.98	53.4	2.30E-12	1

Appendix 3–D

Appendix 3–D Table D1: Table of model selection results for the Gaur (*Bos Gaurus*) relative abundance in Bhutan, from the top 5 N-mixture models, based on country-wide remote camera trapping surveys, Bhutan, 2014-2015. N-mixture models were best fit using the Poisson count model. Covariates are elevation, forest types at 500m radius (BLF= Broad Leaved Forests, Conifers, MCF=mixed conifer forests, Others= Scree, rocks, water bodies, and snow, Sh& Grass= Shrubs and grasslands), forest type at 1km radius, slope at 2 km radius, hhden = house hold density at 4km radius, and number of cattle per camera stations.

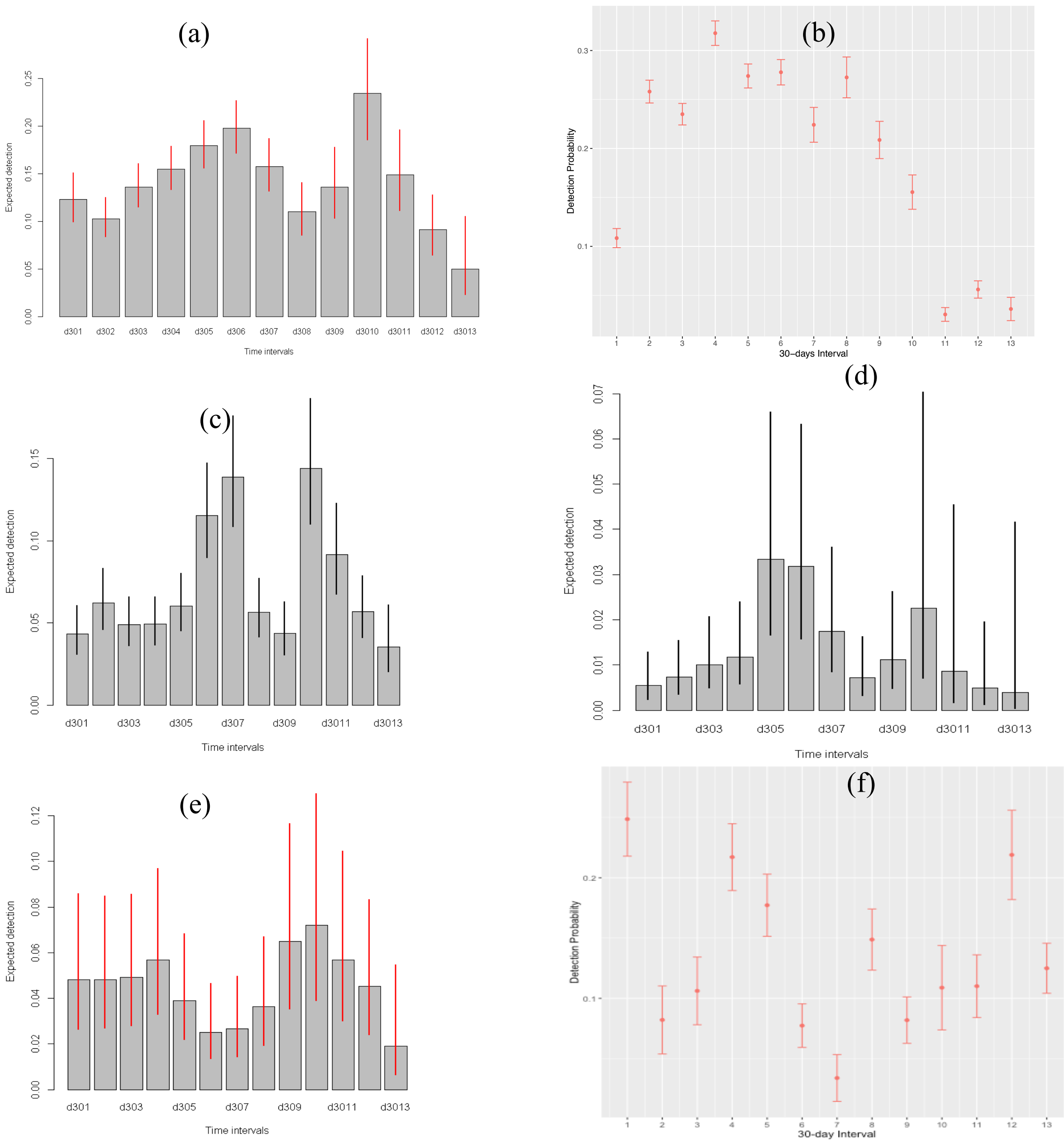
Model	nPars	AIC	Delta	AICwt	cumltvWt
(~d30c-1+trailtype-1 ~ elev+fortype500m-1+hhden4km+human+cattle)	26	17818.48	0	1.00E+00	1
(~d30c-1+trailtype-1 ~ elev+fortype500m-1+slop1km+hhden4km+human+cattle)	27	17864.6	46.12	9.70E-11	1
(~d30c-1+trailtype-1 ~ elev+slop1km+hhden4km+human+cattle)	23	17864.88	46.4	8.40E-11	1
(~d30c-1+trailtype-1 ~ elev+fortype500m-1+human+cattle)	25	17872.9	54.42	1.50E-12	1
(~d30c-1+trailtype-1 ~ elev+human+cattle)	21	17882.76	64.28	1.10E-14	1

Appendix 3–E

Appendix 3-E Table E1: Table of model selection results for the Himalayan serow (*Capricornis thar*) relative abundance in Bhutan, from the top 5 N-mixture models, based on country-wide remote camera trapping surveys, Bhutan, 2014-2015. N-mixture models were best fit using the Poisson count model. Covariates are elevation, forest types at 500m radius (BLF= Broad Leaved Forests, Conifers, MCF=mixed conifer forests, Others= Scree, rocks, water bodies, and snow, Sh& Grass= Shrubs and grasslands) , forest type at 1km radius, slope at 2 km radius, hhden = house hold density at 4km radius, and number of cattle and human per camera stations.

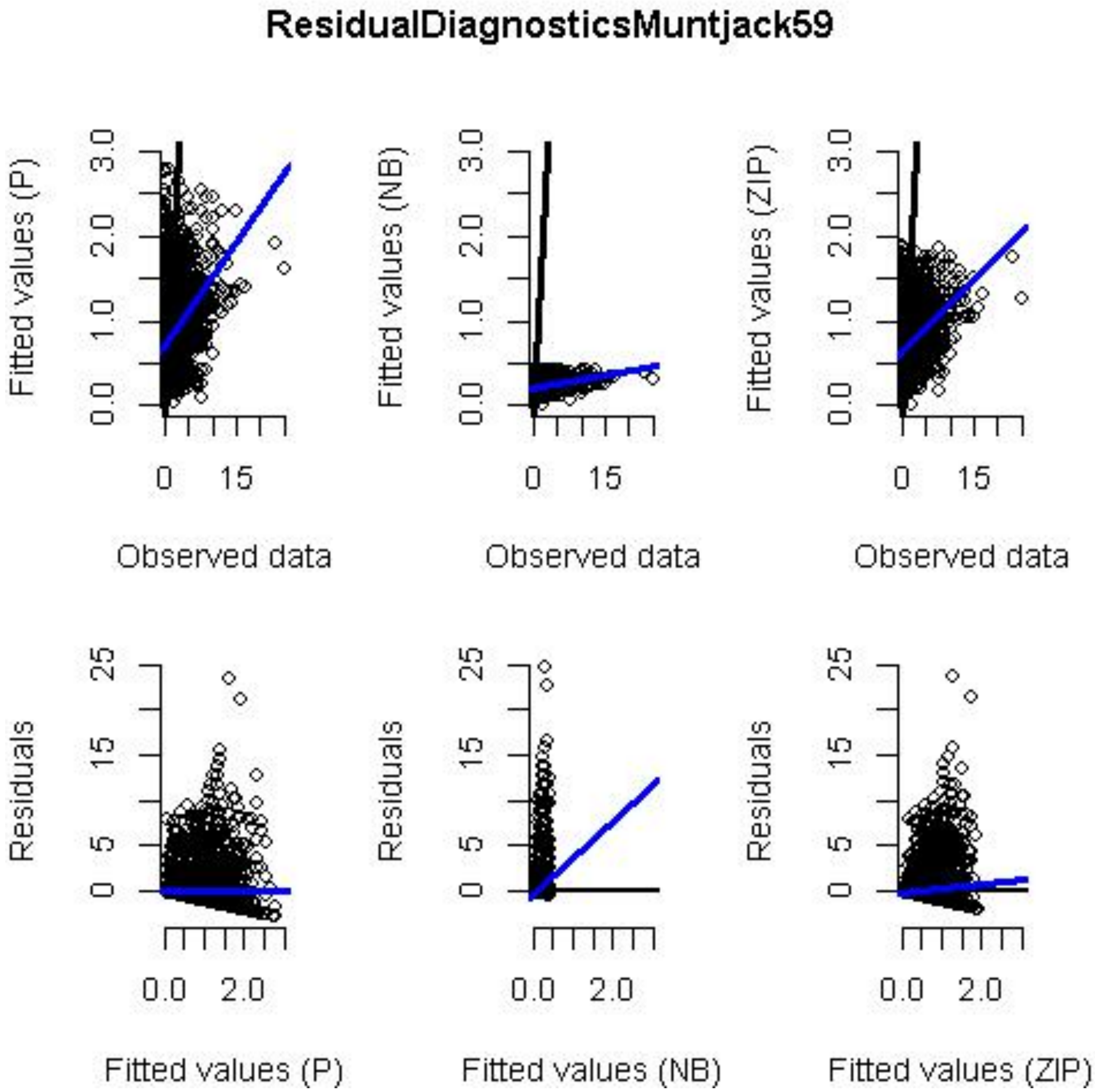
Model	nPars	AIC	Delta	AICwt	cumltvWt
(~d30c-1+trailtype+slop5m ~ elev+fortype500m-1+slop2km+hhden4km+human+cattle)	28	4778.17	0	5.00E-01	0.5
(~d30c-1+trailtype-1+slop5m ~ elev+fortype500m-1+slop2km+hhden4km+cattle)	27	4778.23	0.062	4.90E-01	0.99
(~d30c-1+trailtype-1+slop5m ~ elev+fortype500m-1+slop2km+cattle)	26	4787.69	9.523	4.30E-03	1
(~d30c-1+trailtype-1+slop5m ~ elev+fortype500m-1+slop2km+human+cattle)	27	4787.92	9.756	3.80E-03	1
(~d30c-1+trailtype-1+slop5m ~ fortype500m-1+slop2km+hhden4km+human+cattle)	27	4797.84	19.673	2.70E-05	1

Appendix 3–F

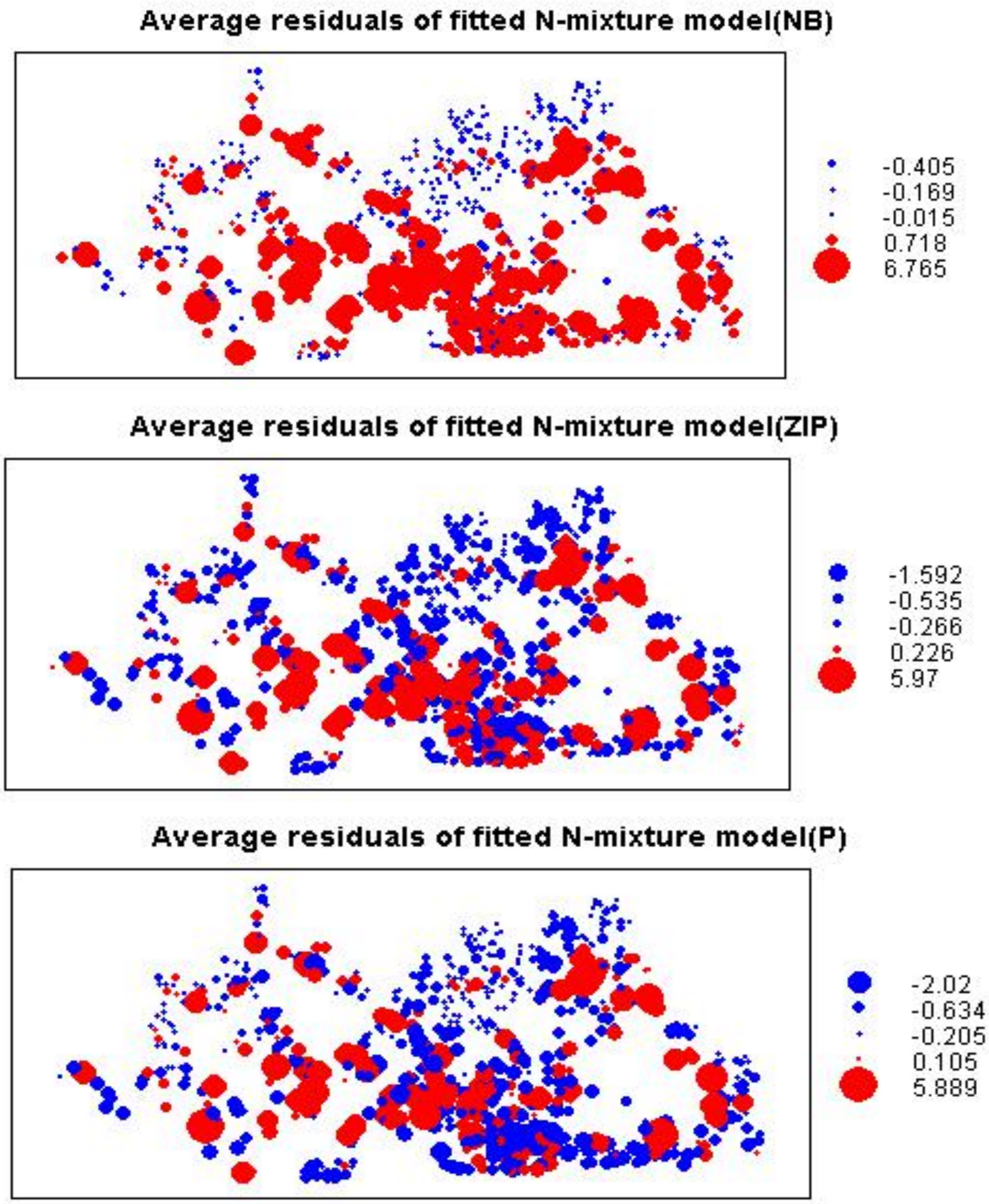


Appendix 3–F Figure F1: Expected detection probability against 30 days time interval: (a) Muntjac (*Muntiacus muntjak*), (b) Sambar (*Rusa unicolor*), (c) Wild pig (*Sus scrofa*), (d) Gaur (*Bos gaurus*), and (e) Himalayan serow (*Capricornis thar*) from the best N-mixture models in Bhutan, Years 2014- 2015. (f) is the detection probability for tiger (*Panthera tigris tigris*) from occupancy model.

