ECOLOGY OF TIGERS IN CHURIA HABITAT AND A NON-INVASIVE GENETIC APPROACH TO TIGER CONSERVATION IN TERAI ARC, NEPAL

Kanchan Thapa

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Marcella J. Kelly (Chair)
Eric Hallerman
Dean Stauffer
Eric Dinerstein

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ABSTRACT

Tigers (*Panthera tigris tigris*) can be viewed as a proxy for intact and healthy ecosystems. Their wild populations have plummeted to fewer than 3,200 individuals in the last four decades and threats to these apex predators are mounting rather than diminishing. Global conservation bodies (Global Tiger Initiative, World Wildlife Fund, Wildlife Conservation Society, Panthera etc.) have recently called for solidarity and scaling up of conservation efforts to save tigers from extinction.

In South Asia, tiger habitat ranges from tropical evergreen forests, dry arid regions and sub-tropical alluvial floodplains, to temperate mixed deciduous forest. The churia habitat is relatively unstudied and is considered a young and geologically fragile mountain range in Nepal. The contribution of the churia habitat to tiger conservation has not been considered, since modern conservation started in 1970's. This study focuses on the ecology of the tiger with respect to population density, habitat use, and prey occupancy and density, in the churia habitat of Chitwan National Park. This study also includes the first assessment of genetic diversity, genetic structure, and gene flow of tigers across the Terai Arc Landscape- Nepal. The Terai Arc Landscape harbors the only remaining tiger population found across the foothills of the Himalayas in Nepal and northwest India. I used a combination of camera-trapping techniques, which have been a popular and robust method for monitoring tiger populations across the landscape, combined with a noninvasive genetic approach to gain information on tigers, thus adding new information relevant to global tiger conservation.

I investigated tiger, leopard (*Panthera pardus fusca*), and prey densities, and predicted the tiger density across the Churia habitat in Chitwan National Park. I used a camera-trap grid with 161 locations accumulating 2,097 trap-nights in a 60 day survey period during the winter season of 2010-2011. Additionally, I used distance sampling techniques for estimating prey density in the churia habitat by walking 136 km over 81 different line transects. The team photographed 31 individual tigers and 28 individual leopards along with 25 mammalian species from a sampling area of 536 km^2 comprising Churia and surrounding areas. Density estimates of tigers and leopards were 2.2 (SE 0.42) tigers and 4.0 (SE 1.00) leopards per 100 km^2. Prey density was estimated at 62.7 prey animals per 100 km^2 with contributions from forest ungulates to be 47% (sambar *Rusa unicolor*, chital *Axis axis*, barking deer *Muntiacus muntjak*, and wild pigs *Sus scrofa*). Churia habitat within Chitwan National Park is capable of supporting 5.86 tigers per 100 km^2 based on applying models developed to predict tiger density from prey density. My density estimates from camera-traps are lower than that predicted based on prey availability, which indicates that the tiger population may be below the carrying capacity. Nonetheless, the churia habitat supports 9 to 36 tigers, increasing estimates of current population size in Chitwan National Park. Based on my finding, the Churia habitat should no longer remain ignored because it has great potential to harbor tigers. Conservation efforts should focus on reducing human disturbance to boost prey populations to potentially support higher predator numbers in Churia.

I used sign surveys within a rigorous occupancy framework to estimate probability of occupancy for 5 focal prey species of the tiger (gaur *Bos gaurus*, sambar, chital, wild pig, and barking deer); as well as probability of tiger habitat use within 537 km^2 of churia habitat in Chitwan National Park. Multi-season, auto-correlation models allowed me to make seasonal (winter versus summer) inferences regarding changes in occupancy or habitat use based on covariates influencing occupancy and detection. Sambar had the greatest spatial distribution across both seasons, occupying 431-437 km^2 of the churia habitat, while chital had the lowest distribution, occupying only 100-158 km^2. The gaur population showed the most seasonal variation from 318- 413 km^2 of area occupied, with changes in occupancy suggesting their migration out of the lowland areas in the summer and into the churia in the winter. Wild pigs showed the opposite, moving into the churia in the summer (444 km^2 area occupied) and having lower occupancy in the winter (383 km^2). Barking deer were widespread in both seasons (329 - 349 km^2). Tiger probability of habitat use $\widehat{\Psi}$ SE($\widehat{\Psi}$) was only slightly higher in winter 0.63 (SE 0.11) than in summer 0.54 (SE 0.21), but confidence intervals overlapped and area used was very similar across seasons, from 337 - 291 km^2. Fine-scale variation in tiger habitat use showed that tigers intensively use certain areas more often than others across the seasons. The proportion of available habitat positively influenced occupancy for the majority of prey species and tigers. Human disturbance had a strong negative influence on the distribution of the majority of prey species but was positively related to tiger habitat use. Tigers appear to live in areas with high disturbance, thus increasing the risk of human-tiger conflict in the churia habitat. Thus, efforts to reduce human disturbance would be beneficial to reducing human wildlife conflict, enriching prey populations, and would potentially support more tigers in churia habitat of Nepal. Overall, I found high prey occupancy and tiger habitat use, suggesting that the churia is highly valuable habitat for tigers and should no longer be neglected or forgotten in tiger conservation planning.

Thirdly, I assessed genetic variation, genetic structure, and gene flow of the tigers in the Terai Arc Landscape, Nepal. I opportunistically collected 770 scat samples from 4 protected areas and 5 hypothesized corridors across the Terai Arc Landscape. Historical landuse change in the Terai Arc was extracted from Anthrome data sets to relate landuse change to potential barriers and subsequent hypothesized bottleneck events in the landscape. I used standard genetic metrics (allelic diversity and heterozygosity) to estimate genetic variation in the tiger population. Using program Structure (non-spatial) and TESS (spatial), I defined the putative genetic clusters present in the landscape. Migrant analysis was carried out in Geneclass and Bayesass for estimating contemporary gene flow. I tested for a recent population bottleneck with the heterozygosity test using program Bottleneck. Of the 700 samples, 396 were positive for tiger (57% success). Using an 8 multilocus microsatellite assay, I identified 78 individual tigers. I found large scale landuse changes across the Terai Arc Landscape due to conversion of forest into agriculture in last two centuries and I identified areas of suspected barriers. I found low levels of genetic variation (expected heterozygosity = 0.61) and moderate genetic differentiation (F_{ST} = 0.14) across the landscape, indicative of sub-population structure and potential isolation of sub-populations. I detected three genetic clusters across the landscape consistent with three demographic tiger sub-populations occurring in Chitwan-Parsa, Bardia, and Suklaphanta protected areas. I detected 10 migrants across all study sites confirming there is still some dispersal mediated gene flow across the landscape. I found evidence of a bottleneck signature, especially around the lowland forests in the Terai, likely caused by large scale landuse change in last two centuries, which could explain the low levels of genetic variation detected at the sub-population level. These findings are highly relevant to tiger conservation indicating that efforts to protect source sites and to improve connectivity are needed to augment gene flow and genetic diversity across the landscape.

Finally, I compared the abundance and density of tigers obtained using two non-invasive sampling techniques: camera-trapping and fecal DNA sampling. For cameras: I pooled the 2009 camera-trap data from the core tiger population across the lowland areas of Chitwan National Park. I sampled 359 km^2 of the core area with 187 camera-trap locations spending 2,821 trap-nights of effort. I obtained 264 identifiable photographs and identified a total of 41 individual tigers. For genetics, I sampled 325 km^2 of the core area along three spatial routes, walking a total of 1,173 km, collecting a total of 420 tiger fecal samples in 2011. I identified 36 tigers using the assay of 8 multilocus genotypes and captured them 42 times. I analyzed both data types separately for estimating density and jointly in an integrated model using both traditional, and spatial, capture-recapture frameworks. Using Program MARK and the model averaged results, my abundance estimates were 46 (SE 1.86) and 44 (SE 9.83) individuals from camera and genetic data, respectively. Density estimates (tigers per 100 km^2) via traditional buffer strip methods using half of the Mean Maximum Distance Moved (½ MMDM) as the buffer surrounding survey grids, were 4.01 (SE 0.64) for camera data and 3.49 (SE 1.04) for genetic data. Spatially explicit capture recapture models resulted in lower density estimates both in the likelihood based program DENSITY at 2.55 (SE 0.59) for camera-trap data and 2.57 (SE 0.88) for genetic data, while the Bayesian based program SPACECAP estimates were 2.44 (SE 0.30) for camera-trap data and 2.23 (SE 0.46) for genetic data. Using a spatially explicit, integrated model that combines data from both cameras and genetics, density estimates were 1.47 (SD 0.20) tigers per 100 km^2 for camera-trap data and 1.89 (SD 0.36) tigers per 100 km^2 for genetic data. I found that the addition of camera-trap data improved precision in genetic capture-recapture estimates, but not visa-versa, likely due to low numbers of recaptures in the genetic data. While a non-invasive genetic approach can be used as a stand-alone capture-recapture method, it may be necessary to increase sample size to obtain more recaptures. Camera-trap data may provide a more precise estimates, but genetic data returns more information on other aspect of genetic health and connectivity. Combining data sets in an integrated modeling framework, aiding in pinpointing strengths and weaknesses in data sets, thus ultimately improving modeling inference.

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Chapter 1

General Background

CHURIA “FORGOTTEN TIGERLAND”

The Churia range, also known as the Siwalikhs, is one of the youngest of the five mountain ranges in Nepal (Hagen 1961). Extending from the Indus River in Pakistan to the Brahmaputra River in India, churia habitat exhibits the highest density of forest cover in Nepal (73% forest cover). The rich faunal diversity includes primates, carnivores, ungulates, birds, and reptiles (Bhuju and Yonzon 2000). Parsa, Chitwan, Bardia, Banke, and Suklaphanta National Parks in the Nepali lowlands, or the Terai, cover prime tiger habitats, which are connected through churia habitat (Wikramanayake et al. 2004).

Lowland areas are the prime habitat of tigers (*Panthera tigris tigris*) and are composed of alluvial floodplain grassland, riparian forest, climax forest, and forest across the foothills of the churia. The churia habitat covers 68% of the core areas of the national park, and is similar across the major tiger conservation landscape (TCL) in Nepal. The southern part of Corbett Tiger Reserve in India, which primarily consists of churia habitat, supports one of the highest tiger densities in the region with 17 individuals per 100 km^2 (Contractor 2007). The 2009 nation-wide tiger survey in Nepal estimated a total of 121 adult tigers; however, this could be grossly underestimated due to exclusion of churia habitat from their sampling (DNPWC 2009). Hence, this proposed study could demonstrate huge potential for churia habitat to support rich tiger density in Nepal. Dhakal et al (2014) on the other hand, estimated 198 tigers in Nepal representing major habitats including churia habitat.

Historically, tiger ecology studies (Seidensticker 1976, Sunquist 1982, Tamang 1983, Smith 1985) have investigated the floodplain habitat, but unfortunately, such studies tend to overlook the churia, even though it occupies a major part of the tiger habitat. Additionally, the churia habitat is under tremendous pressure from illegal hunting of prey animals (which are important to tiger survival) and unsustainable extraction of fodder, fuel wood, timber, and non-timber forest products (see chapter 3 for details). A habitat wide assessment of tiger distribution and abundance is important and crucial for tiger conservation in churia, which holds a significant proportion of land base in the Terai Arc Landscape (Here after referred as Terai Arc). The Government of Nepal recently unveiled its goal of doubling the tiger population by year 2022 (GTRP 2010). This goal may be fulfilled with effective tiger conservation strategies that include the churia habitat. This study, therefore, addresses a gap in understanding of the density of tigers and their prey, habitat use by tigers, and prey occupancy across the important, yet little-known churia habitat. Based on primary field data collected from Churia habitat in Chitwan National Park, the present study covered two main objectives: first, I estimated tiger, leopard, and prey density across the Churia habitat; and second, I examined occupancy of prey and habitat use of tigers in churia habitat. My findings and results are relevant to tiger ecology in the churia habitat, and each study addressing an objectives is presented as a separate paper in chapter 2, chapter 3 in the dissertation, respectively. The titles of these two chapters are entitled as:

- Forgotten tigerland: tigers, leopards, and prey densities in the Churia habitat of the Terai Arc in Chitwan National Park, Nepal (Chapter 2)
- Prey and tigers on the forgotten trail: examining prey occupancy of prey and tiger habitat use in the understudied Churia of Nepal (Chapter 3)

TIGER GENETIC STUDY IN NEPAL

The tiger is the largest felid species in the world and a broadly recognized symbol of wildlife conservation. Dinerstein et al. (2007) documented that tigers are found in 40% less area than they were thought to occupy just a decade ago, and now they are limited to just 7% of their historic range. The global population size is fewer than 3000–4000 animals surviving in fragmented local populations (Morell 2007, Ranganathan et al. 2008). Further, the world's fastest-growing human populations are crowding landscapes where tigers persist.

The Terai Arc is a tiger-inhabited landscape on the southern slope of the Himalayas, with highly productive alluvial grasslands and riverine forests capable of supporting some of the highest tiger densities across the range (Wikramanayake et al. 2004, 2010). Habitat is characterized by savannah grasslands and evergreen and deciduous forest. In this human-dominated landscape, the Government of Nepal and the partners have set the ambitious goal of sustaining 550 tigers (MoFSC 2004). Demographically, core tiger populations are limited to three sub-populations in five protected areas across the landscape: the Chitwan population (Parsa Wildlife Reserve and Chitwan National Park), the Bardia population (Bardia National Park-Banke National Park) and the Suklaphanta population (Suklaphanta Wildlife Reserve), with an estimated 198 adult tigers (Dhakal et al. 2014, Table 1.1).

The potential tiger habitats outside the protected areas are subjected to human pressure and expanding infrastructure development (MoFSC 2007). Analysis of the root cause of biodiversity loss showed that habitat loss and fragmentation are the main drivers for the dwindling number of tigers in the landscape (MoFSC 2004). The good news is that all three sub-populations of tigers are linked to each other by varying degrees of forest connectivity which, when restored, can facilitate gene flow among the respective sub-populations (Dutta et al. 2013, Sharma et al. 2013). The Government of Nepal has identified critical restoration sites across the landscape and is implementing a corridor restoration project. There have been some encouraging results from these efforts; some patches of the forest corridors have been restored, and a camera-trap study in corridors has confirmed the presence of tigers and their use of these restored forest patches to move between core areas (WWF 2006, 2012).

Although the camera-trap data confirm tiger presence, there remains the need to assess genetic admixture between the sub-populations, i.e., to determine whether there is distinct genetic structure or the meta-population is in panmixia. It is imperative to evaluate connectivity to ensure long-term survival of tigers because small subpopulations that become spatially and genetically isolated from the meta-population are more vulnerable to local extinction than those that are connected (Ford et al. 2009). Although tigers occur at high densities in prime habitat within the protected areas of the Terai, these refuges are fast becoming insular. There are indications of inbreeding depression in sub-populations of tigers isolated within particular reserves

With over four decades of conservation history, restoration of functional connectivity raises the hope of improving the probability of long-term persistence in these fragmented tiger populations by increasing gene flow, thereby preserving genetic diversity (Wikramanayake et al. 2010). This hypothesis should be examined by estimation of the rate of gene flow between sub-populations, an estimate that can be obtained through a population genetics study (Sharma et al. 2013). Knowledge of genetic structure also will have implications for assessing the management strategy of restoring forest connectivity across critical areas between sub-populations.

In south Asia, research on tiger genetics has been focused on multiple sites across the tiger conservation landscapes of India (Bhagavatula and Singh 2006, Mondol et al. 2009, Sharma et al. 2009, Reddy et al. 2012a, Reddy et al. 2012b, Dutta et al. 2013, Joshi et al. 2013, Sharma et al. 2013); however, in Nepal, no tiger genetic study has been undertaken in order to assess genetic diversity, genetic structure and gene flow across sub-populations in the fragmented landscape. Camera-trapping has been a reliable technique for estimating population abundance and density (O'Connell et al. 2011). Employing a capture-recapture framework (Williams et al. 2002), population abundance and density can also be estimated using a non-invasive genetics approach (Mondol et al. 2009, Gopalaswamy et al. 2012, Sollmann et al. 2013). I collaborated with the Department of National Park and Wildlife Conservation, the Center for Molecular Dynamics-Nepal and the University of Idaho to undertake Nepal’s first genetic study of tigers employing the molecular scatology (Kohn and Wayne 1997, Reed and Tollit 1997) techniques using tiger fecal samples as the source of DNA. I conducted the study along the Nepali side of the Terai Arc focusing on protected areas and corridors.

My main objectives using the non-invasive genetics approach were to: assess the genetic variation, genetic structure and gene flow among the tiger sub-populations in the Terai Arc; and to compare the abundance and density estimates of the tiger population from the two non-invasive survey techniques: camera-trapping and molecular scatology surveys using both non-spatial and spatially explicit capture-recapture frameworks. These two studies were drafted as separate papers and synthesized in Chapter 4 and Chapter 5 in the dissertation. The titles of these respective papers are:

- Genetic diversity, genetic structure and gene flow of tigers in Terai Arc Landscape, Nepal (Chapter 4)

- Comparison of abundance and density estimates from noninvasive sources: genetic and camera-trap capture-recapture analyses (Chapter 5)

STUDY AREA

Chitwan National Park

Chitwan National Park (CNP) is the first national park in Nepal, established in 1973 and granted the status of World Heritage Site in 1984 (Bhuju et al. 2007). It covers an area of 932 km^2 and is located in the subtropical Inner Terai lowlands of south-central Nepal in the Chitwan district (Figure 1.1). Its elevation ranges from about 100 meters (330 ft.) in the lowland valleys to 815 meters (2,674 ft.) in the churia hills. In the north and west of the protected area, the Narayani - Rapti river system forms a natural boundary to human settlements. Adjacent to the east of CNP is the Parsa Wildlife Reserve, and contiguous in the south is the Valmiki Tiger Reserve. The contiguous protected area of 2,075 km^2 represents the Tiger Conservation Unit (TCU) Chitwan-Parsa-Valmiki, which covers a 3,549-km^2 block of alluvial grasslands and subtropical moist deciduous forests (Wikramanayake et al. 2004). In 1996, a 750-km^2 buffer zone was delineated; 55% agricultural and settlement areas and 45% community forests (DNPWC and PPP 2000) (Figure 1.2). Churia habitat within Chitwan National Park covers an area of 639 km^2 of forested habitat (WWF 2010). The major part of the churia (*Chure* in the local dialect) habitat is located across the eastern part of the Chitwan National Park, covering an estimated area of 363 km^2, the 276 km^2 of forested habitat exists in the western part (Figure 1.2).

CNP is located in the central climatic zone of the Himalayas, where the monsoon starts in mid-June and eases off in late September. Annual precipitation is 2,500 mm. After mid-October, the monsoon clouds retreat, humidity decreases, and the daily temperature gradually subsides until late February. November-February is typically a winter season with sporadic rain. After February, temperature gradually increases and a dry summer season begins, which typically ends in June with the beginning of the monsoon season.

The typical vegetation of the Inner Terai is Himalayan subtropical broadleaf forests with predominantly sal (*Shorea robusta*) trees covering about 70% of the national park area. The purest stands of sal occur on well-drained lowland in the center. Along the southern face of the Churia Hills, sal is interspersed with chir pine (*Pinus roxburghii*). On the northern slopes, sal habitat consists of smaller flowering tree and shrub species, such as beleric (*Terminalia bellirica*), Indian rosewood (*Dalbergia sissoo*), axlewood (*Anogeissus latifolia*), elephant apple (*Dillenia indica*), grey downy balsam (*Garuga pinnata*) and creepers such as *Bauhinia vahlii* and *Spatholobus parviflorus*.

Seasonal bushfires, flooding and erosion drive an ever-changing mosaic of riverine forest and grasslands along the river banks. On recently deposited alluvium and in lowland areas, groups of catechu (*Acacia catechu*) with Indian rosewood (*Dalbergia sissoo*) predominate, followed by groups of kapok (*Bombax ceiba*) and rhino apple trees (*Trewia nudiflora*) (Dinerstein and Wemmer 1988). Understory shrubs of velvety beautyberry (*Callicarpa macrophylla*), hill glory bower (*Clerodendrum viscosum*) and Indian gooseberry (*Phyllanthus emblica*) offer shelter and lairs to a wide variety of species.

Terai-Duar savanna and grasslands cover about 20% of the park's area. More than 50 plant species are found here, including some of the world's tallest grasses, like elephant grass (*Saccharum ravennae*), giant cane (*Arundo donax*), khagra reed (*Phragmites karka*), and several species of true grasses. Kans grass (*Saccharum spontaneum*) is one of the first grasses to colonize new sandbanks and to be washed away by the yearly monsoon floods (Peet et al. 1999, Dinerstein 2003) (Dinerstein 2003; Shrestha and Dongol 2006). The major habitat types of Chitwan National Park are forest (88%), grassland (5%) and other major cover types (11%; Figure 1.3) (Nagendra et al. 2005).

CNP is home to 43 species of mammals (Baral and Shaha 2008). Tigers, leopards (*Panthera pardus fusca*) and dholes (*Cuon alpinus*) are the top carnivores. The estimated adult tiger population size is 125 (SE 21.8) with a density of 4.5 (SE 0.35) tigers per 100 km^2 (Karki et al. 2013). Leopard abundance is estimated at 57 (SE 9.43) adult leopards with a density estimated at 3.45 leopards per 100 km^2 (Thapa 2011). Dholes are concentrated within Churia habitat with trapping rate of 1.02 dhole photographs per 100 trap-nights of effort (Thapa et al. 2013a). In addition to top carnivores, fishing cat (*Prionailurus viverrinus*), jungle cat (*Felis chaus*), leopard cat (*Prionailurus bengalensis*), marbled cat (*Pardofelis marmorata*), golden jackal (*Canis aureus*), sloth bear (*Melursus ursinus*), Bengal fox (*Vulpes bengalensis*), spotted linsang (*Prionodon pardicolor*), large Indian civet (*Viverra zibetha*), small Indian civet (*Viverricula indica*), honey badger (*Mellivora capensis*, Ratel), and yellow-throated marten (*Martes flavigula*) are present. Clouded leopards (*Neofelis nebulosa*) were originally reported in CNP (Dinerstein and Mehta 1989) but translocated to Chitwan from the Butwal area (northwest of Chitwan). In 2012, a clouded leopard was captured by villagers on the outskirts of the buffer zone (Ghimirey et al. 2014) and later captured in a regular camera-trap survey in CNP (WWF 2013).

Four deer species are found in CNP, spotted deer (*Axis axis*), sambar (*Rusa unicolor*), barking deer (*Muntiacus muntjak*), and hog deer (*Axis porcinus*). The wild pig (*Sus scrofa*) is the common feral pig found in CNP. CNP harbors the largest population of gaur (*Bos gaurus*, the Indian bison) in Nepal besides Parsa Wildlife Reserve (WWF 2006). They are predominantly found in the churia range in the southern part of CNP (see Chapter 3 for more details). The Chitwan gaur population increased from 188 to 296 animals between 1997 and 2007 (WWF 2008). I recorded the presence of Himalayan serow (*Capricornis thar*) in my camera-trap survey (see chapter 2 for details) and found indirect evidence of nilgai (*Boselaphus tragocamelus*) and four-horned antelope (*Tetracerus quadricornis*) during the field surveys in churia habitat. The goral (*Naemorhedus goral*) also was photographed during the camera-trap survey in Chitwan National Park (WWF 2013). These ungulates make up the prey base for carnivores in Chitwan National Park.

CNP has a founder population of the one-horned rhinoceros (Dinerstein 2003, Thapa et al. 2013b). The current population size is estimated at 503 individuals (Subedi et al. 2013). Rhinoceros mostly reside in the lowland areas of Nepal and prefer alluvial floodplain grassland and riverine forest across the Rapti and Rue rivers (Dinerstein 2003). There are a few migratory elephants (*Elephus maximus*) that migrate between Parsa Wildlife Reserve and CNP.

Habitat invasion by invasive plants such as *Mikania micrantha* (mile-a-minute weed), is rapid in the moist low land areas of Chitwan National Park (Murphy et al. 2013) and one of the most difficult weeds to manage in tropical areas of Nepal (Poudel et al. 2005). Weed invasion by *Mikania micrantha* is lower in churia habitat except along the moist gullies (personal observation).

The Terai Arc Landscape

The Terai Arc Landscape is a vast conservation landscape covering an area of 49,500 km^2 (E80°04'–E85°30’, N26°45'–N29°07’), stretching from Nepal’s Bagmati River in the east to India’s Yamuna River in the west (Figure 1.4). It links 12 transboundary protected areas from the Parsa Wildlife Reserve in Nepal to Rajaji National Park in India. The protected areas are linked together by the churia hills that run east to west, covering an area within Nepal’s portion of the Terai Arc covering an area of 23,199 km^2. Forested habitat across the churia ranges vary from dense, intact forest to various stages of degradation (MoFSC 2004). The expanding human population, increased development, and extraction of firewood and fodder are the principle causes of disturbances and degradation within the forests (Wikramanayake et al. 2010, Kanagaraj et al. 2011).

Five protected areas found in the Nepal side of Terai Arc: Parsa Wildlife Reserve (499 km^2), Chitwan National Park (932 km^2), Banke National Park (550 km^2), Bardia National Park (968 km^2) and Suklaphanta Wildlife Reserve (305 km^2). Five critical corridors and bottlenecks areas have been identified across the landscape, and habitat restoration has been carried out to save the critical areas for the dispersal of large fauna in the landscape (Wikramanayake et al. 2010, Barber-Meyer et al. 2013, Figure 1.5).

The Terai Arc forms part of the Terai Duar Savannah and Grasslands ecoregion, with subtropical deciduous vegetation ranging from early successional floodplain communities to mature sal (*Shorea robusta*) forests (Barber-Meyer et al. 2013) (Figure 1.6). The Terai Arc, Nepal contains the last remaining alluvial floodplain grassland which holds a high density of tigers and other carnivores. The Terai forests has high-value timber trees species such as Sal, Saj (*Terminalia tomentosa*), Sissoo (*Dalbergia sissoo*) and Khair (*Acacia catechu*) (Figure 1.6). Total forest cover inside the protected areas is 2956 km^2, while forested areas outside the protected areas cover 9395 km^2 within 12 Terai districts found in Terai Arc (Figure 1.7). The average annual rate of deforestation recorded was -0.13% (DoF 2005) (Table 1.2). Forest cover (by area) declined by 34% in the last 50 years (1960-2009) in the Terai Arc (Figure 1.8).

The Terai Arc, Nepal is home to Asia's largest mammals: the tiger (*Panthera tigris*), the elephant (*Elephus maximus*) and the one horned rhinoceros (*Rhinoceros unicornis*). Tiger, leopard, hyena and wild dog are the top predators found in the landscape. Five species of deer (sambar, swamp deer (*Cervus duvaucelli*), chital, barking deer, hog deer), four antelopes (nilgai, goral, four horned antelope and Himalayan serow), wild boar, along with primates common langur (*Semnopithecus entellus*), and common monkey (*Macca mulatta*) forms the important prey base for carnivores in the Terai Arc. Additionally, the river dolphin (*Platanista gangetica*) is a major flagship species found in the major river system in Terai Arc, Nepal.

Domestic livestock, chiefly buffalo, cattle, and goats, graze in the nearby forest and open grazing areas and forming potential prey for carnivores (Madhusudan 2003) in the Terai Arc (Harihar et al. 2009). Today, 6.7 million people of mixed ethnic groups and migrant histories live in the Terai Arc, Nepal. Hill migrants generally settled in the Terai's northern regions and indigenous Tharus populate the southern regions. Migration, particularly from adjoining hill districts, continues to be a leading cause of population growth in the Terai (MoFSC 2004).

People are heavily dependent upon the forest for their subsistence livelihoods for items such as firewood, fodder and non-timber forest products. Agriculture and livestock are key components of the livelihoods of the people in Terai Arc (MoFSC 2004). Poaching remains biggest threat to wild population in the Terai Arc.

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TABLES AND FIGURES

Table 1.1: Summary of estimated tiger abundance (N-hat) in the Terai Arc Landscape (Dhakal et al. 2014). “*” sex ratio calculated based on minimum numbers of tigers identified in the capture-recapture sampling.

Tiger Conservation Unit (TCU)	Protected Areas	Estimated Population Size ($\hat{N}$)	95% CI	Sex Ratio* (M:F)
Chitwan Population	Parsa Wildlife Reserve	7	4-7	1:3
	Chitwan National Park	120	98-139	18-60
Bardia Population	Banke National Park	4	3-7	2:1
	Bardia National Park	50	45-55	14:30
Suklaphanta Population	Suklaphanta Wildlife Reserve	17	13-21	5:8

Table 1.2: Annual rate of change in forest cover (1990-2000) by district in Terai Arc, Nepal (DoF 2005)

S.No	**District**	**Forest Cover (1990/91) (in km^2)**	**Forest Cover (2000/01) (in km^2)**	**Change in Forest Cover (in km^2)**	**Rate of Change**
1	Kanchanpur	545	519	-26	-0.49
2	Kailai	2104	2059	-45	-0.22
3	Bardia	355	337	-18	-0.51
4	Banke	1131	1108	-23	-0.20
5	Dang	1912	1943	31	0.16
6	Kapibastu	646	622	-24	-0.37
7	Rupendhi	273	265	-8	-0.29
8	Nawalparsi	910	932	21	0.23
9	Chitwan	617	636	19	0.30
10	Parsa	189	186	-3	-0.14
11	Bara	496	492	-5	-0.10
12	Rautahat	295	296	1	0.03
13	Protected Areas	2404	2406	2	0.09

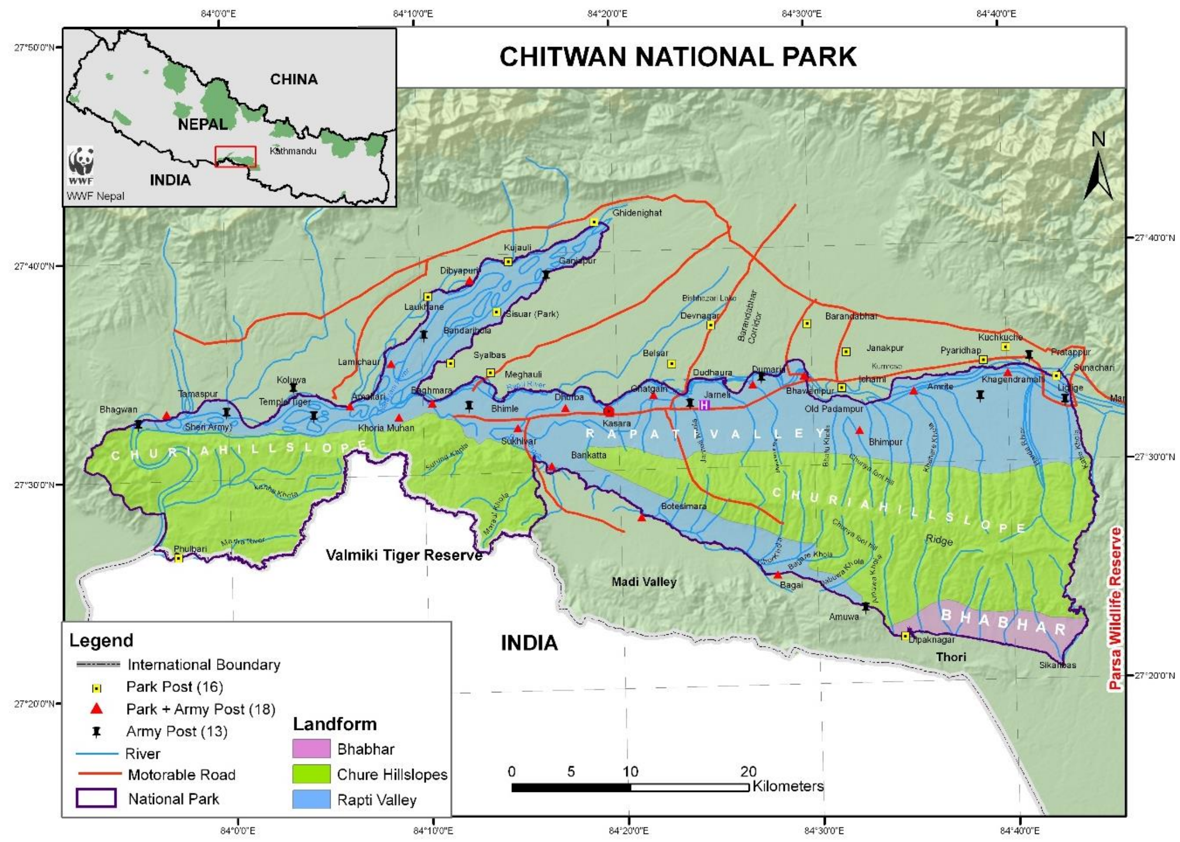

Figure 1.1: Study area in Chitwan National Park.

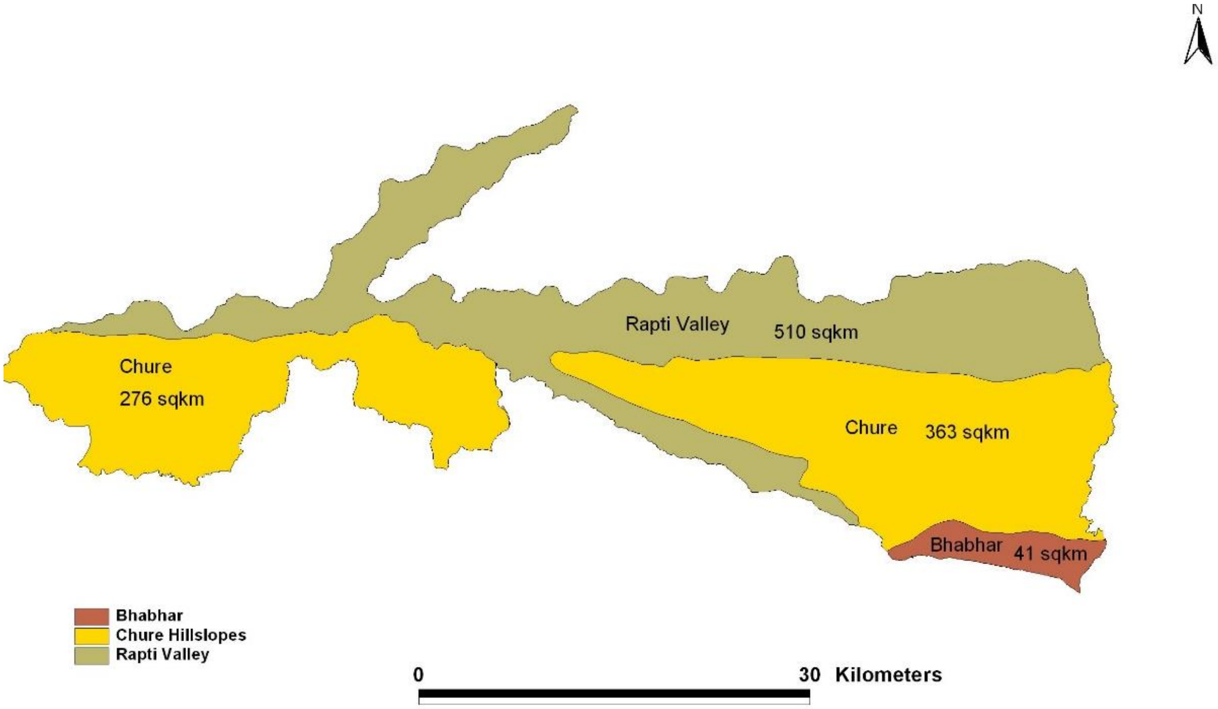

Figure 1.2: Landform classification in Chitwan National Park. Chure refers to the Churia habitat.