Appendix 3–G

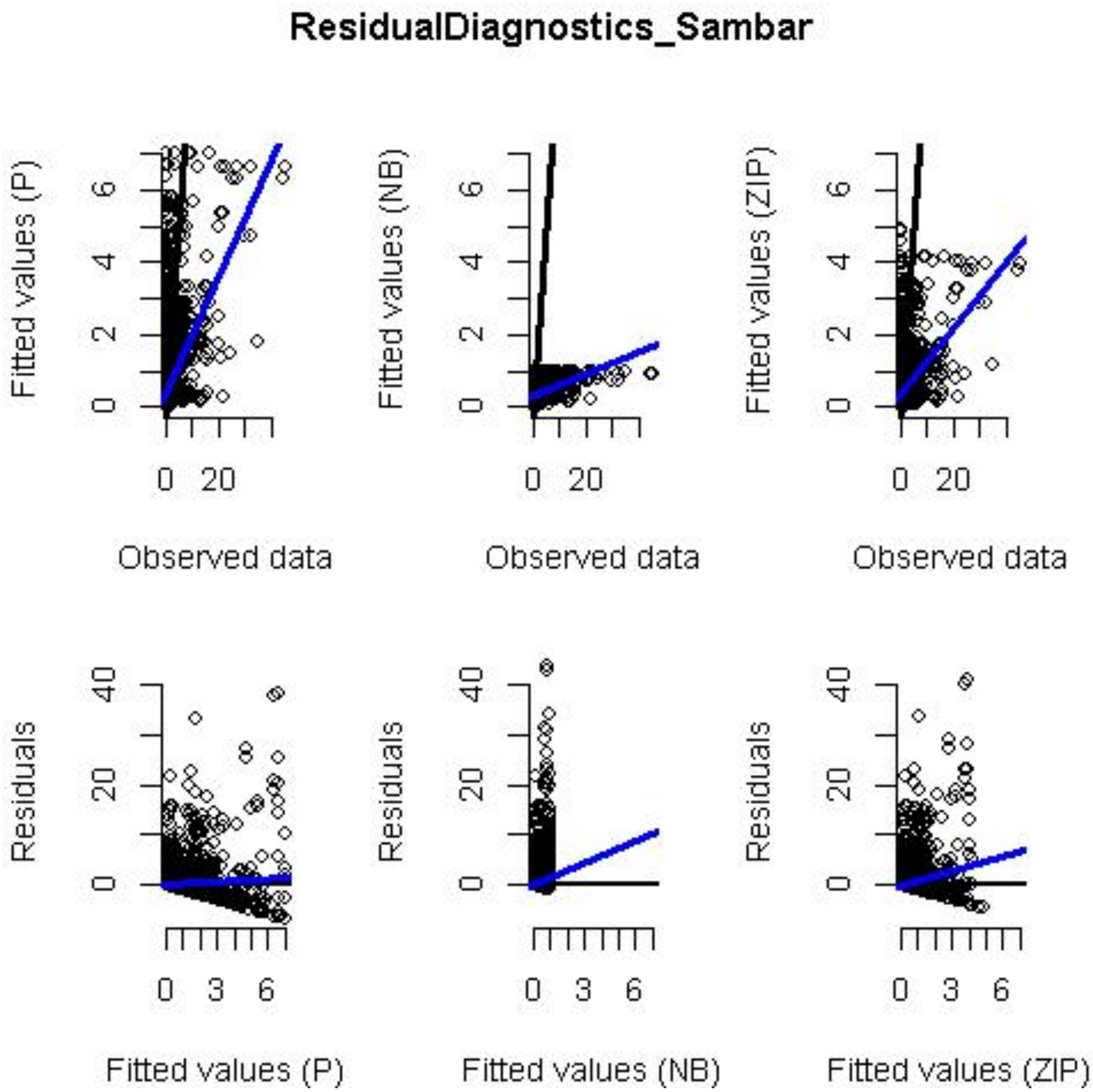


Appendix 3–G Figure G1: Residual diagnostics for the three N-mixture models fitted to the 2014-2015 muntjac counts. Top: Fitted values (1⁄4 expected data) versus observed counts; the black line shows a 1:1 relationship and the blue line is the linear regression line of best fit. Bottom: Residuals versus fitted values (black line denotes a zero residual and the blue line is the linear regression line).

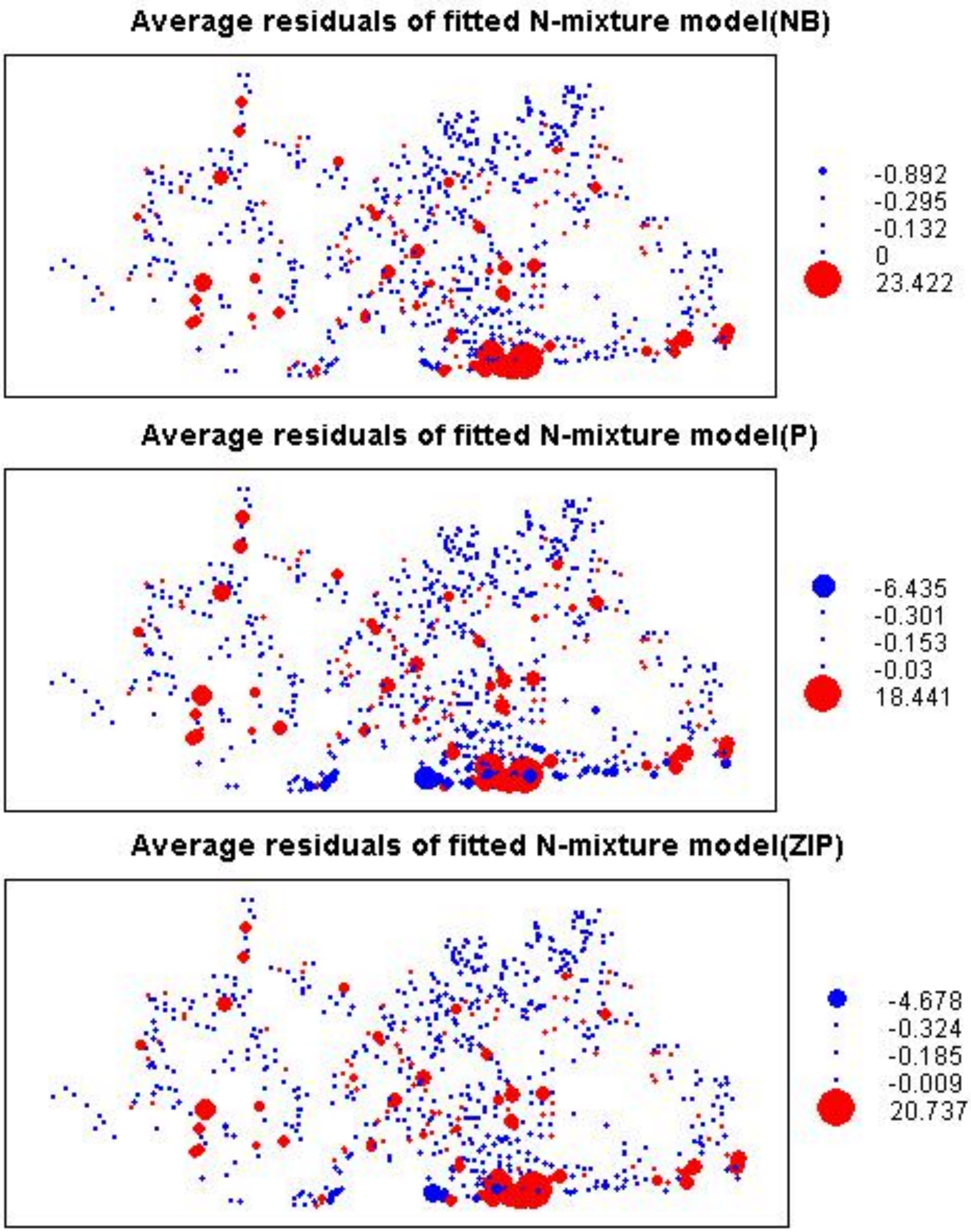


Appendix 3–Figure G2: Maps of the residuals (averaged over replicate surveys) under the AIC-best Poisson, NB, and ZIP N-mixture models for muntjac in 2014-2015

Appendix 3–H

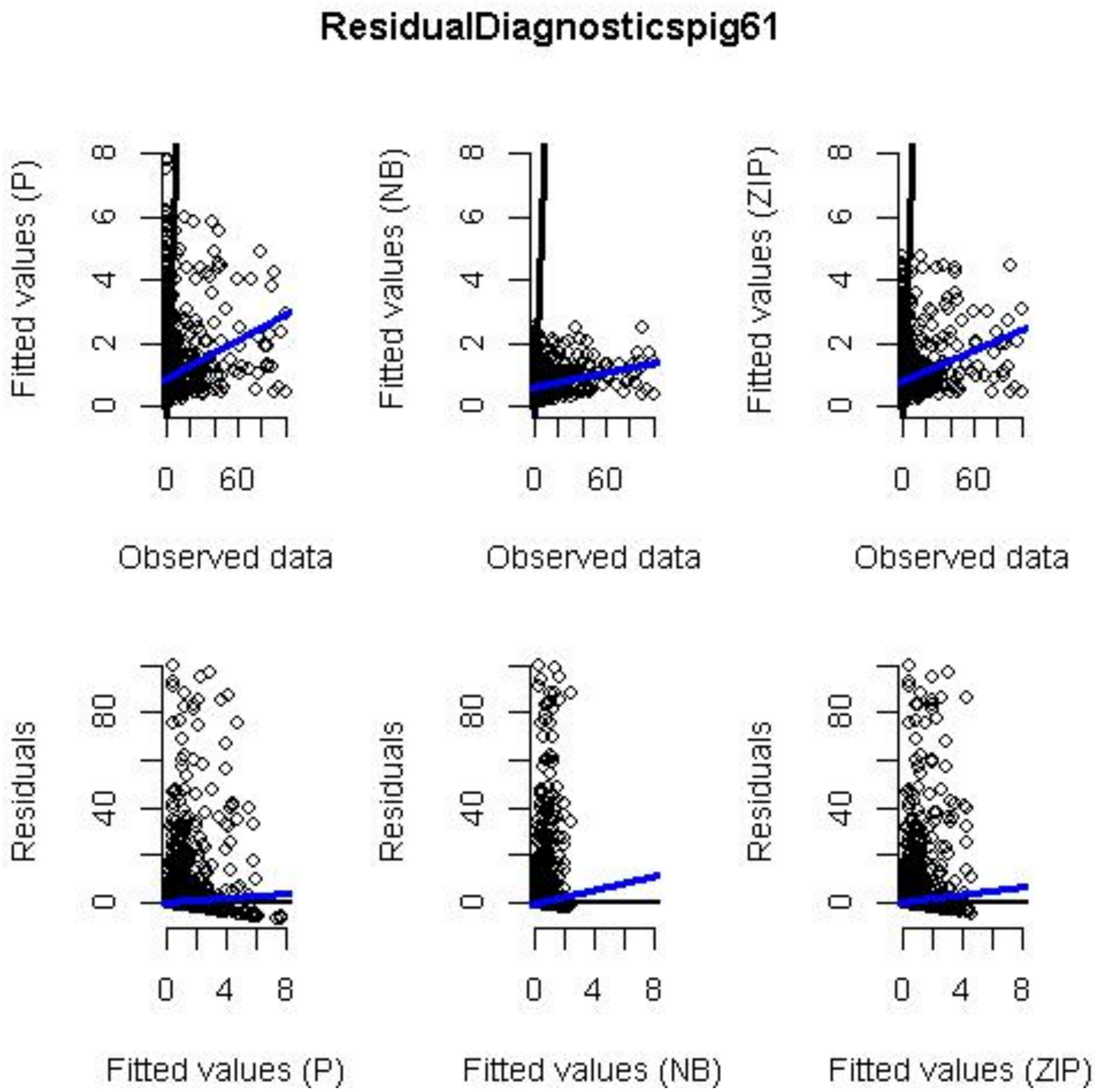


Appendix 3–H Figure H1: Residual diagnostics for the three N-mixture models fitted to the 2014-2015 sambar counts. Top: Fitted values (1⁄4 expected data) versus observed counts; the black line shows a 1:1 relationship and the blue line is the linear regression line of best fit. Bottom: Residuals versus fitted values (black line denotes a zero residual and the blue line is the linear regression line).

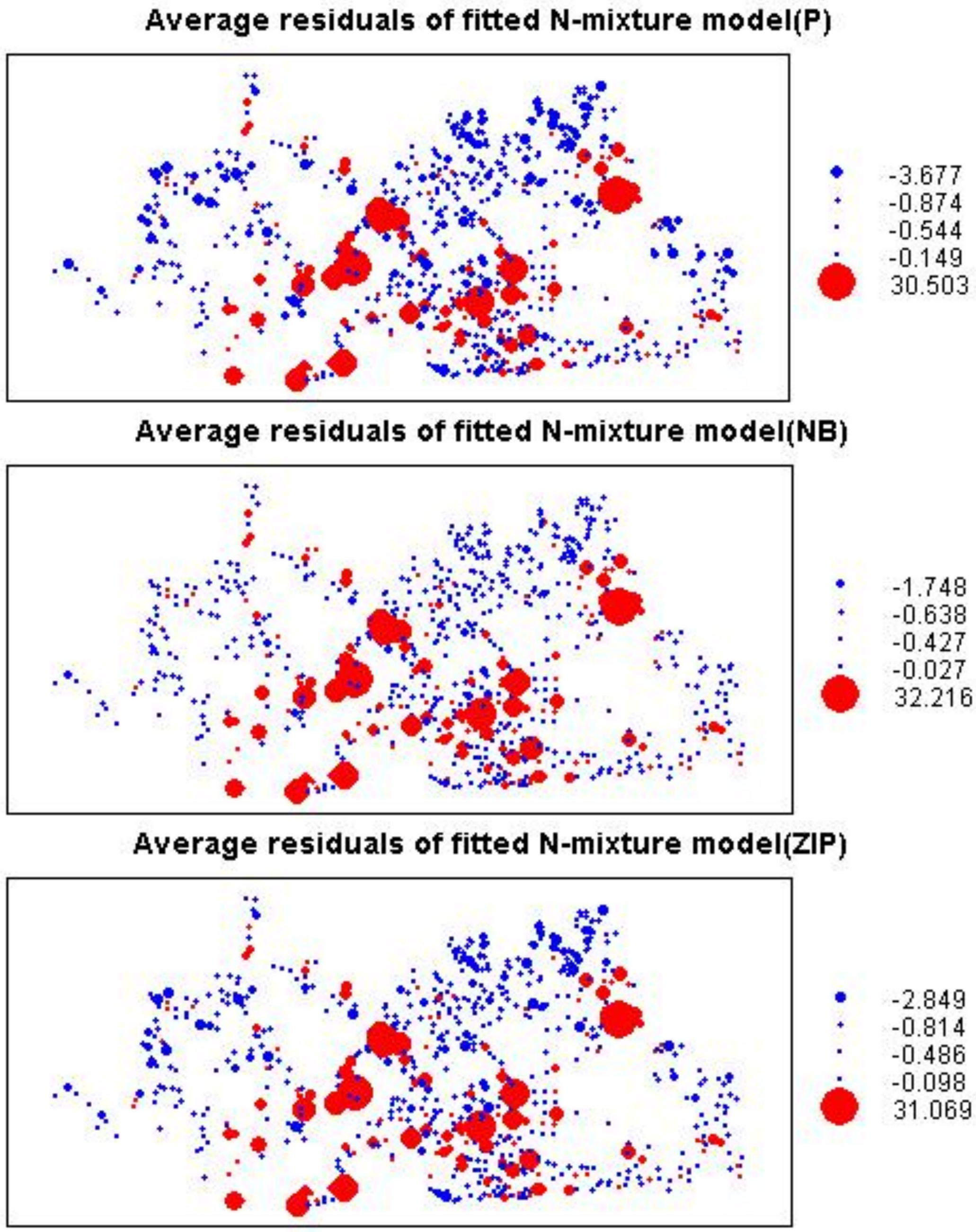


Appendix 3–H Figure H2: Maps of the residuals (averaged over replicate surveys) under the AIC-best Poisson, NB, and ZIP N-mixture models for sambar in 2014-2015.

Appendix 3–I

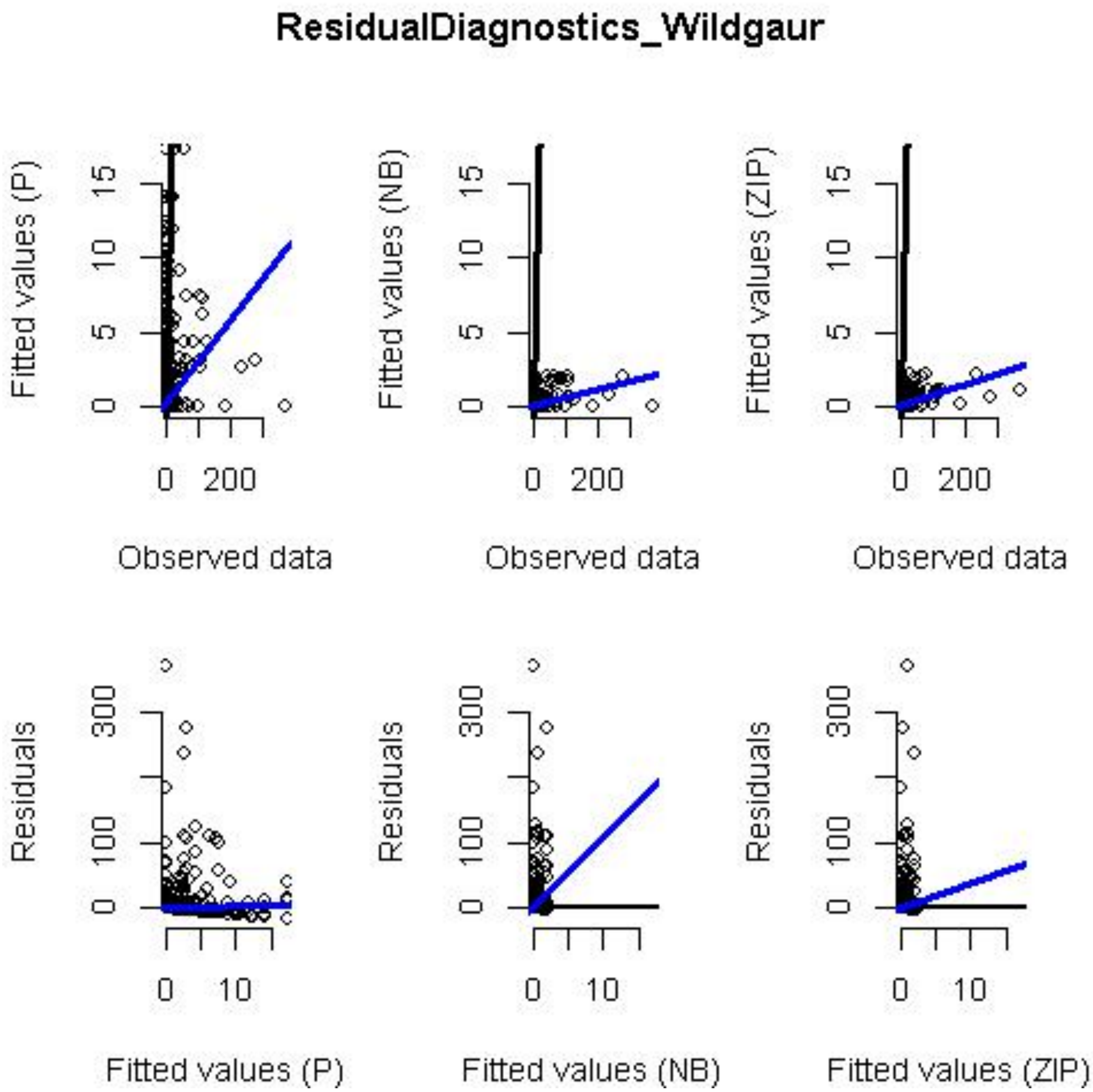


Appendix 3–I Figure I1: Residual diagnostics for the three N-mixture models fitted to the 2014-2015 wild pig counts. Top: Fitted values (1⁄4 expected data) versus observed counts; the black line shows a 1:1 relationship and the blue line is the linear regression line of best fit. Bottom: Residuals versus fitted values (black line denotes a zero residual and the blue line is the linear regression line).

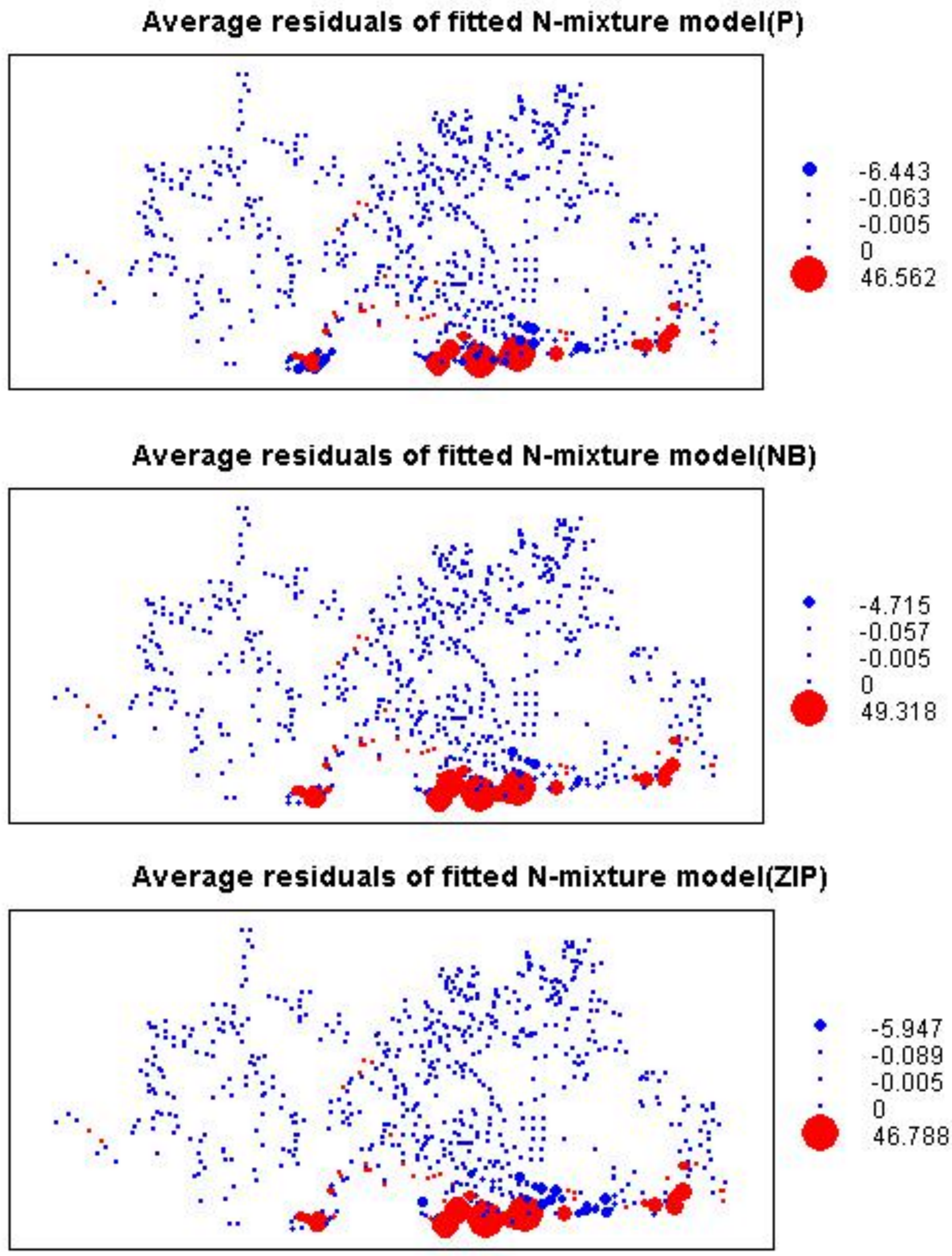


Appendix 3–I Figure I2: Maps of the residuals (averaged over replicate surveys) under the AIC-best Poisson, NB, and ZIP N-mixture models for wild pig in 2014-2015

Appendix 3–J

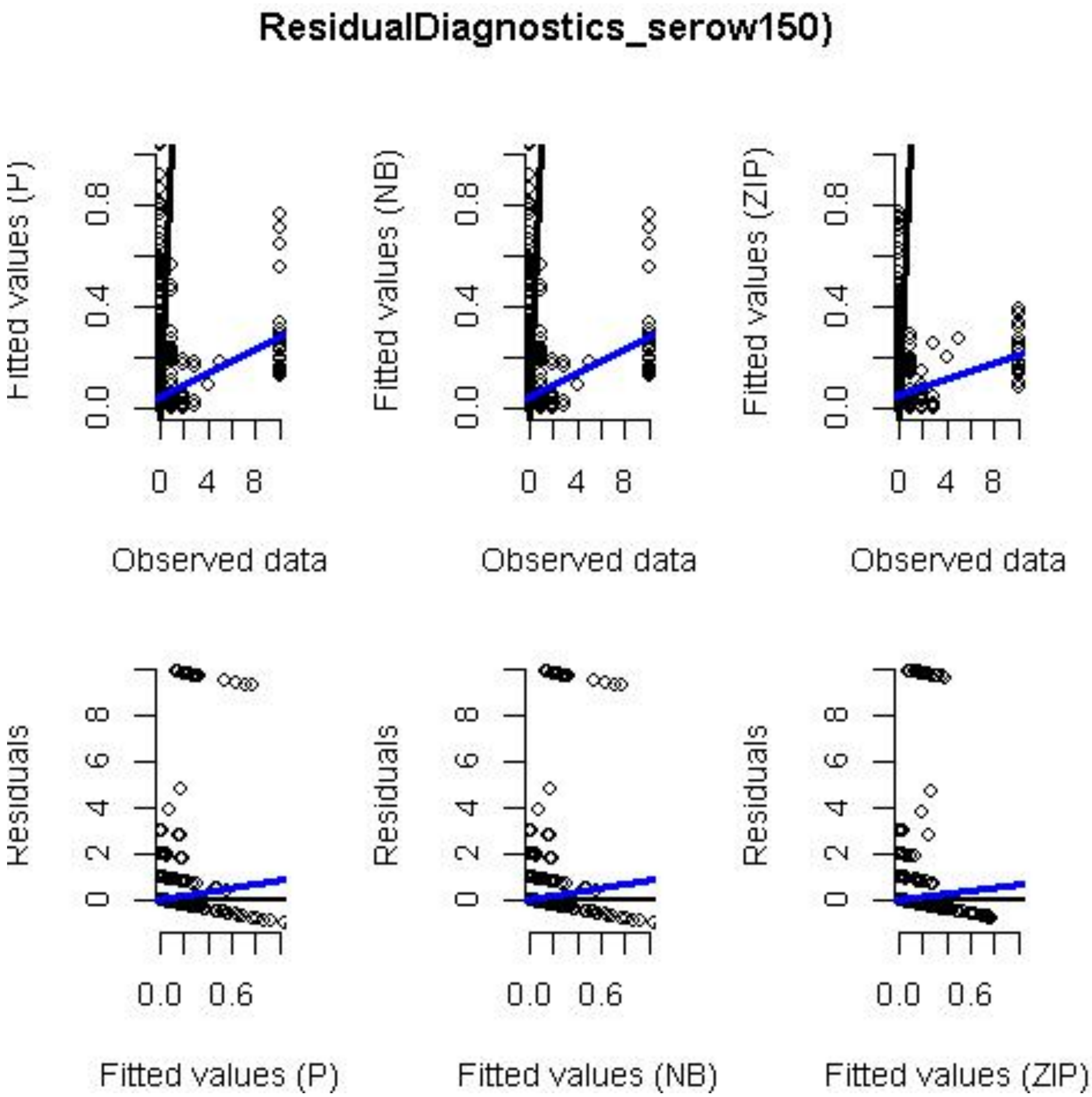


Appendix 3–J Figure J1: Residual diagnostics for the three N-mixture models fitted to the 2014-2015 gaur counts. Top: Fitted values (1⁄4 expected data) versus observed counts; the black line shows a 1:1 relationship and the blue line is the linear regression line of best fit. Bottom: Residuals versus fitted values (black line denotes a zero residual and the blue line is the linear regression line).