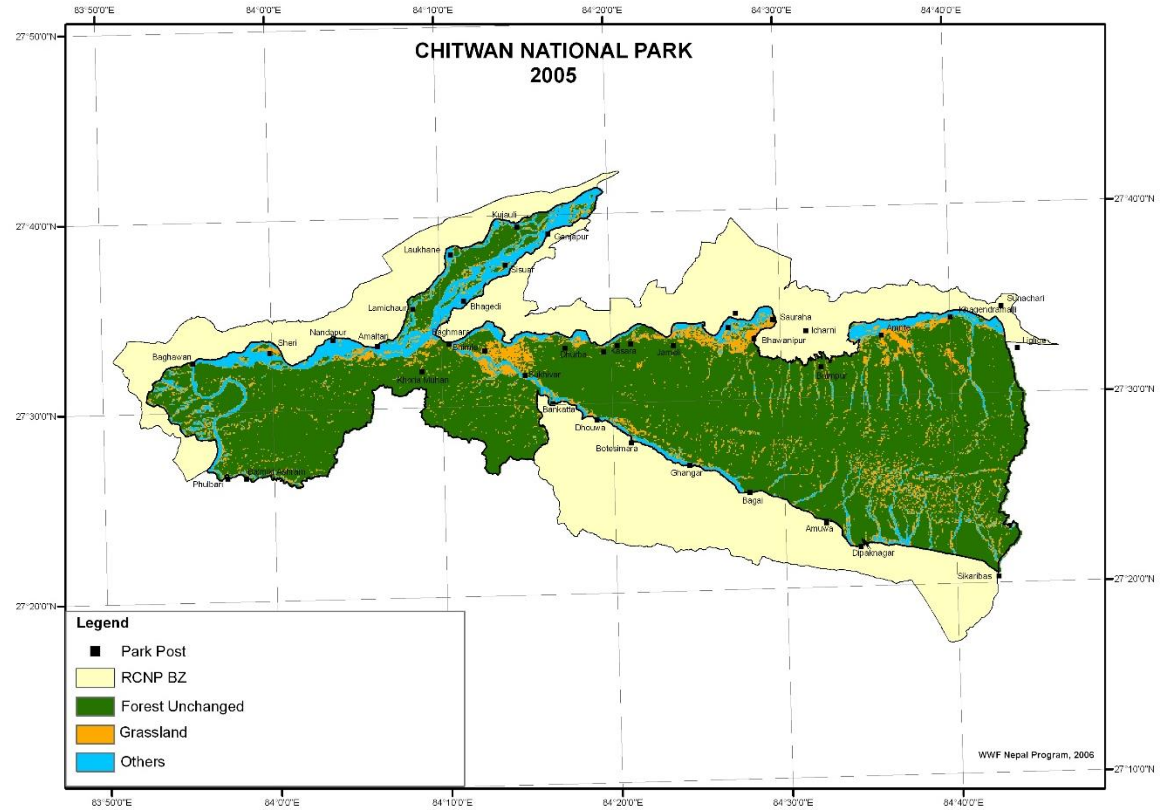

Figure 1.3: Land use of core areas of Chitwan National Park based on 2005 forest classification.

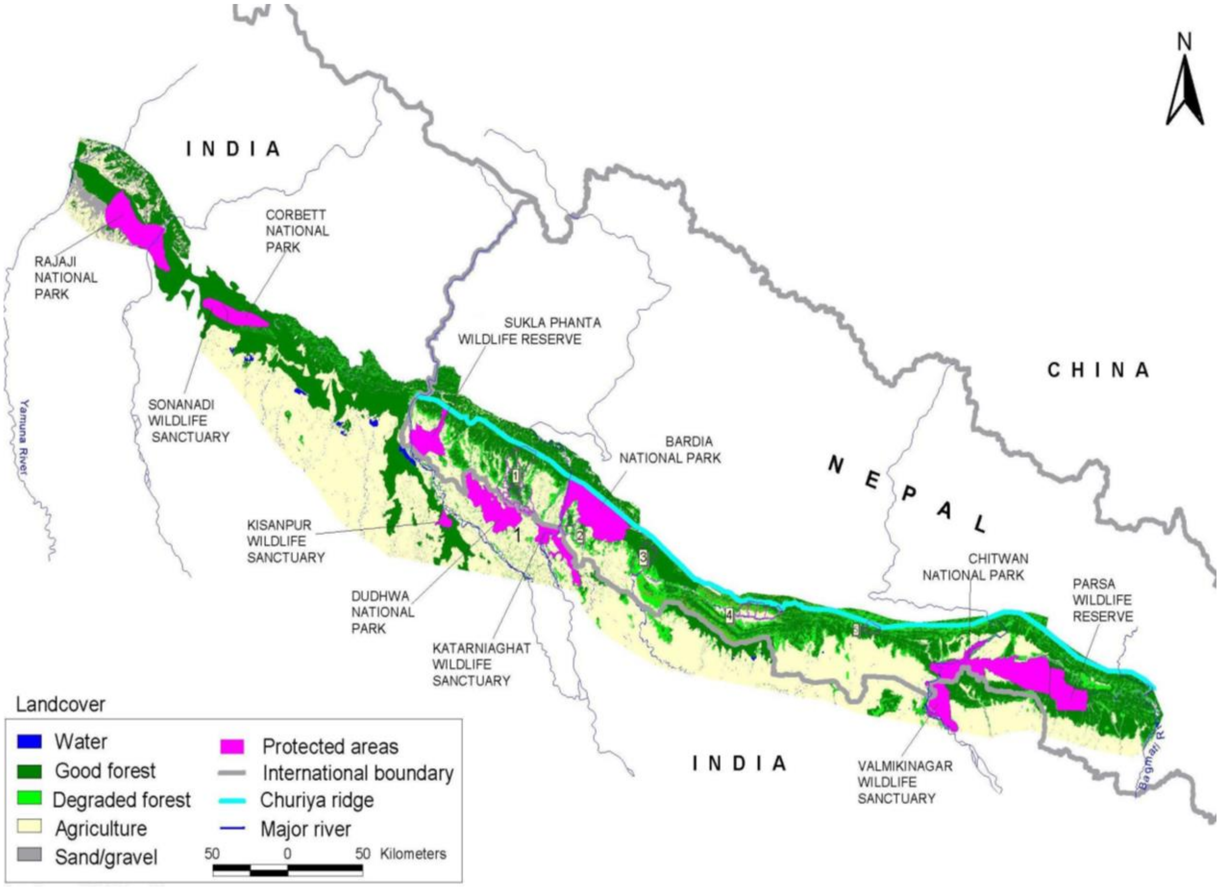

Figure 1.4: The Terai Arc Landscape-Nepal, including seven protected areas in India. Banke National Park adjacent to Bardia National Park in the east was declared in 2011.

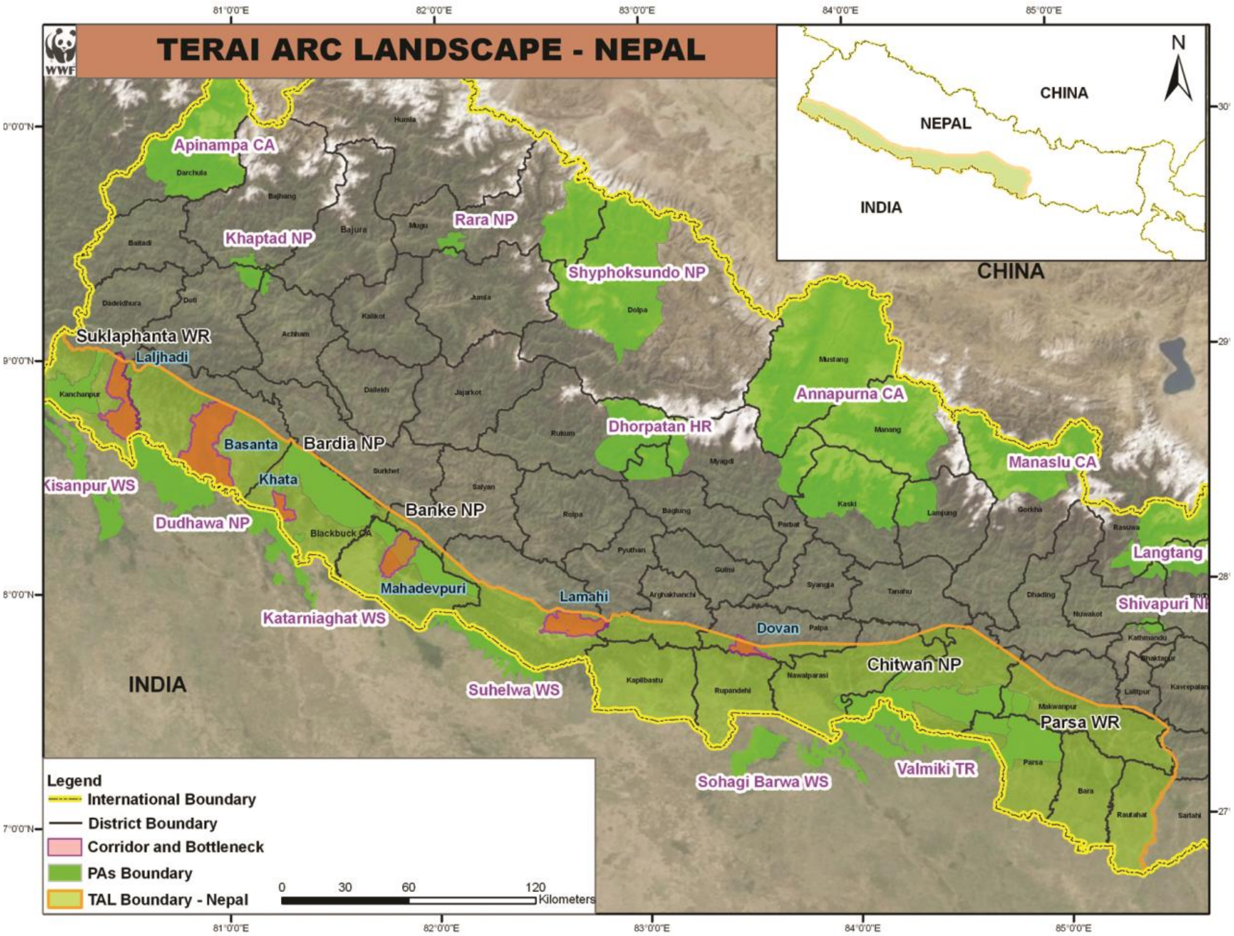

Figure 1.5: Terai Arc Landscape-Nepal, including six critical sites (3 corridors and 3 potential bottleneck areas)

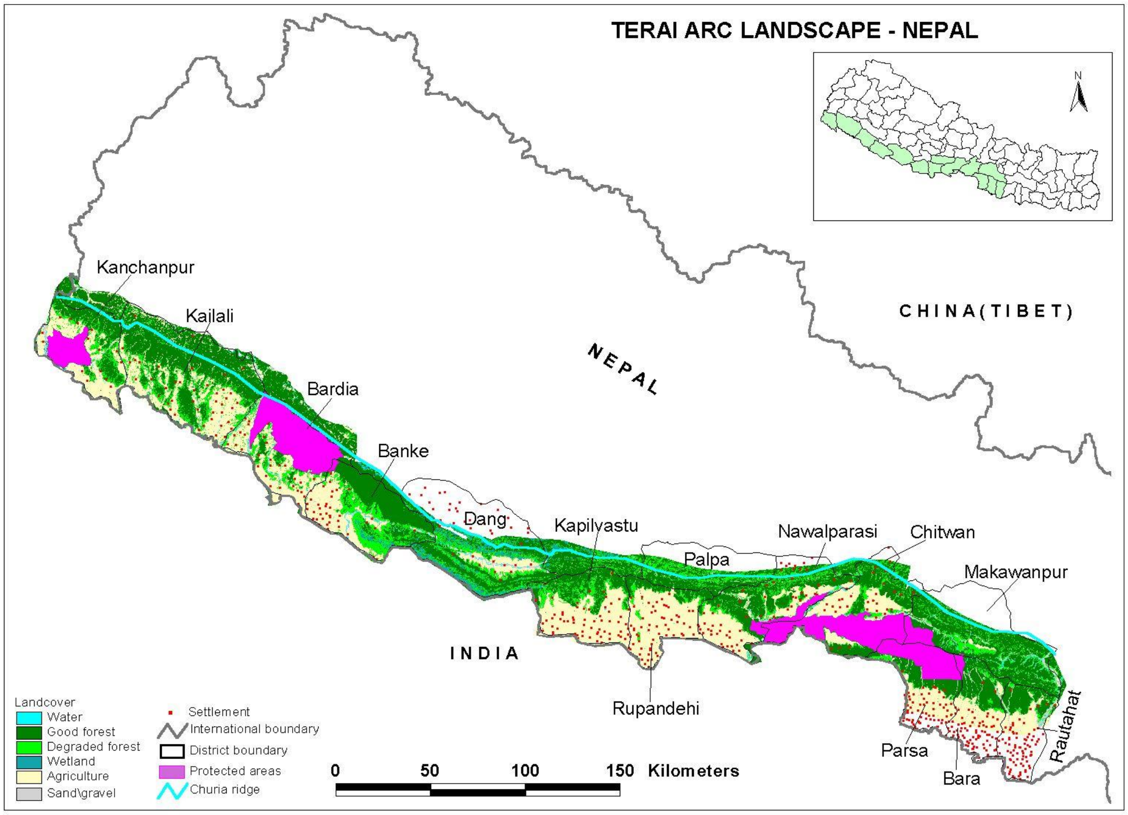

Figure 1.6: Major land-use types across the Terai Arc Landscape-Nepal, including 14 districts.

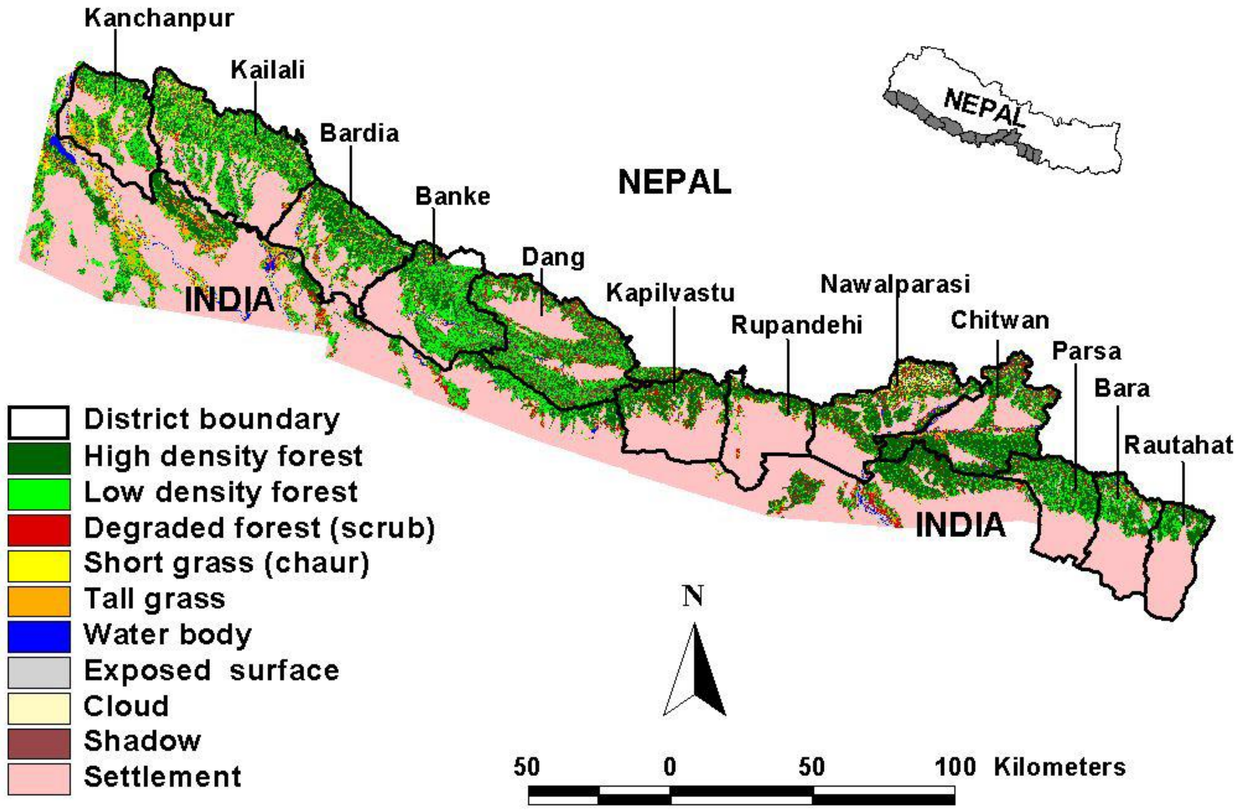

Figure 1.7: Generalized forest classification of Terai Arc Landscape (Joshi et al. 2003)

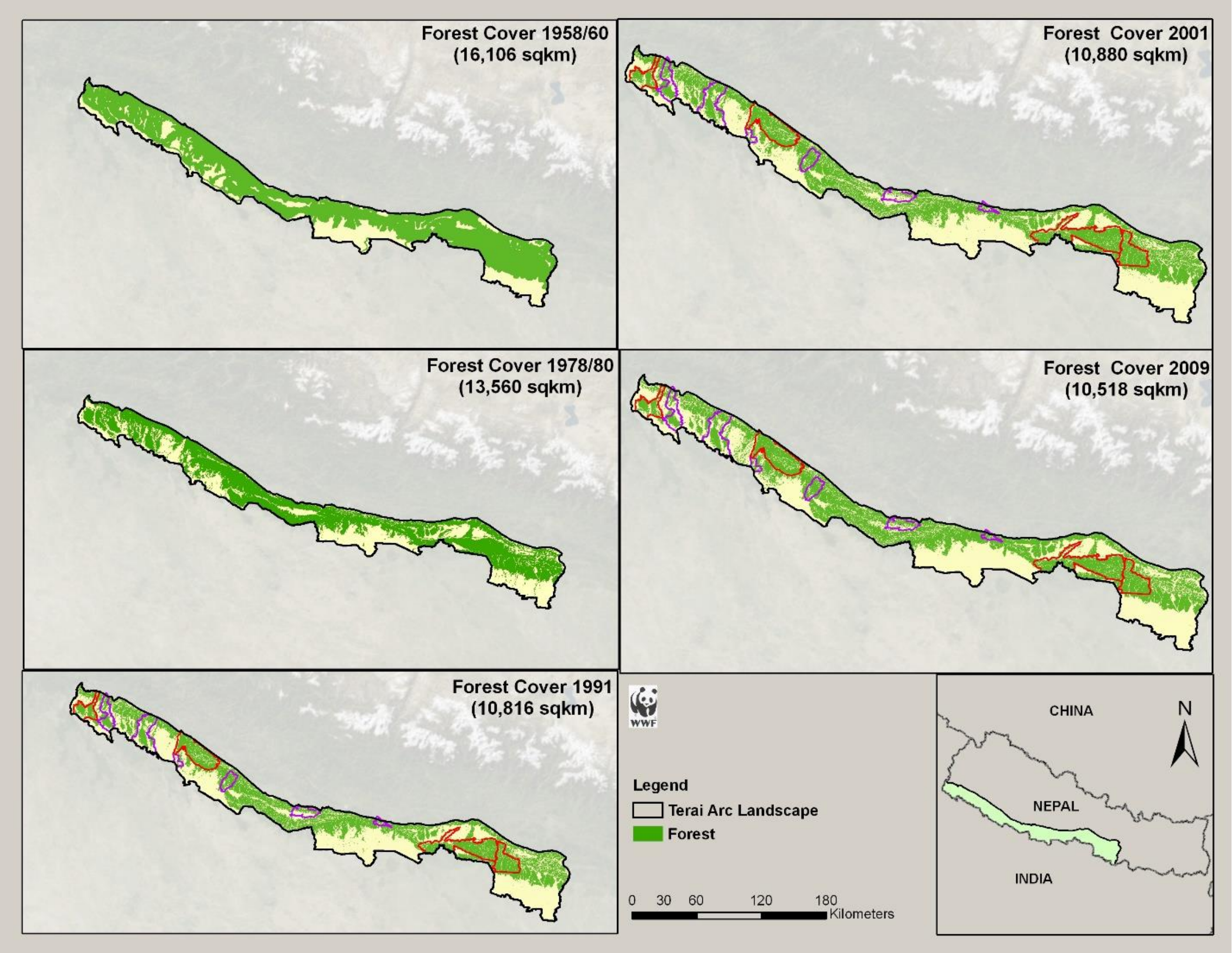

Figure 1.8: Forest cover change in Terai Arc Landscape (1958-2009).

Chapter 2

Forgotten tigerland: tigers, leopards, and prey densities in the Churia habitat of the Terai Arc in Chitwan National Park, Nepal

ABSTRACT

Churia habitat is relatively unknown in terms of the status of tigers and their prey, yet it covers a significant proportion of forested landscape in lowland areas of Nepal. This study investigated tiger, leopard, and prey densities and predicts the tiger density across the churia habitat. I used a camera-trap grid with 161 locations accumulating 2,097 trap-nights in a 60 day survey period during winter of 2010-2011. Additionally, I used distance sampling techniques for estimating prey density in Churia habitat by walking 136 km over 81 different line transects. The team photographed 31 individual tigers and 28 individual leopards along with 25 mammalian species from a sampling area of 536 km^2 comprising Churia and surrounding areas. Using the M_h jackknife estimator, I estimated 36 (SE 6.11) tigers and 55 leopards (SE 12.49) using Program CAPTURE and 32 (SE 3.55) tigers and 43 leopards (SE 10.07) using Program MARK. Density estimates via traditional buffer strip methods (½ MMDM) were 4.16 (SE 0.75) tigers and 6.77 (SE 1.64) leopards per 100 km^2 in churia habitat. Spatially explicit capture recapture (SECR) models resulted in lower density estimates both in likelihood based program DENSITY at 2.26 (SE 0.72) tigers and 3.78 (SE 2.61) leopards per 100 km^2, and Bayesian based program SPACECAP at 2.21 (SE 0.42) tigers and 4.00 (SE 1.00) leopards per 100 km^2 in churia habitat and surrounding areas. To reduce the impact of edge effect caused by animals from the lowlands entering the churia habitat, I also analyzed the core of the churia defined as the area within 2 km of the lowland edge. Density estimates within core of core churia were 2.08 (SE 1.13) tigers and 6.79 (SE 1.99) leopards per 100km^2. Tiger density was found to be similar while leopard density varied across the spatial scale. I recorded 163 detections of potential prey and, using program DISTANCE, estimated density of 62.70 prey animals per 100 km^2 with contribution from forest ungulates to be 47% (sambar, chital, barking deer, and wild pig). Churia habitat within Chitwan National Park is capable of supporting 5.86 tigers per 100 km^2, calculated based on a previous model developed to predict tiger density based on prey density. My density estimates from camera-traps are lower than this ranging from 1.54 - 4.17 tigers per 100km^2 perhaps indicating that the tiger population is below the carrying capacity based on prey availability. Nonetheless, the churia habitat is capable of supporting 9 to 37 tigers, adding additional individuals to the current population in CNP. In addition to its conventional role in forest conservation and watershed protection, the churia habitat should no longer remain a forgotten tigerland because it has great potential to harbor tigers. Conservation initiatives should focus on reducing human disturbance to boost prey populations to potentially support higher predator numbers in Churia.

Keywords: Tiger, camera-trapping, spatially explicit capture recapture, prey density, distance estimation, carrying capacity, leopard, churia habitat

INTRODUCTION

The tiger (*Panthera tigris tigris*) is the top predator in the Indian subcontinent (Sunquist and Sunquist 2002) and plays an important role in shaping prey assemblages in the lower trophic levels (Karanth and Sunquist 1995). Despite their ecologically significant role in ecosystem health (Ritchie et al. 2012) and the long history of concern for their survival, tigers are still being decimated (Seidensticker 2010) and their range has collapsed, to less than 7% of their historic range (Sanderson et al. 2006, Walston et al. 2010). Among the top predators sympatric with the tiger is the leopard (*Panthera pardus fusca*), which is more widely distributed than the tiger because of its ability to live in different environments and its diet flexibility (Bailey 1993). The leopard's range also has collapsed considerably, and now occupies only 65% of the historic range (Ripple et al. 2014). The primary drivers of declines for both carnivores are similar, namely the loss and fragmentation of suitable habitat, depletion of natural prey, and direct persecution by people (Karanth and Stith 1999, Balme et al. 2010, Walston et al. 2010). Conservation of these large carnivores has been a global priority due to their vulnerability to extinction, their potential ability to structure ecosystems (Ripple et al. 2014), and because they serve as "umbrella" species across a wide range of habitats (Wang and Macdonald 2009). In South Asia, these sympatric predators occupy a wide range of habitats including alluvial floodplain grasslands (Smith 1993), seasonally dry sub-tropical deciduous forests in the lowlands (Seidensticker 1976, Odden et al. 2010) and the bhabhar physiographic region (Thapa et al. 2014), and stretching beyond the sub-tropical into temperate areas extending up to alpine regions in the Himalayas for leopards (Wang and Macdonald 2009) and mangrove deltas for tigers in the Sunderbans (Seidensticker 1987, Loucks et al. 2010).

The Terai Arc Landscape (hereafter referred as the Terai Arc) is a high priority landscape for tiger conservation, containing 12 sub-populations connected to varying degrees (Wikramanayake et al. 2004, 2010). The Churia, also called the Siwalikhs, is one of the youngest of the five mountain ranges in Nepal (Hagen 1961) (Figure 2.1) and occupies 13% of the total land surface (LRMP 1986), extending from the Brahmaputra River in the east in India to the Indus River in the west in Pakistan (Jhingran 1981). Due to uplift and erosion of the Himalayas in the Middle Miocene, strata of fluvial mudstone, sandstone, and conglomerates were formed along the Indo–Gangetic foreland basin (Nakayama and Ulak 1999). Forest cover within the Churia is the high (73% has intact forest cover, LRMP 1986), and conservation of Churia is critical to maintain connectivity across the landscape in Nepal and India (Wikramanayake et al. 2004, Seidensticker et al. 2010, Jhala et al. 2011, Barber-Meyer et al. 2013). Nevertheless, the Churia of Nepal generally suffers from degradation (natural and anthropogenic) and over-exploitation (Paudel et al. 2013).

The Churia range extends through a majority of tiger habitat within and outside protected areas across the Terai Arc. However, the majority of classic studies on tiger ecology, including studies of ecological separation (Seidensticker 1976), dispersal and behavior (Smith 1985, 1993), and social organization (Sunquist 1981), have focused instead on the lowland areas comprised of alluvial floodplain grasslands, riverine forests and climax *Shorea robusta* forests (Peet et al. 1999, Dinerstein 2003). I termed the churia habitat as “forgotten tigerland” as its ecological role in tiger conservation has been overlooked because it is generally seen as unsuitable or marginal habitat both inside protected areas and across the landscape. The only data from the Churia come from Karki et al. (2013), who recorded a few individual tigers within the Churia in Chitwan National Park during a camera survey. Thus, if tigers exist in the area, with 600 km^2 of habitat in

Chitwan National Park and 7,642 km^2 across the Terai Arc, the Churia could represent high potential for tiger conservation. To date, however, there have been no studies examining tiger population ecology nor sympatric leopards and the prey base supporting these predators in churia habitat. Thus, habitat and site-specific assessments are needed to make better informed conservation decisions to manage these umbrella species in the forgotten churia habitat.

Against this background, the main objectives of this study were to: 1) estimate population densities of tigers and leopards in the churia habitat using traditional and spatially explicit capture-recapture models in order to estimate densities in an unstudied habitat type and to compare modeling approaches, 2) to estimate potential prey density in the churia habitat using a distance-sampling approach; and 3) to predict tiger abundance within the churia habitat by extrapolating density estimates to the entire area and by scaling the estimated prey density using existing empirical models relating prey biomass to predator energy needs. This study, therefore, addresses a gap in our knowledge of tigers, their co-predators, and prey in this important, yet little-known “forgotten tigerland”. Based on previous studies (Seidensticker et al. 2010, Jhala et al. 2011, Karki et al. 2013), I expected to find a high proportion of tiger and leopard populations existing within the churia habitat, thus positively contributing to the overall population abundance of carnivores and prey populations in Chitwan National Park.

STUDY AREA

This study was conducted in the churia habitat within Chitwan National Park (CNP) located in central Nepal (Figure 2.2). The hilly churia habitat within CNP covers 639 km^2 and is divided into 2 different areas, stretching between the lowland areas on the east (363 km^2) and stretching between the lowland areas of Chitwan National Park and Valmiki Tiger Reserve on the west

(276 km^2). Churia habitat is contiguous with the southern buffer zone, forming a Madi valley with human population density of 440 per km^2 (CBS 2011). The churia habitat is the main corridor joining the Valmiki Tiger Reserve in India and the Parsa Wildlife Reserve in the east to form a Tiger Conservation Landscape (TCL) (Wikramanayake et al. 2004).

The Churia is composed of late tertiary material. This formation contains fine-grained sandstone with deposits of clay, shale, freshwater limestone, and conglomerates (Dinerstein 1979). Churia habitat is an undulating, hilly terrain with elevation ranging from 150 m to 714 m. The ecosystem is dynamic in nature, the substrate conditions are fragile, and as the monsoon season progresses, landslides are common, causing mature trees to fall. Most precipitation occurs between June-September, with annual rainfall of 2,500 mm. After the wet season, the winter season follows for four months (November-February), with lowest temperatures in December and January. The summer season follows for four months from March to June. Deciduous forests shed their leaves at the onset of winter season, and during the following summer season, the area is prone to forest fires which clear most of the ground vegetation. Churia habitat is part of the Rue, East Rapti, and Narayani watersheds. Seasonal and perennial rivers originate in the Churia and cascade down to form important sources of water for wildlife. Perennial rivers like the Kana, Mana, and Sona form the valley within the western part of the churia habitat.

The top soil layer is very thin, with stones and boulders beneath. Churia habitat is composed of mixed deciduous forest. The main vegetation type is Sal forest (*Shorea robusta*) interspersed with other tree species like *Terminalia alata, Syzygium cumini* and *Lagerstroemia parviflora*. Mixed pine (*Pinus roxburgii*) forest emerges at ~400 m elevation and upwards. Bamboo forest is mostly found at the base of the churia hills and across the steep slope areas. Broom grass *Thysanolaena maxima*, asparagus *Asparagus officianalis,* and date palm *Phoenix* *dactylifera* are the main non-timber forest products (NTFP), which are harvested and illegally traded in the local markets.

Tigers, leopards, and dholes (*Cuon alpinus*) are the top carnivores in the churia habitat. Potential prey in the churia include gaur (*Bos garus*), sambar (*Rus unicolor*), chital (*Axis axis*), barking deer (*Muntiacus muntjac*), wild boar (*Sus scrofa*) and primates. In addition, the steep slopes of the churia support four species of antelope: the Himalayan serow (*Capricornis thar*), the goral (*Naemorhedus goral*), the four horned antelope (*Tetracerus quadricornis*) and the nilgai (*Boselaphus tragocamelus*). Churia habitat supports a resident population of elephants (*Elephus maximus*) that extends into the Parsa Wildlife Reserve in the east. Further details on the Chitwan National Park are described elsewhere (Dinerstein 2003, Gurung et al. 2008, Bhattarai and Kindlmann 2012, Karki et al. 2013, Subedi et al. 2013). Illegal logging and NTFP extraction are the two main anthropogenic impacts in the churia habitat. Sporadic poaching incidents have occurred in the western part near the border with India. Livestock grazing within churia habitat is lower than in the lowland forest, yet the impacts are high in the southern part of the habitat.

METHODS

Camera-Trap Survey

I carried out the camera-trap survey from December 2010 to March 2011 to estimate abundance and density of tigers and leopards using a capture-recapture framework (Otis et al. 1978) in which the cats are photographically “captured” and subsequently individually identified by their unique pelage patterns (Karanth and Nichols 1998, 2002b).

Prior to the camera-trap survey, my team and I spent eight days in the field in each survey block conducting a preliminary assessment of potential sites for deploying camera-traps. I also conducted an expert opinion survey with park staff members of the Chitwan National Park (*n* = 6) and other conservation organizations (*n* = 10) regarding their field experience in the churia habitat. Based on the collective information, I divided the study areas into four blocks, each measuring an average of 132 km^2 (SE 23.70) based on the Minimum Convex Polygon (MCP) around camera-traps.

I divided each survey block into a 2km X 2km grid and deployed camera stations within each grid cell. Due to the undulating terrain and ruggedness of the study area, my team (20 field assistants) spent an average of 544 hrs. per block searching for tiger and other carnivore signs (e.g., scrapes, scat, scent marks, claw marks/rakes, pugmarks) to select the appropriate sites in my predetermined camera grids. I non-randomly selected 148 camera-trap locations based primarily on accessibility, with an average of 40 (SE 3.0) camera stations per block. I used combinations of camera-trap models - Moultrie D50, Moultrie D55, and Bushnell. I selected an additional 13 locations in the lowland areas surrounding the churia habitat. The inter-trap distance between two consecutive locations ranged from a minimum of 600 m to maximum of 3,518 m with average distance of 1.56 km (SE 0.09).

Churia habitat is contiguous to lowland forest which is thought to hold the highest density of tigers (2.31 tigers per 100 km^2, DNPWC 2009) in Chitwan National Park. There is a potential edge effect across the boundary between the high density lowland area and the churia habitat, with possible random movement of tigers across the transition zone. Due to large home-range sizes of tigers and leopards, I would expect sharing of habitat between churia and lowland habitat at the transition zone. To discount the potential edge effect (distance to lowland) on detection, abundance, and density, I collected data at three spatial scales (Figure 2.2). In total, I sampled 576 km^2 of churia habitat and surrounding area (denoted CHSA) with 161 locations, then I subsampled 475 km^2 of core area of the churia habitat (denoted CH) with 148 locations, and further subsampled 369 km^2 of the core of core churia (denoted CCC) with 94 locations in Chitwan National Park. For simplicity, I assumed that core animal home-ranges were contained within the core area of the churia habitat (CH). I used a discrete distance of 2 km in from the churia/lowland edge to define the core of the core habitat, and all the carnivores captured within CCC as core animals similar to the approach of Gerber et al. (2012). This geographical division allows comparing population density across the spatial scales.

To maximize capture probabilities, I positioned my camera-traps along river banks (dry and wet, *n* = 119), animal and human trails (*n* = 29), and fire-lines (*n* = 10) where presence of tiger and other carnivore sign was high and because predators are known to follow these routes (Karanth and Nichols 2002b, Karki et al. 2013). Due to the limited number of camera sets, I followed the fourth design protocol (Karanth and Nichols 2002b), with rotation of camera-traps from block to block to cover the area of interest. I followed the standard protocol for deploying the camera-traps (Karanth and Nichols 2002b, Karki et al. 2013) with slight modifications where trap height was fixed relative to the substrate level across the ridges and river banks. Team members were cautious to keep disturbance minimal at each trap location.

I conducted the survey for 64 days during December 2010-March 2011. Team camped for 20 days in each block and all cameras within each block were installed within 2-3 days. Each camera station consisted of 2 camera-traps on opposite sides of the trail and was operational for 15 days in each location and moved to the subsequent block. Camera-traps were active for 24 hrs. and each station was checked every two days for recording purposes and to correct possible malfunctions. I changed the station location 100 m up or down from the original location if there was evidence of trap shyness (e.g., an animal turning away from camera sites, animal moving behind the cameras, etc.). I recorded spatial location with hand-held GPS (Garmin Etrex), time and date, capture details, photo details, battery conditions, and status of memory cards (SanDisk, 2GB) at each visit. I replaced the memory cards at every visit to prevent loss of data due to camera theft and possible camera malfunctions. I had only a few camera malfunctions (*n* = 4), camera theft (*n* = 1), fire damage (*n* = 1), elephant damage (*n* = 2), and theft by langurs (*n* = 1). These problems were resolved by immediate replacement with new camera-traps.

I used the time-lapse image analysis software (Greenberg and Godin 2012) for creating the photo database including the metadata. I imported metadata into Excel (Version 2010) for exploratory data analysis, calculating the independent events, and developing capture histories.

Prey Survey

I used a distance-sampling approach based on line transect surveys for prey density estimation based on visual detection of animals (Buckland et al. 1993, Lancia et al. 1994, Buckland et al. 2001). The team spent a total of 8,160 man hrs. in the field prior to the survey to assess field topography and relative activity of animals across the various sites (Karanth and Sunquist 1992). The relative activity index (trap success: number of independent photo-detections per 100 trap-nights) of potential prey captured during the camera-trap survey aided in designing line transect surveys. The presence of water sources tends to dictate the distribution of the ungulates (Mondal et al. 2013). Due to undulating topographic features leading to difficulty in visually detecting species, I added additional transects to increase the sample size of detections. I located 81 line transects in the churia habitat at variable distances from water sources (seasonal and perennial) and each transect was surveyed twice on alternate days. I stratified transects based on water sources and randomly placed the start of the first location. The team traversed a total of 136 km of line transects in a north-south direction with average transect length of 1.41 km (SE 0.09), minimum 0.2 km and maximum 4.1 km in length. Each transect was marked prior to the survey, and timing between the marking and surveying was kept long to allow recovery following the initial disturbance caused by marking trails. Two observers walked and counted animals on either side of the transect. To maximize visual detections, I carried out the surveys early in the morning between 7:00- 9:00 hrs. and 17:00-19:00 hrs. in the evening (Karanth and Nichols 2002b). I conducted the surveys in the dry seasons of 2011 (eastern section) and 2012 (western section), when visibility is higher due to shedding of the leaves in the deciduous forest and natural clearing of the ground vegetation by early forest fires (Dinerstein 2003).