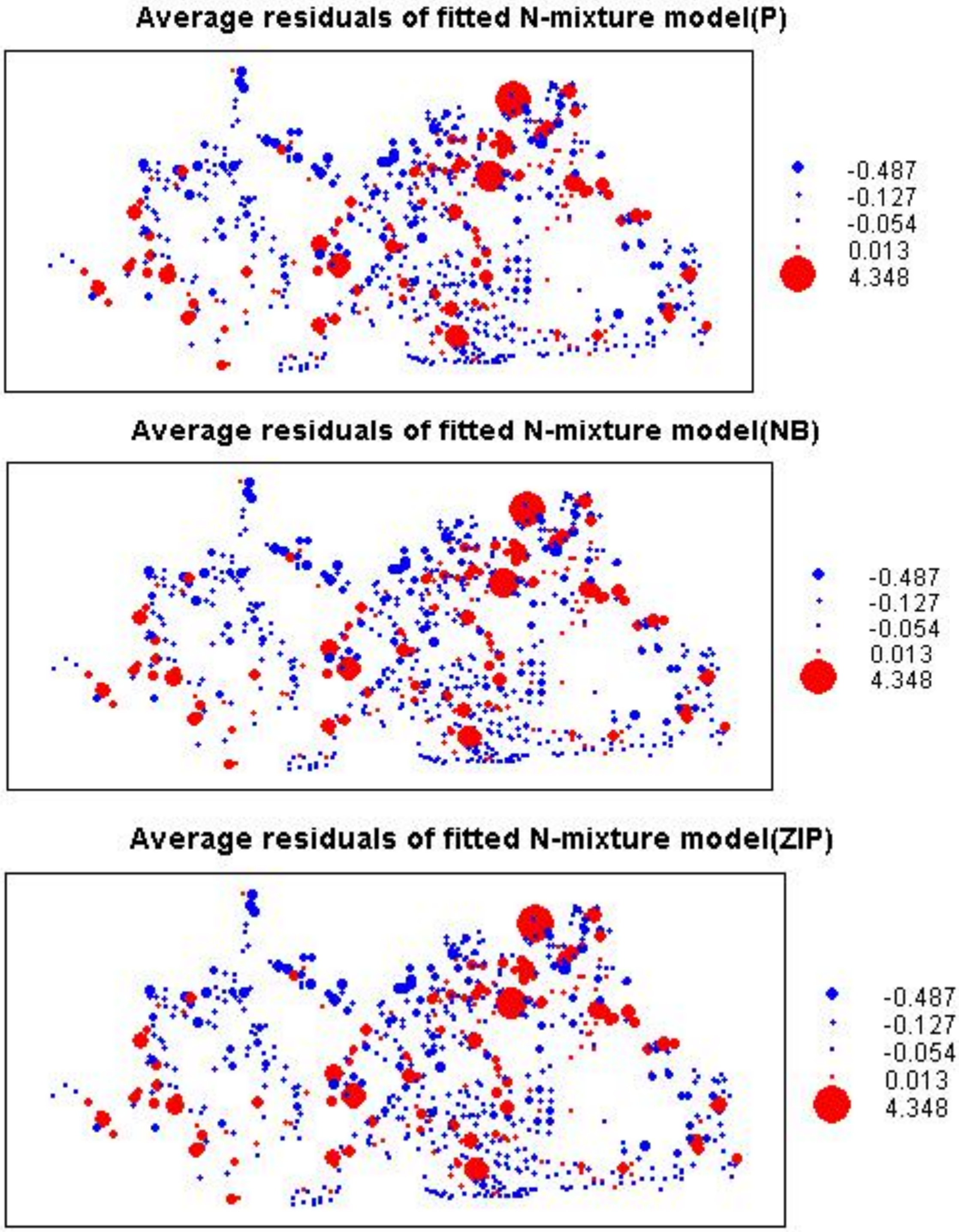


Appendix 3–J Figure J2: Maps of the residuals (averaged over replicate surveys) under the AIC-best Poisson, NB, and ZIP N-mixture models for gaur in 2014-2015.

Appendix 3–K

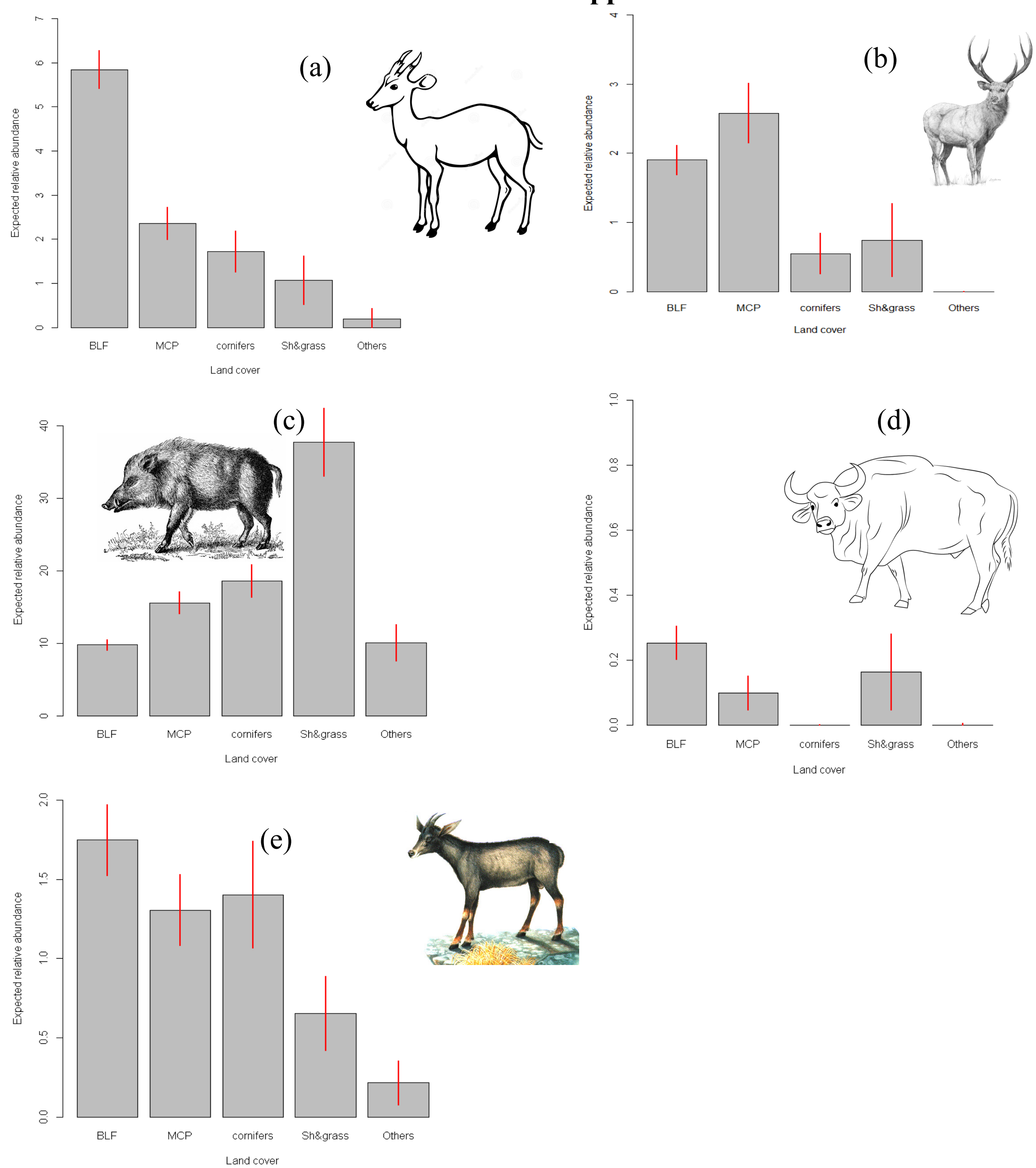


Appendix 3–K Figure K1: Residual diagnostics for the three N-mixture models fitted to the 2014-2015 serow counts. Top: Fitted values (1⁄4 expected data) versus observed counts; the black line shows a 1:1 relationship and the blue line is the linear regression line of best fit. Bottom: Residuals versus fitted values (black line denotes a zero residual and the blue line is the linear regression line).



Appendix 3–K Figure K2: Maps of the residuals (averaged over replicate surveys) under the AIC-best Poisson, NB, and ZIP N-mixture models for serow in 2014-2015.

Appendix 3–L



Appendix 3–L Figure L1: Expected relative abundance of tiger prey species in different forest types : (a) Muntjac (Muntiacus muntjak), (b) Sambar (Rusa unicolor), (c) Wild pig (Sus scrofa), (d) Gaur (Bos gaurus), and (e) Himalayan serow (Capricornis thar) from the best N-mixture models in Bhutan, Years 2014–2015. BFL =broad leaved forest, MCP= mixed conifer forests, sh&grass= grassland, alpine meadows and shrubs, and others=water bodies, rock outcrops, scree, and barren lands.

Chapter 4: Securing the Future of Tigers in the Bhutan Himalayas: A Way Forward

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INTRODUCTION

As one of the most iconic species in the world, the tiger (*Panthera tigris*) continues to fire our imagination and ignite our reverence for the wild (Schaller, 1967, Seidensticker 1996, Nyhus and Tilson 2010). It remains as one of the great symbols of conservation in the 21st Century (Seidensticker 2010). Notwithstanding its charisma and despite the concerted conservation action at both the national and international level, tiger populations continue to plummet in the wild with only about 3200 individuals remaining (Dinnerstein et.al 2007). Having undergone one of the most dramatic range collapses any species have ever witnessed in the last century, habitat loss, prey depletion and direct poaching are the greatest threat to tiger persistence today (Karanth and Gopal 2005, Seidensticker 2010, Goodrich et al. 2015).

Since the enlistment of tiger as an IUCN endangered species in 1969, conservation agencies and governments have rallied around the call to protect and secure the remaining tigers in the wild (Nyhus and Tilson 2010, GTI 2010). Some of the greatest conservation initiatives for tigers was the “Project Tiger” in India (Johnsingh and Goyal, 2015) that resulted in the establishment of many tiger reserves. Todays these areas are the some of the strong holds for Bengal tiger (*P. t. tigris*) conservation in the region (Karanth et.al 2004). New parks and protected areas are continuing to be created in China (Wang 2016). Yet, these areas are increasingly becoming islands of habitat in a sea of humanity, so that focusing solely on protected areas may not be viable for the long-term persistence of the species. To, better allocate limited conservation funding, some conservationists have proposed adopting a triage approach of focusing on the most promising parks and tiger reserves as “source sites” (Karanth et al. 2010a, Walston et al. 2010b). Waltson et al. (2010) identified 42 tiger “source sites” (only 6% of the current tiger habitat) thought to contain 70% of the current tiger population and argued that resources and effort should be directed towards these 42 source sites rather than thinly spreading across to all tiger conservation landscapes. Others have proposed a landscape level approach in the priority Tiger Conservation Landscapes (TCLs) not limited to small patches of “sources sites” (Wikramnayake 2010). According to Sanderson et al. (2010), a Tiger Conservation Landscape (TCL) is a defined as “block of potential effective habitat within 4km of each other, meeting a minimum, habitat-specific size threshold, where tigers haven been confirmed to occur during the last 10 years and are not known to have been extirpated since the last observation”. Of the 75 TCLs spread across all 13 tiger range countries, 20 has been identified as priority TLCs. Depending on which strategy is adopted, funding agencies may decide to allocate funding only to tiger sources site or TCL’s.

Irrespective of these debates around prioritizing of tiger source sites versus a landscape-level approach, Bhutan is thought to harbor approximately 90 tigers (about 3% of the worlds tiger population) (Chapter 2). This number suggests that Bhutan may indeed be a source site for tigers in the wider Himalayan-Indian Manas complex (Chapter 2). Bhutan is also part of Northern Forest Complex - Namdhapha -Royal Manas (NFC-N-RM) tiger conservation landscape, the largest tiger conservation landscape outside of Russian far-east (Sanderson et al., 2010). In addition to potentially harboring significant tiger populations of its own, Bhutan may also be important in connecting the Terai Arc grassland of India and Nepal TCL's to other TCLs in the Northeast India and indeed to the Indochinese tiger (*P. t. corbetti)* in Southeast Asia along the foothills of Himalaya (Sharma et al. 2011). Connectivity along the Indian side has largely been severed by dense settlement and agriculture, but most of the forest in the Bhutan and NFC-N-RM is still intact and in many parts pristine, possibly providing safe corridors for tigers to disperse and move among these TLCs (Sharma et al. 2011). Thus, Bhutan may form the critical linkage for connectivity and gene flow between Bengal tiger populations in the Indian subcontinent with Indochinese tigers.

Recent camera trap evidence demonstrates that tigers in Bhutan successfully breed and inhabit areas from sea-level to over 4000 m (Plate 1 and Plate 2) (Jigme and Tharchen, 2011; Vernes and Rajaratnam, 2012). Well forested landscapes with adequate prey species, coupled with Bhutanese-Buddhist culture, have enabled tigers to freely inhabit these mountain habitats (Chapter 2 and chapter 3). While a network of protected areas connected by biological corridors ensures the availability of such forested habitats into perpetuity, threats for conservation are nevertheless looming. Bhutanese society is undergoing rapid changes as Bhutan has become a constitutional democracy with increasing economic development. Forests are increasingly being cleared for roads, hydroelectric dams, power transmission lines, mines and commercial logging. Over the last 5 years alone, 3 mega hydro-power dams were constructed in prime tiger habitat in Bhutan with growing evidence of the biodiversity threats of hydropower growing through the Himalaya (Pandit and Grumbine 2012). While the proponents of these economic development projects claim that habitat disturbances will be temporary, the scale of development is unprecedented in scale and intensity through Bhutan's history. Therefore, in light of all these changes, it is imperative that we have a way forward for proper management and conservation of tigers and associate wildlife species. Here, we first detail possible factors which have enabled the sanctity of habitats and the abundance of prey and apex predators in Bhutan. We then assess the broader context within which conservation is practiced in Bhutan and described challenges which are unique to the country. Finally, we suggest strategies to ensure the future of tigers in Bhutan and surrounding landscapes.

MATERIALS AND METHODS

Study Area

Bhutan (38,394 km^2) is located in the global biodiversity hotspot of eastern Himalayas, landlocked between the Tibet Autonomous Region of China to the north and India to the east, west, and south (Figure 2-1). It lies between latitudes 26°N and 29°N, and longitudes 88°E and 93°E. Elevation rises from as low as 200 m in the southern foothills to more than 7500 m in north within an aerial distance of 170km. This extreme altitudinal gradient causes great variation in temperature and rainfall, creating different climatic zones ranging from wet sub-tropical in the south to permanent alpine pastures and glaciers in the north and making this landscape a hotspot for biodiversity including wild felids (Tempa et al. 2013).

Bhutan has more than 70% of country under forest cover and more than 50% of the total geographic area under protected areas in the form of national parks and biological corridors. The top predators like tiger, leopard, snow leopard and Asiatic wild dog (*Coun alpinus)* roam these areas supported by diverse prey species (e.g., guar (*Bos gaurus*), sambar (*Rusa unicolor*), 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. Bhutan is also home to many endangered wildlife species including tiger, Indian one-horned rhinoceroses (*Rhinoceros unicornis*), elephants (*Elephas maximus*), Asiatic water buffalos, wild dogs, golden langurs (*Trachypithecus geei*), musk deer (*Moschus chrysogaster*), red panda (*Ailurus fulgens*), and hispid hares (*Caprolagus hispidus*) and critically endangered species like pigmy hogs (*Porcula salvania*) and Chinese pangolin (*Manis pentadactyla*)

Review of Existing Political Leadership, Legislation and Forest Administration

We used existing documents, royal decree, legislations, acts, and rules in Bhutan to assess the policies in place. We used documents from the Ministry of Agriculture and Forests (MoAF), National Assembly, National Environmental Commissions, National land Commission. For the existing human resources and their deployment in the field, we used data based from MoAF human resources database. We also reviewed the current forest management regimes in Bhutan.

Forest Resources and Forest Cover Loss

We used the latest landuse map of Bhutan (MoAF, 2010) to calculate the total forest area in Bhutan. We calculated the total area of potential forests resources (mostly timber) extraction in all of Bhutan both outside and inside protected areas, based on the data made available from Forest Resource Management Division (FRMD). We used ESRI Arcgis 10.3 (ESRI 2016) to calculate the forest lost to date for the construction of roads, electrical power transmission lines, mining and other development. The total length of national highways, feeder roads, and farm roads were provided by the department of roads, under the ministry of works and human settlements. The forest loss for the roads were calculated using width of right of ways for different road categories. For the electrical transmission lines, depending of the voltage capacity of lines (*i.e:* 11kv, 32 kv, 66kv, 132 kv, 220kv, 400kv), we used buffer different buffer width (Table 4.2) to calculated the forest cleared for each different power lines for the existing lines and planned transmission lines. Then we calculated the total forest lost so far with the existing transmission lines and projected the future loss as per the planned and proposed power lines (BPC, 2015).

Socio-Economic Survey in Royal Manas National Park (RMNP)

We conducted socio-economic surveys of residents living in and around RMNP from May-2015- June, 2015, to assess their living condition and dependence on forests resources. We focused on RMNP because RMNP is the prime tiger habitat where we had been studying tigers and their prey base since 2010, and we assume that conditions in RMNP are representative of the most important tiger range in Bhutan. UWICE developed questionnaires and sent 20 enumerators to conduct survey in all the villages in RMNP. The surveyors were trained for a week on how to conduct questionnaires surveys. To estimate nationwide number of household in protected areas and biological corridors, we used data from National Statistical Bureau of Bhutan and used ArcGIS 10.3 to calculate number of houses in the protected areas as well as within the buffer of 500 meters from protected areas.

RESULTS AND DISCUSSION

Review of existing Political Leadership, Legislation and Forest Administration

Leadership is perhaps the most important arbiter of today's conservation success of Bhutan. Under the guidance of the 4th King and the current king of Bhutan, a minimum of 60% of the total land area of Bhutan will be forever retained under forest cover (RGoB, 2008). This constitutional mandate is ensured by the Forest and Nature Conservation (FNC) Act of 1995 being exercised. No tree from private as well as state reserved forests can be harvested without seeking prior approval from the authorized personnel of the Department of Forests and Park Services (FNCA, 1995). A suite of penalties are prescribed and revised within the FNC Act which deters the taking of wildlife (Table 4-1). The highest penalties are for poaching or attempted poaching of tigers (Table 4-1). Between 2012-2016, our surveillance and protection unit confiscated 15 tiger skins imposed Nu.8.6 millions as fines and penalties from 40 individuals (Table 4-3).

Enforcement of the FNC Act and the administration of forest land is carried out by the Department of Forests and Park Services under 12 territorial forests divisions and 10 National Parks and Wildlife Sanctuary. Administrative reach is ensured through a network of offices spread across Bhutan (Figure 4-1). These offices are adequately manned by 1358 forestry officials under different cadres (Figure 4-2). The major focus of these offices is for service delivery to the communities and as a result the main task of foresters in the field are aligned towards resources allocations, forests firefighting, and other community services. Even for the parks, anti-poaching specifically aimed towards curbing wildlife offences is not the major activities, instead they too focus on service delivery activities.

Bhutan's forest lands can be classified under 4 major forms of management regimes (Figure 4-3). The protected areas in the form of national parks and biological corridors has 16,398 km^2 (61%) of the total forest area. The primary objectives of the protected areas are to ensure the persistence of species and wild biodiversity, other forms (Forest Management Units (FMUs) and Community Forests (CFs)) of land use are also managed under scientifically prescribed management plans to sustainably produce timber and other forest goods.

The Forest Management Units (FMUs) with a forests area 2010 km^2 constitute just 7 % of the total forest cover area. FMUs are purely meant for supply of timber and fire wood for commercial purposes and urban areas with proper management plans revised after every 10 years (DoFPS, 20014). However, the rural community within FMUs and nearby can still get the subsidized timer and forest resources from FMUs. The community forests with an area of 315 km^2 constitute just 1% percent of the total forest area in Bhutan. Community forests are areas of forest land handed over to the community forests for management from where they extract forest resource for their own use or for commercial purpose. The remaining 8313 km^2 almost 31 % of the total forest area, is state reserved forests where most of the rural community extract and get their forest resources at subsidized rates.

Communities, Natural Resources and Development

In addition to political leadership, a small population, currently estimated at about 750,000 has perhaps led to lesser pressure on forest lands. It has to be noted that the majority of Bhutanese population are young (Figure 4-4). About 30 % of the Bhutan population is between age group of 1-14 years, 66% of the population between age group of 15-64 years, and only 4% above 65 years (NSB, 2016). As they come of age, rising living standards and development will translate to increasing pressure on forest landscapes and resources.

Today, decision makers usually have to consider over increasing areas to bring under FMUs to meet growing demands for timber (annually estimated at 0.22 million m^3). Most of the extant FMUs suffer from lack of regeneration and growing stock. For example, the Chamgang-Helela Forest Management Unit with an annual allowable cut (AAC) of 13,000 m^3 has been exhausted within 2 management planning cycles of 20 years (10 years in each plan cycle). Such pressures mean that policy makers and bureaucrats often seriously mull and sometimes even suggest that some portions of PAs could be sustainably harvested for timber. Such suggestions are not invalid, given that more than 55 % of productive forests are inside protected areas (FRMD, 2016). However, our constitution mandates 60% of our country to be under forests cover for all times to come, thus our PAs cannot be open for commercial logging.

A small proportion of Bhutanese households also dwell within Protected Areas and Biological Corridors. An estimated 5325 households reside inside the park, and additional 1662 households residing within the buffer of 500 meters from the parks. About 3425 households falls inside the biological corridors and additional 2748 households within the buffer of 500 meters from biological corridors (Figure 4-5). These households depend on forests for timber, fodder, fuel and non-wood forest products. For instance, in the RMNP, a core habitat for tigers, 62 % of HHs depend on forests for fuel and fodder (Figure 4-6). Farming communities are also severely impacted by human-wildlife conflict. More than 50% of the households in RMNP succumb to loss of either crops or livestock to wild animals.

The increasing pace of development has also meant that most of these communities are getting connected by roads and electricity (Figure 4-7). An estimated 60 km^2 (0.15% of the total geographic area) and 41km^2 (0.1% of the total geographic area) of the forests has been lost to electric power transmission cable lines so far (Figure 4-8). The major construction of road networks are completed, huge mega power projects are being planned. A further 50 km^2 will be lost to just planned and proposed power transmission line in near future. Mining, hydropower dam construction sites and other infrastructure development accounts for 21.65 km^2 of the government reserve forest (NEC, 2016).

Poverty, poaching, and trade for tiger parts

Poverty, poaching, and wildlife trades are intricately linked (Challender & MacMillan, 2014; Duffy & St John, 2013). Poaching for tigers is the greatest threat for tiger survival in the tiger range countries (Dinnerstein et al., 2007; Goodrich et al., 2015). The global estimates of trade in tiger parts worth about USD 5.00 million annually (Uhm, 2016). While poaching is not a major threat for tiger in Bhutan so far, the recent trends of tiger skins and parts in the black market are alarming and need to be addressed immediately. Over the past 5 years (2011-2016), about 13 tiger skins and have been seized in Bhutan. Half of these tiger skins came from the tigers in Bhutan, mostly because of human wildlife conflicts. Irrespective of whether accidental or retaliatory killings, tiger skins and parts are being sold via middle men in the black market by farmers give the high values of these parts.

RESPONSE AND CONSERVATION STRATEGIES

National Level Landuse Zonation and Certification of Forests

Protected Areas and Biological Corridor management should be strengthened. As the population increases, the pressure on forest land will increase. With almost 55% of the forest resources potential area locked up in the protected areas, decision makers will increasingly lobby for extracting resources from these areas. To ensure that our protected areas are not exploited and to ease the risk of forest degradation, areas such as forest management units and community forests from where timber is extracted should be strengthen and certified to ensure adequate renewal of forest growth. As tigers and prey base are not only limited in the protected areas, areas outside protected areas should also be managed as wildlife habits.

Habitat Management

With more than 71% of its total geographic area under forest cover, Bhutan has one of the most pristine and contiguous swath of forests in south Asia, enabling tigers and other wildlife to roam freely. Bhutan is one of the few countries, where forest cover has increased over the last few decades (Gilani, et al., 2015; Bruggeman, et al., 2016). As Bhutanese farmers abandoned the old practice of *tseri* agriculture (slash and burn agriculture practices) and trans-migratory livestock herding practice, *tseri* and grasslands are overtaken by woody shrubs and trees (Siebert and Belsky, 2014). Intermediate disturbance regimes like fires and logging trend to increase herbaceous biomass for ungulate which in turn may benefit carnivores (Hebblewhite et al., 2009). Heterogeneous habitat (mixed of grasslands and grazing ground, forests) instead of pure forests covers trend to support more of the tiger's primary prey species (Bhattarai & Kindlmann, 2012; Simcharoen et al., 2014).

Except in small pocket of RMNP, active habitat management is not being carried out in Bhutan. The existing alluvial grasslands are invaded by the trees and other woody shrubs in the south. The traditional grazing ground are also increasingly being lost to trees and woody species in the mid-temperate forests as our farmers are increasingly abandoning their old lifestyle of migratory cattle herding. Therefore, traditional grazing grounds in the temperate mid-altitudes and existing alluvial grasslands in the south should be actively managed to restore traditional landuse practices (Siebert and Belsky 2014), which probably benefit early seral ungulate species and their large carnivore prey, such as tigers.

Community engagement and sustainable development

With 69% of Bhutan's population living in the rural areas and a growing population with aspirations for improved livelihoods, reliance on forest will further increase. Conservation strategies and programs should address energy, food and land conversion issues within forest areas both within and outside protected areas. Bhutan's per capita fuelwood consumption of 1.2 metric tons/year is considered one of the highest in the world (Wangchuk et al., 2014). Interventions should tie in innovative approaches such as subsidizing biogas schemes to reduce fuel intake from forests while promoting effectively use of livestock waste and minimizing greenhouse gas emissions simultaneously.

For example, in a current project supported by the IUCN in the Royal Manas National Park of Bhutan, a total of 150 biogas plants for 150 households (1 biogas plant is sufficient for one household for cooking) will be constructed over the next 3 years. This will substantially reduce the fuel wood consumption for cooking as well as heating. The used cow dung from the biogas digesters will be used as manure for crop lands. To reduce crop loss and prevent retaliatory of tiger prey, a total of 200 km of electrical fencing will be provide in next 3 years to protect farm lands in RMNP. Such interventions not only promote reduction of forest use and mitigate human wildlife conflict but also garner community support for conservation of tigers and other wildlife.