Upon detection, I recorded time, date, species, number of animals, radial sighting distance (measured with a digital range-finder), sighting angle between animal clusters and the transect (measured with a compass), and animal behavior upon, and following, the detection. I also recorded other ancillary information, such as transect number and length, transect bearing, GPS points of start and end points, vegetation types, and weather conditions.

DATA ANALYSIS

Species Identification and Capture Events

I used the Baral and Shaha (2008) manual for species identification in camera-trap pictures. I also used expert opinion (Drs. A.J.T. Johnsingh, E. Wikramanayake, B. Long, and B. Pandav) and the Smithsonian camera-trap picture repository *Smithsonian WILD* for the final identification of species which could not be identified with the manual. Capture events (independent detections) of each species were calculated based on photographs of distinct individuals within a 30-min period at camera stations (O'Brien et al. 2003).

Individual Identification and Capture History

Individual tigers were identified based on their unique natural stripe patterns on their flanks, limbs, foreheads, and tails (Karanth 1995). Similarly, individual leopards were identified based on their unique rosette pelage patterns on their flanks, limbs, and fore-quarters (Miththapala et al. 1989). Three field assistants independently identified individual tigers and leopards. To maximize consensus on photographs, I also compared photographs to the existing photo database from past surveys maintained at the Biodiversity Conservation Center-National Trust for Nature Conservation (BCC-NTNC) in Nepal for drawing conclusions on individual identification. Finally, I double-checked the individually identified carnivores for any discrepancy in the consensus, and any disagreements on individual identification were discarded from further analysis. I developed three datasets of capture histories at three spatial scales: (1) locations (n = 161) representing the churia habitat and the surrounding area (CHSA), (2) locations (n = 148) representing the churia habitat (CH), (3) locations (n = 94) representing core of core churia (CCC) habitat. Although the cameras were operational for 15 days, all of the 161 locations had functional cameras for 12 days continuously. Therefore, I used 12 sampling occasions for developing capture histories.

Assessing the Closure Violation and Edge Effects

I completed the survey in my 4 sampling blocks in a total 60 days. I used two approaches for assessing closure at three spatial scales. I first used the closure test implemented in program CAPTURE (Rexstad and Burnham 1991). I then used the (Stanley and Burnham 1999) closure test that assumes only time variation in recapture probability using the Pradel model (Pradel 1996) in Program MARK version 5.1 (White and Burnham 1999). The Pradel model evaluates geographic closure by estimating site fidelity (ϕ), immigration (f), and recapture probability (p) with regard to entry into and exit, out of the sampling area under the assumption of the geographic closure for the carnivore population over the 60 day sampling period.

I used four discrete distances (0-500 m, 500 m-1 km, 1-1.5 km, 1.5-2 km) to evaluate edge effects due to distance to the lowland area on trap success of carnivores in the churia habitat. Trap success was defined as the number of independent capture events per 100 trap-nights (O'Brien et al. 2003, Kelly et al. 2008).

Abundance and Density Estimation

I used closed population models (Otis et al. 1978) incorporating effects of time, behavior, heterogeneity, and combinations of these factors (Karanth 1995, Karanth and Nichols 1998) implemented in Program CAPTURE to estimate overall capture probability ($\hat{P}$) and abundance ($\hat{N}$). I also used the Huggins Full Closed Capture with heterogeneity modeling platform in Program MARK (White and Burnham 1999) to estimate abundances. These models use a maximum likelihood framework and I fit the 8 models of Otis et al. (1978), which allow capture probabilities to vary over time (p(t)=c(t)), by individual’s heterogeneity (p(h)=c(h)), due to a behavioral response (initial capture being different from recapture probabilities, p(.) c(.)) along with the null model (with no variation in capture probabilities, p(.)=c(.)), and combinations of the above factors. I constructed tiger and leopard capture histories from the one time winter season with 12, 1-day, encounter occasions. I ranked all the models using sample size-adjusted Akaike’s Information Criterion (AICc) and considered all models with $\Delta\mathrm{AIC}_c < 2$ as competing models (Burnham and Anderson 2002). I estimated abundance at all three spatial scales: CHSA, CH, and CCC.

I used the *ad hoc* traditional approach of adding a buffer strip surrounding the camera-trap polygon for calculating the effective trapping area (ETA). I used the abundance estimates from Program CAPTURE and MARK, divided by the ETA to estimate density. Standard errors were calculated using the delta method (Karanth and Nichols 1998). The buffer strip size was calculated using the ½ Mean Maximum Distance Moved (½ MMDM) by animals captured among different camera-traps. Because this method has been shown to underestimate density in other studies (Soisalo and Cavalcanti 2006, Dillon and Kelly 2008), I also buffered the camera polygon with the full MMDM as a buffer. I removed all the non-habitat area (settlements and agriculture areas) from the buffered area following the procedure of Karanth & Nichols (1998) and Karki et al. (2013). I used the ½ MMDM and full MMDM approaches for density estimates for the CHSA and CH scales only, because the CCC area was too small to accurately reflect the MMDMs.

In the CCC, no buffer width was added because I defined the core area as within 2-km within from the edge of the churia/lowland habitat transition. I used the population estimates for the CCC divided by this predetermined survey area to obtain density estimates. The variance was calculated by dividing the N variance by the square of predetermined survey area (Weinberg and Abramowitz 2008).

To address the shortcomings of the traditional approach in estimating tiger and leopard density, I also used recently developed spatially explicit capture recapture (SECR/SCR) techniques that use spatial information more directly in the density estimation process (Efford 2004, Borchers and Efford 2008, Royle et al. 2009a, Royle et al. 2009b). I compared the maximum likelihood-SECR (ML-SECR) and Bayesian SCR (B-SCR) approaches in estimating density without the need to estimate an effective trapping area using the traditional *ad hoc* buffering approach. In Program DENSITY, I used the estimated log likelihood and root pooled spatial variance (RPSV) of varying integration buffers (Efford et al. 2004, Tredick and Vaughan 2009) for determining the appropriate buffer size surrounding the trapping grid. Then I selected the appropriate detection process either as half-normal, hazard rate, or negative exponential. Using the appropriate detection function, I then allowed g_0 (the capture probability at the center of an individual's home-range) and sigma (a function of the scale of animal movement) to vary using 2-class finite mixture (h2) and/or a behavioral response (b). Thus, a half-normal detection function model with constant g_0 and 2-class finite mixture of sigma would be represented as HN g_0(.) sig(h2). I ranked all the models using sample size-adjusted Akaike's Information Criterion (AICc) and used model-averaging techniques to determine density estimates at all spatial scales (CHSA, CH, and CCC).

I used a Bayesian SCR approach (Royle et al. 2009a) in program SPACECAP (Gopalaswamy et al. 2012) version 1.1.0 (Gopalaswamy et al. 2014) implemented in R package version 3.10, to estimate tiger and leopard density at all spatial scales. I used the habitat extent of 15 km around the MCP delineated by the camera-traps of the CHSA to represent all the probable tiger and leopard habitat and generated a grid of hypothetical home-range centers with equally spaced points (3,254: habitat; 2,076: non-habitat), each 1 km^2 apart. The habitat extent (15 km) roughly represents Chitwan valley and the Valmiki Tiger Reserve, which are historically known to have tiger and leopard habitat (Dinerstein 2003, Seidensticker et al. 2010). After removing the 2,086 km^2 area of settlements (villages and agriculture areas), the area of carnivore habitat over which these activity centers were uniformly distributed was 3,255 km^2. I used the Google Earth map features to delineate the habitat extent. I used all three standard input data files (animal capture locations and dates, trap deployment dates and locations, and hypothetical activity centers). I assumed the half-normal detection function and behavioral response present in the detection process. I performed 300,000 iterations, of which the initial 50,000 were discarded as the burn-in period, a thinning rate was set at 10, and augmentation values of 300 individuals (five times the expected number of ~50 animals) was used in CHSA, 180 individuals in CH and 180 individuals in CCC for both tigers and leopard, respectively. I used the Geweke diagnostic statistics (Geweke 1992) and the |z| score to check for the lack of convergence (Gopalaswamy et al. 2012c).

Prey Activity Index

I segregated the photographs of tiger and leopard potential prey species and calculated photographic trapping rates (trap success) as a surrogate measure of prey activity in the churia habitat. I then calculated trap effort based on the number of the trap-nights at each station, minus any nights where cameras were malfunctioning. A camera-trap activity index of prey was calculated as the number of independent prey photographic events per 100 trap-nights (TN) (Karanth et al. 2003).

Distance Sampling Approach

I used Program DISTANCE (Thomas et al. 2010) to estimate density of each of the potential prey species in the churia habitat. I used exploratory data analysis to check for potential violations of the assumptions such as heaping and evasive movements, data truncation to remove outliers, and readjusted bin sizes for detection functions to improve the model fit. I used the conventional density sampling (CDS) analysis engine in program DISTANCE for modelling the appropriate detection functions and generating final density estimates. I used the uniform key function with cosine adjustments, half-normal key function with cosine or hermite-polynomial adjustments, and hazard-rate key function with simple polynomial adjustments as candidate sets of detection functions. I used the best model to estimate final detection probabilities and density estimates based on lowest AIC value and goodness-of-fit (GoF-p) tests. In the situation of the competing models (e.g. models with < 2 ΔAIC), I calculated the model weight (*w*) and used model averaging techniques incorporating the most parsimonious models for deriving the final estimates (Burnham and Anderson 2002). Due to low detection and sample sizes, I did not use any covariates to evaluate influence on prey density estimates. Due to low detection and differing detection functions for each species, I summed up the species-specific density estimates to present overall ungulate density in churia habitat (Karanth and Nichols 1998) rather than pooling all the detections and estimating a single overall prey estimate. I calculated the overall biomass of prey found in CH using average body size of the potential prey species taken from literature (Karanth and Sunquist 1995, Harihar et al. 2011).

Predicting the Tiger Density

The churia habitat within the Chitwan National Park spans 639 km^2, and I predicted the tiger density (Karanth et al. 2004, O'Kelly et al. 2012, Harihar et al. 2014) that could be supported based on the ungulate density estimates. Predicting tiger densities based on preferred prey (sambar and wild pig) potentially yields results describing the carrying capacity of tigers (Hayward et al. 2012, Harihar et al. 2014). However, no information on preferred prey from churia habitat is available. While sambar and wild pig are preferred prey, chital and muntjac are preyed upon in accordance with their availability (Hayward et al. 2012). I used these 4 prey species density estimates for predicting potential tiger densities. I used the scaling relationship $T_j = \frac{0.10}{50} U_j \ddot{a}_j$ developed by Karanth et al. (2004) specific to tigers, where T_j is the predicted density of tigers and U_j is the density of prey at a site j and, $\ddot{a}_j$ is a mean one random variable which is estimated in the model. The model also reflects the cropping rate by tiger to be 10% from all the available prey (Karanth and Sunquist 1992) and average kill rate of 50 ungulates per tiger per year (Karanth and Stith 1999).

RESULTS

Species Identified in Churia Habitat

Team amassed a total of 35,130 photographs in 2,097 trap-nights of effort after removing 123 trap-nights of camera malfunctions. A total of 15.64% of the animal photos were of 25 mammalian species, including 12 species of carnivores (Table 2.1). I gathered a total of 477 photographs of carnivores including the top predators in the churia: tigers (*n* = 85), leopards (*n* = 67), and dholes (*n* = 22) (Table 2.1). I recorded two events of a leopard and a tiger with cubs, indicating potential breeding populations in the churia.

Individual Identification and Closure Assumption

Two independent observers agreed on 100% and 96% of the individual identifications from the total independent captures of tigers (*n* = 57) and leopards (*n* = 43) respectively. We visually assessed adults (e.g. > 1 year) and found 31 individual tigers and 28 individual leopards in the churia and surrounding area (CHSA). Non-consensus capture events of leopards (*n* = 2) were discarded from further analysis. At the scale of just the churia habitat (CH), we identified 26 individual tigers and 24 individual leopards, while in the core area CCC we found 6 individual tigers and 13 individual leopards. Based on the closure test (Otis et al. 1976) implemented in Program CAPTURE, there were no violations of the closed population assumption in the 60-day sampling period at all spatial scales, except with the tiger population in CCC (Table 2.2). The Stanley and Burnham (1999a) test in program MARK similarly supported the closed population assumptions at all spatial scales including CCC, as models containing site fidelity (ϕ) set to one and immigration (f) set to zero were given full support (Table 2.3). Hence, I used the population estimates for CCC assuming the temporary geographic closure for the tiger population in CCC.

Assessing Edge Effects on the Trap Success of Tigers and Leopards in the Churia Habitat

Trap success (# independent photos/100 trap-nights (TN)) for tigers decreased steadily with increasing distance from the edge of the lowland area (Figure 2.3). Tigers had relatively high trap success (5.11 per 100 TN) at 0.5 km from the edge of the lowland habitat that declined by more than half (1.92 per 100 TN) at 1.5-2.0 km from the edge. Leopards also had high trap success (3.78 per 100 TN) at 0.5 km from the edge of the lowland, but trapping rate dropped at the intermediate distance (0.5-1.0 km) from the edge and then sharply rose again as distance increased to 1 and 2 km from the lowland edge.

Abundance and Density Estimation

Models incorporating M_o and M_h were the two top models for both tigers and leopards based on their discriminant function score from Program CAPTURE. Models incorporating heterogeneity (M_h) are often regarded as the most biologically realistic model (Karanth 1995, Karanth and Nichols 1998, O'Connell et al. 2011) for top carnivores like tigers and leopards based on factors such as territoriality, different trapping rates of males versus females, and home-ranges that only partially overlap the camera grid. The M_h jackknife model produced abundance estimates $\widehat{N}$ (SE) of 36 (SE 6.11) tigers and 55 (SE 12.49) leopards, with average capture probabilities ($\hat{p}$) of 0.11 for tigers and 0.05 for leopards in the CH. In Program MARK, three models accounted for 100% of the AIC weights, supporting variation in the behavior, heterogeneity, and constant (null model) for both tigers and leopards. Due to imprecise estimates for the M_b model for both species and the fact that individuals are unlikely to have constant detectability, I used the model incorporating heterogeneity (M_h), which resulted in abundance estimates of 32 (SE 3.55) tigers and 43 (SE 10.07) leopards with $\hat{p}\ (SE)$ of 0.13 (SE 0.02) and 0.06 (SE 0.01), respectively. The point estimates for both predators varied predictably among spatial scales, with highest abundance occurring in the largest area (the CHSA) and lowest in smallest area (the CCC) (Figure 2.4; Table 2.2).

Based on the traditional approach using buffer-strip methods (½ MMDM), density estimates $\widehat{D}\ (SE)$ via Program CAPTURE were 4.17 (SE 0.79) tigers and 6.47 (SE 1.43) leopards per 100 km^2 and via Program MARK density estimates were 3.42 (SE 0.41) tigers and 5.33 (SE 1.21) leopards per 100 km^2 in the CHSA (Figure 2.5). While in CH, density estimates via Program CAPTURE were 4.16 (SE 0.75) tigers per 100 km^2 and 6.24 (SE 1.50) leopards per 100 km^2 and via Program MARK density estimates were 3.70 (SE 0.47) tigers per 100 km^2 and 4.86 (SE 1.21) leopards per 100 km^2. The ½ MMDM density estimates were predictably higher than density estimates using the full MMDM (Figure 2.4). For the CCC, using the abundance estimate from Program CAPTURE divided by the predetermined survey area size (i.e., $\widehat{N}$÷A), the density estimates of tigers and leopards were 2.16 (SE 0.01) and 10 (SE 0.02) individuals per 100 km^2 respectively.

Using the ML-SECR models implemented in Program DENSITY with the appropriate detection function (hazard (HZ), negative-exponential (NE) and half-normal (HN)) along with variation in σ and g_o explained by behavior and/or heterogeneity, provided the best fit for the CHSA, CH, and CCC datasets, respectively (Table 2.5 and 2.6). The model averaged density estimates for tigers and leopards respectively in CHSA were 2.28 (SE 0.74) and 3.32 (SE 2.29) individuals per 100 km^2; in CH they were 2.26 (SE 0.72) and 3.78 (SE 2.61) individuals per 100

km^2; and in CCC they were 2.08 (SE 1.13) and 9.75 (SE 13.72) individuals per 100 km^2. Using B-SCR models implemented in Program SPACECAP, density estimates for tigers and leopards respectively were 2.85 (SE 0.50) and 4.63 (SE 0.92) individuals per 100 km^2 in CHSA; 2.21 (SE 0.42) and 3.94 (SE 0.95) individuals per 100 km^2 in CH, and, in the CCC, were 2.08 (SE 1.13) and 6.79 (SE 1.99) individuals per 100 km^2 respectively (Table 2.7-2.9).

Prey Assemblage in Churia Habitat (CH)

Eight species of the ungulates were identified within the churia habitat (CH) based on camera-trap photographs (Table 2.1), direct observation, and indirect evidence (pellets and tracks). The common principal wild prey species of tigers, leopards, and dholes are: large-sized animals (>50 kg) - gaur, sambar and nilgai (rare); medium-sized animals (20-50 kg) - chital, barking deer, wild pig, himalayan serow (rare), and four-horned antelope (rare). In addition to ungulates, the small-bodied primates (< 20 kg) - common langurs (*Semnopithecus entellus*) and rhesus monkeys (*Macaca mulatta*), were also recorded in the churia habitat (CH).

Prey Density

Along the 136 km of surveying, team recorded 117 sightings of four species of ungulates (sambar, chital, muntjac, and wild pig) and 46 sightings of two species of primates (grey langur and macaque). I had only 2 detections of gaur ($n = 2$) and thus gaur were discarded from further analysis. Among the principal prey, sambar had the highest densities at 9.55 (SD 1.76) animals per km^2 (Table 2.10), while chital density was lowest at 5.19 (SD 1.11) animals per km^2 (Table 2.10). Summing the top 4 species-specific densities (sambar, chital, wild pig and muntjac) into one estimate resulted in overall prey density of 29.3 prey per km^2 in the churia habitat (Table 2.10). Overall density of all wild prey was 62.7 prey per km^2 with contributions from the top 4 wild ungulates of 47%. The overall estimated biomass of all wild ungulates was 2,450 kg per km^2.

Potential Tiger Densities

Based on Karanth et al. (2004) equation, an ungulate prey density of 29.3 individuals per km^2 would be capable of supporting 5.9 tigers per 100 km^2 within the 639 km^2 of churia habitat (CH), which translates into a total of 37 individuals.

DISCUSSION

This was the first detailed study to investigate densities of tigers, their common sympatric predator, the leopard, and their prey in the churia habitat since the commencement of the classic Terai ecology project in 1970s (Dinerstein 2003, Seidensticker et al. 2010). The results serve as baseline information and add additional animals to the overall tiger number estimate for the Terai Arc. In the churia habitat (CH) : 1) recorded 12 species of carnivores with tigers (*Panthera tigris tigris*), leopards (*Panthera pardus fusca*), and wild dog (dholes) (*Cuon alpinus*) being the top carnivores, including evidence of breeding for tigers and leopards; 2) determined tiger activity to be higher closer to the lowland forest (1-2 km) than inside the CCC; 3) found higher numbers of leopards than tigers, at nearly double the density; 4) recorded 8 species of potential prey with body size greater than 15 kg including new records for himalayan serow, four-horned antelope, and nilgai; 5) determined pooled prey density to be 62.7 per km^2, 47% (29.3 per km^2) of which consist of 4 species of wild ungulates; and 6) found estimated tiger densities to be lower than that predicted by ungulate density in the churia habitat (CH). As hypothesized, current population size estimated for tigers represents 4 to 30% of the total population size when considering the additional tiger numbers from CCC to CHSA (Dhakal et al. 2014). Additionally, the population size of leopards from only the churia habitat (CH) is similar to the total population size of leopards estimated for Chitwan National Park (Thapa 2012), suggesting underestimated population sizes for the Chitwan National Park. These findings contradict the conventional view of the churia as unsuitable or marginal habitat (Smith et al. 1999) for tigers and leopards. While tiger density in the CH is lower by half than to the density in the lowland areas of Chitwan National Park (Karki et al. 2013) and Bardia National Park (Dhakal et al. 2014), it is still comparable to sites in India such as Pakke Tiger Reserve (Chauhan et al. 2006), Chilla range (Harihar et al. 2011), Tadoba and Bhadra tiger reserves (Karanth et al. 2004) and higher in density than those for tigers in Bhutan (Wang and Macdonald 2009), Myanmar (Lynam et al. 2009) and Malaysia (Kawanishi and Sunquist 2004). Leopard density, on the other hand, is very similar to high-density areas in the bhabhars of Parsa Wildlife Reserve in Nepal (Thapa et al. 2014), the mountains of Kuiburi National Park in Thailand (Steinmetz et al. 2013), Manas Tiger Reserve in India (Borah et al. 2013) and the Irrigated Valley in Akole Tahsil, Maharastra, India (Athreya et al. 2013).

Expert opinion and reconnaissance surveys aided in fine-tuning the design protocol for the camera-trap survey and distance-based, line transect survey in a relatively unknown habitat. Refined sampling design coupled with high sampling effort per km^2 (~4.5 trap-nights effort per km^2) in the churia habitat resulted in similar capture probability (0.08 per occasion) as in the high tiger density areas in Nagarhole (0.11, Karanth and Nichols 1998), Chitwan (0.06, Karki et al. 2013) and Kaziranga (0.19, Karanth et al. 2004).

My density estimates for both carnivores show variation based on the type of estimator (spatial and non-spatial) used. I generally found higher estimates with ½ MMDM than SECR/SCR models, supporting the findings of earlier studies (Kalle et al. 2011, Gerber et al.

2012, Sunarto et al. 2013). My estimates were similar for both spatially explicit approaches for the tiger. The SECR model relaxes the problem with geographic closure, potentially lessening the impact of the potential edge effect at the churia/lowland boundary area; hence, SECR estimates are likely more accurate than traditional approaches, which are likely to underestimate survey area and hence overestimate density. Leopard density estimates however, were more variable than those for tigers between the spatial models. Recent research shows that trap deployment and small trapping polygon could affect the estimates from SECR/SCR models (Tobler and Powell 2013). However, trapping grids in my study were large, ranging from 370 km^2 for CCC to 557 km^2 for CHSA and multiple camera-traps were deployed within each animal's home-range (10.6-50.4 km^2 home-range for tigers - Smith et al. 1987 and 47 km^2 home-range for leopards - Odden and Wegge 2009) to allow sufficient captures and recaptures (Noss et al. 2012) for deducing accurate density estimates. Nevertheless, I would suggest further work to confirm the stability of my estimates for leopards given the relatively high estimate and poor precision for the CCC.

Combined ungulate density in churia habitat was low compared to those at multiple sites in Nepal and India (Karanth and Nichols 2002a, Jhala et al. 2011, Karki 2011, GoN 2013, Harihar et al. 2014). Gaur and sambar deer are the large body-sized potential prey of tigers found in the churia. However, gaur distribution was highly clustered and their detection was too low to estimate density. Nevertheless, another study calculating their probability of occupancy revealed occupancy ($\widehat{\psi}(SE\widehat{\psi})$ to be high at 0.76 (0.12) in churia habitat. Predation on such large herbivores is very rare, and therefore their biomass contribution to support the tiger population is only occasional (Sunquist 1981) due to their heavy body weight and the high energy needed to kill gaur while avoiding injury, especially in the undulating terrain conditions. Sambar was most abundant and was most likely to be the preferred prey species of tigers (Karanth and Sunquist 1995, Stoen and Wegge 1996, Hayward et al. 2012). Sambar is a forest ungulate showing preference for deciduous forest with high understory (Schaller 1967, Dinerstein 1980), which is highly restricted to the churia hilly terrain across the Terai Arc (Johnsingh et al. 2004). My observations concur with these findings in the churia within CNP, with reported ecological density and its spatial distribution in churia habitat $\widehat{\psi}(\mathrm{SE}\ \widehat{\psi}) = 0.81(\mathrm{SE}\ 0.72)$. Barking deer were the most abundant medium-sized ungulate, likely due to their preference for closed forest habitat and high under-growth (Dinerstein 1980, Teng et al. 2004, Wegge et al. 2009), both of which are found in the churia.

Carnivore densities are directly correlated with prey densities (Carbone and Gittleman 2002, Karanth et al. 2004). Sambar and wild boar are the preferred prey species of tiger (Hayward et al. 2012). Availability of abundant sambar and medium-sized prey like barking deer could explain the tiger's higher-than-expected density in churia habitat. Leopards, on the other hand, preferentially prey upon species within a weight range of 10-40 kg (Hayward et al. 2006). Abundant medium-sized ungulate prey (size: 35-50 kg, density: 13.3 animals per km^2) in addition to primates (33.39 animals per km^2) could explain the high leopard density in the churia habitat. Leopards have been shown to use habitat not used by tigers, purportedly to avoid fierce competition with them (Seidensticker 1976, Odden et al. 2010). I found relatively dense leopard population inside the core of the core churia (6.8 animals per 100 km^2), and increasing leopard trap rates starting at 1.0 km from the lowland edge. Leopard predominance in the core of the churia habitat could be related to avoiding higher dense tiger population in the lowland habitat and the high availability of medium-sized prey (Karki et al. 2013).

The density of tigers was similar at all spatial scales; while density of leopards appeared to increase in core of core churia rather than in churia habitat as a whole (Figure 2.4). The transition zone (~2km) formed between the edges of CH and CCC is important from management point of view, as both tiger and leopard activity is very high within this zone. Anti-poaching strategies for protected areas like SMART (Spatial Monitoring and Reporting Tool) (ESS 2009, Thapa et al. 2013) also should include targeting this transition zone within their standard operating protocol for securing high performance areas within churia habitat.

The tiger population in the churia habitat within CNP may be lower than capacity, according to the prey density extrapolation relative to the densities estimated from camera-traps. My density estimates ranged from 1.5 to 4.2 tigers per 100km^2, translating to 10 to 27 tigers across the 639 km^2 of churia habitat in CNP, whereas tiger density extrapolated from prey density is 5.9 tigers per 100 km^2 or 37 tigers in the churia. Therefore, it is important to maintain the integrity of the churia habitat for tiger conservation. Human disturbance, including resource extraction, is known to have damaging effects on wildlife (Hebblewhite and Merrill 2008, Burdett et al. 2010), including their Darwinian fitness (Leblond et al. 2013). Direct persecution of prey species by humans in churia habitat is known to occur in the form of illegal hunting, which is prevalent across the transboundary with India, and illegal harvest of non-timber forest products is high. Decreasing such illegal activities could enrich the potential prey populations, thereby increasing the carrying capacity for tigers (O'Kelly et al. 2012, Harihar et al. 2014) across the churia habitat in CNP. If similar prey densities prevail across the churia habitat outside CNP, then the 1,200 km^2 of churia habitat in the Chitwan valley alone could support up to ~70 tigers following the Karanth et al. (2004) models applied in this study. The total area of churia habitat within Terai Arc is 7,642 km^2, representing the potential for holding substantially more tigers. Enhancement of prey populations and predominance of a successful community forest program (Agrawal and Ostrom 2001, Seidensticker et al. 2010) outside the core areas should be a win-win situation for tigers and prove beneficial to sympatric leopards as well. Chitwan National Park is contiguous with Valmiki Tiger Reserve, sharing a majority of the churia habitat. Transboundary efforts in reducing human -elated disturbances in churia habitat and churia-specific monitoring of the tiger and leopard populations could aid in better understanding of the conservation status of predator populations in Valmiki Tiger Reserve (Jhala et al. 2011).

The Government of Nepal has proposed an east-west road and railway project in lowland areas of Nepal, and its proposed alignment passes through the matrix of habitat types including churia habitat in Chitwan National Park. This developmental project would trigger habitat fragmentation and conversion, causing devastating effects on the habitat, including a negative effect on large mammals (Terborgh 2004, Fahrig and Rytwinski 2009). Chitwan National Park holds the largest source population of tigers in the Terai Arc (Karki et al. 2013), the only founder population of rhinoceros (Subedi et al. 2013, Thapa et al. 2013), and the few remaining floodplain grassland habitats in the country (Lehmkuhl 1994, Peet et al. 1999, Dinerstein 2003), as well as the understudied churia habitat. These natural legacies would be jeopardized by this road and rail project, and implementation of the project would call into question the commitment of the government of Nepal to double the tiger population by 2022 (GTRP 2010).

This study was first of its kind to focus on a specific habitat thought to be unsuitable/poor quality for tigers, and the results should highlight the inference that the churia habitat should no longer remain a “forgotten tigerland”. Simply by inclusion of this habitat as suitable, albeit at lower density, but likely holding 9 to 36 tigers, I have shown that more tigers occur in Chitwan than previously thought (Smith et al. 1999), thus contributing to the country’s goal of doubling the tiger population by 2022. In addition to its conventional role in forest conservation and watershed protection (Gautam et al. 2004, Pandit et al. 2007), the churia habitat also is important in fostering tiger conservation across the Terai Arc (Seidensticker et al. 2010, Wikramanayake et al. 2010). Conservation initiatives should include the churia as suitable habitat and focus on reducing human disturbance and protecting and possibly boosting prey populations in order to potentially support even higher numbers of threatened and endangered carnivores.

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TABLES AND FIGURES

Table 2.1: Activity index (number of independent photo-captures per 100 trap-nights) of mammalian species identified in the churia camera-trap survey and their conservation status in Nepal (*NPCA 1973) and regionally based on the IUCN Red List (IUCN 2013).

Name of species recorded	**Activity index**	**IUCN Red list Status**	**Nepal Protected Animal List**
CARNIVORES			
Tiger (*Panthera tigris tigris*)	4.05	Endangered	Yes
Leopard (*Panthera pardus fusca*)	3.19	Near Threatened	No
Dhole (*Cuon alpinus*)	1.02	Endangered	Yes
Leopard Cat (*Prionailurus bengalensis)*	1.00	Least Concern	Yes
Fishing Cat (*Prionailurus viverrinus*)	0.24	Endangered	No
Jungle Cat (*Felis chaus*)	0.14	Least Concern	No
Sloth bear (*Melursus ursinus)*	1.53	Vulnerable	No
Asiatic jackal (*Canis aureus)*	0.62	Least Concern	No
Large indian civet (*Viverra zibetha)*	4.10	Near Threatened	No
Small indian civet (*Viverricula indica)*	1.34	Least Concern	No
Common palm civet (*Paradoxurus hermaphroditus)*	0.91	Least Concern	No
Crab eating mongoose (*Herpestes urva*)	1.86	Least Concern	No
HERBIVORES			
Indian crested porcupine (*Hystrix indica)*	2.72	Least Concern	No
Yellow throated martin (*Martes flavigula)*	0.05	Least Concern	No
Indian hare (*Lepus nigricollis)*	0.29	Least Concern	No
Gaur (*Bos gaurus*)	1.38	Vulnerable	Yes
Sambar (*Rusa unicolor*)	13.26	Vulnerable	No
Chital (*Axis axis*)	7.15	Least Concern	No
Barking deer (*Muntiacus muntjak*)	5.48	Least Concern	No
Wild pig (*Sus scrofa*)	3.48	Least Concern	No
Himalayan serow (*Capricornis thar)*	0.29	Near Threatened	No
Rhesus monkey (*Macaca mulatta*)	1.19	Least Concern	No
Grey langur (*Semnopithecus entellus*)	4.29	Least Concern	No
Asian elephant (*Elephus maximus*)	2.72	Endangered	Yes
Greater one-horned rhinoceros (*Rhinoceros unicornis*)	5.53	Vulnerable	Yes

* Nepal Protected Area and Wildlife Act

Table 2.2: Population closure test from program CAPTURE, population abundance ($\widehat{N}$) standard error (SE), detection ($\hat{p}$) and trap success of leopards and tigers across the different spatial scales. CHSA: Churia Habitat and Surrounding Area; CH: Churia Habitat; CCC: Core of Core Churia

Spatial Scale	**Predator**	**Closure Test**		**Heterogeneity Based Model from CAPTURE**		**Heterogeneity Based Model from MARK**		**Trap Success (Independent Capture events / 100 trap-nights)**
		Z	**P**	$\widehat{N}$ **(SE)**	$\widehat{P}$	$\widehat{N}$ **(SE)**	$\widehat{P}$	
CHSA	Tiger	0.978	0.83	48 (8.77)	0.10	39 (4.34)	0.12	4.42
	Leopard	-1.381	0.08	57 (11.71)	0.06	47 (9.93)	0.07	3.41
CH	Tiger	0.636	0.74	36 (6.11)	0.12	32 (3.55)	0.13	4.05
	Leopard	-1.613	0.05	55 (12.49)	0.05	43 (10.07)	0.06	3.19
CCC	Tiger	-1.890	0.03*	8 (3.40)	0.09	10 (3.93)	0.07	1.79
	Leopard	-1.491	0.07	37 (10.58)	0.04	38 (28.30)	0.03	2.72

*Violation of the closed population assumption

Table 2.3: Model selection summary for geographic closure for tiger and leopard populations across the three spatial scales in the churia habitat. CHSA: Churia Habitat and Surrounding Area); CH: Churia Habitat; CCC: Core of Core Churia.

Predator	**Spatial Scale**	**Model**	**AICc**	**ΔAICc**	**AICc Weights (ω)**	**Model Likelihood**	**Number of Parameters (*k*)**	**Deviance**
Tiger	CHSA	Φ (1).p(time).f(0)	325.10	0.00	0.41	1.00	12	104.33
	CH	Φ (1).p(time).f(0)	287.11	0.00	0.74	1.00	12	101.89
	CCC	Φ (1.)p(time).f(0)	-14.99	0.00	0.78	1.00	12	17.50
Leopard	CHSA	Φ (1).p(time).f(.)*	245.32	0.00	0.61	1.00	12	68.68
	CH	Φ (1).p(time).f(0)	222.29	0.00	0.69	1.00	12	67.61
	CCC	Φ (1.)p(time).f(0)	204.78	0.00	1.00	1.00	12	15.02

Φ, site fidelity; p, recapture probability; f, immigration onto the study area. Parameters with “1” and “0” indicate the parameter is fixed. “.” indicates a constant value. Akaike’s information criterion corrected for small sample size (AICc), difference in AIC value between top model and ith model (Δ AICc), weight of support for each model (AICc weights, **ω**); * support for migration from the sampling area for leopard population in CHSA in italic.

Table 2.4: Capture and recapture estimates of tiger and leopard abundance ($\widehat{N}$) and density ($\widehat{D}$ per 100 km^2) across the Churia Habitat and Surrounding Areas (CHSA), Churia Habitat (CH) and Core of Core Churia (CCC) in Chitwan National Park. Traditional density estimates based on ½ MMDM and FMMDM with the estimated population size from Program CAPTURE and MARK. MCP: Minimum Convex Polygon, M_{t+1}: Number of Animal Captured; ETA: Effective Trapping Area.

Spatial Scale	**MCP**	**Predator**	**M_{t+1}**	**Recaptured Individuals**	**Estimator**	**Abundance $\widehat{N}$ (SE)**	**ETA**	**Buffer Type**	**Density $\widehat{D}$ (SE)**
CHSA	558.00	Tiger	31	16	Capture	48 (8.77)	1152.25	½ MMDM	4.17 (0.79)
					Mark	40 (4.34)			3.42 (0.41)
					Capture	48 (8.77)	1581.34	FMMDM	3.03 (0.57)
					Mark	40 (4.34)			2.49 (0.29)
		Leopard	28	9	Capture	57 (11.71)	880.8	½ MMDM	6.47 (1.43)
					Mark	47 (9.93)			5.33 (1.21)
					Capture	57 (11.71)	1208.10	FMMDM	4.71 (1.02)
					Mark	47 (9.93)			3.89 (0.87)
CH	475.83	Tiger	26	15	Capture	36 (6.11)	864.58	½ MMDM	4.16 (0.75)
					Mark	32 (3.55)			3.70 (0.47)
					Capture	36 (6.11)	1226.35	FMMDM	2.93 (0.52)
					Mark	32 (3.55)			2.60 (0.32)
		Leopard	24	9	Capture	55 (12.49)	819.96	½ MMDM	6.24 (1.50)
					Mark	43 (10.07)			4.86 (1.21)
					Capture	55 (12.49)	1143.78	FMMDM	4.80 (1.14)
					Mark	43 (10.07)			3.74 (0.92)
CCC	369.79	Tiger	6	1	Capture	8 (3.40)	369.79	N÷A	2.16 (0.01)
					Mark	10 (3.93)			2.61 (0.01)
		Leopard	13	2	Capture	37 (10.58)	369.79		10.00 (0.02)
					Mark	38 (28.30)			10.37(0.01)

Table 2.5: Model selection results from tiger density estimates ($\widehat{D}$ per 100 km^2) using photographic capture-recapture data for tiger populations in Program DENSITY (ML-SECR) across three spatial scales: Churia Habitat and Surrounding Areas (CHSA), Churia Habitat (CH) and Core of Core Churia (CCC) in Chitwan National Park. The g_o is the capture probability at home-range center, s is the spatial scale parameter of capture function, h2 is the 2-class finite mixture probability for heterogeneity, and b is the variation due to behavioral response. Akaike's Information Criterion was adjusted for small sample size by AICc.