Majority of the Bhutanese population are Buddhist with core beliefs that respects all life forms. As our younger generations are exposed to outside world, we are increasingly our traditional beliefs systems and ethos. For example, Buddhist monks in Arunachal Pradesh played very important role in banning the hunting of wildlife and visit by His Holiness Dalia Lama in 2003 had reduced hunting by local communities (Velho and Laurance 2013). In the Tibetan plateau, Buddhist monks plays important role in conservation of endangered wildlife (Li et al. 2014). This is high time that we bring on board our central monistic body in the conservation programs and encourage our monks and high lamas (teachers) to convey conservation messages during their sermons and teachings. This will strengthen our beliefs systems and help to prevent our communities from harming or poaching of wildlife.

Anti-poaching and cross border cooperation

One of the most serious impediments to tiger persistence is the poaching of tigers (Chapron et al.2008, Robinson et al. 2015). In Bhutan, poaching has never been considered as major threat for wildlife conservation. This is obvious from the recent announcement by the Minister of Agriculture and Forests, that wild pigs should be killed as one of the measures for human-wildlife conflict (Kuensel, 2017). While Bhutan have one of the most stringent policies and acts in place for conservation, this kind of announcement promoting lethal control of problem wildlife from one of the top decision makers in the country can have many negative effect for the future conservation. Although organized wildlife poaching and trade do not occur at the scale seen elsewhere in the region, Bhutan is not immune from the ills of wildlife trafficking. If the recent trends in wildlife products in the market is of any indication, it gives us reasons to be worried and warrant immediate intervention. Even in most parks, anti-poaching is not a regular activity and it is often treated as some optional activities. Most of the park staff are engaged in numerous biodiversity surveys, community activities, socio-economic survey, and resources allocations in the park. This approach should be changed, and staff particularly in the protected areas should focus more on anti-poaching. At the park and division level, we should institute dedicated patrolling unit, and identify anti-patrol trails and tracks. These trails should be regularly patrol. Regular anti-poaching patrols are known to substantially reduce the poaching activities and endangered wildlife populations rebound in many protected areas (Messer, 2010). In Bhutan, government do not allocate enough funds for anti-poaching activities even in protected areas where the primary goal is for protection of wildlife. This need to be changed and fund and resources must be mobilized for anti-poaching activities. Both within and outside of PAs, interventions such as SMART patrolling should be implemented at a national level.

Informant sharing networks should be strengthened within Bhutan and cross border initiatives should be supported to share information to prevent poaching and illegal transactions. Most of the confiscations of tiger and other wildlife parts in the market in Bhutan were confiscated because of information sharing and network of our forest surveillance team. This unit has to be strengthen and more staff has to be recruited. Surveillance unit needs to be established in each park and division in addition to regular patrolling team.

Penalties for illegal activities could also be increased to act as a greater deterrent. For example, in Bhutan, the penalties for poaching a tiger has been raised to Nu 50,000 (~USD 1,000.00) to Nu. 1.00 Million (~USD 50,000.00) in 2017 (DoFPS, 2017). Likewise, for tiger prey that are included as protected species the penalties have also been increased accordingly (Table 4-1). Between 2009 to 2016, fines and penalties imposed and collected on forest offences (that include illegal harvesting of timber, killing of wildlife and trade, fishing, extraction of sands and stones from forest and river banks) has increased more than four folds, from Nu. 8.56 (~150,000 USD) to Nu. 45.03 Million (~900,000 USD) in 2015 and Nu. 36.45 (~750,000 USD) in 2016 (Figure 4-9). Around the same time, the Department of Forests and Park Services established the “Forest Protection and Surveillance Unit” and as a result, the number of forest crime detections also increased. What is needed in addition to raising penalties is the support from the legal court system for adequately tackling illegal issues.

Institution Building

Institutions such as the Department of Forests and Park Services which in Bhutan has the express mandate to protect, monitor and allocate forest resources should be strengthened. Human resources capacity at all levels of the Department should be enhanced through regular short-terms capacity building trainings. Staff and offices should be furnished with communications and mobility. The newly established regional center for tiger and cats research at Gelephu should be operationalized soon to provide timely technical expertise and technical backstopping to parks and territorial divisions.

Scientifically Rigorous Monitoring

Monitoring of wildlife population is one of the most important management programs that helps managers and decision makers to detect the extent and direction of wildlife population changes (Karanth et al., 2003; Mills 2012; Oli and Mills, 2013). Targeted, or hypotheses based monitoring (Nichols and Williams 2006) should be incorporated as part of our programs for tigers and other wildlife in Bhutan. This will not only detect the changes in the wildlife population trends, but also help identify the cause of such changes. For example, if poaching is a primary threat for tiger conservation in Bhutan, then designing monitoring protocols to detect poaching activities along the boarders will provide information on the severity of poaching and its impact to tigers. This will enable managers to take appropriate management actions, rather than waiting to see the trend of population decline and then beginning to ask if poaching or disease or other factors are the main cause of the decline.

Independent institutions such as Ugyen Wangchuck Institute for Conservation and Environmental Research (UWICER) and newly established regional center for tiger and cats research should take a lead in monitoring tiger and their prey population on regular basis. The problem of monitoring of important wildlife population like tigers by park's own staff and management is it often leads to higher counts animals than the ground reality (Avinandan et al., 2008; Check, 2006). Therefore, in collaboration with the parks, an independent monitoring is critical to ensure the proper monitoring of the status of tigers and their prey population.

Camera trapping has become one of the most important tools for monitoring the tiger populations (Chapter 2, 3). This should be carried out on regular basis in the protected area. Such monitoring should be expended to other tiger habitat at national level every 5 years. To monitor tiger movements and fine scale resources selection and to address prevent human wildlife conflicts radio-telemetry studies must be conducted. Social demographics and public perception monitoring should be carried out every 5 years in the protected areas.

International Agreements and Conservation Efforts

Bhutan as one of the members of tiger range countries had pledged to double tiger numbers by 2022 during the Global Tiger Summit, 2010 at St. Petersburg, Russia (GTI, 2010). As a follow up to this pledge, Bhutan participates in all international and regional discourse on tigers' recovery plans. Three rounds of Asia Ministerial Conference on Tiger Conservation have been conducted till date with specific objectives to fulfil the goal of doubling tiger numbers by 2022. Bhutan is also a member and signatory to the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES), TRAFFIC, and IUCN. These international agreements and memberships are very important for Bhutan not only for securing funding and support, but also to collaborate and corporate in species recovery and curbing illegal trade of wildlife and wildlife products. Currently IUCN is providing a funding of 700,000 euros for *Integrated Tiger Habitat Conservation Program Bhutan*, and likewise Global Environment

Facility (GEF) |and other international organizations had funded numerous projected for wildlife protection and conservations.

The regional and transboundary corporation is very important for Bhutan, India, Myanmar, and Nepal for tigers to thrive. The Northern Forest Complex (Myanmar) – Namdhapha (India) -Royal Manas (Bhutan) (NFC-N-RM) tiger conservation landscape is very important for tigers and this landscape must be secure and protected for tigers. An international NGOs like World Wildlife Fund for Nature (WWF) should take a lead to initiate dialogue and discourse for regional corporations and collaboration to protect this large tract of forests for tigers and other wildlife.

The Trans-boundary Manas Conservation Area (TraMCA) was initiated as the pilot project between RMNP and Indian Manas to collaborate and corporate in conservation and research in 2010. This was informal agreement that two parks agreed upon, but by 2013 this program has become a flagship program endorsed by both India and Bhutan governments. While no drastic changes in the tiger numbers are apparent within Bhutan, Indian Manas Tiger Reserve witnessed tiger numbers increasing more than threefold from 9 individuals in 2010-2011to 32 individuals in 2015-2016 (Borah et al., 2012; Ahmed et al., 2016). Tigers in Indian Manas were locally extinct due to militant insurgents from late 1980s to early 2000s (Goswami and Ganesh 2011; Soud et al. 2013; Goswami and Ganesh 2014). The recovery of tiger population in Indian Manas Tiger Reserve underpins the importance of transboundary and regional collaboration and cooporation. Bhutan and India should start similar transboundary initiatives with the neighboring Indian state of Arunachal Pradesh (Pakke Tiger Reserve) and West Bengal (Buxa Tiger Reserve).

The regional connectivity is a key for tiger survival in the regions. Indian Manas tiger reserve, Buxa tiger reserve, and Sonai Rupai Wildlife Sanctuary are small patch of tiger habitats in the middle of human settlement. The forests of Bhutan provide the critical linkages among these reserves in India (Sharma et al., 2011). The tigers from Bhutan are known to go both westwards towards Sikkim (borders western Bhutan) and Eastwards to Arunachal Pradesh (borders eastern Bhutan) (Oberoi, 2009; Chanda, 2017).

CONCLUSION

Bhutan with its vast tracts of contiguous forests offers the best hope for conserving tigers in the Himalayas. With proper formulation of conservation programs aided by effective implementation, tiger habitats can be secured and living standards of communities in and around protected areas can be enhanced. Bhutan can effectively serve as a source site for tigers in the region with benefits spreading across connected habitats towards India, Myanmar, and further afield. Our paper demonstrates that conservation issues are not only restricted to species protection but should address issues arising from land-use change, community development, legal frameworks and institution building. This means that conservation scientists should be able to engage in and influence concerns beyond just monitoring tigers in the wild.

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Table 4- 1: List of penalties for killing wildlife in Bhutan. Source: MoAF

Offences	Penalties in FNCR,2006	Revised Penalties in FNCR,2017
Attempt to catch or injure a tiger	-	500,000 (~USD 10,000)
Killing of Tiger	50,000 (~USD 1000)	1,000,000 (~USD 50,000)
Killing of Gaur	10000 (~USD 200)	10,000 (~USD 200)
Killing of Wild buffalo	10000 (~USD 200)	10,000 (~USD 200)
Killing of Sambar	10000 (~USD 200)	10,000 (~USD 200)
Killing of Serow	5,000 (~USD 100)	10,000 (~USD 200)

Table 4- 2: The width of the right of way for different voltage of electric transmission lines.

Source: Bhutan Power Corporation, 2017, Thimphu Bhutan.

Voltage of the transmission line	Right of Way (Meters)
415 V	7
11 kV	9
33 kv	12
66 kV	18
132 kV	27
220 kv	35
400 kV	52

Table 4- 3: Table of the list of tiger skins and bone sets confiscated by the surveillance and protection unit of the department of forests and park services between 2012-2016 in Bhutan. The fines in (Nu, 1USD~60 Nu). Source: DoFPS, 2017

SL.NO	Location	Date	Tiger Parts	Fines (Nu.)	No. of People	Remarks
1	Phuntsholing town	9/1/13	1no.tiger skin	100,000	3	Case settled in P/Ling Range
2	Norbugang Ngalam	26/3/12	1no.tiger skin	100,000	3	Case settled Ngalam Range
3	Gelephu town	20/09/13	1no.tiger skin and bones	100,000	1	Case settled in Gelephu Range
4	Bumthang town	23/03/14	1no.tiger skin and bones	100,000	4	Case settled in, Bumthang Division
5	Doban,Chunzom Geog	05/05/14	1no.tiger skin and bones	100,000	2	Case settled in Sarpang Range office
6	Thimphu town	15/08/14	1no.tiger skin	100,000	5	Case settled in Thimphu Division settlement
7	Norbugang geog	4/8/15	1no.skin	1,000,000	4	Settled in Sarpang Range office
8	Babesa	18/10/15	1 sets of tiger bones	1,000,000	2	Settled in Thimphu Forest division
9	Norbugang Geog	17/01/16	1no.Tiger skin and sets of bones	1,000,000	3	Settled in Gelephu
10	Gelephu town	12/06/16	1no.tiger skin and bones	1,000,000	3	Settled in Gelephu
11	Thimphu		3 skins	3,000,000	7	Settled in Thimphu Range
12	S/Jongkhar	2016	1 skin	-	2	Case in Supreme Court
13	Sarpang	2016	1	1,000,000	1	Settled in Gelephu

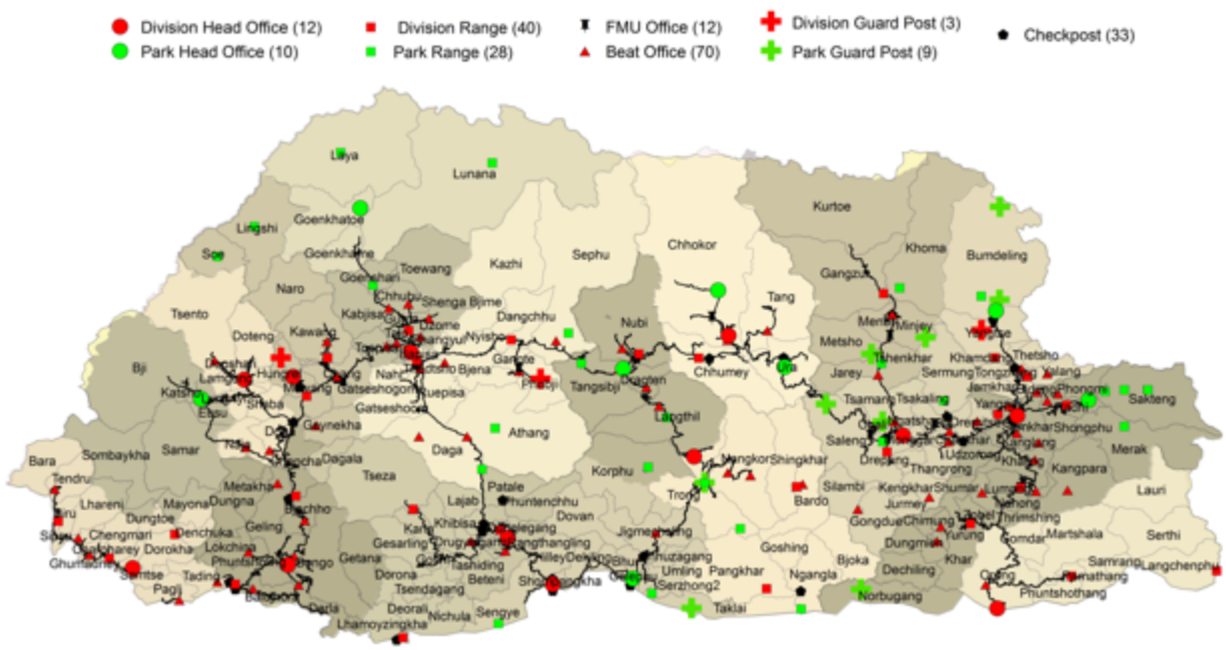

Figure 4- 1: Maps of forests offices under the department of forests and park services across Bhutan.

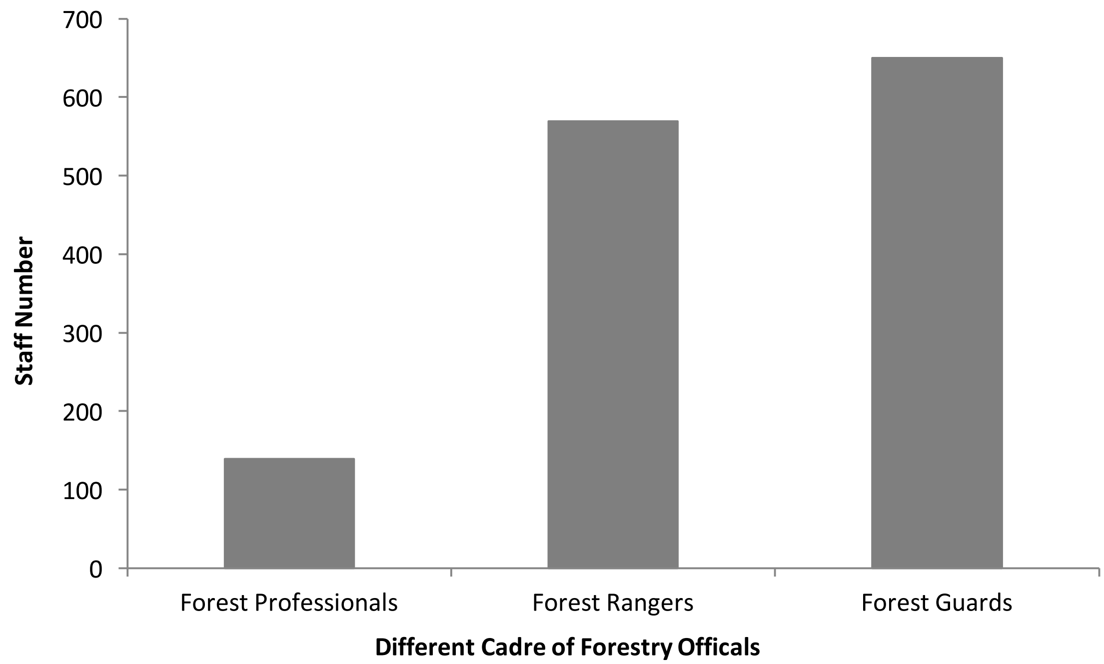

Figure 4- 2: The graph showing cadre of forests officials in the department of forests and park services manning forest offices.

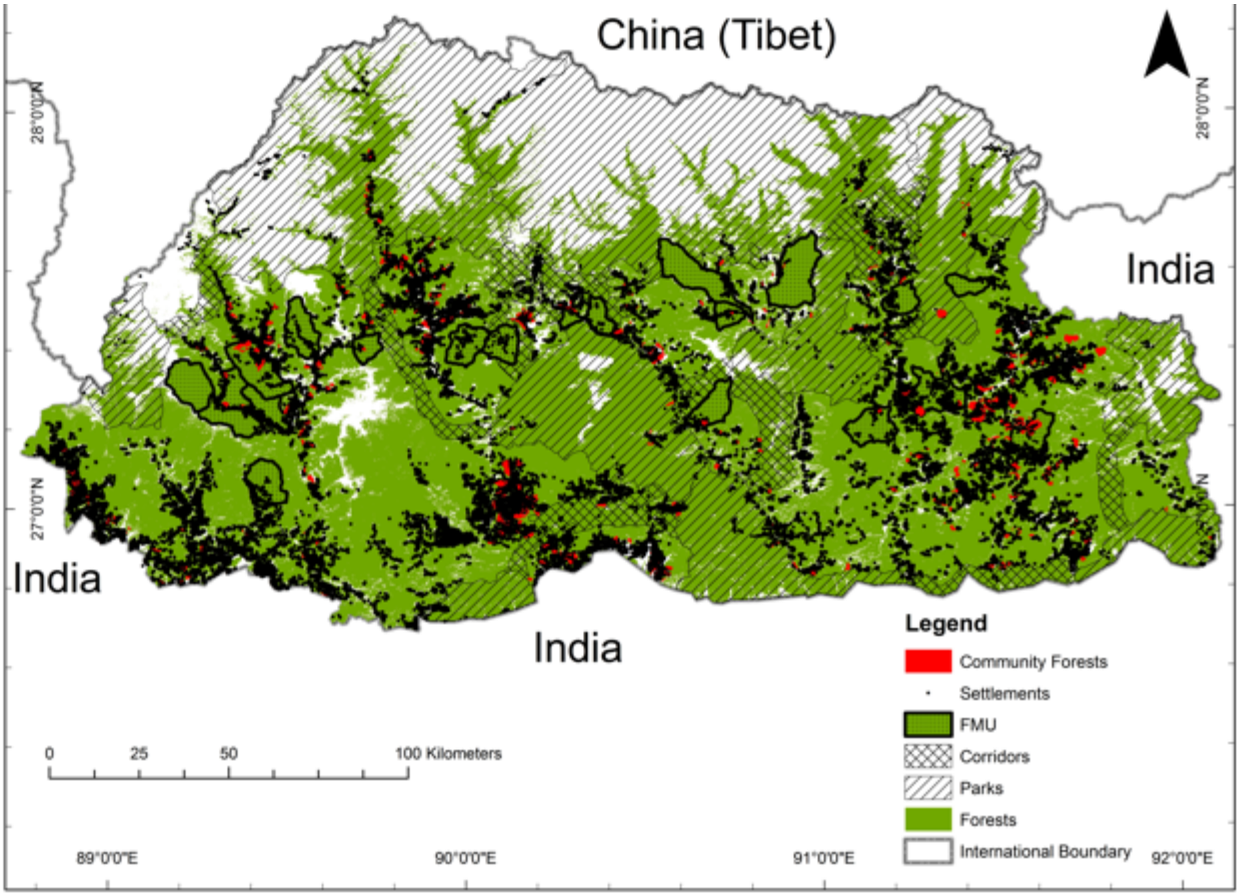

Figure 4- 3: Map of Bhutan showing forests under different management regimes.

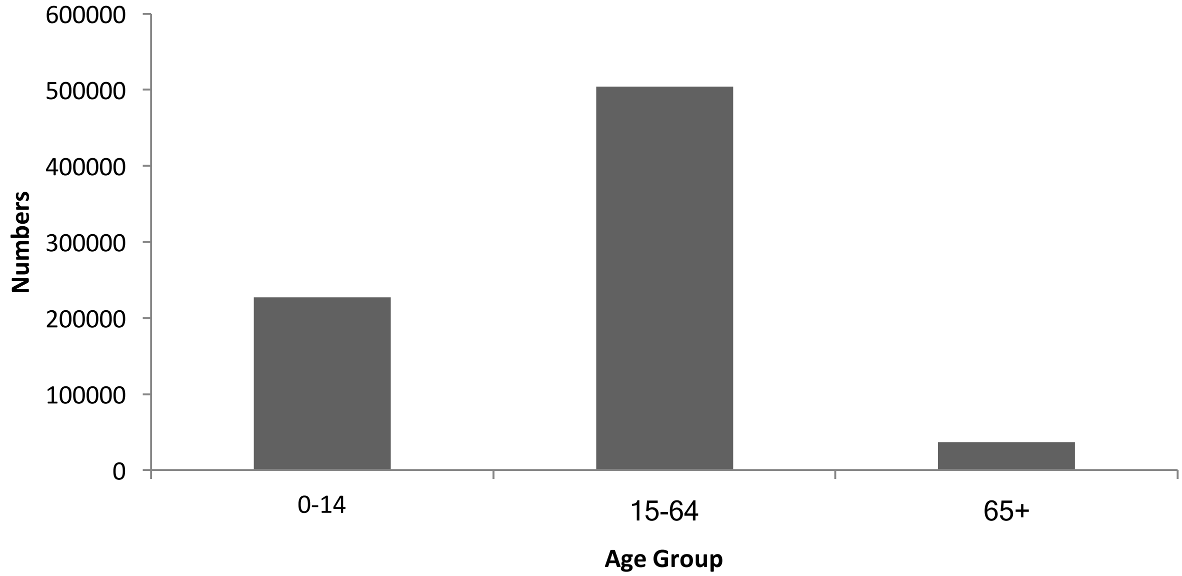

Figure 4-4: Graph showing different age group of Bhutanese population (2016)

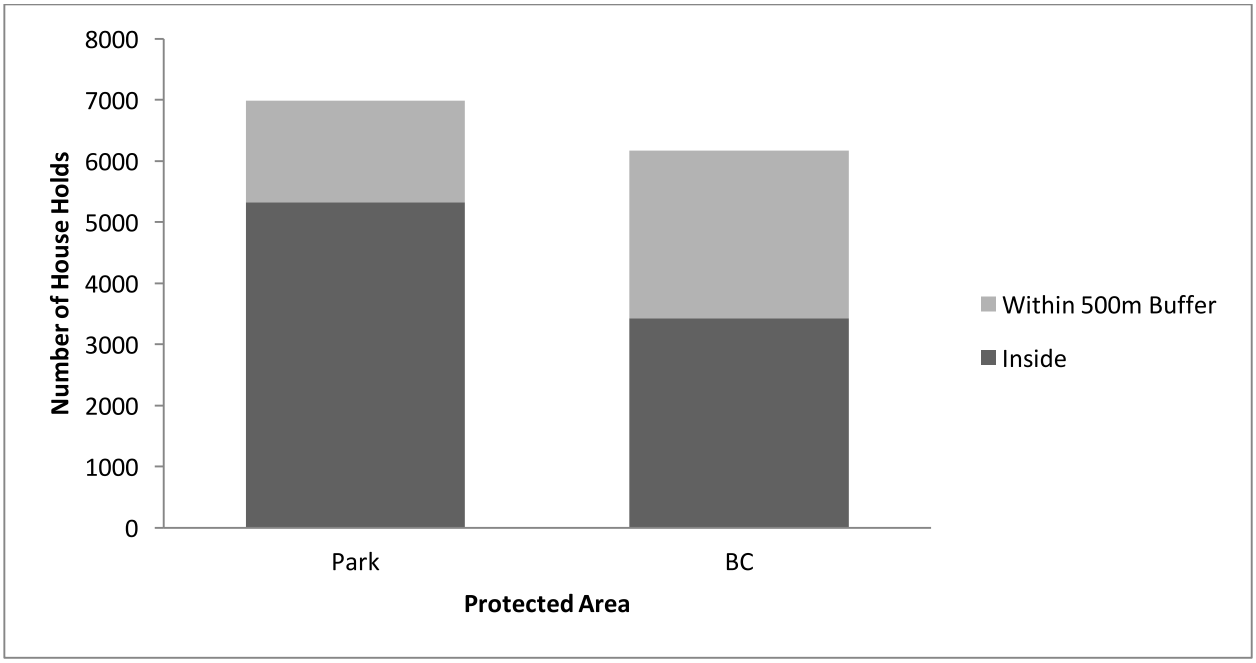

Figure 4-5: Number of households inside the park and biological corridors (dark color) and number of households within 500m buffer from parks and BC (gray color).

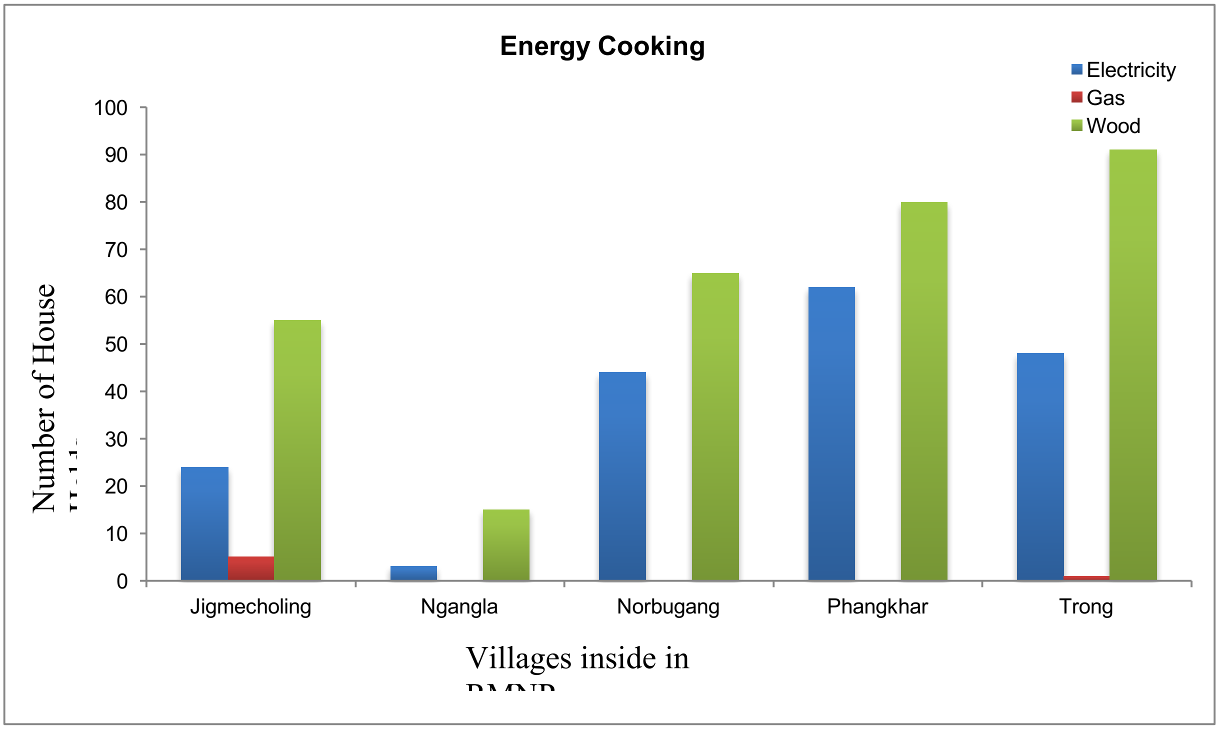

Figure 4-2: The reliance of communities on forests for energy (cooking) in 5 villages inside RMNP. All most all the villages have electricity supply.