Scale	Buffer Size (m)	Model selection	K	AIC	AICc	ΔAICc	w	Model Likelihood	Density $\boldsymbol{\widehat{D}}$ (SE)
CHSA	12,000	HZ g0[b]s[.]	4	796.72	798.25	0	0.46	1.00	2.31 (0.67)
		HZ g0[b]s[b]	5	797.31	799.71	1.46	0.22	0.48	2.58 (0.82)
		HZ g0[.]s[.]	3	800.1	800.99	2.74	0.12	0.25	2.84 (0.80)
		HZ g0[.]s[b]	4	799.74	801.28	3.03	0.10	0.22	2.30 (0.67)
		HZ g0[b]s[h2]	6	800.52	804.02	5.77	0.03	0.06	2.34 (0.69)
		HZ g0[bh2]s[.]	6	800.72	804.22	5.97	0.02	0.05	2.30 (0.67)
CH	15,000	NE g0[b]s[.]	4	722.88	724.78	0	0.30	1.00	1.80 (0.45)
		NE g0[.]s[h2]	5	722.16	725.16	0.38	0.25	0.82	3.08 (0.94)
		NE g0[b]s[b]	5	722.57	725.57	0.79	0.20	0.67	2.21 (0.64)
		NE g0[.]s[.]	3	724.63	725.72	0.94	0.19	0.62	2.10 (0.52)
		NE g0[.]s[b]	4	726.03	727.93	3.15	0.06	0.20	1.85 (0.54)
CCC	5,000	HN g0[.]s[b]	3	136.46	148.46	0	0.50	1.00	1.55 (1.02)
		HN g0[b]s[.]	3	136.48	148.48	0.02	0.49	0.99	1.60 (1.00)
		HN g0[b]s[b]	4	138.44	178.44	29.98	0.00	-	1.50 (1.03)

K: number of parameters, AICc: Akaike Information Criteria; AICc: AIC corrected for small sample size; w: Akaike model weight. [.] represents the null model or constant. HZ: Hazard rate, NE: Negative exponential, and HN: Half normal

Table 2.6: Model selection results from leopard density estimates ($\widehat{D}$ per 100 km^2) using photographic capture-recapture data for leopard populations in Program DENSITY (ML-SECR) across three spatial scales: Churia Habitat and Surrounding Areas (CHSA), Churia Habitat (CH) and Core of Core Churia (CCC) in Chitwan National Park. The g_o is the capture probability at home-range center, s is the spatial scale parameter of capture function, h2 is the 2-class finite mixture probability for heterogeneity, and b is the variation due to behavioral response. Akaike's Information Criterion was adjusted for small sample size by AICc.

Predator	Buffer Size (m)	Model selection	K	AIC	AICc	ΔAICc	w	Model likelihood	Density $\widehat{\boldsymbol{D}}$(SE)
CHSA	12000	NE,g0[.]s[b]	3	-234.64	475.28	0	0.35	1.00	2.00 (0.84)
		NE g0[b]s[.]	3	-234.84	475.69	0.41	0.29	0.81	3.00 (0.77)
		NE g0[.]s[.]	2	-236.96	477.91	2.11	0.12	0.34	4.00 (1.27)
		NE g0[h2]s[.]	4	-234.33	476.66	2.12	0.12	0.34	8.00 (3.78)
		NE g0[b]s[b]	4	-234.61	477.22	2.68	0.09	0.26	2.00 (0.99)
CH	15000	NE g0[.]s[b]	3	434.69	435.89	0	0.27	1.00	2.48 (0.09)
		NE g0[b]s[.]	3	434.99	436.19	0.30	0.24	0.86	2.94 (0.08)
		NE g0[.]s[.]	2	435.84	436.41	0.52	0.21	0.77	4.20 (1.25)
		NE g0[h2]s[.]	4	434.39	436.49	0.6	0.20	0.74	7.33 (3.70)
		NE g0[b]s[b]	4	436.65	438.76	2.87	0.06	0.23	2.61 (1.07)
CCC	5000	HN g0[.]s[b]	3	178.07	180.47	0	0.43	1.00	8.9 (1.36)
		HN g0[b]s[.]	3	178.08	180.48	0.01	0.43	0.99	9.8 (1.36)
		HN g0[b]s[b]	4	179.97	184.41	3.94	0.06	0.13	11.9 (1.65)
		HN g0[h2]s[.]	4	180.16	184.60	4.13	0.06	0.12	16.0 (1.19)

K: number of parameters, AICc: Akaike Information Criteria; AICc: AIC corrected for small sample size; w: Akaike model weight. [.] represents the null model or constant. NE: Negative exponential, and HN: Half normal

Table 2.7: The posterior summaries of model parameters from Bayesian spatially explicit capture recapture (B-SCR) for tigers across the Churia Habitat and Surrounding Areas (CHSA), Churia Habitat (CH) and Core of Core Churia (CCC) in Chitwan National Park implemented in SPACECAP (Gopalaswamy et al. 2012) along with Geweke diagnostic statistic. Sigma (σ) is the range parameter of the species, lam0 (λ_0) is the intercept of expected encounter frequency, psi (Ψ) is the ratio of the number of animals present within the state space, S, to the maximum allowable number. Beta (β) is the regression coefficient which measures the behavioral response, N is the number of activity centers in S. p is the detection probability. Density (D) is N divided by S representing number of animals per 100km^2. A |z score| shows convergence of the estimated parameters (less than 1.6)

Scale	Parameter	Posterior Mean	Posterior SD	95% Lower HPD Level	95% Lower HPD Level	Geweke's Statistics |z score|
CHSA	σ	3534.77	373.53	2816.33	4267.13	-0.65
	λ_0	0.02	0.00	0.01	0.03	1.01
	Ψ	0.33	0.07	0.21	0.46	0.27
	N	93.05	16.66	62.00	125.00	0.22
	D	2.86	0.51	1.94	3.87	
	p	0.02	0.00	0.01	0.03	
CH	σ	3757.74	414.41	2972.09	4581.41	-1.51
	λ_0	0.03	0.01	0.02	0.04	0.99
	β	-0.33	0.56	-1.43	0.73	-0.58
	Ψ	0.35	0.07	0.21	0.50	0.53
	N	72.06	13.69	46.00	98.00	0.57
	D	2.21	0.42	1.41	3.01	
	$p1$	0.03	0.01	0.02	0.04	
	$p2$	0.02	0.01	0.00	0.04	
CCC	σ	1537.74	785.03	558.52	3137.74	-1.02
	λ_0	0.05	0.03	0.01	0.12	0.22
	Ψ	0.36	0.20	0.05	0.78	-0.20
	N	67.54	36.69	10.00	143.00	-0.19
	D	2.08	1.13	0.31	4.39	
	p	0.05	0.03	0.01	0.11	

Table 2.8: The posterior summaries of model parameters from Bayesian spatially explicit capture recapture B-SCR) for leopards across the Churia Habitat and Surrounding Areas (CHSA), Churia Habitat (CH) and Core of Core Churia (CCC) in Chitwan National Park implemented in SPACECAP (Gopalaswamy et al. 2012) along with Geweke diagnostic statistic. Sigma (σ) is the range parameter of the species, lam0 (λ_0) is the intercept of expected encounter frequency, psi (Ψ) is the ratio of the number of animals present within the state space, S, to the maximum allowable number. N is the number of activity centers in S. *p* is the detection probability. Density (D) is N divided by S representing number of animals per 100km^2. A |z score| shows convergence of the estimated parameters (less than 1.6).

Scale	Parameter	Posterior Mean	Posterior SD	95% Lower HPD Level	95% Lower HPD Level	Geweke's Statistics |z score|
CHSA	σ	2983.08	540.52	2061.05	4039.33	2.15
	λ_0	0.01	0.00	0.00	0.02	-2.20
	Ψ	0.72	0.15	0.48	1.00	-1.34
	N	150.61	29.93	99.00	206.00	-1.38
	D	4.63	0.92	3.04	6.33	
	p	0.01	0.00	0.00	0.02	
CH	σ	3106.18	613.24	2107.57	4287.85	-0.23
	λ_0	0.01	0.00	0.00	0.02	-0.94
	Ψ	0.63	0.15	0.36	0.95	1.40
	N	128.26	30.93	72.00	190.00	1.41
	D	4.00	1.00	2.00	6.00	
	p	0.01	0.00	0.00	0.02	
CCC	σ	2377.11	2337.41	423.55	7597.51	0.86
	λ_0	0.02	0.02	0.00	0.06	-1.51
	Ψ	0.70	0.21	0.32	1.00	-2.13
	N	220.86	64.62	102.00	314.00	-2.11
	D	6.79	1.99	3.13	9.65	
	p	0.02	0.02	0.00	0.06	

Table 2.9: Summary of density estimates ($\widehat{D}$ per 100 km^2) for the tiger and leopard across three spatial scales in Chitwan National Park. CHSA: Churia Habitat and Surrounding Area; CH: Churia Habitat; CCC: Core of Core Churia.

Spatial Scale	**Predator**	**Density Estimator**	**Buffer Type**	**Density (SE)**
CHSA	Tiger	$\hat{\boldsymbol{N}}$ /ETA-CAPTURE	½ MMDM	4.17 (0.79)
			FMMDM	3.03 (0.57)
		$\hat{\boldsymbol{N}}$ /ETA-MARK	½ MMDM	3.42 (0.41)
			FMMDM	2.49 (0.29)
		ML-SECR	-	2.28 (0.74)
		B-SCR	-	2.85 (0.50)
	Leopard	$\hat{\boldsymbol{N}}$ /ETA-CAPTURE	½ MMDM	6.47 (1.43)
			FMMDM	4.71 (1.02)
		$\hat{\boldsymbol{N}}$ /ETA-MARK	½ MMDM	5.33 (1.21)
			FMMDM	3.89 (0.87)
		ML-SECR	-	3.32 (2.29)
		B-SCR	-	4.63 (0.92)
CH	Tiger	$\hat{\boldsymbol{N}}$ /ETA-CAPTURE	½ MMDM	4.16 (0.75)
			FMMDM	2.93 (0.52)
		$\hat{\boldsymbol{N}}$ /ETA-MARK	½ MMDM	3.70 (0.47)
			FMMDM	2.60 (0.32)
		ML-SECR	-	2.26 (0.72)
		B-SCR	-	2.22 (0.42)
	Leopard	$\hat{\boldsymbol{N}}$ /ETA-CAPTURE	½ MMDM	6.24 (1.50)
			FMMDM	4.80 (1.14)
		$\hat{\boldsymbol{N}}$ ETA- MARK	½ MMDM	4.86 (1.21)
			FMMDM	3.74 (0.92)
		ML-SECR	-	3.78 (2.61)
		B-SCR	-	4.00 (1.00)
CCC	Tiger	$\hat{\boldsymbol{N}}$ ÷A	-	2.16 (0.01)
		ML-SECR	-	1.54 (1.00)
		B-SCR	-	2.08 (1.13)
	Leopard	$\hat{N}$ ÷A	-	10 (0.02)
		ML-SECR	-	9.75 (13.72)
		B-SCR	-	6.79 (1.99)

Table 2.10: Detections, transect survey effort, detection function used, probability of detection, prey density ($\widehat{D}$ per km^2), the associated confidence intervals (CI), and coefficients of variation (CV) modeled in Program DISTANCE of the major prey species of the churia habitat (CH). Prey body mass was calculated based on the existing literature (Karanth and Sunquist 1992, Harihar et al. 2011). T: Truncation.

Species	**No of detections**	**Detection function**	**Probability of detection**	**$\widehat{D}$ per km^2 (SE)**	**95% CI**	**CV%**	**Body Weight (kg)**	**Biomass (kg per km^2)**
Sambar	47	HN_Cos_T50	0.55	9.55 (1.76)	6.62-13.76	18.52	185	1757.5
Barking Deer	19	UN_Cos_T80	0.50	7.71 (1.19)	5.60-10.62	15.45	25	192.75
Wild Boar	28	HN_Cos_T70	0.67	6.86 (1.59)	4.33-10.87	23.21	35	240.10
Chital	23	HZ_Cos_T100	0.61	5.19 (1.11)	3.37-8.01	21.44	50	259.50
All Ungulates combined				29.31				2449.85
Primates	46	HN_Cos_T80	0.75	33.39	22.21-50.20	20.70		
Overall Prey				62.70				

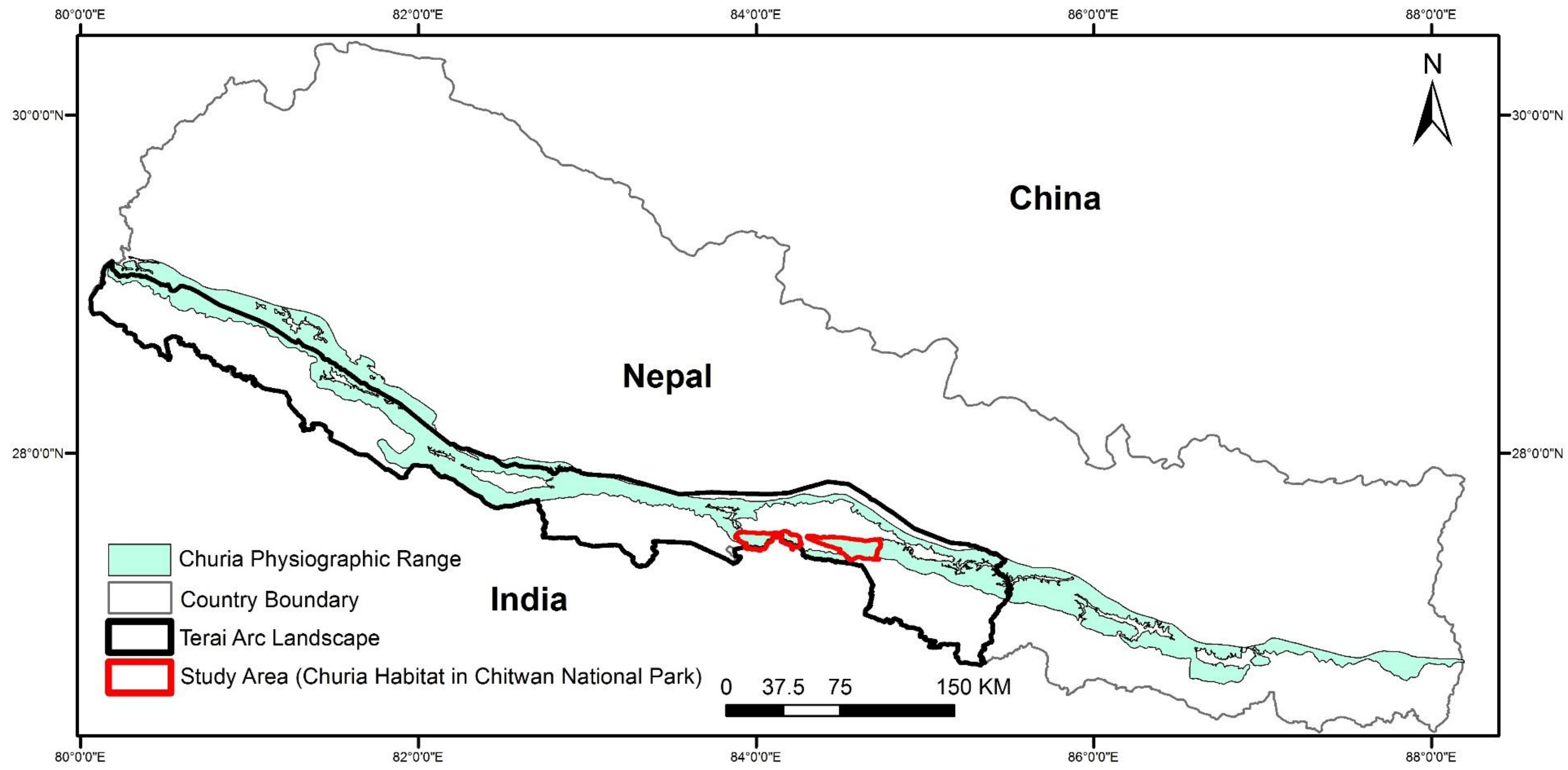

Figure 2.1: Churia physiographic range in Nepal covers 639 km^2 within Chitwan National Park (Study Area) and covers 7,642 km^2 across the Terai Arc Landscape.

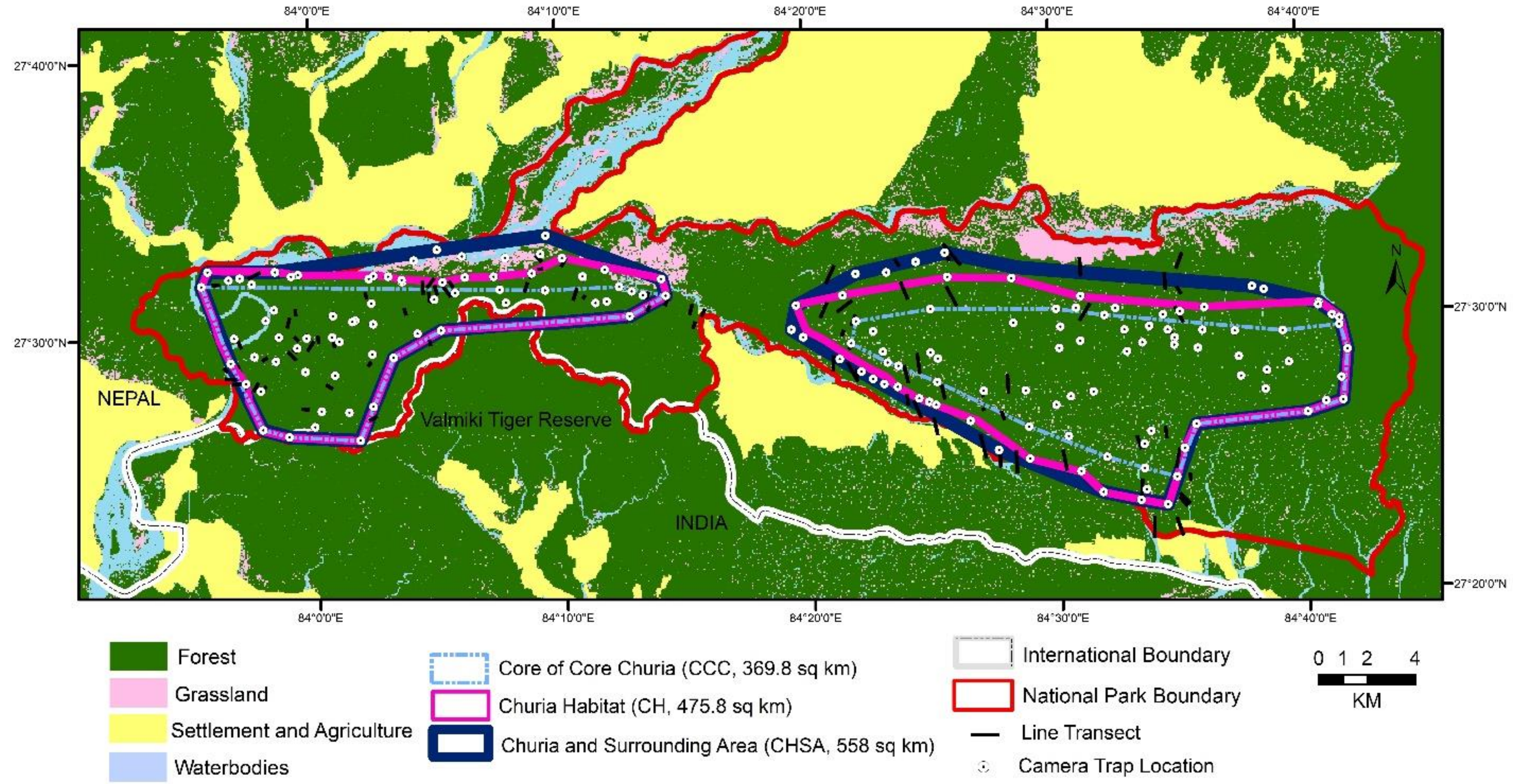

Figure 2.2: Study area showing camera-trap and line transect locations in Chitwan National Park. Note that the pink line is underneath the dark and light blue lines in part of the figure.

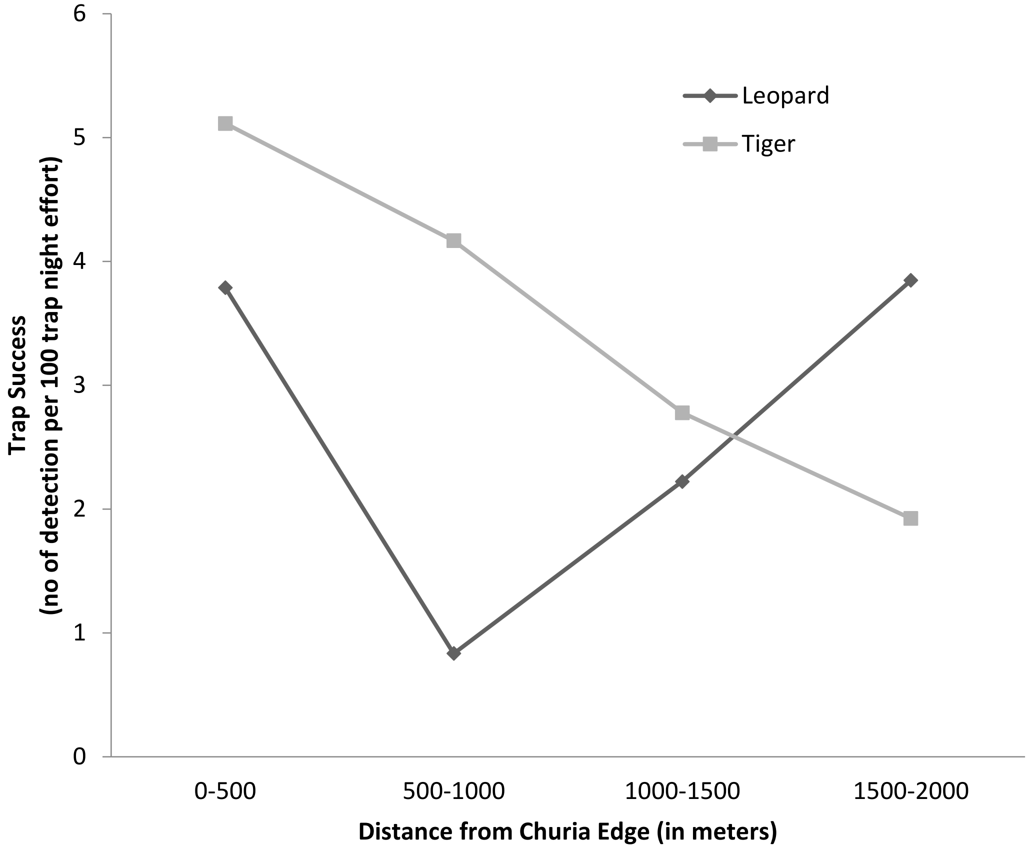

Figure 2.3: Edge Effect of edge in the transition zone between Churia Habitat (CH) and Core of Core Churia (CCC) on the trap success (number of detections per 100 trap-nights) for tigers and leopards in churia habitat.

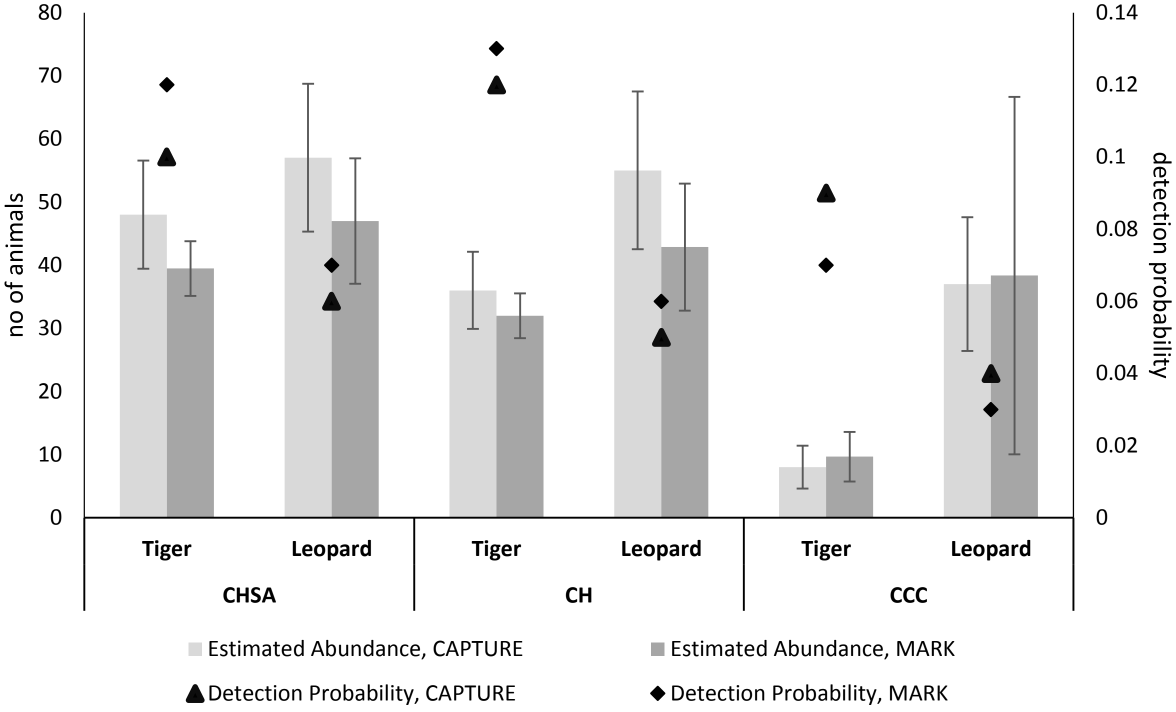

Figure 2.4: Population estimates ($\widehat{N}$) and detection probabilities ($\hat{p}$) from Programs CAPTURE and MARK based on M_h (incorporating heterogeneity in detection) for tiger and leopard populations at three spatial scales: Churia Habitat and Surrounding Area (CHSA), Churia Habitat (CH) and Core of Core Churia (CCC). Model average estimates are presented from program MARK for CCC in Chitwan National Park, Nepal. Error bars represents 95% CI on the abundance estimates.

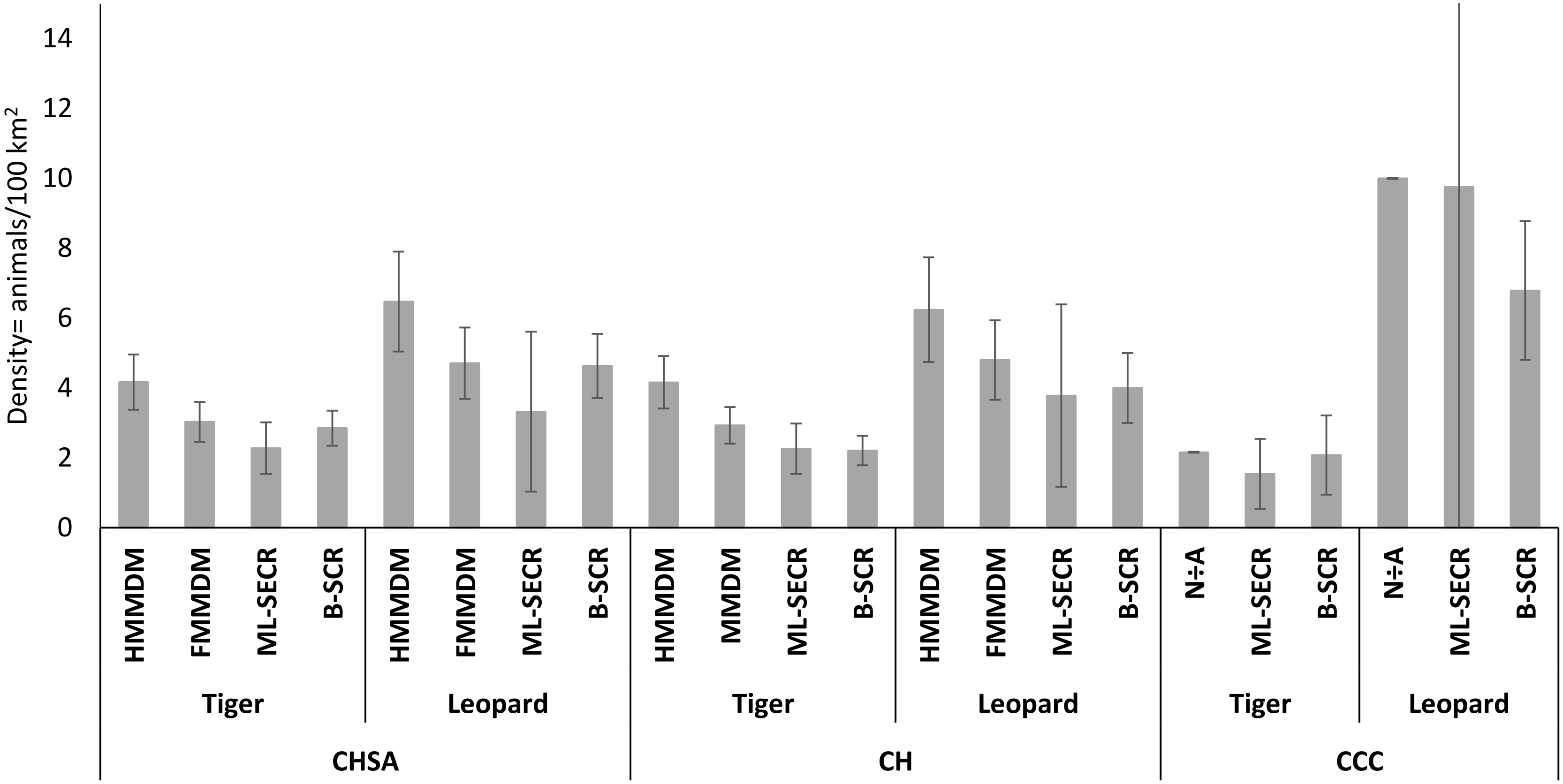

Figure 2.5: Density estimates per 100 km^2 for tigers and leopards from four different density estimators across the three spatial scales in churia habitat. Traditional methods use the ½ MMDM and the Full MMDM to buffer camera-traps to determine area surveyed. SECR models using maximum likelihood (ML-SECR) and Bayesian (B-SCR) approaches were implemented in Churia Habitat and Surrounding Area (CHSA), Churia Habitat (CH), and Core of Core Churia (CCC). N÷A represents estimated population size (N) divided by predetermined area (A) of the CCC: as the area embedded within churia at distance of 2 km from churia/lowland edge.

Chapter 3

Prey and tigers on the forgotten trail: examining prey occupancy and tiger habitat use in the Churia of Nepal

ABSTRACT

Forest ungulates are important determinants of local carnivore presence. Their spatial distribution also is important for fostering conservation efforts especially in areas that are relatively unknown in terms of species occurrence. I used sign surveys within a rigorous occupancy framework to estimate probability of occupancy for 5 focal prey species of the tiger (gaur, sambar, chital, wild pig, and barking deer); as well as probability of tiger habitat use within 537 km^2 of churia habitat in Chitwan National Park, Nepal. I divided the churia habitat into grid cells each measuring 3.25 km^2 and selected grid cells in a checker board fashion for conducting sign surveys. I conducted analysis at two spatial scales: at the grid cell level (3.25 km^2) for measuring both prey occupancy and tiger habitat use, and at the fine-scale, 600 m transect level, for further measuring habitat use of tigers only. Multi-season, auto-correlation models allowed me to make seasonal (winter versus summer) inferences regarding changes in occupancy or habitat use based on covariates influencing occupancy and detection. Sambar had the largest spatial distribution across both seasons occupying 431- 437 km^2 of the churia habitat, while chital had the smallest distribution occupying only 100-158 km^2. The gaur population showed the most seasonal variation from 318 - 413 km^2 of area occupied, with changes in occupancy suggesting their migration out of the lowland areas in the summer and into the churia in the winter. Wild pigs showed the opposite, moving into the churia in the summer (444 km^2 area occupied) and having lower occupancy in the winter (383 km^2). Barking deer were widespread in both seasons (329 - 349 km^2). Tiger habitat use $\widehat{\Psi}$ SE($\widehat{\Psi}$) was only slightly higher in winter 0.63 (SE 0.11) than in summer 0.54 (SE 0.21), but confidence intervals overlapped and area used was very similar across seasons, from 337 - 291 km^2. Fine scale variation in tiger habitat use showed that tigers intensively use certain areas more often than others across the seasons. The proportion of available habitat positively influenced occupancy for the majority of prey species and tigers. Human disturbance had a strong negative influence on the distribution of the majority of prey species but was positively related to tiger habitat use. Tigers appear to live in areas with high disturbance, thus increasing the risk of human-tiger conflict in the churia habitat. Thus, efforts to reduce human disturbance would be beneficial to reducing human wildlife conflict, enriching prey populations, and would potentially support more tigers in churia habitat of Nepal. Overall, I found high prey occupancy and tiger habitat use, suggesting that the churia is highly valuable habitat for tigers and should no longer be neglected or forgotten in tiger conservation planning.

Keywords: occupancy modelling, habitat use, tiger, prey, churia habitat, disturbances

INTRODUCTION

Conservation of key prey species is crucial for the survival of any large carnivores because changes in preferred prey abundance can alter population status of large carnivores (Hayward et al. 2006b, Hayward et al. 2007, Wegge et al. 2012), which already occur at naturally low densities (Carbone and Gittleman 2002). Presently, 36% of the world's carnivores and ungulates combined are now threatened with extinction (IUCN 2012, Di Marco et al. 2014), higher than any other mammal group. Prey populations, particularly large ungulates (>15 kg body mass), are often directly affected by human persecution, such as hunting and poaching, causing declines in their densities and subsequent potential risk of extinction for several species. In addition, direct threats to their habitat (Pringle et al. 2007) can also cause prey declines, affecting the predator populations which depend upon them, thus potentially changing ecosystem structure and dynamics (Estes et al. 2011).

Cervid and bovid prey species are fundamental determinists of tiger (*Panthera tigris tigris)* ecological density (Karanth and Sunquist 1992, Karanth et al. 2004, Hayward et al. 2012). These prey types form an important guild of ungulates within seasonally dry forests of Asia because they are the primary food source for large carnivores. Additionally, they are important agents of ecosystem change, acting to create spatial heterogeneity by changing nutrient cycles in their environment through depositing feces and churning soil, and they modulate successional processes by influencing the net primary production of plant communities (Hobbs 1996). Collectively, large mammalian prey species provide a broad diet allowing tigers to live wherever these prey species are available (Seidensticker 1986, Karanth and Sunquist 1995, Miquelle et al. 1999, Ramakrishnan et al. 1999). In South Asia, prey populations of large carnivores are found to reside in a wide range of habitats such as forests, grasslands, and cultivated and agricultural landscapes (Schaller 1967, Dinerstein 1979,1980, Wegge et al. 2000, Karanth et al. 2009).

The churia habitat is a relatively unknown and understudied habitat across the Terai Arc of Nepal even though it occupies a significant portion of the forested landscape. Within the churia of Chitwan National Park, tigers are known to occur, albeit at lower density than in the contiguous lowland areas, but the churia has remained overlooked ever since modern conservation began in the 1970s (Heinen and Kattel 1992). Addressing tiger conservation needs in this forgotten land requires knowledge of the distribution and habitat requirements of tigers and their prey, which are fundamental for effective wildlife management (Sinclair et al. 2006). Understanding prey distribution is an important first step in targeting conservation efforts for tigers in the churia habitat. Species distribution models are valuable in addressing key biological questions, including the impacts of ecological and anthropogenic factors that influence distribution and habitat use patterns for species of conservation concern (Sinclair et al. 2006).

In this study, I used presence-absence data collected from sign surveys of tigers and their prey within an occupancy modelling framework (MacKenzie et al. 2002). This framework provides useful metrics for assessing prey distribution and habitat use of tigers across the matrix of churia habitat, while accounting for imperfect detection. While, in general, occupancy techniques have been used for carnivores at larger spatial scales to measure true occupancy (Karanth et al. 2011, Sunarto et al. 2012, Barber-Meyer et al. 2013), the methods can also be used to model habitat use of tigers at a finer scale (Sunarto et al. 2012). Prey occupancy analyses in Nepal and India, are relatively new and have only been conducted in combination with estimating ungulate densities under occupancy based approaches (Gopalaswamy et al. 2012). Prey animal distribution patterns across the landscape are typically non-uniform due to varying habitat characteristics (MacKenzie et al. 2003, Royle 2006). Therefore incorporating biologically relevant covariates into occupancy models is important. In this study, I focused on five major tiger prey species (Table 3.1): gaur (*Bos gaurus*), sambar (*Cervus unicolor*), chital (*Axis axis*), barking deer (*Muntiacus muntjac*), and wild pig (*Sus scrofa*), found in the Chitwan National Park in order to estimate prey occupancy (proportion of area occupied), seasonal changes in occupancy, and tiger habitat use in the little known churia habitat.

A multi scale analysis of spatial distribution is of practical importance in addressing wildlife conservation needs (Scott et al. 2002, Hartley and Kunin 2003). Tigers, as a case study, have been a suitable example in this regard because collating the spatial distribution of tigers across the entire Tiger Conservation Landscape (TCL) has been helpful in planning global tiger conservation strategies (GTRP 2010, Walston et al. 2010, Wikramanayake et al. 2011). At a regional level: landscape-wide assessment of tiger distribution aided in identification of source populations, meta population structure, and functional corridors including anthropogenic impacts therein (Smith et al. 1998, Ranganathan et al. 2008b, Karanth et al. 2011, Barber-Meyer et al. 2013). At the finer scale, patterns of habitat use in source areas where tigers are known to occur, provide insight into the local factors driving habitat use and thus are important for devising the local management options (Sunarto et al. 2012, Srivathsa et al. 2014). Habitat use analyses that include multiple spatial scales can improve our understanding of wildlife-habitat relationships (Johnson 1980, McDonald et al. 2012). In this study, in addition to large scale prey occupancy, I focused on tiger habitat use through an occupancy framework at a fine scale on the 537 km^2 of the churia habitat within a tiger source site in Chitwan National Park (Karki et al. 2013).

The objectives of my study were: 1) to investigate the factors affecting the probability of occupancy of the tiger's principal prey (gaur, sambar, chital, barking deer, and wild pig); 2) to examine habitat use of tigers at a fine scale using occupancy modeling; 3) to measure seasonal variation in prey occupancy and seasonal habitat use of tigers; and 4) to develop a predictive prey distribution maps based on spatially explicit occupancy models for species across the churia habitat. No studies on species distribution and habitat use characteristics by wildlife are available from the churia habitat. Based on existing literature, I hypothesized that prey occupancy and tiger habitat use across the forest matrix in churia habitat are affected by ecological and anthropogenic factors at the landscape scale and at the finer, micro-habitat scale. I expected to find to high occupancy of some prey species in some seasons to support the carnivore population in churia habitat

STUDY AREA

This study was conducted in the churia habitat, a 639 km^2 subset of the Chitwan National Park (CNP) located in central Nepal (Figure 3.1). The hilly churia habitat stretches between the flat lowland areas on the eastern side (363 km^2) and between the lowland forest of Chitwan National Park and Valmiki Tiger Reserve on the western side (276 km^2). The occupancy survey grid cells cover 537 km^2 out of the available 639 km^2 of churia habitat. Churia habitat is contiguous with the southern buffer zone to form a Madi valley with a human population density of 440 per km^2 (CBS 2011). Churia habitat is the main corridor joining the Valmiki Tiger Reserve in India and the Parsa Wildlife Reserve in the east to form a Tiger Conservation Landscape (TCL) (Wikramanayake et al. 2004).

Churia habitat is an undulating, hilly terrain with elevation ranging from 150 m to 714 m. The ecosystem is dynamic in nature as the substrate conditions are fragile. The top soil layer is very thin with stones and boulders beneath it. As the monsoon season progress, landslides are prevalent and mature trees fall down. Three seasons exist in the churia. Most of the precipitation occurs during the wet season between June-September with annual precipitation of 2,437 mm. After the wet season, the winter season follows for four months (November-February) with lowest temperatures in December and January. The summer season follows for four months from March to June. Deciduous forest trees shed their leaves at the onset of the winter season and the forest is prone to fire in the summer season. Most of the ground vegetation and forest floor is cleared by forest fires in the summer. Seasonal and perennial rivers originate in the churia and cascade down to form important sources of the water for wildlife. Churia habitat is composed of mixed deciduous forest. Mixed pine (*Pinus roxburgii*) forests emerge at ~400 m elevation and upwards. Broom grass *Thysanolaena maxima,* asparagus *Asparagus officianalis* and date palm *Phoenix dactylifera* are the main non-timber forest products (NTFP) which are harvested and illegally traded in the local markets.

Prey in the churia include gaur, sambar, barking deer, chital, wild pig, and primates, supporting a density of 62.5/ km^2 for all large to small size prey species combined (See Chapter 2). In addition to the cervids and bovids, the steep slopes of the Churia support four species of the antelope: the Himalayan serow (*Capricornis thar*), the goral (*Naemorhedus griseus*), the four horned antelope (*Tetracerus quadricornis*) and the nilgai (*Boselaphus tragocamelus*). Tigers, leopards (*Panthera pardus*), and dholes (*Cuon alpinus*) are the top carnivores in the churia habitat (Thapa et al. 2013a). Further details on the Chitwan National Park are described elsewhere (Dinerstein 2003, Gurung et al. 2008, Bhattarai and Kindlmann 2012, Karki et al. 2013, Subedi et al. 2013). Sporadic poaching incidents have been observed in the western part of the churia near the border with India. Livestock grazing is lower than the lowland forest areas, yet the impacts are thought to be high in the southern part of the churia.

METHODS

I employed occupancy modeling techniques using detection/non-detection data of animal signs while explicitly addressing the issue of imperfect detection (MacKenzie et al. 2002). Stronger inference can be derived from occupancy modelling because it makes full use of available information, decomposing true absence from non-detection, within a probabilistic framework (MacKenzie and Royle 2005, MacKenzie et al. 2006, Royle 2006). I created a grid across the churia using small grid cells of size 3.24 km^2 to investigate occupancy of potential tiger prey and the effects of ecological and anthropogenic factors influencing occupancy across the churia habitat. Because most prey species have very small home-ranges (< 3.25 km^2), occupancy can be used to predict prey distribution across the landscape. For animals with larger home-ranges such as tigers, occupancy models can also yield reliable estimates of probability of habitat-use at finer spatial scales (e.g. within the home-range, see tigers: Sunarto et al. 2012, and dholes: Srivastava et al. 2014). The technique is known to produce precise estimates of probability of habitat use and the nuisance parameter, detection probability. I investigated tiger habitat use at the grid cell (3.24 km^2) level and at an even finer scale of 600 m replicated spatial transects. To account for seasonal, spatial variation in occupancy and habitat use, I carried out surveys in the winter and summer seasons across the churia habitat to investigate changes in prey occupancy and tiger habitat use across seasons.

Prey Occupancy

I choose a small grid cell size of 3.24 km^2, overlaid on 537 km^2 of the churia forest habitat within Chitwan National Park, to measure occupancy of forest ungulates following Gopalaswamy et al. (2012). This grid cell size circumscribes the expected daily ungulate movement based on home-range size and movement rates reported in the field sites (Table 3.1) for gaur (Conry 1989, Sankar *et al.* 2001), sambar (Schaller 1967, Dinerstein 1980, Mishra 1982, Nowak 1999, Francis 2008, Sankar and Acharya 2004), chital (Schaller 1967, Mishra 1982, Mishra and Wemmer 1987, Moe and Wegge 1994), muntjac (Mishra 1982, Barrette 1977, Odden and Wegge 2007), and wild pig (Singer 1981, Baber and Coblentz 1986, Caley 1997). Team searched for common signs of ungulates such as tracks, pellets, dung, prey remains, calls, and direct sightings of prey during the field survey. I chose to survey grid cells in a checker board pattern (Figure 3.1). Within each alternate grid cell, I sampled 8 spatial replicates, with each replicate consisting of a 600m transect. Total survey effort within each 3.24 km^2 grid cell was 4.8 km. I conducted the survey in the same grid cells twice, once each in both the winter and summer seasons. For the prey occupancy analysis, detection and non-detection of prey animals was coded either a “1” for presence or “0” for absence for each transect such that there were 8 sampling occasions within each grid cell represented by the eight, 600 m long transects.

Tiger Habitat Use

For tigers, probability of habitat use was based on observations conducted at two fine scales: the grid cell level (3.25 km^2) similar to the prey survey noted above with 8 spatial replicates (sampling occasions) per grid cell, and also at the transect level (600 m), similar to Sunarto et al. (2012) for Sumatran tigers. Tiger sign (e.g. tracks, scrapes, scats, urine, etc.) at the grid level was collected at the same time as the prey data. At the transect level, each 600 m transect was considered as the site, and sampling occasions were represented by six, 100 m segments. Detection of tiger sign was recorded in every 100 m segment for 6 encounter occasions within each transect.

Selection of Covariates at the Grid Level

I collected covariates at two spatial scales: geographical information system (GIS) based landscape covariates and ground based field covariates for each grid cell. I extracted GIS-based, landscape-level covariates for each grid cell using a data source downloaded from GIS public domain and with permission from the WWF Nepal Conservation Science Unit. These landscape level covariates are believed to influence prey occupancy and tiger habitat use in the churia habitat and are listed in detail in Table 3.2. These data include two weather variables: temperature and precipitation; two terrain parameters: elevation and terrain ruggedness (Riley et al. 1999) computed from a digital elevation model (DEM) with-90m resolution data; a variable indexing vegetation characteristics that indicates the amount of primary productivity: Normalized Difference Vegetation Index (NDVI) extracted for winter; two variables characterizing habitat: habitat available (HAB) and tree canopy cover (CC); and finally distance to nearest settlement (DNS) as a surrogate measure of disturbance factors at the landscape level. Available habitat is measure as the proportion of *sal* dominant mixed deciduous forest within each grid cell. I used either constant detection probability (*p*) or modelled the influence of seasonal variation (winter versus summer) on detection. All variables were extracted and values were averaged at the grid cell level.

Field based covariates were collected within the 100 m replicates (Table 3.3). Upon detection of animal sign within each 100 m segment, I collected information on three variables defining structural characteristics of the habitat: ground cover (GC) using ocular estimates of % cover of vegetation, horizontal cover (HC) by visualizing the extent of 5 equally spaced colored bands across a 1.5 m stick from a distance of 25 m (1 representing high cover, to 5 representing low cover) (Shrestha 2004), and canopy cover (CC) using ocular estimates of % of vegetation overhead (Daubenmire 1959). I constructed three indices characterizing disturbance factors (DIST), carnivore activity (CAR), and prey activity (PREY). The disturbance index characterizing the disturbance impact on vegetation and species was calculated following Barber-Meyer et al. 2012: DIST= 0.35*evidence of poaching + 0.2*livestock presence + 0.25* impact on vegetation + 0.2*fire). I made modifications to the DIST formula excluding the impact of forest fire as it was hard to characterize forest fire quantitatively. I re-parameterized the equation as $\mathrm{DIST}_{\mathrm{revised}}$=0.5*poaching incident + 0.3*livestock presence + 0.2* impact on vegetation. The index characterizing carnivore activity (CAR) was calculated as the sum of all carnivore detection events divided by total sampling effort of 4.8 km within each grid cell. An index characterizing prey activity (PREY) affecting habitat use of the tiger was calculated as the sum of all prey detection events divided by the total sampling effort of 4.8 km. All the ground based variables collected along the sampling route were averaged for each grid cell. In addition to quantitative covariates, I used two qualitative variables: presence of forest fire and water sources ("1" for presence or "0" for absence), based on observations made along the sampling route for every 100 m and later at the 600 m scale during the analysis phase.

Selection of Covariates at the Transect Level

In addition to the grid level analysis, I also used the transect level (600 m) at each site for investigating habitat use of tigers at a fine scale. I developed habitat use models with different sets of covariates (landscape and field) extracted across the transects. For continuous variables, I extracted and averaged landscape-level and field-level information for the grid level from two circles surrounding the starting and ending points of each 600-m transect, each with a radius of 0.25 km. For binary variables such as presence of water and forest fires, information at the grid level was coded as “1” for presence or “0” for absence based on the observations made along the sampling route for every 100 m.

Selection of the first grid cell was random and consequent alternate grid cells in checker board pattern aided in minimizing spatial autocorrelation among grid cells. I randomly selected the starting point of the first transect within each grid cell and followed a compass azimuth for the transect in an approximate, S-shaped pattern. Each team was comprised of 2-3 skilled field personnel who searched the sampling routes to locate animal sign. Only fresh signs or direct sightings were considered to minimize false detections that could occur from the presence of very old sign (MacKenzie et al. 2006). While I realize that aging sign is difficult, my methods are conservative because i did not include sign that appeared old and weathered. For both tigers and prey, the team collected information on detection and non-detection, and collected data on field level covariates within each 100 m segment, whether animals were detected or not. The team searched for sign along the transects following probable animal travel routes including firelines, riverbanks, ridge lines, and water holes that were deemed to have high likelihood of finding sign (Barber-Meyer et al. 2013). To optimize detection, I deviated from search routes (<25 m) looking for signs but ensured uniformity in spatial coverage within each grid cell. All grid cells were surveyed on average for 4-5 hrs. (Gopalaswamy et al. 2012) to assume spatial closure (i.e. to minimize the bias from movement of animals from the surrounding grid cells). The survey was conducted in the winter (January-March, 2011) and the summer (April-June, 2011; April-June, 2012) seasons.

DATA ANALYSIS

I used the standard occupancy framework (MacKenzie et al. 2002) to model prey occupancy across the landscape and tiger occupancy at the within-habitat scale, maximizing the likelihood of observing the detection history at the sites. I used single species, multi-season correlated occupancy models in Program PRESENCE version 6.8, that explicitly take into account spatial autocorrelation in detection across the 600 m transects within each grid cell or within in the contiguous 100 m segments (Hines et al. 2014). In addition, I used Hines et al. (2014) models to derive the probability of occupancy or habitat use for the summer season and for changes in occupancy over time (λ) for each species.

Probability of occupancy for all the prey species (gaur, sambar, barking deer, chital, and wild pig) was measured at the grid level denoted, Ψ_{GRID}, while probability of tiger habitat use was measure at both the grid cell, Ψ_{GRID}, and the transect, Ψ_{TRAN}, levels. The landscape level covariates (extracted using GIS) and the field measured covariates were used to investigate detection, occupancy and habitat use probabilities in churia habitat.

Before modeling, all the covariates were screened for collinearity (Table 3.4). Highly correlated variables ($|r_s| \geq 0.77$) were either removed or not used in combination within the same model. For example: NDVI and ELE were not used in combination due to high correlation between the variables ($r_{\mathrm{NDVI\text{-}ELE}}$=0.81). I retained the variables which better explained the parameter of interest based on: ecological relevance, correspondence with earlier studies, ease in data collection across the study areas, and simplest in explanation of the model outcomes. All covariates used in modelling were normalized using the z transformation and/or scaled using constant value (Sunarto et al. 2012) except the proportion of habitat available (Donovan and Hines 2007) as this already represents a scaled parameter.

I first compared the standard models of Mackenzie et al. (2002), and Hines et al. (2014) without additional covariates to choose the appropriate model type for subsequent analysis. I used a two stage approach to modeling the parameter of interest at the grid level (Karanth et al. 2011, Harihar and Pandav 2012). First, I modeled detection probability (p) employing either the season-specific or the constant detection probability model, while using the global model (most parameterized model that included all the landscape and field covariates) for occupancy (Ψ_{GRID}). The spatial dependence parameter (e.g. the autocorrelation parameter at the transect level) are θ^0, representing the probability that the species is present locally, given the species was not present in the previous transect (spatial replicate); and θ^1 representing the probability that a species is present locally, given it was present in the previous spatial replicate. I used the constant model for θ^0 and θ^1 in all analyses. Secondly, I modelled the influence of all covariates (landscape and field level) on occupancy (Ψ_{GRID}) by using either seasonal influence on detection probability or constant detection.

Similarly, at the fine scale, I first modeled detection probability (p) employing either the season-specific or the constant detection probability model, while using the global model (most parameterized model that included all the landscape and field covariates) for habitat use (Ψ_{TRAN}). I then modelled the probability of habitat use (Ψ_{TRAN}) with covariates using either constant or seasonal influence on detectability. I followed the approach of Sunarto et al. (2012) by building models for covariates influencing the parameter of interest at both the spatial scales (grid and transect level). I modeled covariates in a stepwise, univariate fashion such that if the covariate improved model fit it was retained in the model and combined with other covariates in multivariate models. I only used the combination of covariates as additive effects in the models. No interaction models were used due to complexity that arises with general covariates to model different species with no prior information on their distribution. I eliminated models from the candidate set that did not converge. For model selection, I ranked all models using Akaike's Information Criterion (AICc) and chose the best model based on lowest AIC scores. I considered all models with $\Delta AIC_c < 2$ as competing models (Burnham and Anderson 2002). I used model averaging techniques to determine the cell-specific probabilities of occupancy (Ψ_{GRID}) and habitat use (Ψ_{TRAN}) considering all the competing models.

I used inferences from surveyed cells to estimate occupancy and habitat use for the un-surveyed cells based on landscape level characteristics only. I modeled site specific probabilities of prey occupancy and tiger habitat use as linear functions of the covariates (environmental, habitat and anthropogenic) using the logit link functions (MacKenzie et al. 2002, 2006). The value of untransformed estimates coefficients (i.e. betas, β), reflects the magnitude and direction (sign) of the influence of covariates on the probabilities of occupancy and habitat use. I considered the influence of covariates as important and supported if their estimates of β and the 95% confidence limits did not include zero (Dupont 2002). For comparison, I reported the beta estimates for the best model, univariate model, and model averaged estimates. I computed the model average estimates of cell specific $\widehat{\Psi}$ by considering all the plausible alternative models. I reported the final estimates (probability of occupancy and habitat use) as well as changes in occupancy (lamda, λ) from both the standard models and the models containing covariates on the parameter of interests. To estimate overall prey occupancy ($\widehat{\Psi}$) and tiger probability of habitat use within the churia habitat of Chitwan National Park, I weighed the cell-specific occupancy estimates by potential habitat within each grid cell ($3.24\ km^2$) (Karanth et al. 2011). The computation of variance was done using a parametric bootstrapping approach (Karanth et al. 2011). I prepared predicted maps of occupancy for all ungulate prey species and tiger habitat maps based on inferences made from the model averaged outputs in ArcGIS 10.1

RESULTS

Summary of Effort and Detections

During the survey, the team walked a total of 643 km of trails in the winter and summer seasons combined and detected prey sign 1,317 times and tiger sign 301 times on the 600 m transect level and in 71 of the 76 grid cells surveyed (Table 3.5). At the segment level, the team detected tiger sign on 308 of the 100 m segments of the 616 segments surveyed. Overall, the team recorded a total of 2,284 fresh signs of prey, 308 fresh signs of tigers, and 605 signs of carnivores (tiger and leopard combined) at 100 m segment level in 76 grid cells in two seasons across the trails of the churia habitat.

Test for Spatially Correlated Occupancy Model

Because the team searched for the animal sign across trails (animal, human, riverbanks, etc.) there is a high likelihood of spatial dependence in sign detection along the spatial segments. The spatial autocorrelation models (Hines et al. 2014) fit the data best as indicated by the lowest AIC values for all species (Table 3.6) and confirmed lack of independence between detections across spatial replicates compared to the standard model which assumes independence between detection events. Therefore, I included autocorrelation in all subsequent models.

Modelling Detection Probability

The global models for occupancy with the landscape covariates for gaur, wild pig, and tigers revealed the influence of season on detection probabilities across transects (Table 3.7- 3.13). Gaur and tigers had high detectability in winter and low detectability in summer, while, wild pigs had the opposite with low detectability in winter and high detectability in summer. Sambar, chital, and barking deer had a constant detectability across seasons. When using the global model with field level covariates; all species showed similar trends as for landscape level covariates except for sambar, with detectability varying by season while tigers had a constant detectability (Table 3.7- Table 3.13).

Modelling the Influence of Covariates on Prey Occupancy

Among all landscape covariates, proportion of available habitat (HAB) had a strong positive effect with on occupancy of prey species as indicated by β values (Figure 3.2). Other landscape variables tended to have varying degrees of influence but the estimates overlapped zero indicating inconclusive effects (Table 3.14). Among the large body sized prey (> than 50 kg), the model incorporating available habitat was the top model for sambar, while for gaur, the top model included additive effects of environmental covariates (terrain ruggedness index: tri, and normalized difference vegetation index: NDVI) influencing occupancy. Among the medium sized prey (25-50 kg): the model incorporating anthropogenic (DNS: distance to nearest village) and habitat (CC: canopy cover) characteristics was the top model for chital having negative impacts on occupancy; but with low β coefficients for all covariates and CIs including zero. Distance to nearest village was the top model for barking deer, negatively influencing occupancy, however, effect size was low for the species. For the wild pig, the additive effects of anthropogenic (DNS), habitat (HAB), and environmental (NDVI) variables were included in the top model. The largest effect size effect came from the covariate available habitat (HAB) which positively affected occupancy, while DNS and NDVI negatively, but more weakly influenced-wild pig occupancy in churia habitat.

Among the field level covariates, disturbance (DIST) had a strong negative effect on gaur and sambar occupancy, while presence of forest fire (FIRE) had a strong negative influence on occupancy of sambar and a strong positive influence on chital occupancy (Figure 3.2; Table 3.15). Effects of ground cover (GC) and horizontal cover (HC) were found to have strong negative and positive influences respectively on the occupancy of barking deer only. The carnivore activity (CAR) index had a strong negative influence only on occupancy of wild pigs (Table3.15). Presence of fire (FIRE) had positive effects on chital, and had a negative effects on sambar (Figure 3.3). The large number of competing models using both set of covariates (landscape and field) point to the uncertainties in modelling prey occupancy and tiger habitat use in churia habitat.

Estimates of Prey Occupancy in Churia habitat

The model averaged estimates of probability of occupancy $\widehat{\Psi}\ SE(\widehat{\Psi})$ (initial and derived) based on landscape covariates were found to be highest for sambar at 0.80 (SE 0.11) in winter and 0.82 (SE 0.21) in summer (Table 3.8) and lowest for chital at 0.30 (SE 0.13) in winter and 0.19 (SE 0.07) in summer (Table 3.9; Figure 3.4). The model averaged changes in occupancy across season (lamda, λ) showed increases from winter to summer in occupancy for wild pigs (λ = 1.11), sambar (λ = 1.02), and barking deer, although barking deer was basically stable (λ = 1.00). The opposite occurred for gaur (λ = 0.76) and chital (λ = 0.65) with decreases in occupancy from winter to summer in churia habitat (Figure 3.9). Similar trends in occupancy estimates were observed using field level predictor covariates (Tables 3.7-3.13) across the seasons but they differed in point estimates between the covariates types (landscape versus field).

The final model averaged estimates of prey occupancy for the churia habitat, including non-surveyed grid cells was highest for sambar at 0.80 (SE 0.12) in winter and 0.81 (SE 0.22) in summer, and again lowest for chital at 0.29 (SE 0.13) in winter and 0.19 (SE 0.13) in summer (Figure 3.5). In winter, the area of available habitat occupied out of the total 537 km^2 of potential available churia habitat by each prey species was: gaur, 413 km^2: sambar, 431 km^2; chital, 158 km^2; wild pig, 383 km^2; and barking deer, 329 km^2 . In summer, the area of available habitat occupied was: gaur, 318 km^2; sambar, 437 km^2; chital, 100 km^2; wild pig, 444 km^2; and barking deer, 349 km^2. I estimated the site specific $\widehat{\Psi}$ using the model averaged estimates for all species and showed the matrix of site specific variation in occupancy across the geographical space in churia habitat (Figure 3.6-3.8).

Modelling Tiger Habitat Use

At the grid level (3.25 km^2), the probability of detecting tiger sign $\hat{p}_{\mathrm{t(GRID)}}$ (SE) was influenced by season being much higher at 0.72 (SE 0.06) in winter than in summer at 0.40 (SE 0.07) when using the global model of all the landscape covariates for occupancy. Therefore, I used seasonal variation in detectability in the subsequent analyses for modelling probability of tiger habitat use.

Among all landscape covariates, proportion of available habitat (HAB) was the top model for tigers and had a high positive effect size on tiger habitat use with CIs that did not overlap zero (Figure 3.2, Table 3.14). Among field level covariates, additive effects of disturbance (DIST), presence of forest fire (FIRE), and presence of water (PW) were included in the top model. Tiger habitat use was unexpectedly positively influenced by disturbance factors, while forest fire had large positive effect but was not strong on tiger habitat use and presence of water positive influenced tiger habitat use in churia (Table 3.15). Model averaged β estimates revealed no covariates had important impacts although the size effect was high for some habitat variables, but CIs overlapped zero (Table 3.15).

At the fine grain, transect level (600m), I did not find any influence of seasonal variation on detection probability, hence the constant model was used for detection with both sets of covariates. Among the landscape variables, additive effects of temperature (TEMP, positive) and distance to nearest village (DNS, negative) were included in the top model influencing tiger habitat use (Table 3.14), suggesting tigers tend to use warm areas during the winter season and use areas closer to villages (Table 3.14). However, model averaged beta estimates overlapped zero revealing no distinct impact of landscape level variables except for NDVI, which had a strong negative influence on tiger habitat use at the fine grained level (Ψ_{TRAN}).

With field level covariates, the combined model incorporating disturbance(DIST), forest fire (FIRE), horizontal cover (HC), prey activity(PREY), and presence of water (PW) was the top model based on the lowest AIC values. DIST and HC had a weak positive influence; while, FIRE had a weak negative influence on tiger habitat use in churia habitat. PW had a strong positive influence on habitat use by tigers, while PREY was found to have a significant negative influence on tiger habitat use - opposite to my predictions (Table 3.15). Except for PW, no other field level covariates were found to have important impact on probability of habitat use of tiger at the transect level.

Estimates of Tiger Habitat Use in Churia Habitat

At the grid level, the model averaged estimates of probability $\widehat{\Psi}\ SE(\widehat{\Psi})$ of tiger habitat use (initial and derived) based on landscape covariates were 0.61 (SE 0.11) in winter and 0.56 (SE 0.21) in summer, among the surveyed cells in the churia habitat (Figure 3.4, Table 3.12). Similar trends in model averaged probabilities of habitat use were observed with field level covariates across the seasons but differed in point estimates between covariates types (landscape versus field covariates).

The final model averaged estimates of probability of tiger habitat use $\hat{\Psi}\ SE(\hat{\Psi})$ in the churia habitat were 0.63 (SE 0.15) in winter, 0.54 (SE 0.23) in summer. The area of available habitat occupied out of the total 537 km^2 of potential available churia habitat by tiger was: 337 km^2 and 291 km^2 in winter and summer respectively. The model averaged changes in occupancy (lamda, λ) showed a decrease in tiger habitat use from winter to summer, $\hat{\lambda}$ (SE) = 0.77 (SE 0.50), by almost 23% from winter to summer seasons. The site specific variation (high to low) in habitat use of tigers (Figure 3.8-3.9) shows that tigers intensively used certain habitat more often than other across the seasons.

At the transect level, the model averaged estimates of probability of tiger habitat use (initial and derived) based on landscape covariates were 0.65 (SE 0.20) in winter and 0.38 (SE 0.14) in summer, among the surveyed cells in the churia (Table 3.13). Similar trends in model averaged estimates were observed with field level covariates across the seasons but differed in point estimates between the covariates types (landscape versus field covariates).

DISCUSSION

This is the first study to estimate occupancy of principal tiger prey and prey seasonal variation in churia habitat employing the robust design occupancy modelling approach (MacKenzie et al. 2006). Ease in collecting occupancy data (Bailey et al. 2013) through a simple sign surveys aided in estimating and predicting species distributions (Karanth et al. 2011, Sunarto et al. 2012, Barber-Meyer et al. 2013, Srivathsa et al. 2014) across a relatively unknown landscape.

Occupancy estimates are more robust than the traditional presence and absence approach, which is likely to under estimate true occupancy by up to 30% in the case of gaur in winter and 17% in case of barking deer in summer season calculated based on naïve occupancy estimates. Employing Hines et al. (2014) spatial autocorrelation models aided in overcoming bias and provided more precise occupancy estimates of prey species across churia habitat. For example, gaur occurred across as 413 km^2 of the churia in winter and 318 km^2 in summer; higher than naïve estimates of 247 km^2 in winter and 166 km^2 in summer. Thus, detection and non-detection data combined with a rigorous occupancy approach provides better inference about spatial distributions of prey species, specifically addressing problems of underestimation that occurs when detectability is not incorporated. Using covariates in models of prey occupancy also increases realism and is therefore believed to be superior to other techniques, especially those using presence only detection models (Bhattarai and Kindlmann 2013, Simcharoen et al. 2014).

Sign surveys are often prone to observation error (failing to differentiate between preys signs) (Royle and Link 2006, Shea et al. 2011), which cannot be ignored in this study. At the field level, field assistants in my study had considerable experience in differentiating among animal signs, and experts were well mixed among the survey groups to minimize error (Barber-Meyer et al. 2013). Techniques allowing false detection error into spatial dependence models could provide the better occupancy estimates, however these methods are not yet available in the current modeling platform (Hines et al. 2014).

This study was able to estimate probability of occupancy of multiple forest ungulates simultaneously in the little known churia habitat. Unfortunately, there were many competing models for each species while using both sets of covariates (landscape and field level). These uncertainties that arise may be due to inclusion of covariates that are too general rather than prey-species specific. I did find, however, that proportion of area occupied by prey was high for some species and variable across species. The large bodied gaur and sambar were widely distributed. Gaur, exhibited a decrease in occupancy from winter to summer ($\lambda = 0.76$). This indicates that gaur use the churia intensively in winter but then move out of the churia as they migrate to the low lying areas in the summer season, supporting previous research (Prater 1980, Prayurasiddhi 1997). My findings of little seasonal change in occupancy (~2%) for sambar in the churia concurs with earlier studies that noted its restricted distribution in the hilly tracts across the Terai Arc (Johnsingh et al. 2004). The high occupancy estimates across seasons suggest sambar are resident throughout the churia (McKay- and Eisenberg 1974) and that they prefer mixed deciduous habitat (Karanth and Sunquist 1992) within rugged terrain in that the churia provides (Shrestha 2004). Considering that this is a favored prey of tigers, it is likely that churia habitat can support tigers in the area.

I found wild pigs as the most widely distributed medium sized prey (20-50 kgs) in churia habitat. The wild pig is a generalist species (Bratton 1975) with a highly plastic diet contributing to their wide distribution (Ballari and Barrios-García 2014). The large increase in occupancy for wild pigs seasonally from winter to summer (λ =1 .11) suggests that wild pigs range into the churia habitat in the summer from the surrounding areas, opposite of gaur, which migrate out. Above ground resources are scarce in churia during the winter season (Baron 1982) and pigs must rely on rooting which I found to be the most common sign in winter. In summer, delays in forest fires in churia makes above ground plants more easily available as the summer progress and new shoots of herbs are more abundant. This phenomenon is heightened after forest fires in summer and could be one reason for their increased occupancy in the summer season.

Chital are described as a habitat generalist (Schaller 1967) and their distribution is limited especially in the winter season. Chital prefer to live in open grassland intermixed with forest for shelter (Schaller 1967, Dinerstein 1980). The preponderance of only mixed deciduous habitat within the churia habitat could be limiting their distribution there. Barking deer, on the other hand, are forest animals (Schaller 1967) preferring dense vegetation structure that provides good cover (Chapman et al. 1994, McCullough et al. 2000), such as that available in the churia habitat. Stable occupancy estimates across seasons suggest their adherence to mixed deciduous forests (Dinerstein 1980, Shrestha 2004, Teng et al. 2004) as residents of in churia habitat.

Based on the top models: two of the environmental landscape covariates, precipitation and elevation, were non-influential and weak in predicting prey occupancy or tiger habitat use in the churia habitat. This indicates that winter rain or rainfall patterns in the Chitwan Valley do not affect the forest ungulate distributions. Other studies found only a weak relationship between prey density and rainfall pattern across the multiple sites in India (Karanth et al. 2004).

For gaur, occupancy was high in relatively flat to moderate terrain and not in the steeper slopes of the churia habitat. Large body size (400-1,000 kg) likely leads to higher amount of energy expenditure in steep terrain and could restrict their distribution to relatively moderate terrain. In other areas, presence of water sources were shown to be the prime reason for gaur tolerance of more rugged terrain and denser forest (Smith et al. 2010). Gaur occupancy was also affected positively by the productivity of vascular plants, measured by winter "NDVI" (Fairbanks and McGwire 2004), a measure of habitat productivity, which is lower in the summer in the *sal* dominated deciduous forest of churia habitat. Timing of forest fires in the churia habitat is delayed relative to the lowland areas (personal observation) causing more sprouting of palatable grass for bovids earlier on in the lowlands than in the churia and additionally, water sources become depleted as the summer progress within the churia habitat. Decreases in summer occupancy for gaur therefore are likely due to their summer migration downhill as fire in the lowlands increase forage, and as productivity decreases and water dries up in the churia as the summer progress. Hence habitat productivity (this study) and water availability (Smith et al. 2012) are likely important determinants of gaur distribution.

Proportion of habitat available within grid cells is an important ecological factor driving occupancy of sambar and wild pigs. Available habitat within the churia is defined as predominately composed of *sal* dominant mixed deciduous forest with varying levels of canopy cover. This reveals the importance of forest patches for sambar (Timmins et al. 2008) and wild pig occupancy in churia habitat. Trisurat et al. (2010) found sambar avoiding steep terrain and preferring open habitat. However, terrain related covariates did influence sambar in this study (TRI and ELE). Perhaps because they were not highly variable across the undulating landscape of the churia habitat. Sambar distribution has been shown to be very patchy in lowland areas of Chitwan National Park (Bhattarai and Kindlmann 2013), yet my results show that, within the churia, sambar are widespread.

Among the field collected variables: canopy cover, as proxy for shade (Dinerstein 1979) had weak or no influence on prey distribution across the churia habitat. As expected, disturbance had a negative effect on prey occupancy (Dave and Jhala 2011, Barber-Meyer et al. 2013) for all species but wild pigs. Disturbances in churia mostly include impacts on vegetation from people from factors like collection of non-timber forest products (NTFPs), firewood, timber, and direct persecution (e.g. hunting/poaching) by humans. For the large bodied gaur and sambar, the negative influence of disturbance on occupancy could explain the low level of human wildlife conflict as they avoid the areas of human settlements in the Chitwan Valley. Forest fire disturbance in general, does not impact all cervids equally (McShea et al. 2011). Forest fire negatively influenced sambar occupancy in this study but their ability to rapidly adjust their feeding strategy (Dinerstein 1979) could explain their high occupancy throughout the season. Alternatively forest fires facilitate increased productivity of ground vegetation. The chital's preference for grass (Schaller 1967, Johnsingh and Sankar 1991) and their attraction to young vigorous grass sprouts in freshly burned areas could explain the positive influence of fire on occupancy (Mishra 1982). Negative but weak influence of carnivore activity on all prey but gaur, suggests gaur distribution is independent of carnivore activity in the churia habitat.

Multiple scale analyses of tiger habitat use in the churia habitat provides a better understand the species-habitat relationships. The high probability of habitat use by tigers (0.54 - 0.63), suggests the churia habitat is highly suitable for tigers despite uncertainties in model selection. The 95% CIs of seasonal occupancy estimates for tiger habitat use overlap suggesting weak seasonal effects in tiger habitat use of churia habitat. Nonetheless, water availability could explain difference since water is depleted as summer progress in churia. Proportion of available habitat is an important factor driving tiger habitat use within the churia concurring with other studies showing that tigers require large tracts of forest at the landscape scale with dense understory at a fine scale (Sunarto et al. 2012). Presence of water is also important for tigers and water within the churia habitat is available in pockets across the gullies and at the base of the churia hills (personal observation). The majority of water drainages inside churia are seasonal and depend upon rainfall patterns for replenishment. Water sources get recharged and cascade down to low lying areas as important sources of water for wildlife in Chitwan National Park.