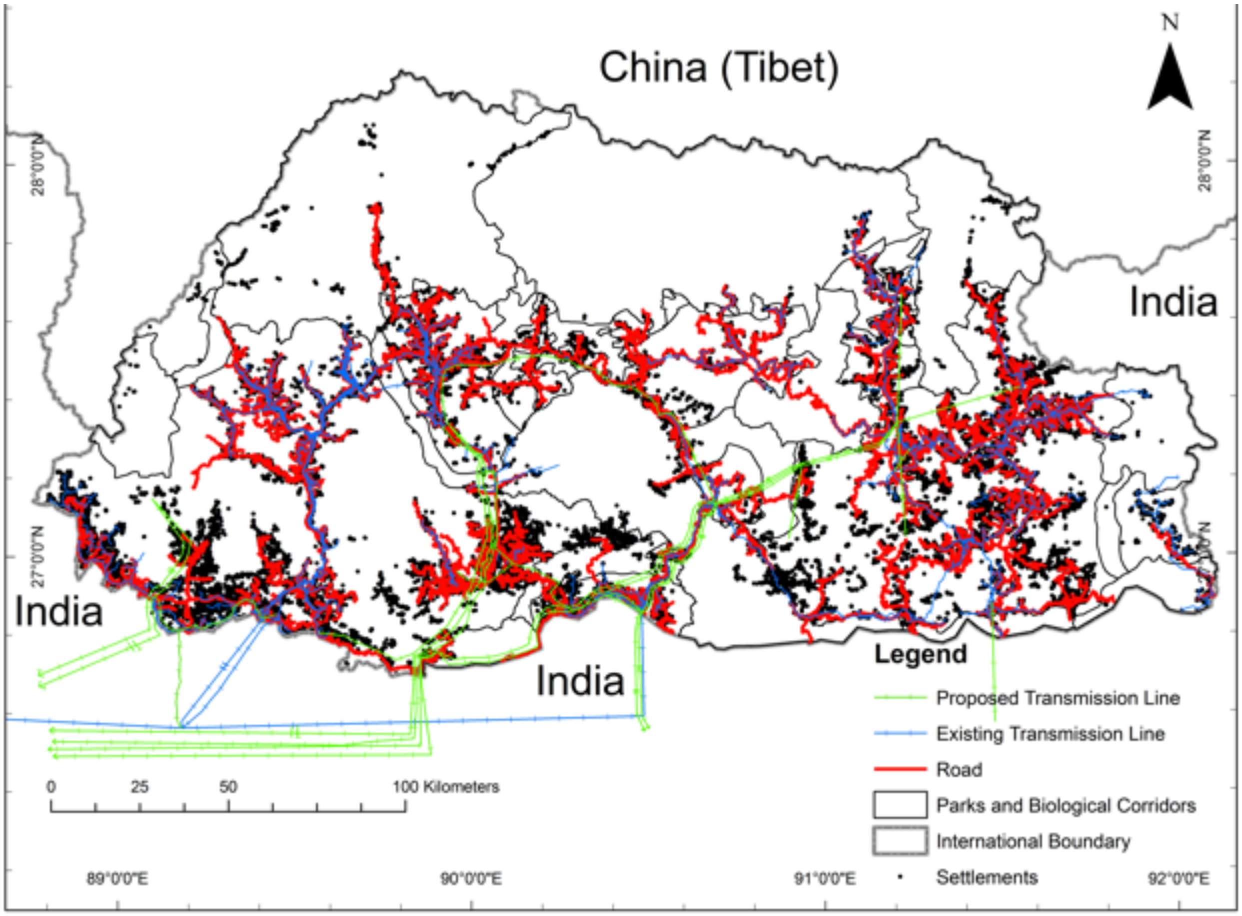

Figure 4- 7: The map of Bhutan with road network (red lines), existing power transmission lines (blue line) and proposed transmission lines (green lines). The power transmission lines has been plotted beyond Bhutan Borders into India to indicate where power supply is going and will go in future.

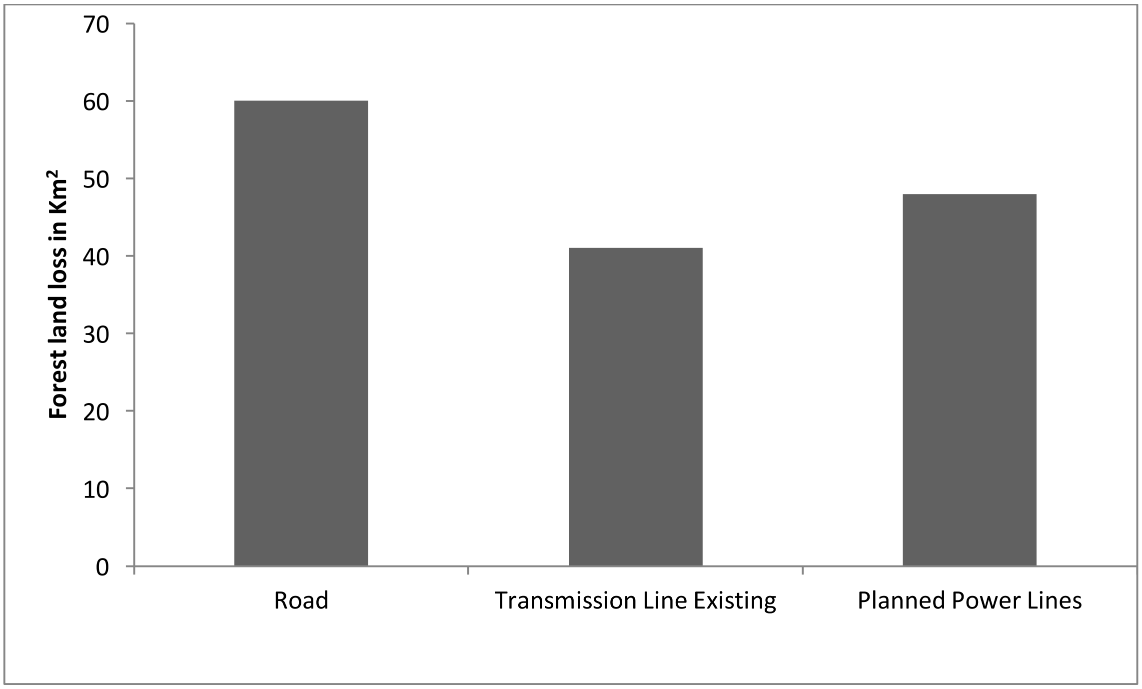

Figure 4- 8: Forest lost (km^2) so far for road construction and existing power transmission lines. The planned power lines indicate how much forest will be lost in near future from the planned power transmission lines.

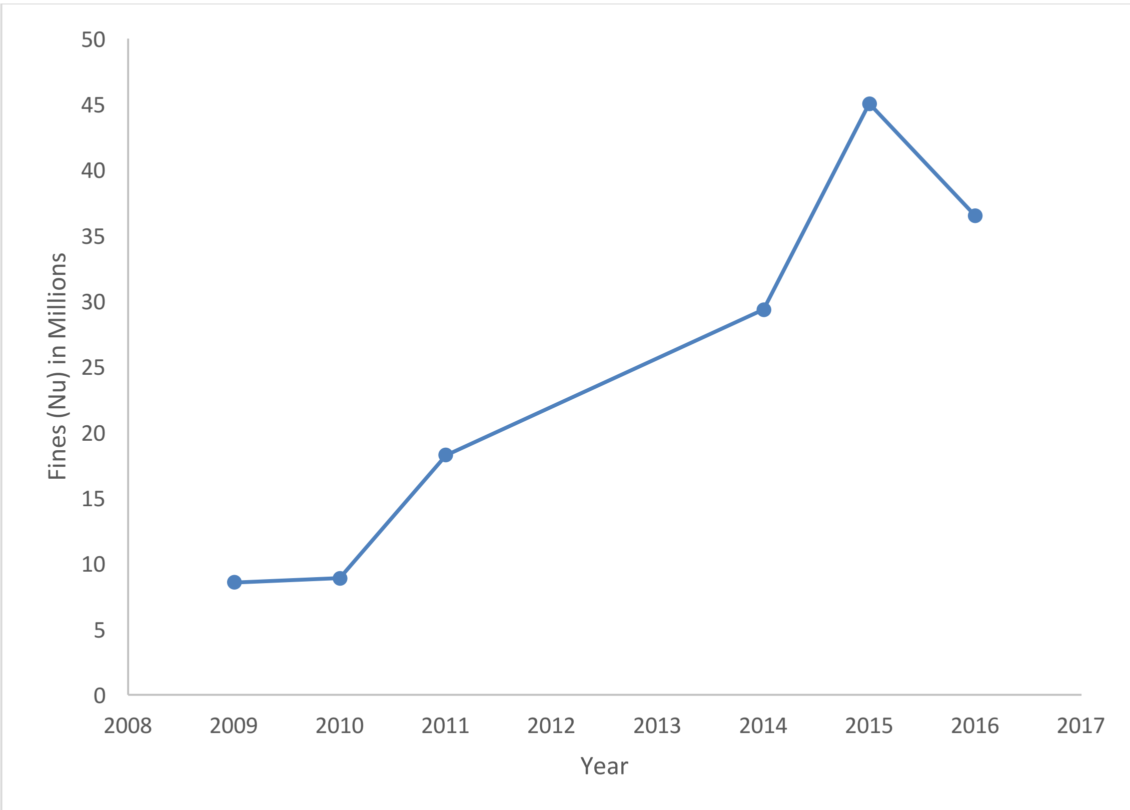

Figure 4-9: The penalties and fines collected from 2009 till 2016 from forestry offences (that include wildlife poaching and trade, fishing, illegal harvesting of timer and smuggling of forest resources, stones, sand, encroachment of forest land).

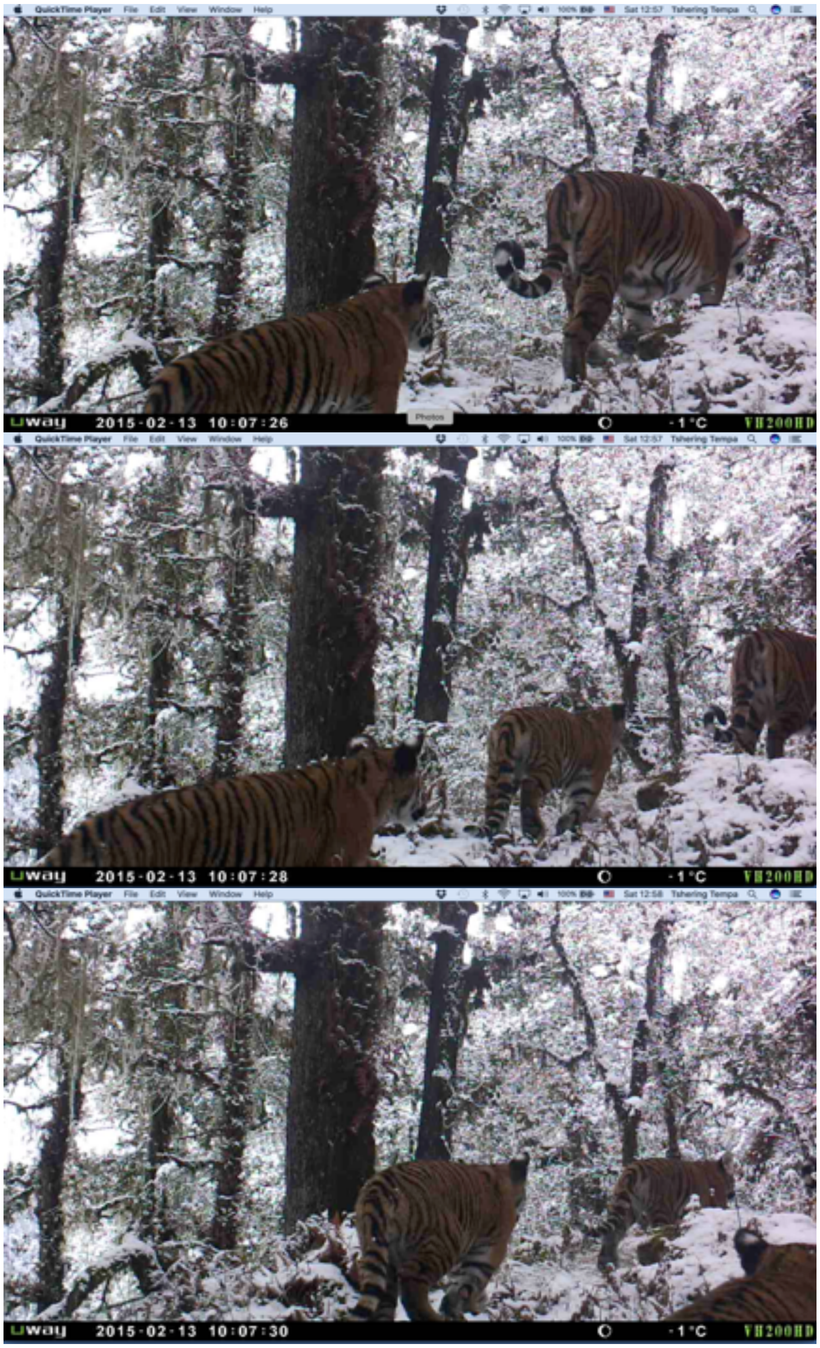

Plate 4-1: Bengal tiger (*Panthera tigris tigris*) with three young cubs in Bhutan, 2014-2015.

Plate 4- 2: Images of Bengal tigers (*Panthera tigris tigris*) photographed by our remote camera traps at different elevation. A sub-adult male tiger was captured in 2011 at elevation of 300 amsl in RMNP, the same tiger was captured in camera trap at an elevation of 3900 amsl in JSWNP in 2013.

Plate 4- 3: Images of Bengal tigers (*Panthera tigris tigris*) photographed by our remote camera traps in 2010 in RMNP. The stripe pattern of tiger skin confiscated at Gelephu, Bhutan in 2012 matched to the stripe pattern of tiger camera trapped 2010 in RMNP.