Tigers appear to use areas with high levels disturbance in churia, opposite from my prediction. Of the main disturbances recorded in churia habitat is the collection of thatched grass and fodder and NTFPs. These activities put people in close proximity to tigers, often as they work alone, and typify the main activities of victims who are killed by tigers in Chitwan (Gurung et al. 2008). It is possible that there are not many areas where tigers can avoid contact with humans throughout the churia and they may be forced to use areas with human disturbance such as in case of buffer zones surrounding protected areas. Tiger habitat use of areas with human disturbances should not be equated with co-existence between tigers and humans. Recent debates (Goswami et al. 2013, Karanth et al. 2013) draw attention to the controversial terminology equating co-occurrence between tigers and humans as “co-existence” (Carter et al. 2012). Additionally, high tiger density lowland areas of Chitwan (Dhakal et al. 2014) may compel tigers to use the contiguous churia habitat or extend their territories into the surrounding buffer zone areas drawing humans and wildlife into a conflict nexus (Harihar and Pandav 2012, Karki et al. 2013). The inevitable repercussion is human-tiger conflict and fatal human casualties in the Chitwan National Park and buffer zones (Gurung et al. 2008). Between 1999 and 2009, 50% of the total human casualties (n = 88) from tigers were reported within the churia habitat in the Chitwan Valley, and 30% were reported from this study area (Gurung et al. 2008). However, 635 km^2 of the core churia habitat is within the protected area, but lacks adequate enforcement to break the human compulsion to disturb the churia habitat for human needs.

Contiguous land cover patches facilitate movement and dispersal of animals across the landscape (Boscolo et al. 2008, Kanagaraj et al. 2011, Short Bull et al. 2011, Sunarto et al. 2012) and influences habitat use on a fine scale (Sunarto et al. 2012). Churia habitat provides continuous forest cover for tigers and their prey with a majority of patches occupied and used across the seasons. The churia habitat as part of a tiger source site in Chitwan and hence provides an opportunity for augmenting tiger densities based on the high prey occupancy I found in this study. Functional wildlife habitats distributed across the tiger range are connected by forested habitat such as the churia, which can enhance connectivity among source sites (Smith et al. 2011). The churia provides a hospitable habitat for dispersing between source sites within the Valmiki-Chitwan Conservation Landscape.

The Government of Nepal (GoN) has proposed a road and railway project through Chitwan National Park, which would trigger habitat fragmentation, impacting species assemblages within the churia ecosystem. Occupancy modelling from other studies has shown that such type of disturbance could have serious impact on prey occupancy and tiger habitat use on multiple scales (Kerley et al. 2002, Sunarto et al. 2012, Barber-Meyer et al. 2013). Impacts could include, reducing species abundance (Dyer et al. 2001, Kerley et al. 2002, Gravel et al. 2012) through a barrier effect or increased mortality (Kerley et al. 2002, Fahrig and Rytwinski 2009), and/or reduced structural connectivity causing further isolation and potential threats caused by reduced population sizes (Epps et al. 2005, Proctor et al. 2005). Road construction through one of the very few tiger source sites likely would be highly detrimental to tiger conservation and calls into question the commitment of the GoN to double the wild tiger population by 2022.

Availability of habitat patches, distribution of water sources, and human disturbances were top ranked variables influencing the spatial distribution of prey and habitat use of tiger at different scales. Spatial distribution of prey is broad within the churia and does not require any immediate habitat management interventions. Creation of waterholes is an important habitat management practice in seasonally dry, sub-tropical forest, but would be an expensive investment under such porous substrate conditions in the churia. Considering the possibly unavoidable situation that tigers must live in disturbed areas, while prey tend to avoid such disturbed areas, calls for conservation efforts to strengthen the protection strategies in this valuable churia habitat. Three approaches could be considered for securing the churia habitat: 1) timing the patrolling to correspond to the phenology of harvesting of non-timber forest products (e.g.: *Asparagus racemose*); 2) focusing on protection of the transition zone between the edge of the churia habitat and core of core churia (~2km in); and 3) strengthening the transboundary anti-poaching measures. The churia habitat is highly valuable and should not be forgotten in the conservation of tigers and their prey. I encourage heightened protection and expanded studies of this unknown habitat type in other parts of the Terai Arc, and recommended inclusion of the churia in the tiger conservation management plans.

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TABLES AND FIGURES

Table 3.1: Natural History attributes of ungulates species. Adapted from (William et al. 2011).

Attribute	**Gaur** *Bos gaurus*	**Sambar** *Rusa unicolor*	**Chital** *Axis axis*	**Wild pig** *Sus scrofa*	**Barking Deer** *Muntiacus muntjak*
Body weight (kg)	400-1,000	180-260	70-90	25-40	20-30
Home-range (km^2)	27.8	0.1-1	0.15-0.2	2.04-0.20	1.5-2.5
Average Daily Movement (km)	4.2	N/A	3-4	N/A	N/A
Mean group size	2-42	4-3	5-17	6-20	1-2
Birth season	Nov-Mar	May-August	Oct-Apr	NA	Nov-May
Birth season (months)	5	4	7	4	8
Diet	Grazer , grass, forbs, browse	Browse, ferns, grass, forbs	Grass, browse, fruits	Browse, graze, rooting, Omnivores	Browse, forbs
Range extent in South Asia (*10000 sq. km)	NA	438.8	127.5	NA	415.7
% protected (range)	NA	0.09	0.05	NA	0.09
IUCN Red list Status	VU	VU	LC	LC	LC

NA: Not Available; VU: Vulnerable; LC: Least Concern;

Table 3.2: Landscape level predictor variables used as potential factors affecting prey occupancy and tiger habitat use in the churia habitat. The “+” and “-“indicate the *apriori* predictions regarding the hypothesized direction of the effect. GR: Gaur; SAM: sambar; CHI: Chital; BD: Barking deer; WB: Wild pig; TIG: Tiger

Covariates	**Description**	**Value Range**			**Apriori Relationship**					
		Min	Max	Av. (SD)	GR	SAM	CHI	BD	WB	TIG
Distance to Nearest Settlement (DNS) (in km)	Generated a surface by calculating the Euclidean distance from settlement data extracted from Nepal Survey Department 1996 digital topographic data (ref) and world settlement data (Ref).	0	11	5.05 (2.6)	+	+	+	+	+	+
Normalized Difference Vegetation Index (NDVI)	Derived from Landsat 6 Thematic Mapper imagery (28.5 m X 28.5 m resolution) of the study area during the ‘winter season’ (November, 2011) and summer season (May 2011). Used as a measure of vegetation productivity (Nathalie Pettorelli et al. 2009). Download from : http://Glovis.usgs.gov	0.19	0.50	0.43 (0.05)	+	+	+	+	+	+
Win temperature (TEMP) ˚C	Extracted from World Climate data at 1 km^2 resolution (Hijmans et al 2005); Downloaded from www.climate.org	16.35	19.46	17.76 (0.84)	+	+	+	+	+	+
Precipitation (PREP)	Extracted from World Climate data at 1 km^2 resolution (Hijmans et al. 2005); Downloaded from www.climate.org	40	70.50	57.12 (7.13)	+	+	+	+	+	+
Elevation (ELE)	Derived from Digital elevation Model/DEM at 90-m resolution from the Shuttle Radar Topographic Mission dataset (SRTM) (Jarvis et al. 2008); Downloaded from: http://srtm.usgs.gov	154.24	680.09	412.71 (139.16)	-	-	-	-	-	-
Topographic Ruggedness Index (TRI)	Computed using the SRTM digital elevation model-90m (Riley et al., 1999)	71.31	276.48	175.69 (46.51)	-	-	-	-	-	-
Habitat Available (HAB) (km^2)	Derived and extracted for the study area from 2010 supervised classification Landsat 6 Thematic Mapper imagery (28.5 m X 28.5 m resolution) with permission from WWF Nepal. Download from : http://Glovis.usgs.gov	0.08	2.64	2.52 (0.39)	+	+	+	+	+	+
Canopy Cover (CC) (km^2)	Derived and extracted for the study area from 2011 supervised classification of Landsat 4–5 Thematic Mapper imagery (30 m X 30 m resolution) with permission from WWF Nepal.	0	2.56	1.98 (0.56)	+	+	+	+	+	+

Table 3.3: Field level predictor variables evaluated as covariates affecting prey occupancy and tiger habitat use in the churia habitat. The "+" and "-"indicate the *apriori* predictions regarding the hypothesized direction of the effect. GR: Gaur; SAM: sambar; CHI: Chital; BD: Barking deer; WB: Wild pig; TIG: Tiger

Covariate	**Description**	**Value Range**			**Apriori Relationship**					
		Min	**Max**	**Av. (SD)**	GR	SAM	CHI	BD	WB	TIG
disturbance index (dist)	combined index using the equation modified after Barber et al. 2012; dist= 0.2*(impact to vegetation)+ 0.3* (livestock presence)+ 0.5*(poaching)	0	28.15	8.24 (6.41)	-	-	-	-	-	-
presence of fire (fire)	presence "1" or absence of fire "0" observed at the site along the route	0	1	-	-	-	-	-	-	-
presence of water (pw)	presence "1" or absence of water "0" observed at the visible distance from the route	0	1	-	+	+	+	+	+	+
canopy cover (cc)	visual estimation of canopy cover (in %)	3.11	68.13	44.44 (14.23)	+	+	+	+	+	+
horizontal cover (cc)	number of color bands (0-5) observed from 25 m distance. Number ranges from zero to five represent high to low cover.	2.00	5.00	4.00 (1.00)	+	+	+	+	+	+
ground cover (gc)	visual estimation of percent of ground cover by vegetation.	0	74.09	26.16 (19.49)	+	+	+	+	+	+
carnivore activity index (car)	total unique detection of fresh sign of tiger/leopard/dhole along each 600m transect walk divided by total number of detection and multiplied with scalar factor 100	0	272.92	135.57 (46.55)	-	-	-	-	-	
Prey activity index (prey)	total unique detection of prey (sambar, gaur, chital, barking deer, wild pig) along the 600m transect walk divided by total number of detection, and multiplied with scalar factor 100	0	125	15.61 (22.27)						+

Table 3.4: Spearman correlation coefficients between the predictor variables. Those with very high correlations ($|r_s| \geq 0.70$) were not used together in the same model. Number of grid cells surveyed = 77; Number of transects surveyed = 616

Landscape Variables	DNS	ELE	TRI	CC	Hab	NDVI	TEMP	PREP
DNS	1.00							
ELE	0.34	1.00						
TRI	0.24	0.87	1.00					
CC	-0.13	0.00	-0.14	1.00				
HAB	-0.07	-0.07	-0.03	0.55	1.00			
NDVI	0.27	0.67	0.48	0.31	-0.09	1.00		
TEMP	-0.25	-0.98	-0.83	-0.04	0.10	-0.71	1.00	
PREP	0.26	0.97	0.80	0.08	-0.07	0.71	-0.98	1.00

Field Variables	DIST	HC	CC	CAR	PREY
DIST	1.00				
HC	0.17	1.00			
CC	-0.13	0.11	1.00		
CAR	0.15	0.02	0.06	1.00	
PREY	0.31	0.12	0.33	0.11	1.00

DNS: Distance to Nearest Settlement; ELE: Elevation; TRI: Terrain Ruggedness Index; CC: Canopy cover; HAB: Habitat Available; NDVI: Normalized Difference Vegetation Index; TEMP: Temperature; PREP: Precipitation. DIST: Disturbance; HC: Horizontal Cover; CC: Canopy Cover; CAR: Carnivore Index; PREY: Prey Index

Table 3.5: Summary of survey effort at two spatial scales (grid and transect levels) during the sign surveys of forest ungulates and tigers in churia habitat in Chitwan National Park, Nepal.

SCALE	SPECIES	Season	Number of units surveyed	Proportion with detections (Naïve occupancy)	Total sign detected
Grid (3.25 km^2)	Gaur	Winter	69	0.46	79
		Summer	65	0.31	45
	Sambar	Winter	69	0.83	272
		Summer	65	0.91	293
	Barking Deer	Winter	69	0.57	133
		Summer	65	0.57	114
	Chital	Winter	69	0.25	45
		Summer	65	0.16	28
	Wild pig	Winter	69	0.62	126
		Summer	65	0.80	182
	Tiger	Winter	69	0.46	100
		Summer	65	0.42	55
Transect (600 m)	Tiger	Winter	552	0.18	196
		Summer	520	0.11	105

Table 3.6: Comparisons between the standard occupancy model (MacKenzie et al. 2003) and the multi-season model including potential auto-correlation of sign detection (Hines et al. 2014) used to estimate occupancy of prey species at the 3.24 km^2 grid level (Ψ_{GRID}) and probability of tiger habitat use at both the grid level (Ψ_{GRID}) and the 600m transect level (Ψ_{TRAN}). Surveys were conducted in winter and summer season in the churia habitat of Chitwan National Park, Nepal. AIC is Akaike's information criterion, ΔAIC is the difference in AIC value of the focal model and the best AIC model in the set, K is the number of model parameters and –2Loglik is -2 of the logarithm of the likelihood function evaluated at the maximum.

Scale	Species		MODEL	AIC	ΔAIC	Model Like-lihood	K	Deviance
Ψ_{GRID}	Gaur	CSRM	$\Psi_{GRID}(.), \theta^{0}_{GRID}(.), \theta^{1}_{GRID}(.), \gamma_{GRID}(.), \varepsilon_{GRID}(.), p_{t(GRID)}(.)$	658.83	0	1	1	644.83
		SMSM	$\Psi_{GRID}(.), \gamma_{GRID}(.), \varepsilon_{GRID}(.), p_{t(GRID)}(.)$	679.81	20.98	0	0	671.81
	Sambar	CSRM	$\Psi_{GRID}(.), \theta^{0}_{GRID}(.), \theta^{1}_{GRID}(.), \gamma_{GRID}(.), \varepsilon_{GRID}(.), p_{t(GRID)}(.)$	1243.66	0	1	7	1229.66
		SMSM	$\Psi_{GRID}(.), \gamma_{GRID}(.), \varepsilon_{GRID}(.), p_{t(GRID)}(.)$	1338.18	94.52	0	4	1330.18
	Barking Deer	CSRM	$\Psi_{GRID}(.), \theta^{0}_{GRID}(.), \theta^{1}_{GRID}(.), \gamma_{GRID}(.), \varepsilon_{GRID}(.), p_{t(GRID)}(.)$	989.63	0	1	7	975.63
		SMSM	$\Psi_{GRID}(.), \gamma_{GRID}(.), \varepsilon_{GRID}(.), p_{t(GRID)}(.)$	1029.71	40.08	0	4	1021.71
	Chital	CSRM	$\Psi_{GRID}(.), \theta^{0}_{GRID}(.), \theta^{1}_{GRID}(.), \gamma_{GRID}(.), \varepsilon_{GRID}(.), p_{t(GRID)}(.)$	365.78	0	1	7	351.78
		SMSM	$\Psi_{GRID}(.), \gamma_{GRID}(.), \varepsilon_{GRID}(.), p_{t(GRID)}(.)$	414.64	48.86	0	4	406.64
	Wild pig	CSRM	$\Psi_{GRID}(.), \theta^{0}_{GRID}(.), \theta^{1}_{GRID}(.), \gamma_{GRID}(.), \varepsilon_{GRID}(.), p_{t(GRID)}(.)$	1139.97	0	1	7	1125.97
		SMSM	$\Psi_{GRID}(.), \gamma_{GRID}(.), \varepsilon_{GRID}(.), p_{t(GRID)}(.)$	1178.18	38.21	0	4	1170.18
	Tiger	CSRM	$\Psi_{GRID}(.), \theta^{0}_{GRID}(.), \theta^{1}_{GRID}(.), \gamma_{GRID}(.), \varepsilon_{GRID}(.), p_{t(GRID)}(.)$	744.96	0	1	7	730.96
		SMSM	$\Psi_{GRID}(.), \gamma_{GRID}(.), \varepsilon_{GRID}(.), p_{t(GRID)}(.)$	780.32	35.36	0	4	772.32
Ψ_{TRAN}	Tiger	CSRM	$\Psi_{TRAN}(.), \theta^{0}_{TRAN}(.), \theta^{1}_{TRAN}(.), \gamma_{TRAN}(.), \varepsilon_{TRAN}(.), p_{t(TRAN)}(.)$	1590.72	0	1	7	1576.72
		SMSM	$\Psi_{TRAN}(.), \gamma_{TRAN}(.), \varepsilon_{TRAN}(.), p_{t(TRAN)}(.)$	1611.15	20.43	0	4	1603.15

θ^0 = spatial dependence parameter representing the probability that the species is present locally, given the species was not present in the previous spatial replicate; θ^1 = spatial dependence parameter representing the probability that a species is present locally, given it was present at the previous spatial replicate. γ is the probability that the site is occupied in summer season, given that it was unoccupied in winter season. ε is the probability that the site is unoccupied in summer season, given that it was occupied in winter season. CSRM: Correlated Multiple Season Model. SMSM: Standard Multiple Season Model.

Table 3.7: Top models for gaur (> 50 kg) including the influence of covariates on the probability of occupancy (Ψ_{GRID}) based on detection history data collected at the grid level (3.24 km^2) in the churia habitat of Chitwan National Park, Nepal.

Co-variates	Model	AIC	ΔAIC	w_i	Model like-lihood	K
Land-scape	$\Psi_{GRID}(\text{tri+ndvi}),\theta^{0}_{GRID}(.),\theta^{1}_{GRID}(.), \gamma_{GRID}(.), \varepsilon_{GRID}(.), p_{t(GRID)}(\text{season})$	651.07	0	0.26	1	10
	$\Psi_{GRID}(\text{tri}), \theta^{0}_{GRID}(.),\theta^{1}_{GRID}(.), \gamma_{GRID}(.), \varepsilon_{GRID}(.), p_{t(GRID)}(\text{season})$	652.94	1.87	0.10	0.39	9
	$\Psi_{GRID}\ (\text{tri+ndvi+cc}), \theta^{0}_{GRID}(.),\theta^{1}_{GRID}(.), \gamma_{GRID}(.), \varepsilon_{GRID}(.), p_{t(GRID)}(\text{season})$	652.99	1.92	0.1	0.38	11
	$\Psi_{GRID}(\text{tri+ndvi+dns}), \theta^{0}_{GRID}(.),\theta^{1}_{GRID}(.), \gamma_{GRID}(.), \varepsilon_{GRID}(.), p_{t(GRID)}(\text{season})$	653.05	1.98	0.10	0.37	11
	$\Psi_{GRID}(\text{tri+ndvi+hab}), \theta^{0}_{GRID}(.),\theta^{1}_{GRID}(.), \gamma_{GRID}(.), \varepsilon_{GRID}(.), p_{t(GRID)}(\text{season})$	653.07	2	0.10	0.37	11
	$\Psi_{GRID}(\text{tri+hab}), \theta^{0}_{GRID}(.),\theta^{1}_{GRID}(.), \gamma_{GRID}(.), \varepsilon_{GRID}(.), p_{t(GRID)}(\text{season})$	654.52	3.45	0.05	0.18	10
	$\Psi_{GRID}(\text{prep}), \theta^{0}_{GRID}(.),\theta^{1}_{GRID}(.), \gamma_{GRID}(.), \varepsilon_{GRID}(.), p_{t(GRID)}(\text{season})$	654.63	3.56	0.04	0.17	9
	$\Psi_{GRID}(\text{tri+dns}), \theta^{0}_{GRID}(.),\theta^{1}_{GRID}(.), \gamma_{GRID}(.), \varepsilon_{GRID}(.), p_{t(GRID)}(\text{season})$	654.74	3.67	0.04	0.16	10
	$\Psi_{GRID}(\text{tri+cc}), \theta^{0}_{GRID}(.),\theta^{1}_{GRID}(.), \gamma_{GRID}(.), \varepsilon_{GRID}(.), p_{t(GRID)}(\text{season})$	654.92	3.85	0.04	0.15	10
	$\Psi_{GRID}(\text{tri+ndvi+cc+hab}), \theta^{0}_{GRID}(.),\theta^{1}_{GRID}(.), \gamma_{GRID}(.), \varepsilon_{GRID}(.), p_{t(GRID)}(\text{season})$	654.99	3.92	0.04	0.14	12
	$\Psi_{GRID}(\text{temp}), \theta^{0}_{GRID}(.), \theta^{1}_{GRID}(.), \gamma_{GRID}(.), \varepsilon_{GRID}(.), p_{t(GRID)}(\text{season})$	655.01	3.94	0.04	0.14	9
	$\Psi_{GRID}(\text{prep+hab}), \theta^{0}_{GRID}(.), \theta^{1}_{GRID}(.), \gamma_{GRID}(.), \varepsilon_{GRID}(.), p_{t(GRID)}(\text{season})$	655.87	4.8	0.02	0.09	10
	$\Psi_{GRID}(\text{temp+hab}), \theta^{0}_{GRID}(.), \theta^{1}_{GRID}(.), \gamma_{GRID}(.), \varepsilon_{GRID}(.), p_{t(GRID)}(\text{season})$	656.39	5.32	0.02	0.07	10
	$\Psi_{GRID}(.), \theta^{0}_{GRID}(.), \theta^{1}_{GRID}(.), \gamma_{GRID}(.), \varepsilon_{GRID}(.), p_{t(GRID)}(\text{season})$	658.15	7.08	0.01	0.03	8
Field	$\Psi_{GRID}(\text{dist}), \theta^{0}_{GRID}(.)\ ,\theta^{1}_{GRID}(.), \gamma_{GRID}(.), \varepsilon_{GRID}(.), p_{t(GRID)}(\text{season})$	625.52	0.00	0.19	1.00	9
	$\Psi_{GRID}(\text{dist+cc}), \theta^{0}_{GRID}(.), \theta^{1}_{GRID}(.), \gamma_{GRID}(.), \varepsilon_{GRID}(.), p_{t(GRID)}(\text{season})$	626.32	0.80	0.13	0.67	10
	$\Psi_{GRID}(\text{dist+car}), \theta^{0}_{GRID}(.), \theta^{1}_{GRID}(.), \gamma_{GRID}(.), \varepsilon_{GRID}(.), p_{t(GRID)}(\text{season})$	626.81	1.29	0.10	0.52	10
	$\Psi_{GRID}\ (\text{dist+fire}), \theta^{0}_{GRID}(.), \theta^{1}_{GRID}(.), \gamma_{GRID}(.), \varepsilon_{GRID}(.), p_{t(GRID)}(\text{season})$	627.47	1.95	0.07	0.38	10
	$\Psi_{GRID}(\text{dist+gc}), \theta^{0}_{GRID}(.), \theta^{1}_{GRID}(.), \gamma_{GRID}(.), \varepsilon_{GRID}(.), p_{t(GRID)}(\text{season})$	627.50	1.98	0.07	0.37	10
	$\Psi_{GRID}(\text{dist+pw}), \theta^{0}_{GRID}(.), \theta^{1}_{GRID}(.), \gamma_{GRID}(.), \varepsilon_{GRID}(.), p_{t(GRID)}(\text{season})$	627.51	1.99	0.07	0.37	10
	$\Psi_{GRID}(\text{dist+cc+car}), \theta^{0}_{GRID}(.), \theta^{1}_{GRID}(.), \gamma_{GRID}(.), \varepsilon_{GRID}(.), p_{t(GRID)}(\text{season})$	627.75	2.23	0.06	0.33	11
	$\Psi_{GRID}(\text{dist+cc+fire}), \theta^{0}_{GRID}(.), \theta^{1}_{GRID}(.), \gamma_{GRID}(.), \varepsilon_{GRID}(.), p_{t(GRID)}(\text{season})$	628.19	2.67	0.05	0.26	11
	$\Psi_{GRID}\ (\text{dist+cc+pw}), \theta^{0}_{GRID}(.), \theta^{1}_{GRID}(.), \gamma_{GRID}(.), \varepsilon_{GRID}(.), p_{t(GRID)}(\text{season})$	628.22	2.70	0.05	0.26	11

Co-variates	**Model**	**AIC**	**ΔAIC**	***w*$_i$**	**Model like-lihood**	**K**
	Ψ_{GRID} (dist+cc+gc), $\theta^{0}_{GRID}(.)$, $\theta^{1}_{GRID}(.)$, $\gamma_{GRID}(.)$, $\varepsilon_{GRID}(.)$, $p_{t(GRID)}$(season)	628.32	2.80	0.05	0.25	11
	Ψ_{GRID} (dist+car+fire), $\theta^{0}_{GRID}(.)$, $\theta^{1}_{GRID}(.)$, $\gamma_{GRID}(.)$, $\varepsilon_{GRID}(.)$, $p_{t(GRID)}$(season)	628.75	3.23	0.04	0.20	11
	Ψ_{GRID} (dist+car+pw), $\theta^{0}_{GRID}(.)$, $\theta^{1}_{GRID}(.)$, $\gamma_{GRID}(.)$, $\varepsilon_{GRID}(.)$, $p_{t(GRID)}$(season)	628.80	3.28	0.04	0.19	11
	Ψ_{GRI} (dist+car+gc), $\theta^{0}_{GRID}(.)$, $\theta^{1}_{GRID}(.)$, $\gamma_{GRID}(.)$, $\varepsilon_{GRID}(.)$, $p_{t(GRID)}$(season)	628.81	3.29	0.04	0.19	11
	$\Psi_{GRID}(.)$, $\theta^{0}_{GRID}(.)$, $\theta^{1}_{GRID}(.)$, $\gamma_{GRID}(.)$, $\varepsilon_{GRID}(.)$, $p_{t(GRID)}$(season)	631.48	5.96	0.01	0.05	8.00

Ψ_{GRID} = probability of site occupancy/habitat use at the grid level; p = probability of detection; θ^0 = spatial dependence parameter representing the probability that the species is present locally, given the species was not present in the previous spatial replicate; θ^1 = spatial dependence parameter representing the probability that a species is present locally, given it was present at the previous spatial replicate. γ is the probability that the site is occupied in summer season, given that it was unoccupied in winter season. ε is the probability that the site is unoccupied in summer season, given that it was occupied in winter season. Hab: habitat available; cc: canopy cover; ndvi: normalized difference vegetation index; ele: elevation; tri: terrain ruggedness index; prep: precipitation; dist: disturbance index; gc: ground cover; pw: presence of water; car: carnivore activity index; K: number of parameters in the model.

Table 3.8: Top models for sambar (> 50 kg) including the influence of covariates on the probability of occupancy (Ψ_{GRID}) based on detection history data collected at the grid level (3.24 km^2) in the churia habitat of Chitwan National Park, Nepal.

Co-variates	Model	AIC	ΔAIC	w_i	Model like-lihood	K
Land-scape	$\Psi_{GRID}(hab), \theta^0_{GRID}(.), \theta^1_{GRID}(.), \gamma_{GRID}(.), \varepsilon_{GRID}(.), p_{t(GRID)}(.)$	1243.09	0.00	0.09	1.00	8
	$\Psi_{GRID}(hab+dns), \theta^0_{GRID}(.), \theta^1_{GRID}(.), \gamma_{GRID}(.), \varepsilon_{GRID}(.), p_{t(GRID)}(.)$	1243.22	0.13	0.09	0.94	9
	$\Psi_{GRID}(.),\theta^0_{GRID}(.),\theta^1_{GRID}(.), \gamma_{GRID}(.), \varepsilon_{GRID}(.), p_{t(GRID)}(.)$	1243.66	0.57	0.07	0.75	7
	$\Psi_{G}(hab+cc), \theta^0_{GRID}(.), \theta^1_{GRID}(.), \gamma_{GRID}(.), \varepsilon_{GRID}(.), p_{t(GRID)}(.)$	1244.40	1.31	0.05	0.52	9
	$\Psi_{GRID}(cc), \theta^0_{GRID}(.), \theta^1_{GRID}(.), \gamma_{GRID}(.), \varepsilon_{GRID}(.), p_{t(GRID)}(.)$	1244.43	1.34	0.05	0.51	8
	$\Psi_{GRID}(dns), \theta^0_{GRID}(.), \theta^1_{GRID}(.), \gamma_{GRID}(.), \varepsilon_{GRID}(.), p_{t(GRID)}(.)$	1244.58	1.49	0.04	0.47	8
	$\Psi_{GRID}(hab+dns+cc), \theta^0_{GRID}(.), \theta^1_{GRID}(.), \gamma_{GRID}(.), \varepsilon_{GRID}(.), p_{t(GRID)}(.)$	1244.62	1.53	0.04	0.47	10
	$\Psi_{GRID}(hab+ndvi), \theta^0_{GRI}(.), \theta^1_{GRID}(.), \gamma_{GRID}(.), \varepsilon_{GRID}(.), p_{t(GRID)}(.)$	1244.74	1.65	0.04	0.44	9
	$\Psi_{GRI}(hab+ele), \theta^0_{GRID}(.) ,\theta^1_{GRID}(.), \gamma_{GRID}(.), \varepsilon_{GRID}(.), p_{t(GRID)}(.)$	1244.80	1.71	0.04	0.43	9
	$\Psi_{GRID}(hab+prep), \theta^0_{GRID}(.) ,\theta^1_{GRID}(.), \gamma_{GRID}(.), \varepsilon_{GRID}(.), p_{t(GRID)}(.)$	1244.87	1.78	0.04	0.41	9
	$\Psi_{GRID}(hab+temp), \theta^0_{GRID}(.), \theta^1_{GRID}(.), \gamma_{GRID}(.), \varepsilon_{GRID}(.), p_{t(GRID)}(.)$	1244.93	1.84	0.04	0.40	9
	$\Psi_{GRID}(ndvi), \theta^0_{GRID}(.), \theta^1_{GRID}(.), \gamma_{GRID}(.), \varepsilon_{GRID}(.), p_{t(GRID)}(.)$	1245.02	1.93	0.03	0.38	8
	$\Psi_{GRID}(hab+cc+ndvi), \theta^0_{GRID}(.), \theta^1_{GRID}(.), \gamma_{GRID}(.), \varepsilon_{GRID}(.), p_{t(GRID)}(.)$	1245.03	1.94	0.03	0.38	10
	$\Psi_{GRID}(hab+tri), \theta^0_{GRID}(.), \theta^1_{GRID}(.), \gamma_{GRID}(.), \varepsilon_{GRID}(.), p_{t(GRID)}(.)$	1245.07	1.98	0.03	0.37	9
	$\Psi_{GRID}(hab+dns+temp), \theta^0_{GRID}(.), \theta^1_{GRID}(.), \gamma_{GRID}(.), \varepsilon_{GRID}(.), p_{t(GRID)}(.)$	1245.14	2.05	0.03	0.36	10
	$\Psi_{GRID}(hab+dns+prep), \theta^0_{GRID}(.), \theta^1_{GRID}(.), \gamma_{GRID}(.), \varepsilon_{GRID}(.), p_{t(GRID)}(.)$	1245.15	2.06	0.03	0.36	10
	$\Psi_{GRID}(hab+dns+ele), \theta^0_{GRID}(.), \theta^1_{GRID}(.), \gamma_{GRID}(.), \varepsilon_{GRID}(.), p_{t(GRID)}(.)$	1245.156	2.07	0.03	0.36	10
	$\Psi_{GRID}(hab+dns+ndvi), \theta^0_{GRID}(.), \theta^1_{GRID}(.), \gamma_{GRID}(.), \varepsilon_{GRID}(.), p_{t(GRID)}(.)$	1245.163	2.07	0.03	0.36	10
	$\Psi_{GRID}(hab+dns+tri), \theta^0_{GRID}(.), \theta^1_{GRID}(.), \gamma_{GRID}(.), \varepsilon_{GRID}(.), p_{t(GRID)}(.)$	1245.22	2.13	0.03	0.34	10
	$\Psi_{GRID}(prep), \theta^0_{GRID}(.), \theta^1_{GRID}(.), \gamma_{GRID}(.), \varepsilon_{GRID}(.), p_{t(GRID)}(.)$	1245.25	2.16	0.03	0.34	8
	$\Psi_{GRID}(temp), \theta^0_{GRID}(.), \theta^1_{GRID}(.), \gamma_{GRID}(.), \varepsilon_{GRID}(.), p_{t(GRID)}(.)$	1245.31	2.22	0.03	0.33	8
	$\Psi_{GRID}(ele), \theta^0_{GRID}(.), \theta^1_{GRID}(.), \gamma_{GRID}(.), \varepsilon_{GRID}(.), p_{t(GRID)}(.)$	1245.32	2.23	0.03	0.33	8
	$\Psi_{GRID}(dist+fire),\theta^0_{GRID}(.), \theta^1_{GRID}(.), \gamma_{GRID}(.), \varepsilon_{GRID}(.), p_{t(GRID)}(season)$	1182.53	0.00	0.23	1.00	10

Co-variates	**Model**	**AIC**	**ΔAIC**	***w_i***	**Model likelihood**	**K**
Field	Ψ_{GRID}(dist+fire+hc), θ^0_{GRID}(.),θ^1_{GRID}(.), γ_{GRID}(.), ε_{GRID}(.), $p_{t(GRID)}$(season)	1182.57	0.04	0.23	0.98	11
	Ψ_{GRID}(dist+fire+cc), θ^0_{GRID}(.), θ^1_{GRID}(.), γ_{GRID}(.), ε_{GRID}(.), $p_{t(GRID)}$(season)	1184.27	1.74	0.10	0.42	11
	Ψ_{GRID}(dist+fire+gc), θ^0_{GRID}(.), θ^1_{GRID}(.), γ_{GRID}(.), ε_{GRID}(.), $p_{t(GRID)}$(season)	1184.32	1.79	0.10	0.41	11
	Ψ_{GRID}(dist+fire+car), θ^0_{GRID}(.), θ^1_{GRID}(.), γ_{GRID}(.), ε_{GRID}(.), $p_{t(GRID)}$(season)	1184.44	1.91	0.09	0.38	11
	Ψ_{GRID}(dist), θ^0_{GRID}(.), θ^1_{GRID}(.), γ_{GRID}(.), ε_{GRID}(.), $p_{t(GRID)}$(season)	1184.72	2.19	0.08	0.33	9
	Ψ_{GRID}(dist+hc), θ^0_{GRID}(.), θ^1_{GRID}(.), γ_{GRID}(.), ε_{GRID}(.), $p_{t(GRID)}$(season)	1185.56	3.03	0.05	0.22	10
	Ψ_{GRID}(dist+car), θ^0_{GRID}(.), θ^1_{GRID}(.), γ_{GRID}(.), ε_{GRID}(.), $p_{t(GRID)}$(season)	1186.48	3.95	0.03	0.14	10
	Ψ_{GRID}(dist+cc), θ^0_{GRID}(.), θ^1_{GRID}(.), γ_{GRID}(.), ε_{GRID}(.), $p_{t(GRID)}$(season)	1186.64	4.11	0.03	0.13	10
	Ψ_{GRID}(dist+gc), θ^0_{GRID}(.), θ^1_{GRID}(.), γ_{GRID}(.), ε_{GRID}(.), $p_{t(GRID)}$(season)	1186.70	4.17	0.03	0.12	10
	Ψ_{GRID}(fire), θ^0_{GRID}(.), θ^1_{GRID}(.), γ_{GRID}(.), ε_{GRID}(.), $p_{t(GRID)}$(season)	1189.49	6.96	0.01	0.03	9
	Ψ_{GRID}(dist+pw), θ^0_{GRID}(.), θ^1_{GRID}(.), γ_{GRID}(.), ε_{GRID}(.), $p_{t(GRID)}$(season)	1189.73	7.20	0.01	0.03	10

Ψ_{GRID} = probability of site occupancy/habitat use at the grid level; p = probability of detection; θ^0 = spatial dependence parameter representing the probability that the species is present locally, given the species was not present in the previous spatial replicate; θ^1 = spatial dependence parameter representing the probability that a species is present locally, given it was present at the previous spatial replicate. γ is the probability that the site is occupied in summer season, given that it was unoccupied in winter season. ε is the probability that the site is unoccupied in summer season, given that it was occupied in winter season. Hab: habitat available; cc: canopy cover; ndvi: normalized difference vegetation index; ele: elevation; tri: terrain ruggedness index; prep: precipitation; temp: ambient air temperature; dist: disturbance index; gc: ground cover; hc: horizontal cover; pw: presence of water; car: carnivore activity index; K: number of parameters in the model.

Table 3.9: Top model for chital (20-50 kg) including the influence of covariates on the probability of occupancy (Ψ_{GRID}) based on detection history data collected at the grid level (3.25 km^2) in the churia habitat of Chitwan National Park, Nepal.

Covariates	Model	AIC	ΔAIC	w_i	Model likelihood	K
Landscape	$\Psi_{GRID}(cc+dns),\theta^{0}_{GRID}(.), \theta^{1}_{GRID}(.), \gamma_{GRID}(.), \varepsilon_{GRID}(.), p_{t(GRID)}(.)$	365.29	0.00	0.10	1.00	9
	$\Psi_{GRID}(cc), \theta^{0}_{GRID}(.), \theta^{1}_{GRID}(.), \gamma_{GRID}(.), \varepsilon_{GRID}(.), p_{t(GRID)}(season)$	365.33	0.04	0.10	0.98	8
	$\Psi_{GRID}(.),\theta^{0}_{GRID}(.), \theta^{1}_{GRID}(.), \gamma_{GRID}(.), \varepsilon_{GRID}(.), p_{t(GRID)}(season)$	365.78	0.49	0.08	0.78	7
	$\Psi_{GRID}(dns), \theta^{0}_{GRID}(.), \theta^{1}_{GRID}(.), \gamma_{GRID}(.), \varepsilon_{GRID}(.), p_{t(GRID)}(season)$	365.95	0.66	0.07	0.72	8
	$\Psi_{GRID}(cc+dns+prep), \theta^{0}_{GRID}(.) ,\theta^{1}_{GRID}(.), \gamma_{GRID}(.), \varepsilon_{GRID}(.), p_{t(GRID)}(season)$	366.69	1.40	0.05	0.50	10
	$\Psi_{GRID}(cc+dns+temp), \theta^{0}_{GRID}(.),\theta^{1}_{GRID}(.), \gamma_{GRID}(.), \varepsilon_{GRID}(.), p_{t(GRID)}(season)$	366.73	1.44	0.05	0.49	10
	$\Psi_{GRID} (cc+dns+ndvi), \theta^{0}_{GRID}(.), \theta^{1}_{GRID}(.), \gamma_{GRID}(.), \varepsilon_{GRID}(.), p_{t(GRID)}(season)$	367.00	1.71	0.04	0.43	10
	$\Psi_{GRID}(ndvi), \theta^{0}_{GRID}(.), \theta^{1}_{GRID}(.), \gamma_{GRID}(.), \varepsilon_{GRID}(.), p_{t(GRID)}(season)$	367.07	1.78	0.04	0.41	8
	$\Psi_{GRID}(cc+temp), \theta^{0}_{GRID}(.), \theta^{1}_{GRID}(.), \gamma_{GRID}(.), \varepsilon_{GRID}(.), p_{t(GRID)}(season)$	367.14	1.85	0.04	0.40	9
	$\Psi_{GRID}(cc+prep), \theta^{0}_{GRID}(.), \theta^{1}_{GRID}(.), \gamma_{GRID}(.), \varepsilon_{GRID}(.), p_{t(GRID)}(season)$	367.17	1.88	0.04	0.39	9
	$\Psi_{GRI} (cc+tri), \theta^{0}_{GRID}(.), \theta^{1}_{GRID}(.), \gamma_{GRID}(.), \varepsilon_{GRID}(.), p_{t(GRID)}(season)$	367.23	1.94	0.04	0.38	9
	$\Psi_{GRID}(cc+hab), \theta^{0}_{GRID}(.), \theta^{1}_{GRID}(.), \gamma_{GRID}(.), \varepsilon_{GRID}(.), p_{t(GRID)}(season)$	367.25	1.96	0.04	0.38	9
	$\Psi_{GRI} (cc+dns+tri), \theta^{0}_{GRID}(.), \theta^{1}_{GRID}(.), \gamma_{GRID}(.), \varepsilon_{GRID}(.), p_{t(GRID)}(season)$	367.27	1.98	0.04	0.37	9
	$\Psi_{GRID}(cc+ele), \theta^{0}_{GRID}(.), \theta^{1}_{GRID}(.), \gamma_{GRID}(.), \varepsilon_{GRID}(.), p_{t(GRID)}(season)$	367.29	2.00	0.04	0.37	10
	$\Psi_{G}(temp), \theta^{0}_{GRID}(.), \theta^{1}_{GRID}(.), \gamma_{GRID}(.), \varepsilon_{GRID}(.), p_{t(GRID)}(season)$	367.32	2.03	0.04	0.36	9
	$\Psi_{GRID}(prep), \theta^{0}_{GRID}(.), \theta^{1}_{GRID}(.), \gamma_{GRID}(.), \varepsilon_{GRID}(.), p_{t(GRID)}(season)$	367.72	2.43	0.03	0.30	8
	$\Psi_{GRID}(tri), \theta^{0}_{GRID}(.), \theta^{1}_{GRID}(.), \gamma_{GRID}(.), \varepsilon_{GRID}(.), p_{t(GRID)}(season)$	367.77	2.48	0.03	0.29	8
	$\Psi_{GRID}(ele), \theta^{0}_{GRID}(.), \theta^{1}_{GRID}(.), \gamma_{GRID}(.), \varepsilon_{GRID}(.), p_{t(GRID)}(season)$	367.78	2.49	0.03	0.29	8
	$\Psi_{GRID}(fire+dist), \theta^{0}_{GRID}(.), \theta^{1}_{GRID}(.), \gamma_{GRID}(.), \varepsilon_{GRID}(.), p_{t(GRID)}(season)$	357.81	0.00	0.15	1.00	9
	$\Psi_{GRID}(fire), \theta^{0}_{GRID}(.), \theta^{1}_{GRID}(.), \gamma_{GRID}(.), \varepsilon_{GRID}(.), p_{t(GRID)}(season)$	358.20	0.39	0.12	0.82	8
	$\Psi_{GRID}(fire+cc), \theta^{0}_{GRID}(.), \theta^{1}_{GRID}(.), \gamma_{GRID}(.), \varepsilon_{GRID}(.), p_{t(GRID)}(season)$	358.47	0.66	0.11	0.72	9
	$\Psi_{G}(fire+dist+cc), \theta^{0}_{GRID}(.), \theta^{1}_{GRID}(.), \gamma_{GRID}(.), \varepsilon_{GRID}(.), p_{t(GRID)}(season)$	358.68	0.87	0.10	0.65	10
	$\Psi_{GRI} (fire+dist+pw), \theta^{0}_{GRID}(.), \theta^{1}_{GRID}(.), \gamma_{GRID}(.), \varepsilon_{GRID}(.), p_{t(GRID)}(season)$	359.31	1.50	0.07	0.47	10
	$\Psi_{GRID}(fire+dist+cc+pw),\theta^{0}_{G}(.), \theta^{1}_{G}(.), \gamma_{G}(.), \varepsilon_{G}(.), p_{t(G)}(.)$	359.62	1.81	0.06	0.40	11

Co-variates	**Model**	**AIC**	**ΔAIC**	***w_i***	**Model like-lihood**	**K**
Field	Ψ_{GRID}(fire+pw), θ^0_{GRID}(.), θ^1_{GRID}(.), γ_{GRID}(.), ε_{GRID}(.), $p_{t(GRID)}$(season)	359.69	1.88	0.06	0.39	9
	Ψ_{GRID}(fire+dist+car), θ^0_{GRID}(.), θ^1_{GRID}(.), γ_{GRID}(.), ε_{GRID}(.), $p_{t(GRID)}$(season)	359.80	1.99	0.06	0.37	10
	Ψ_{GRID}(fire+car), θ^0_{GRID}(.), θ^1_{GRID}(.), γ_{GRID}(.), ε_{GRID}(.), $p_{t(GRID)}$(season)	360.02	2.21	0.05	0.33	9
	Ψ_{GRID}(fire+gc), θ^0_{GRID}(.), θ^1_{GRID}(.), γ_{GRID}(.), ε_{GRID}(.), $p_{t(GRID)}$(season)	360.18	2.37	0.05	0.31	9
	Ψ_{GRID}(fire+hc), θ^0_{GRID}(.), θ^1_{GRID}(.), γ_{GRID}(.), ε_{GRID}(.), $p_{t(GRID)}$(season)	360.19	2.38	0.05	0.30	9
	Ψ_{GRID}(dist), θ^0_{GRID}(.), θ^1_{GRID}(.), γ_{GRID}(.), ε_{GRID}(.), $p_{t(GRID)}$(season)	361.53	3.72	0.02	0.16	8
	Ψ_{GRID}(dist+cc), θ^0_{GRID}(.), θ^1_{GRID}(.), γ_{GRID}(.), ε_{GRID}(.), $p_{t(GRID)}$(season)	361.61	3.80	0.02	0.15	9
	Ψ_{GRID}(dist+fire+cc+pw+car), θ^0_{GRID}(.), θ^1_{GRID}(.), γ_{GRID}(.), ε_{GRID}(.), $p_{t(GRID)}$(season)	361.62	3.81	0.02	0.15	12
	Ψ_{GRID}(cc), θ^0_{GRID}(.), θ^1_{GRID}(.), γ_{GRID}(.), ε_{GRID}(.), $p_{t(GRID)}$(season)	361.99	4.18	0.02	0.12	8
	Ψ_{GRID}(dist+cc+pw), θ^0_{GRID}(.) ,θ^1_{GRID}(.), γ_{GRID}(.), ε_{GRID}(.), $p_{t(GRID)}$(season)	362.59	4.78	0.01	0.09	10
	Ψ_{GRID}(.),θ^0_{GRID}(.), θ^1_{GRID}(.), γ_{GRID}(.), ε_{GRID}(.), $p_{t(GRID)}$(season)	362.71	4.90	0.01	0.09	7
	Ψ_{GRID}(pw), θ^0_{GRID}(.), θ^1_{GRID}(.), γ_{GRID}(.), ε_{GRID}(.), $p_{t(GRID)}$(season)	364.25	6.44	0.01	0.04	8

Ψ(Psi) = probability of site occupancy/habitat use; *p* = probability of detection; θ^0 = spatial dependence parameter representing the probability that the species is present locally, given the species was not present in the previous spatial replicate; θ^1 = spatial dependence parameter representing the probability that a species is present locally, given it was present at the previous spatial replicate. γ is the probability that the site is occupied in summer season, given that it was unoccupied in winter season. ε is the probability that the site is unoccupied in summer season, given that it was occupied in winter season. Hab: habitat available; cc: canopy cover; ndvi: normalized difference vegetation index; ele: elevation; tri: terrain ruggedness index; prep: precipitation; temp: ambient air temperature; dist: disturbance index; gc: ground cover; hc: horizontal cover; pw: presence of water; car: carnivore activity index; K: number of parameters in the model.

Table 3.10: Top models for barking deer (20-50 kg) including the influence of covariates on the probability of occupancy (Ψ_{GRID}) based on detection history data collected at the grid level (3.25 km2) in the churia habitat of Chitwan National Park, Nepal.

Co-variates	**Model**	**AIC**	**ΔAIC**	**w_i**	**Model likelihood**	**K**
Land-scape	$\Psi_{GRID}(dns),\theta^0_{GRID}(.), \theta^1_{GRID}(.), \gamma_{GRID}(.), \varepsilon_{GRID}(.), p_{t(GRID)}(.)$	989.20	0.00	0.09	1.00	8
	$\Psi_{GRID}(.),\theta^0_{GRID}(.), \theta^1_{GRID}(.), \gamma_{GRID}(.), \varepsilon_{GRID}(.), p_{t(GRID)}(.)$	989.63	0.43	0.07	0.81	7
	$\Psi_{GRID}(dns+cc), \theta^0_{GRID}(.), \theta^1_{GRID}(.), \gamma_{GRID}(.), \varepsilon_{GRID}(.), p_{t(GRID)}(.)$	989.91	0.71	0.06	0.70	9
	$\Psi_{GRID}(dns+ele), \theta^0_{GRID}(.), \theta^1_{GRID}(.), \gamma_{GRID}(.), \varepsilon_{GRID}(.), p_{t(GRID)}(.)$	990.33	1.13	0.05	0.57	9
	$\Psi_{GRID}(hab), \theta^0_{GRID}(.),\theta^1_{GRID}(.), \gamma_{GRID}(.), \varepsilon_{GRID}(.),p_{t(GRID)}(.)$	990.38	1.18	0.05	0.55	8
	$\Psi_{GRID}(dns+temp), \theta^0_{GRID}(.), \theta^1_{GRID}(.), \gamma_{GRID}(.), \varepsilon_{GRID}(.), p_{t(GRID)}(.)$	990.42	1.22	0.05	0.54	9
	$\Psi_{GRID}(cc), \theta^0_{GRID}(.), \theta^1_{GRID}(.), \gamma_{GRID}(.), \varepsilon_{GRID}(.), p_{t(GRID)}(.)$	990.48	1.28	0.05	0.53	8
	$\Psi_{GRID}(dns+hab), \theta^0_{GRID}(.), \theta^1_{GRID}(.), \gamma_{GRID}(.), \varepsilon_{GRID}(.), p_{t(GRID)}(.)$	990.52	1.32	0.05	0.52	9
	$\Psi_{GRID}(dns+tri), \theta^0_{GRID}(.), \theta^1_{GRID}(.), \gamma_{GRID}(.), \varepsilon_{GRID}(.), p_{t(GRID)}(.)$	990.61	1.41	0.04	0.49	9
	$\Psi_{GRID}(dns+prep), \theta^0_{GRID}(.), \theta^1_{GRID}(.), \gamma_{GRID}(.), \varepsilon_{GRID}(.), p_{t(GRID)}(.)$	990.68	1.48	0.04	0.48	9
	$\Psi_{GRID}(dns+ele+cc), \theta^0_{GRID}(.), \theta^1_{GRID}(.), \gamma_{GRID}(.), \varepsilon_{GRID}(.), p_{t(GRID)}(.)$	990.76	1.56	0.04	0.46	10
	$\Psi_{GRID}(dns+cc+temp), \theta^0_{GRID}(.), \theta^1_{GRID}(.), \gamma_{GRID}(.), \varepsilon_{GRID}(.), p_{t(GRID)}(.)$	990.87	1.67	0.04	0.43	10
	$\Psi_{GRID}(temp), \theta^0_{GRID}(.), \theta^1_{GRID}(.), \gamma_{GRID}(.), \varepsilon_{GRID}(.), p_{t(GRID)}(.)$	990.91	1.71	0.04	0.43	8
	$\Psi_{GRID}(dns+cc+prep), \theta^0_{GRID}(.), \theta^1_{GRID}(.), \gamma_{GRID}(.), \varepsilon_{GRID}(.), p_{t(GRID)}(.)$	991.06	1.86	0.03	0.39	10
	$\Psi_{GRID}(tri), \theta^0_{GRID}(.), \theta^1_{GRID}(.), \gamma_{GRID}(.), \varepsilon_{GRID}(.), p_{t(GRID)}(.)$	991.14	1.94	0.03	0.38	8
	$\Psi_{GRID}(dns+ndvi), \theta^0_{GRID}(.), \theta^1_{GRID}(.), \gamma_{GRID}(.), \varepsilon_{GRID}(.), p_{t(GRID)}(.)$	991.18	1.98	0.03	0.37	9
	$\Psi_{GRID}(ele), \theta^0_{GRID}(.), \theta^1_{GRID}(.), \gamma_{GRID}(.), \varepsilon_{GRID}(.), p_{t(GRID)}(.)$	991.19	1.99	0.03	0.37	8
	$\Psi_{GRID}(prep), \theta^0_{GRID}(.), \theta^1_{GRID}(.), \gamma_{GRID}(.), \varepsilon_{GRID}(.), p_{t(GRID)}(.)$	991.23	2.03	0.03	0.36	8
	$\Psi_{GRID}(ndvi), \theta^0_{GRID}(.), \theta^1_{GRID}(.), \gamma_{GRID}(.), \varepsilon_{GRID}(.), p_{t(GRID)}(.)$	991.45	2.25	0.03	0.32	8
	$\Psi_{GRID}(dns+cc+hab), \theta^0_{GRID}(.), \theta^1_{GRID}(.), \gamma_{GRID}(.), \varepsilon_{GRID}(.), p_{t(GRID)}(.)$	991.59	2.39	0.03	0.30	10
	$\Psi_{GRID}(cc+hab), \theta^0_{GRID}(.), \theta^1_{GRID}(.), \gamma_{GRID}(.), \varepsilon_{GRID}(.), p_{t(GRID)}(.)$	991.61	2.41	0.03	0.30	9
Field	$\Psi_{GRID}(gc+hc+dist), \theta^0_{GRID}(.), \theta^1_{GRID}(.), \gamma_{GRID}(.), \varepsilon_{GRID}(.), p_{t(GRID)}(.)$	934.75	0.00	0.24	1.00	10
	$\Psi_{GRID}(gc+hc+dist+pw), \theta^0_{GRID}(.), \theta^1_{GRID}(.), \gamma_{GRID}(.), \varepsilon_{GRID}(.), p_{t(GRID)}(.)$	936.30	1.55	0.11	0.46	11
	$\Psi_{GRID}(gc+hc+dist+fire), \theta^0_{GRID}(.), \theta^1_{GRID}(.), \gamma_{GRID}(.), \varepsilon_{GRID}(.), p_{t(GRID)}(.)$	936.55	1.80	0.10	0.41	11
	$\Psi_{GRID}(gc+hc+dist+cc), \theta^0_{GRID}(.), \theta^1_{GRID}(.), \gamma_{GRID}(.), \varepsilon_{GRID}(.), p_{t(GRID)}(.)$	936.56	1.81	0.10	0.40	11

Co-variates	**Model**	**AIC**	**ΔAIC**	***w*$_i$**	**Model like-lihood**	**K**
	$\Psi_{GRID}(gc+dist), \theta^{0}_{GRID}(.), \theta^{1}_{GRID}(.), \gamma_{GRID}(.), \varepsilon_{GRID}(.), p_{t(GRID)}(.)$	936.88	2.13	0.08	0.34	9
	$\Psi_{GRID}(gc+hc), \theta^{0}_{GRID}(.), \theta^{1}_{GRID}(.), \gamma_{GRID}(.), \varepsilon_{GRID}(.), p_{t(GRID)}(.)$	937.11	2.36	0.07	0.31	9
	$\Psi_{GRID}(gc), \theta^{0}_{GRID}(.), \theta^{1}_{GRID}(.), \gamma_{GRID}(.), \varepsilon_{GRID}(.), p_{t(GRID)}(.)$	937.87	3.12	0.05	0.21	8
	$\Psi_{GRID}(gc+hc+pw), \theta^{0}_{GRID}(.), \theta^{1}_{GRID}(.), \gamma_{GRID}(.), \varepsilon_{GRID}(.), p_{t(GRID)}(.)$	938.35	3.60	0.04	0.17	10
	$\Psi_{GRID}(gc+hc+fire), \theta^{0}_{GRID}(.), \theta^{1}_{GRID}(.), \gamma_{GRID}(.), \varepsilon_{GRID}(.), p_{t(GRID)}(.)$	938.35	3.60	0.04	0.17	10
	$\Psi_{GRID}(gc+hc+cc), \theta^{0}_{GRID}(.), \theta^{1}_{GRID}(.), \gamma_{GRID}(.), \varepsilon_{GRID}(.), p_{t(GRID)}(.)$	938.54	3.79	0.04	0.15	10
	$\Psi_{GRID}(gc+cc), \theta^{0}_{GRID}(.), \theta^{1}_{GRID}(.), \gamma_{GRID}(.), \varepsilon_{GRID}(.), p_{t(GRID)}(.)$	938.74	3.99	0.03	0.14	9
	$\Psi_{GRID}(gc+fire), \theta^{0}_{GRID}(.), \theta^{1}_{GRID}(.), \gamma_{GRID}(.), \varepsilon_{GRID}(.), p_{t(GRID)}(.)$	939.01	4.26	0.03	0.12	9
	$\Psi_{GRID}(gc+ pw), \theta^{0}_{GRID}(.), \theta^{1}_{GRID}(.), \gamma_{GRID}(.), \varepsilon_{GRID}(.), p_{t(GRID)}(.)$	939.08	4.33	0.03	0.11	9
	$\Psi_{GRID}(gc+car), \theta^{0}_{GRID}(.), \theta^{1}_{GRID}(.), \gamma_{GRID}(.), \varepsilon_{GRID}(.), p_{t(GRID)}(.)$	939.63	4.88	0.02	0.09	9

Ψ_{GRID} = probability of site occupancy/habitat use at the grid level; p = probability of detection; θ^0 = spatial dependence parameter representing the probability that the species is present locally, given the species was not present in the previous spatial replicate; θ^1 = spatial dependence parameter representing the probability that a species is present locally, given it was present at the previous spatial replicate. γ is the probability that the site is occupied in summer season, given that it was unoccupied in winter season. ε is the probability that the site is unoccupied in summer season, given that it was occupied in winter season. Hab: habitat available; cc: canopy cover; ndvi: normalized difference vegetation index; ele: elevation; tri: terrain ruggedness index; prep: precipitation; temp: ambient air temperature; dist: disturbance index; gc: ground cover; hc: horizontal cover; pw: presence of water; car: carnivore activity index; K: number of parameters in the model.

Table 3.11: Top models for wild pig (20-50 kg) including the influence of covariates on the probability of occupancy (Ψ_{GRID}) based on detection history data collected at the grid level (3.24 km^2) in the churia habitat of Chitwan National Park, Nepal.

Co-variates	Model	AIC	ΔAIC	w_i	Model like-lihood	K
Land-scape	Ψ_{GRID}(hab+dns+ndvi),θ^0_{GRID}(.), θ^1_{GRID}(.), γ_{GRID}(.), ε_{GRID}(.), $p_{t(GRID)}$(season)	1126.33	0.00	0.51	1.00	11
	Ψ_{GRID}(hab+dns), θ^0_{GRID}(.), θ^1_{GRID}(.), γ_{GRID}(.), ε_{GRID}(.), $p_{t(GRID)}$(season)	1127.63	1.30	0.27	0.52	10
	Ψ_{GRID}(hab+dns+ele), θ^0_{GRID}(.), θ^1_{GRID}(.), γ_{GRID}(.), ε_{GRID}(.), $p_{t(GRID)}$(season)	1129.23	2.90	0.12	0.23	11
	Ψ_{GRID}(ndvi+hab), θ^0_{GRID}(.), θ^1_{GRID}(.), γ_{GRID}(.), ε_{GRID}(.),$p_{t(GRID)}$(season)	1130.64	4.31	0.06	0.12	10
	Ψ_{GRID}(ndvi+dns), θ^0_{GRID}(.), θ^1_{GRID}(.), γ_{GRID}(.), ε_{GRID}(.), $p_{t(GRID)}$(season)	1126.33	0.00	0.51	1.00	11
Field	Ψ_{GRID}(car+pw+gc), θ^0_{GRID}(.), θ^1_{GRID}(.), γ_{GRID}(.), ε_{GRID}(.) ,$p_{t(GRID)}$(season)	1102.36	0.00	0.14	1.00	10
	Ψ_{GRID}(car+pw+hc+gc+fire),θ^0_{GRID}(.), θ^1_{GRID}(.), γ_{GRID}(.), ε_{GRID}(.), $p_{t(GRID)}$(season)	1103.20	0.84	0.09	0.66	12
	Ψ_{GRI} (car+pw+hc), θ^0_{GRID}(.), θ^1_{GRID}(.), γ_{GRID}(.), ε_{GRID}(.), $p_{t(GRID)}$(season)	1103.22	0.86	0.09	0.65	10
	Ψ_{GRID}(car+pw+fire), θ^0_{GRID}(.), θ^1_{GRID}(.), γ_{GRID}(.), ε_{GRID}(.), $p_{t(GRID)}$(season)	1103.30	0.94	0.08	0.63	10
	Ψ_{GRID}(car+pw), θ^0_{GRID}(.), θ^1_{GRID}(.), γ_{GRID}(.), ε_{GRID}(.), $p_{t(GRID)}$(season)	1103.31	0.95	0.08	0.62	9
	Ψ_{GRID}(car+pw+gc+hc), θ^0_{GRID}(.), θ^1_{GRID}(.), γ_{GRID}(.), ε_{GRID}(.), $p_{t(GRID)}$(season)	1103.54	1.18	0.08	0.55	11
	Ψ_{GRID}(car+pw+hc+fire), θ^0_{GRID}(.),θ^1_{GRID}(.), γ_{GRID}(.), ε_{GRID}(.), $p_{t(GRID)}$(season)	1103.57	1.21	0.07	0.55	11
	Ψ_{GRID}(gc+car), θ^0_{GRID}(.), θ^1_{GRID}(.), γ_{GRID}(.), ε_{GRID}(.), $p_{t(GRID)}$(season)	1104.22	1.86	0.05	0.39	9
	Ψ_{GRID}(car+hc), θ^0_{GRID}(.), θ^1_{GRID}(.), γ_{GRID}(.), ε_{GRID}(.), $p_{t(GRID)}$(season)	1104.78	2.42	0.04	0.30	9
	Ψ_{GRID}(car), θ^0_{GRID}(.), θ^1_{GRID}(.), γ_{GRID}(.), ε_{GRID}(.), $p_{t(GRID)}$(season)	1104.94	2.58	0.04	0.28	8
	Ψ_{GRID}(gc), θ^0_{GRID}(.), θ^1_{GRID}(.), γ_{GRID}(.), ε_{GRID}(.), $p_{t(GRID)}$(season)	1105.09	2.73	0.03	0.26	8
	Ψ_{GRID}(car+fire), θ^0_{GRID}(.), θ^1_{GRID}(.), γ_{GRID}(.), ε_{GRID}(.), $p_{t(GRID)}$(season)	1105.17	2.81	0.03	0.25	9
	Ψ_{GRID}(pw), θ^0_{GRID}(.), θ^1_{GRID}(.), γ_{GRID}(.), ε_{GRID}(.), $p_{t(GRID)}$(season)	1105.34	2.98	0.03	0.23	8
	Ψ_{GRID}(.),θ^0_{GRID}(.), θ^1_{GRID}(.), γ_{GRID}(.), ε_{GRID}(.), $p_{t(GRID)}$(season)	1105.66	3.30	0.03	0.19	7
	Ψ_{GRID}(hc), θ^0_{GRID}(.), θ^1_{GRID}(.), γ_{GRID}(.), ε_{GRID}(.), $p_{t(GRID)}$(season)	1105.80	3.44	0.02	0.18	8
	Ψ_{GRID}(fire), θ^0_{GRID}(.), θ^1_{GRID}(.), γ_{GRID}(.), ε_{GRID}(.), $p_{t(GRID)}$(season)	1106.22	3.86	0.02	0.15	8
	Ψ_{GRID}(pw+hc+fire), θ^0_{GRID}(.) θ^1_{GRID}(.), γ_{GRID}(.), ε_{GRID}(.), $p_{t(GRID)}$(season)	1106.33	3.97	0.02	0.14	10

Ψ_{GRID}= probability of site occupancy/habitat use at the grid level; p = probability of detection; θ^0 = spatial dependence parameter representing the probability that the species is present locally, given the species was not present in the previous spatial replicate; θ^1 = spatial dependence parameter representing the probability that a species is present locally, given it was present at the previous spatial replicate. γ is the probability that the site is occupied in summer season, given that it was unoccupied in winter season. ε is the probability that the site is unoccupied in summer season, given that it was occupied in winter season. Hab: habitat available; cc: canopy cover; ndvi: normalized difference vegetation index; ele: elevation; tri: terrain ruggedness index; prep: precipitation; temp: ambient air temperature; dist: disturbance index; gc: ground cover; hc: horizontal cover; pw: presence of water; car: carnivore activity index; K: number of parameters in the model.

Table 3.12: Top models for tiger, including the influence of covariates on the probability of habitat use (Ψ_{GRID}) based on detection history data collected at the grid level (3.25 km^2) in the churia habitat of Chitwan National Park, Nepal.

Co-variates	Model	AIC	ΔAIC	w_i	Model like-lihood	K
Landscape	Ψ_{GRID}(hab), θ^0_{GRID}(.), θ^1_{GRID}(.), γ_{GRID}(.), ε_{GRID}(.), $p_{t(GRID)}$(season)	731.51	0.00	0.20	1.00	9
	Ψ_{GRID}(hab+temp), θ^0_{GRID}(.), θ^1_{GRID}(.), γ_{GRID}(.), ε_{GRID}(.), $p_{t(GRID)}$(season)	732.95	1.44	0.10	0.49	10
	Ψ_{GRID}(hab+ndvi), θ^0_{GRID}(.), θ^1_{GRID}(.), γ_{GRID}(.), ε_{GRID}(.), $p_{t(GRID)}$(season)	733.09	1.58	0.09	0.45	10
	Ψ_{GRID}(hab+dns), θ^0_{GRID}(.), θ^1_{GRID}(.), γ_{GRID}(.), ε_{GRID}(.), $p_{t(GRID)}$(season)	733.11	1.60	0.09	0.45	10
	Ψ_{GRID}(hab+prep), θ^0_{GRID}(.), θ^1_{GRID}(.), γ_{GRID}(.), ε_{GRID}(.), $p_{t(GRID)}$(season)	733.21	1.70	0.09	0.43	10
	Ψ_{GRID}(hab+tri), θ^0_{GRID}(.), θ^1_{GRID}(.), γ_{GRID}(.), ε_{GRID}(.), $p_{t(GRID)}$(season)	733.46	1.95	0.08	0.38	10
	Ψ_{GRID}(hab+cc), θ^0_{GRID}(.), θ^1_{GRID}(.), γ_{GRID}(.), ε_{GRID}(.), $p_{t(GRID)}$(season)	733.51	2.00	0.07	0.37	10
	Ψ_{GRID}(hab+dns+temp), θ^0_{GRID}(.), θ^1_{GRID}(.), γ_{GRID}(.), ε_{GRID}(.), $p_{t(GRID)}$(season)	734.49	2.98	0.05	0.23	11
	Ψ_{GRID}(hab+dns+prep), θ^0_{GRID}(.), θ^1_{GRID}(.), γ_{GRID}(.), ε_{GRID}(.), $p_{t(GRID)}$(season)	734.79	3.28	0.04	0.19	11
	Ψ_{GRID}(hab+dns+tri), θ^0_{GRID}(.),θ^1_{GRID}(.), γ_{GRID}(.), ε_{GRID}(.), $p_{t(GRID)}$(season)	735.01	3.50	0.03	0.17	11
	Ψ_{GRID}(hab+tri+ndvi), θ^0_{GRID}(.), θ^1_{GRID}(.), γ_{GRID}(.), ε_{GRID}(.), $p_{t(GRID)}$(season)	735.06	3.55	0.03	0.17	11
	Ψ_{GRID}(hab+dns+cc), θ^0_{GRID}(.), θ^1_{GRID}(.), γ_{GRID}(.), ε_{GRID}(.), $p_{t(GRID)}$(season)	735.10	3.59	0.03	0.17	11
	Ψ_{GRID}(hab+tri+cc), θ^0_{GRID}(.), θ^1_{GRID}(.), γ_{GRID}(.), ε_{GRID}(.), $p_{t(GRID)}$(season)	735.46	3.95	0.03	0.14	11
	Ψ_{GRID}(.),θ^0_{GRID}(.),θ^1_{GRID}(.), γ_{GRID}(.), ε_{GRID}(.),$p_{t(GRID)}$(season)	736.55	5.04	0.02	0.08	8
Field	Ψ_{GRID}(dist+pw+fire),θ^0_{GRID}(.), θ^1_{GRID}(.), γ_{GRID}(.), ε_{GRID}(.), $p_{t(GRID)}$(.)	683.49	0.00	0.38	1.00	10
	Ψ_{GRID}(dist+pw+fire+prey), θ^0_{GRID}(.), θ^1_{GRID}(.), γ_{GRID}(.), ε_{GRID}(.), $p_{t(GRID)}$(.)	685.18	1.69	0.17	0.43	11
	Ψ_{GRID}(dist+pw+fire+cc), θ^0_{GRID}(.), θ^1_{GRID}(.), γ_{GRID}(.), ε_{GRID}(.), $p_{t(GRID)}$(.)	685.45	1.96	0.14	0.38	11
	Ψ_{GRID}(dist+pw+fire+cc+prey), θ^0_{GRID}(.),θ^1_{GRID}(.), γ_{GRID}(.), ε_{GRID}(.), $p_{t(GRID)}$(.)	686.51	3.02	0.08	0.22	12
	Ψ_{GRID}(dist+pw), θ^0_{GRID}(.) ,θ^1_{GRID}(.), γ_{GRID}(.), ε_{GRID}(.), $p_{t(GRID)}$(.)	687.05	3.56	0.06	0.17	9
	Ψ_{GRID}(car+pw+cc), θ^0_{GRID}(.), θ^1_{GRID}(.), γ_{GRID}(.), ε_{GRID}(.), $p_{t(GRID)}$(.)	687.44	3.95	0.05	0.14	10
	Ψ_{GRID}(dist+pw+hc), θ^0_{GRID}(.), θ^1_{GRID}(.), γ_{GRID}(.), ε_{GRID}(.), $p_{t(GRID)}$(.)	688.11	4.62	0.04	0.10	10
	Ψ_{GRID}(car+pw+prey), θ^0_{GRID}(.), θ^1_{GRID}(.), γ_{GRID}(.), ε_{GRID}(.), $p_{t(GRID)}$(.)	688.83	5.34	0.03	0.07	10

Ψ(Psi) = probability of site occupancy/habitat use; p = probability of detection; θ^0 = spatial dependence parameter representing the probability that the species is present locally, given the species was not present in the previous spatial replicate; θ^1 = spatial dependence parameter representing the probability that a species is present locally, given it was present at the previous spatial replicate. γ is the probability that the site is occupied in summer season, given that it was unoccupied in winter season. ε is the probability that the site is unoccupied in summer season, given that it was occupied in winter season. Hab: habitat available; cc: canopy cover; ndvi: normalized difference vegetation index; ele: elevation; tri: terrain ruggedness index; prep: precipitation; temp: ambient air temperature; dist: disturbance index; gc: ground cover; hc: horizontal cover; pw: presence of water; car: carnivore activity index; K: number of parameters in the model**.**

Table 3.13: Top models for tiger, including the influence of covariates on the probability of habitat use (Ψ_{TRAN}) based on detection history data collected at the transect level (600 m) in the churia habitat of Chitwan National Park, Nepal.

Co-variates	**Model**	**AIC**	**ΔAIC**	**w_i**	**Model like-lihood**	**K**
Land-scape	$\Psi_{TRAN}(temp), \theta^0_{TRAN}(.), \theta^1_{TRAN}(.), \gamma_{TRAN}(.), \varepsilon_{TRAN}(.), p_{t(TRAN)}(.)$	1579.38	0.00	0.18	1.00	9
	$\Psi_{TRAN}(ele+dns), \theta^0_{TRAN}(.), \theta^1_{TRAN}(.), \gamma_{TRAN}(.), \varepsilon_{TRA}(.), p_{t(TRAN)}(.)$	1579.55	0.17	0.17	0.92	9
	$\Psi_{TRAN}(ele), \theta^0_{TRAN}(.), \theta^1_{TRAN}(.), \gamma_{TRAN}(.), \varepsilon_{TRAN}(.), p_{t(TRAN)}(.)$	1580.02	0.64	0.13	0.73	8
	$\Psi_{TRAN}(ndvi), \theta^0_{TRAN}(.), \theta^1_{TRAN}(.), \gamma_{TRAN}(.), \varepsilon_{TRAN}(.), p_{t(TRAN)}(.)$	1580.55	1.17	0.10	0.56	8
	$\Psi_{TRAN}(temp+dns+hab), \theta^0_{TRAN}(.), \theta^1_{TRAN}(.), \varepsilon_{TRAN}(.), p_{t(TRAN)}(.)$	1580.74	1.36	0.09	0.51	10
	$\Psi_{TRAN}(temp), \theta^0_{TRAN} (.), \theta^1_{TRAN}(.), \gamma_{TRAN}(.), \varepsilon_{TRAN}(.), p_{t(TRAN)}(.)$	1581.18	1.80	0.07	0.41	8
	$\Psi_{TRAN}(ele+dns+hab), \theta^0_{TRAN}(.), \theta^1_{TRAN}(.), \gamma_{TRAN}(.), \varepsilon_{TRAN}(.), p_{t(TRAN)}(.)$	1581.42	2.04	0.07	0.36	10
	$\Psi_{TRAN}(ele+hab), \theta^0_{TRAN}(.), \theta^1_{TRAN}(.), \gamma_{TRAN}(.), \varepsilon_{TRAN}(.), p_{t(TRAN)}(.)$	1581.49	2.11	0.06	0.35	9
	$\Psi_{TRAN}(prep+dns), \theta^0_{TRAN}(.), \theta^1_{TRAN}(.), \gamma_{TRAN}(.), \varepsilon_{TRAN}(.), p_{t(TRAN)}(.)$	1582.17	2.79	0.05	0.25	9
	$\Psi_{TRAN}(ndvi+hab), \theta^0_{TRAN}(.), \theta^1_{TRAN}(.), \gamma_{TRAN}(.), \varepsilon_{TRAN}(.), p_{t(TRAN)}(.)$	1582.52	3.14	0.04	0.21	9
	$\Psi_{TRAN}(prep), \theta^0_{TRAN}(.) ,\theta^1_{TRAN} (.), \gamma_{TRAN}(.), \varepsilon_{TRAN}(.), p_{t(TRAN)}(.)$	1583.30	3.92	0.03	0.14	8
	$\Psi_{TRAN}(dns), \theta^0_{TRAN}(.), \theta^1_{TRAN}(.), \gamma_{TRAN}(.), \varepsilon_{TRAN}(.), p_{t(TRAN)}(.)$	1588.19	8.81	0.00	0.01	8
Field	$\Psi_{TRAN}(pw+prey+hc+fire+dist), \theta^0_{TRAN}(.), \theta^1_{TRAN}(.), \gamma_{TRAN}(.), \varepsilon_{TRAN}(.), p_{t(TRAN)}(.)$	1559.69	0.00	0.11	1.00	12
	$\Psi_{TRAN}(pw+prey+hc+fire), \theta^0_{TRAN}(.), \theta^1_{TRAN}(.), \gamma_{TRAN}(.), \varepsilon_{TRAN}(.), p_{t(TRAN)}(.)$	1559.78	0.09	0.11	0.96	11
	$\Psi_{TRAN}(pw+prey+hc+fire+cc), \theta^0_{TRAN}(.), \theta^1_{TRAN}(.), \gamma_{TRAN}(.), \varepsilon_{TRAN}(.), p_{t(TRAN)}(.)$	1559.93	0.24	0.10	0.89	12
	$\Psi_{TRAN}(pw+prey+hc+dist), \theta^0_{TRAN}(.), \theta^1_{TRAN}(.), \gamma_{TRAN}(.), \varepsilon_{TRAN}(.), p_{t(TRAN)}(.)$	1560.05	0.36	0.09	0.84	11
	$\Psi_{TRAN}(pw+prey+fire), \theta^0_{TRAN}(.), \theta^1_{TRAN}(.), \gamma_{TRAN}(.), \varepsilon_{TRAN}(.), p_{t(TRAN)}(.)$	1560.14	0.45	0.09	0.80	10
	$\Psi_{TRAN}(pw+prey+fire+cc), \theta^0_{TRAN}(.), \theta^1_{TRAN}(.), \gamma_{TRAN}(.), \varepsilon_{TRAN}(.), p_{t(TRAN)}(.)$	1560.15	0.46	0.09	0.79	11
	$\Psi_{TRAN}(pw+prey+hc+cc), \theta^0_{TRAN}(.), \theta^1_{TRA}(.), \gamma_{TRAN}(.), \varepsilon_{TRAN}(.), p_{t(TRAN)}(.)$	1560.17	0.48	0.09	0.79	11
	$\Psi_{TRAN}(pw+prey+dist+fire), \theta^0_{TRA} (.), \theta^1_{TRA}(.), \gamma_{TRAN}(.), \varepsilon_{TRAN}(.), p_{t(TRAN)}(.)$	1560.33	0.64	0.08	0.73	11
	$\Psi_{TRAN}(pw+prey), \theta^0_{TRAN}(.), \theta^1_{TRAN}(.), \gamma_{TRAN}(.), \varepsilon_{TRAN}(.), p_{t(TRAN)}(.)$	1560.35	0.66	0.08	0.72	9
	$\Psi_{TRAN}(pw+prey+hc+cc+dist+fire), \theta^0_{TRAN}(.),\theta^1_{TRAN}(.), \gamma_{TRAN}(.), \varepsilon_{TRAN}(.), p_{t(TRAN)}(.)$	1560.82	1.13	0.06	0.57	13
	$\Psi_{TRAN}(pw+prey+cc), \theta^0_S(.), \theta^1_S(.), \gamma_S(.), \varepsilon_S(.), p_{t(S)}(.)$	1561.02	1.33	0.06	0.51	10
	$\Psi_{TRAN}(pw+hc), \theta^0_S(.), \theta^1_S(.), \gamma_S(.), \varepsilon_S(.), p_{t(S)}(.)$	1562.75	3.06	0.02	0.22	9

Ψ_{TRAN} = probability of site occupancy/habitat use at the transect level; p = probability of detection; θ^0 = spatial dependence parameter representing the probability that the species is present locally, given the species was not present in the previous spatial replicate; θ^1 = spatial dependence parameter representing the probability that a species is present locally, given it was present at the previous spatial replicate. γ is the probability that the site is occupied in summer season, given that it was unoccupied in winter season. ε is the probability that the site is unoccupied in summer season, given that it was occupied in winter season. Hab: habitat available; cc: canopy cover; ndvi: normalized difference vegetation index; ele: elevation; tri: terrain ruggedness index; prep: precipitation; temp: ambient air temperature; dist: disturbance index; gc: ground cover; hc: horizontal cover; pw: presence of water; car: carnivore activity index; K: number of parameters in the model.

Table 3.14: Summary of estimates of β coefficients from the logit link function based on the best univariate top model for each species, and the model averaged (ave) estimates for competing models within 2 delta AIC of the top model or containing a model weight more than 95%, based on landscape level covariates hypothesized to influence probability of prey occupancy at the grid level (Ψ_{GRID}) and probability of tiger habitat use at both the grid (Ψ_{GRID}) and transect (Ψ_{TRAN}) level; SE represents unconditional standard errors; NC: not converged. Models in bold and underlined represent the best models and models in italics represent robust beta estimates (95% CI do not include zero).

Scale	**Species**	**Model**	**β_{O} (SE)**	**β_{DNS} (SE)**	**β_{ELE} (SE)**	**β_{TRI} (SE)**	**β_{HAB} (SE)**	**β_{CC} (SE)**	**β_{TEMP} (SE)**	**β_{PREP} (SE)**	**β_{NDVI} (SE)**
Ψ_{GRID}	Gaur	Best model				**-2.94 (1.57)**					**1.28 (0.78**)
		Univariate	NA	-0.05 (0.39)	NC	-1.67 (1.19)	-1.83 (3.37)	0.34 (0.50)	3.32 (2.53)	-3.12 (1.90)	-1.67(1.28)
		Model ave	3.13 (5.56)	-0.00 (0.21)		-2.23 (1.54)	-0.29 (2.07)	-0.03(0.30)	0.15 (0.87)	-0.20 (0.96)	-0.81 (0.76)
	Sambar	Best model					***2.29 (1.40)***				
		Univariate	NA	-0.35 (0.33)	-0.22 (0.38)	-0.04 (0.40)	*2.29 (1.40)*	0.40 (0.34)	0.22 (0.39)	-0.24 (0.39)	-0.31 (0.41)
		Model ave	-2.25 (4.01)	-0.15 (0.28)	-0.02 (0.14)	0.00 (0.11)	1.56 (1.40)	0.07 (0.21)	0.02 (0.14)	-0.02 (0.15)	-0.04 (0.19)
	Chital	Best model		**-0.44 (0.32)**				**-0.55 (0.35**)			
		Univariate	NA	-0.40 (0.31)	0.03 (0.32)	-0.03 (0.33)	-0.13 (1.48)	-0.53 (0.37)	-0.08 (0.32)	0.04 (0.32)	-0.24 (0.28)
		Model ave	-0.75 (0.85)	-0.17 (0.27)	0.00 (0.08)	0.00 (0.11)	0.01 (0.31)	-0.35 (0.34)	-0.02 (0.13)	0.02 (0.14)	0.00 (0.13)
	Barking Deer	Best model		**0.51 (0.37)**							
		Univariate	NA	0.51 (0.37)	-0.21 (0.32)	-0.22 (0.32)	1.60 (1.35)	0.37 (0.35)	0.27 (0.34)	-0.21 (0.34)	0.14 (0.32)
		Model ave	0.18 (1.85)	0.29 (0.32)	-0.05 (0.18)	-0.01 (0.07)	0.19 (0.69)	0.11 (0.25)	0.04 (0.16)	-0.03 (0.14)	0.01 (0.08)
	Wild pig	Best model		**-1.11 (0.69)**			***5.20 (2.49)***				**-1.14 (1.06)**
		Univariate	NA	-0.68 (0.32)	-0.41 (0.32)	-0.19 (0.35)	*3.63 (1.56)*	0.14 (0.32)	0.38 (0.33)	-0.37 (0.37)	*-1.10 (0.56)*

Scale	Species	Model	β_O (SE)	β_{DNS} (SE)	β_{ELE} (SE)	β_{TRI} (SE)	β_{HAB} (SE)	β_{CC} (SE)	β_{TEMP} (SE)	β_{PREP} (SE)	β_{NDVI} (SE)
	Tiger	Model ave	-11.94 (6.26)	-1.03 (0.64)	-0.03 (0.16)		*5.18 (2.60)*				-0.64 (0.86)
		Best model					***4.86 (2.26)***				
		Univariate	NA	0.03 (0.35)	-0.26 (0.32)	-0.03 (0.34)	*4.86 (2.26)*	0.28 (0.35)	0.32 (0.32)	-0.25 (0.32)	-0.23 (0.39)
		Model ave	-11.31 (6.23)	-0.07 (0.24)		-0.01 (0.19)	4.64 (2.46)	0.00 (0.18)	0.04 (0.18)	-0.03 (0.16)	-0.04 (0.23)
Ψ_{TRAN}	Tiger	Best model		**-0.49 (0.27)**					***0.72 (0.29)***		
		Univariate	NA	-0.54 (0.33)	*-0.82 (0.42)*	-0.26 (0.23)	7.74 (9.24)	0.08 (0.16)	0.90 (0.50)	-0.80 (0.40)	*-4.51 (1.74)*
		Model ave	0.47 (2.62)	-0.35 (0.31)	-0.22 (0.34)		1.13 (5.64)		0.27 (0.36)		*-0.64 (1.63)*

Ψ = probability of site occupancy/habitat use at the grid (Ψ_{GRID}) and/or transect level (Ψ_{TRAN}); β is the beta coefficient explaining the magnitude and direction of covariate in a model; β_O represent the intercept; dns: distance to nearest settlement; hab: habitat available; cc: canopy cover; ndvi: normalized difference vegetation index; ele: elevation; tri: terrain ruggedness index; prep: precipitation; temp: ambient air temperature.

Table 3.15: Summary of estimates of β coefficient for the logit link function based on the best univariate top model for each species, and the model averaged (ave) estimates for competing models within 2 delta AIC of the top model or containing a model weight more than 95%, based on field level covariates hypothesized to influence probability of prey occupancy at grid level (Ψ_{GRID}) and probability of tiger habitat use at both the grid (Ψ_{GRID}) and transect (Ψ_{TRAN}) levels. SE represents unconditional standard errors. Models in bold and underlined represent the best models and models in italics represent robust beta estimates (95% CI do not include zero).

Scale	**Species**	**Model**	**β_{O} (SE)**	**β_{DIST} (SE)**	**β_{FIRE} (SE)**	**β_{GC} (SE)**	**β_{CC} (SE)**	**β_{HC} (SE)**	**β_{CAR} (SE)**	**β_{PREY} (SE)**	**β_{PW} (SE)**
Ψ_{GRID}	Gaur	Best Model		***-1.19 (0.57)***							
		Univariate	NA	*-1.19 (0.57)*	0.13 (1.09)	0.08 (0.40)	0.66 (0.42)	0.92 (0.82)	0.28 (0.45)		0.20 (0.90)
		Model ave	1.16 (0.80)	-1.05 (0.51)	-0.11 (0.61)	0.00 (0.19)	0.19 (0.34)	0.00 (0.00)	0.09 (0.26)		0.02 (0.41)
	Sambar	Best Model		***-1.01 (0.35)***	***-1.84 (0.93)***						
		Univariate	NA	*-0.86 (0.33)*	-1.25 (0.78)	0.04 (0.34)	0.06 (0.35)	-7.51 (4.44)	-0.27 (0.28)		-0.67 (0.90)
		Model ave	2.60 (1.04)	*-1.00 (0.42)*	-1.50 (1.03)	0.02 (0.17)	0.02 (0.17)	-0.29 (0.65)	-0.01 (0.11)		
	Chital	Best Model		**-0.64 (0.47)**	***1.84 (0.87)***						**-0.64 (0.47)**
		Univariate	NA	-0.68 (0.44)	*1.88 (0.83)*	0.02 (0.30)	0.54 (0.35)	0.03 (0.30)	-0.11 (0.31)		-0.45 (0.66)
		Model ave	-1.04 (0.56)	-0.30 (0.39)	*1.61 (0.82)*	0.00 (0.07)	0.23 (0.31)	0.00 (0.07)	-0.01 (0.20)		-0.27 (0.57)
	Barking Deer	Best Model		**-0.92 (0.49)**		***-1.67 (0.65)***		***1.07 (0.54)***			
		Univariate	NA	-0.43 (0.34)	-0.84 (0.70)	*0.93 (0.40)*	0.01 (0.32)	0.13 (0.30)	-0.07 (0.30)		0.85 (0.66)
		Model ave	1.11 (0.79)	-0.55 (0.46)	-0.12 (0.51)	*-1.40 (0.65)*	0.05 (0.22)	0.70 (0.51)	0.00 (0.05)		0.12 (0.43)
	Wild pig	Best Model				**0.54 (0.35)**			***-0.57 (0.29)***		**1.24 (0.65)**
		Univariate	NA	-0.20 (0.27)	0.85 (0.77)	0.45 (0.31)	-0.07 (0.26)	0.35 (0.27)			0.87 (0.57)
		Model ave	0.07 (0.58)		0.51 (0.75)	0.13 (0.28)		0.13 (0.23)	-0.46 (0.30)		0.82 (0.77)

Scale	Species	Model	β_{O} (SE)	β_{DIST} (SE)	β_{FIRE} (SE)	β_{GC} (SE)	β_{CC} (SE)	β_{HC} (SE)	β_{CAR} (SE)	β_{PREY} (SE)	β_{PW} (SE)
	Tiger	Best Model		***10.41 (4.55)***	**7.09 (3.99)**						***6.91 (3.40)***
		Univariate	NA	*4.14 (1.60)*	-0.22 (0.83)	-0.17 (0.33)	-0.51 (0.45)	0.34 (0.37)		0.57 (0.46)	*2.13 (1.08)*
		Model ave	0.53 (1.45)	9.56 (6.54)	6.34 (5.24)		-0.08 (0.54)	0.02 (0.14)		0.32 (1.08)	6.48 (5.20)
Ψ_{TRAN}	Tiger	Best Model		**0.49 (0.48)**	**-0.81 (0.62)**			**0.45 (0.31)**		***-0.56 (0.27)***	***2.67 (1.09)***
		Univariate	NA	-0.31 (0.45)	-0.50 (0.32)	-0.24 (0.16)	*-0.33 (0.16)*	0.40 (0.32)		*-0.37 (0.15)*	1.81 (0.95)
		Model ave	-0.90 (0.73)	0.15 (0.34)	-0.45 (0.52)		-0.10 (0.16)	0.20 (0.24)		-0.44 (0.24)	*1.92 (0.95)*

Ψ = probability of site occupancy/habitat use at the grid (Ψ_{GRID}) and/or transect level (Ψ_{TRAN}); β is the beta coefficient explaining the magnitude and direction of covariate in a model; β_{O} represent the intercept; dist: disturbance index; gc: ground cover; hc: horizontal cover; fire: presence of forest fire pw: presence of water; car: carnivore activity index; prey: prey activity index

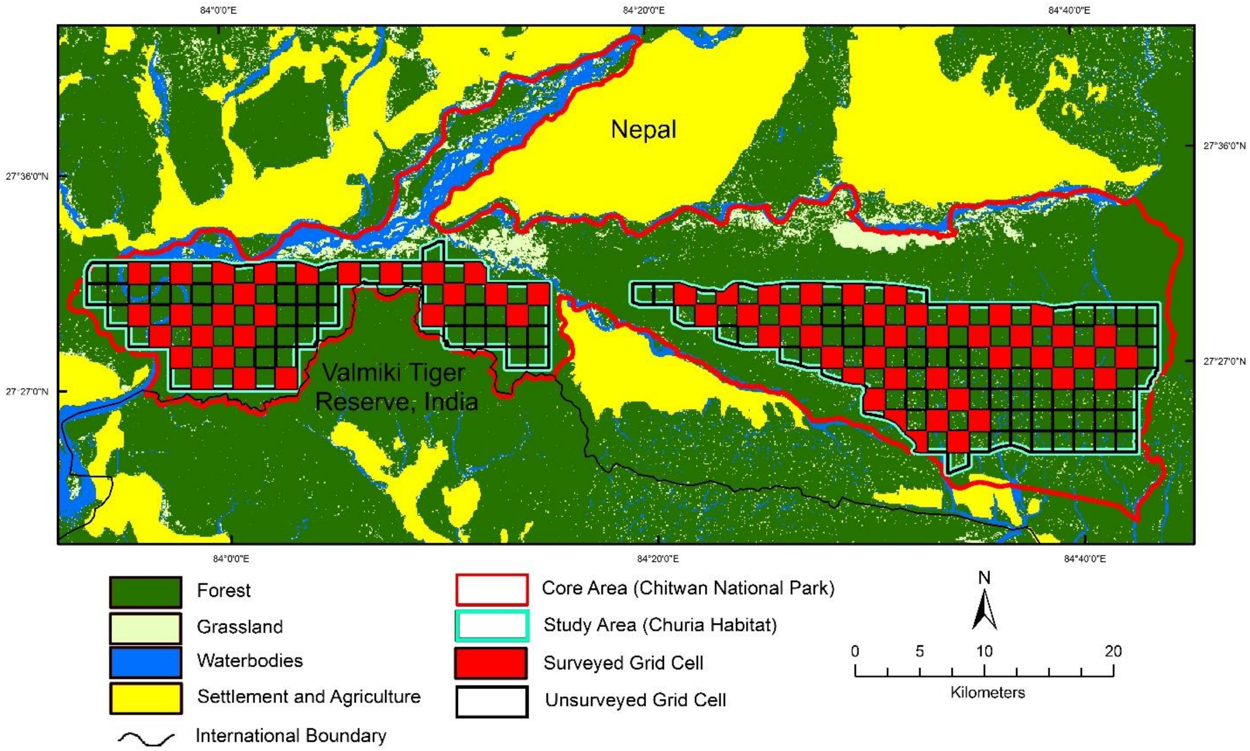

Figure 3.1: Study areas and study design showing spatial distribution of grid cells measuring 3.24 km^2 in checker board pattern across the Churia in Chitwan National Park.

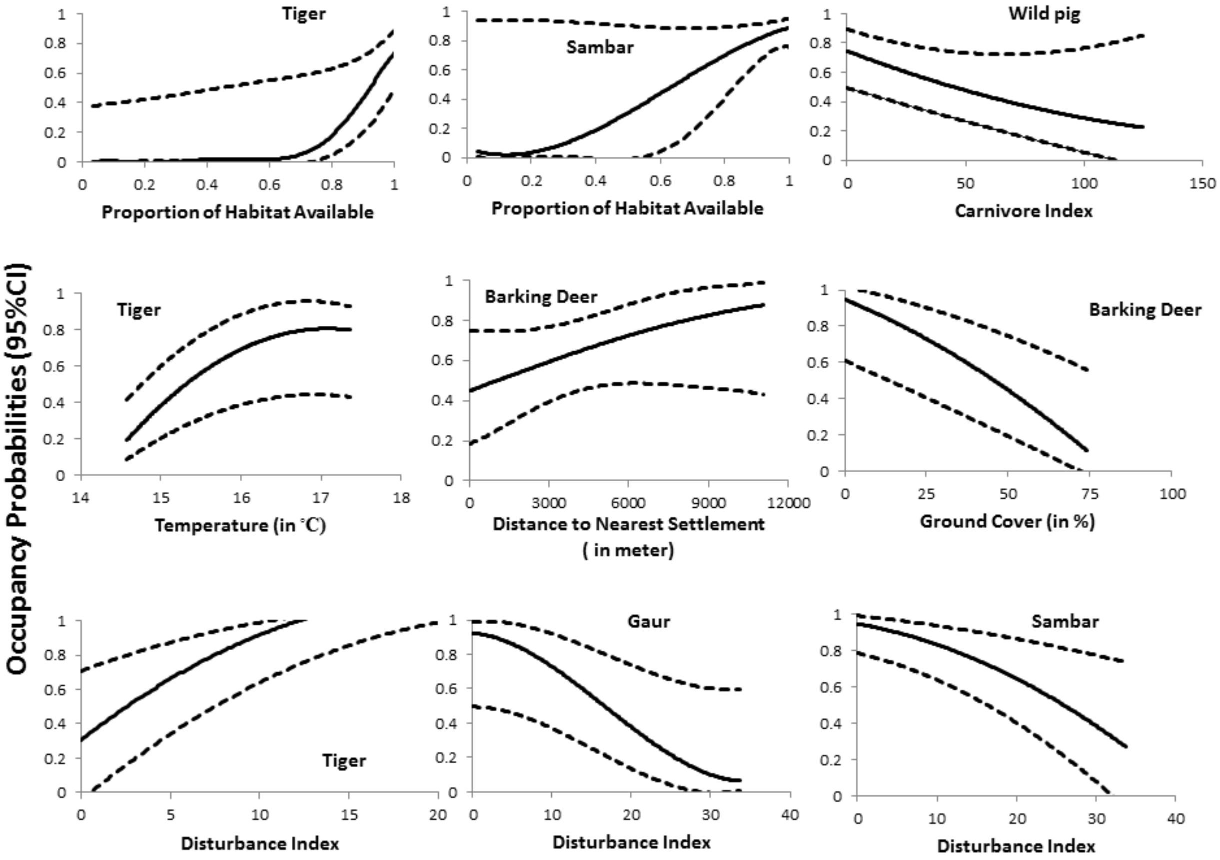

Figure 3.2: Relationship between the highly influential continuous covariates (based on beta estimates (β) from top models) and the probability of prey occupancy or tiger habitat use in Churia habitat.

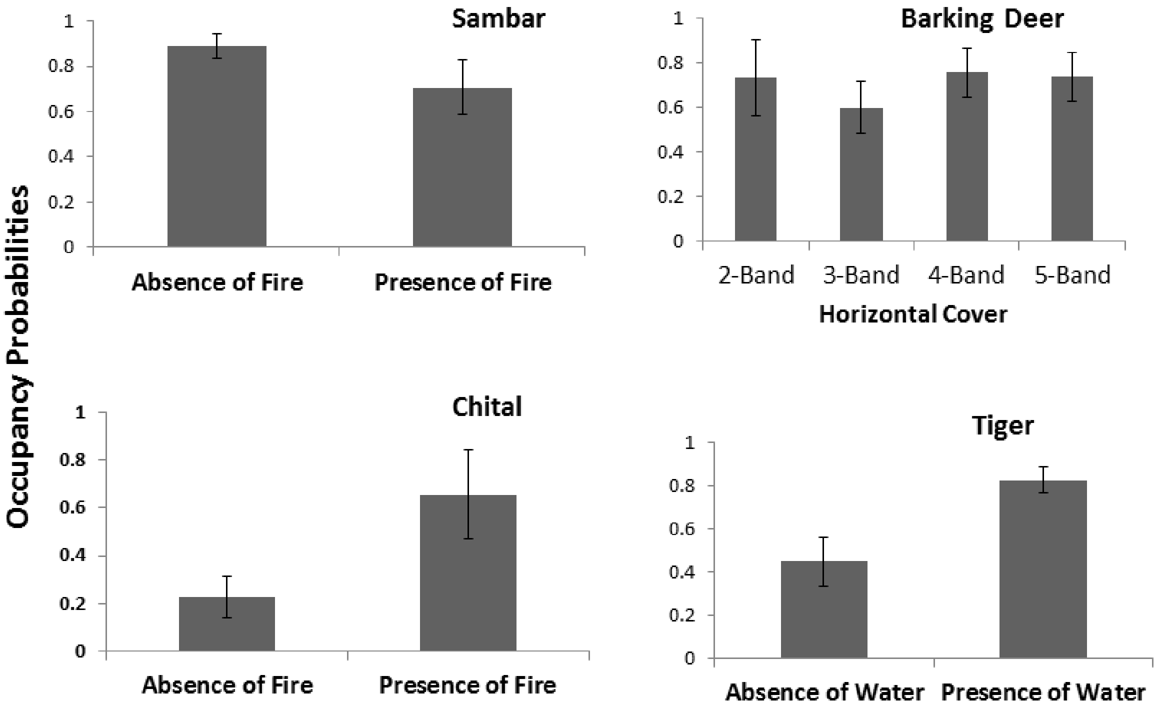

Figure 3.3: Relationship between the highly influential covariates (based on beta estimates (β) from top models) and the probability of occupancy or habitat use in Churia habitat. Covariates considered are the categorical variables.

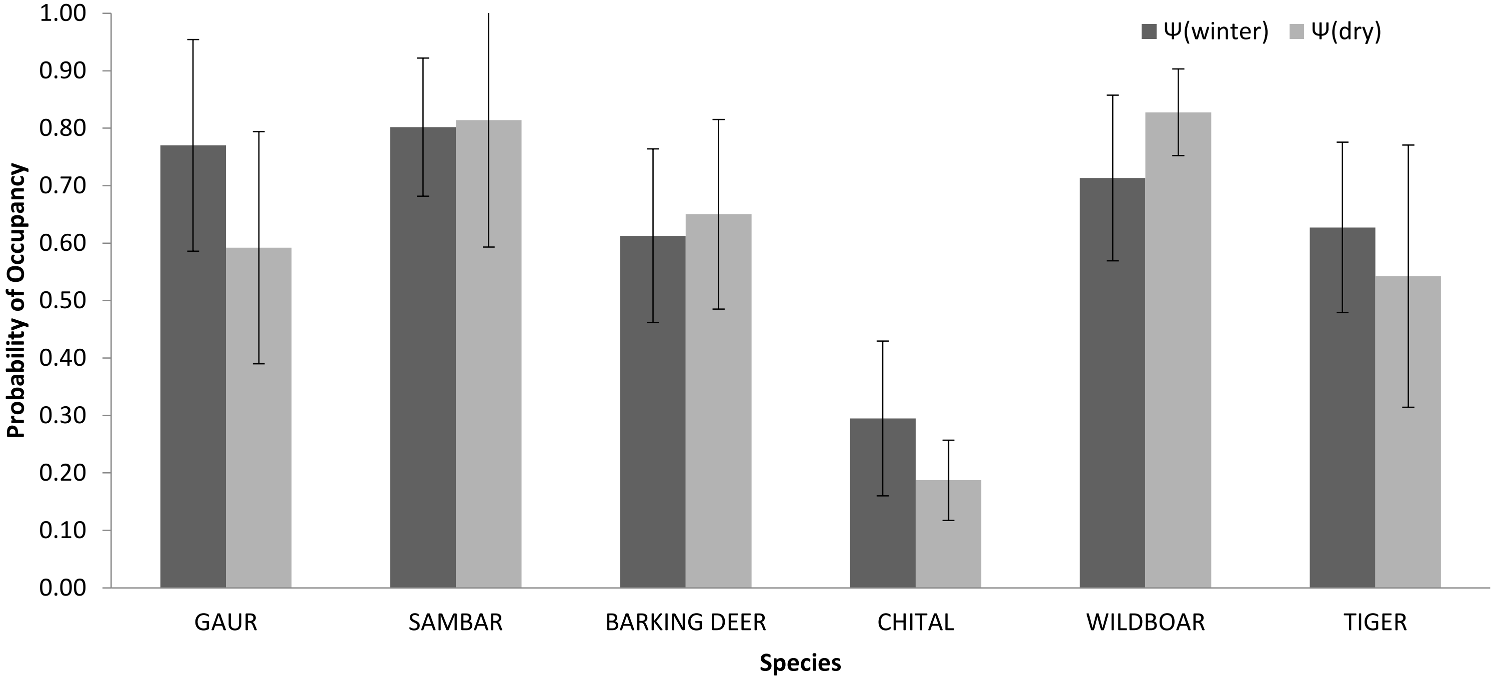

Figure 3.4: Model averaged estimates of occupancy (Ψ) and error bar represents model predicted 95% CI based on landscape level covariates for prey species and probability of habitat use of tigers in Churia habitat.

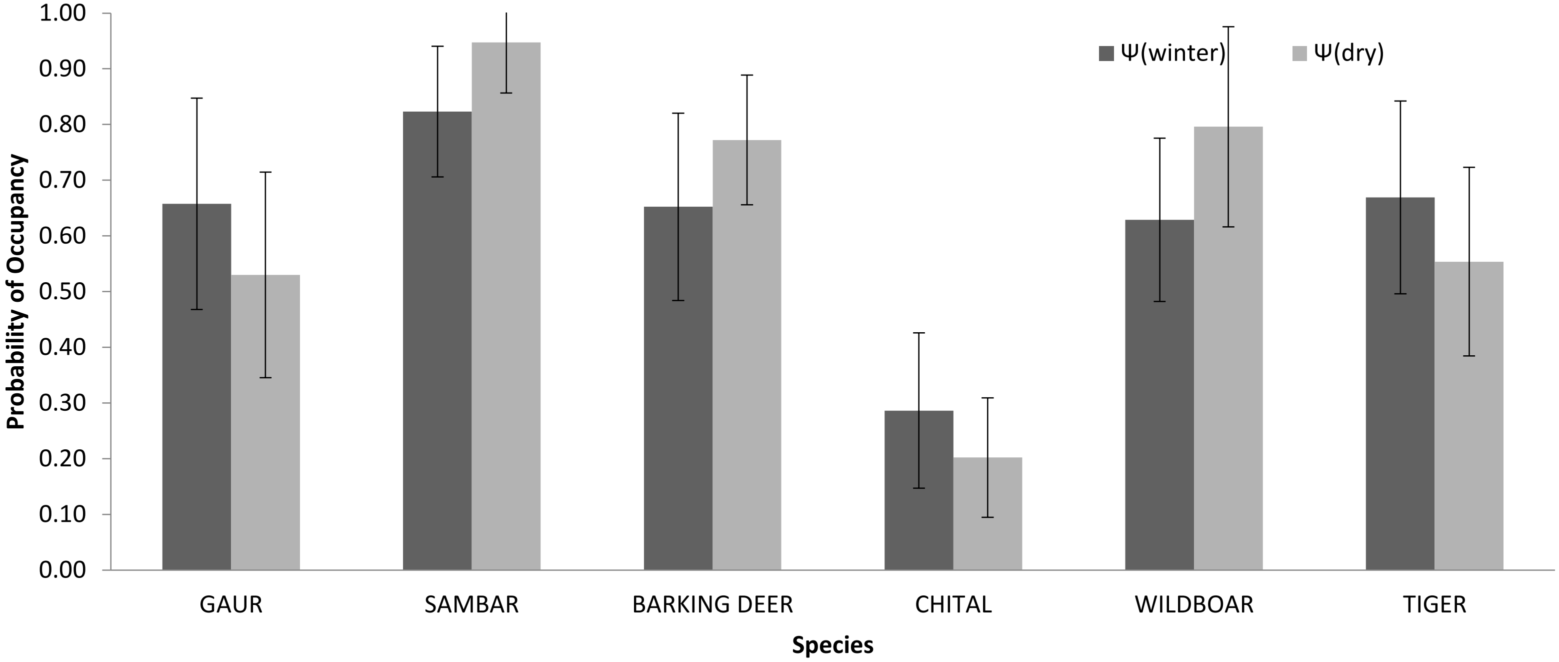

Figure 3.5: Model averaged estimates of occupancy (Ψ) and error bar represents model predicted 95% CI based on field level covariates for prey species and probability of habitat use of tiger in Churia habitat.

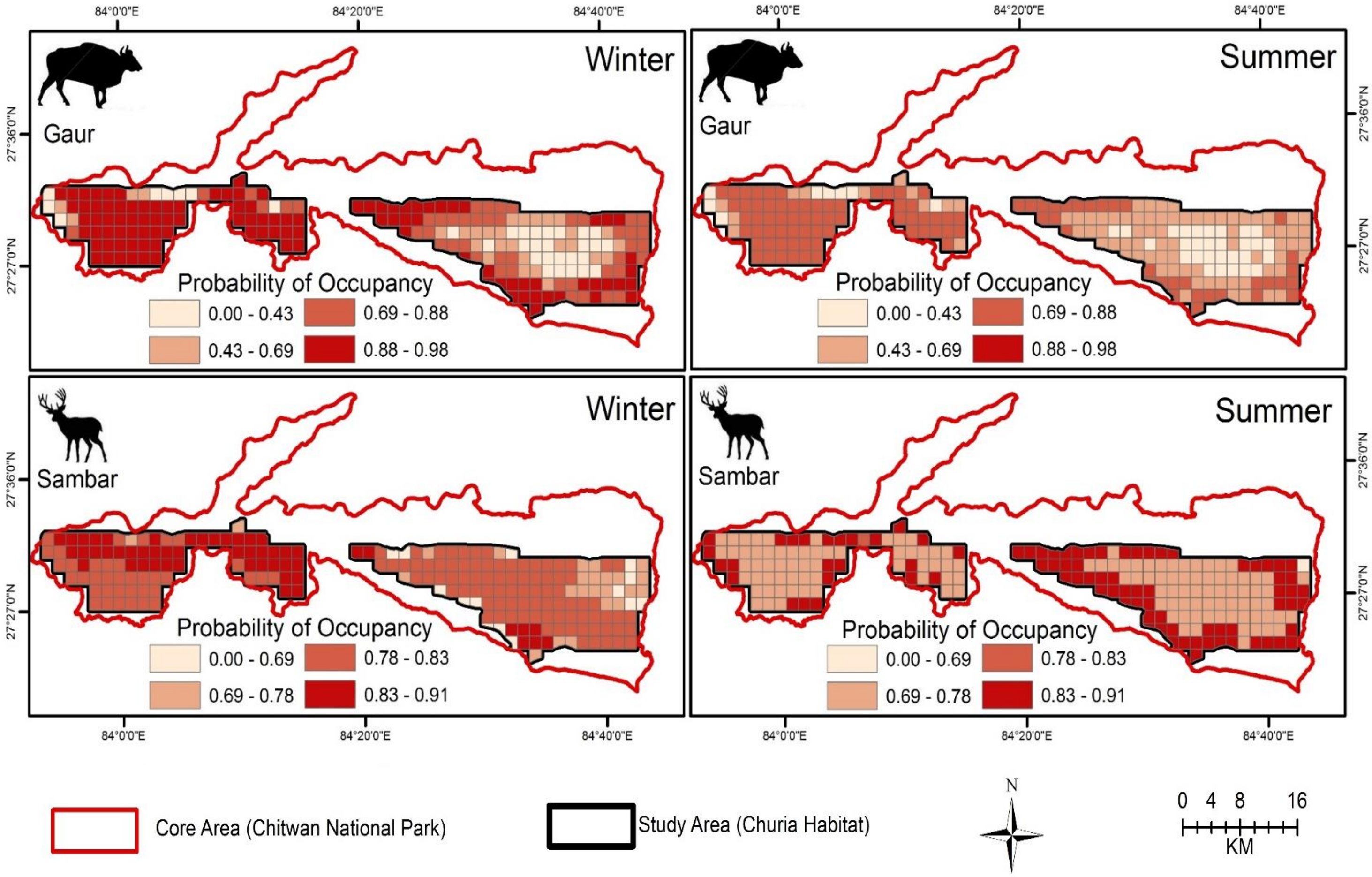

Figure 3.6: Gaur and sambar distribution patterns across the churia habitat in Chitwan National Park, Nepal. Grid cells shading shows the seasonal pattern based on estimated probabilities of occupancy in the winter (left panel) to the derived probabilities of occupancy in summer season (right panel). Lamda values indicate decrease in occupancy estimates for gaur (λ=0.76) and slight increase in occupancy estimates for sambar (λ=1.02) across the seasons (winter to summer) in churia habitat.

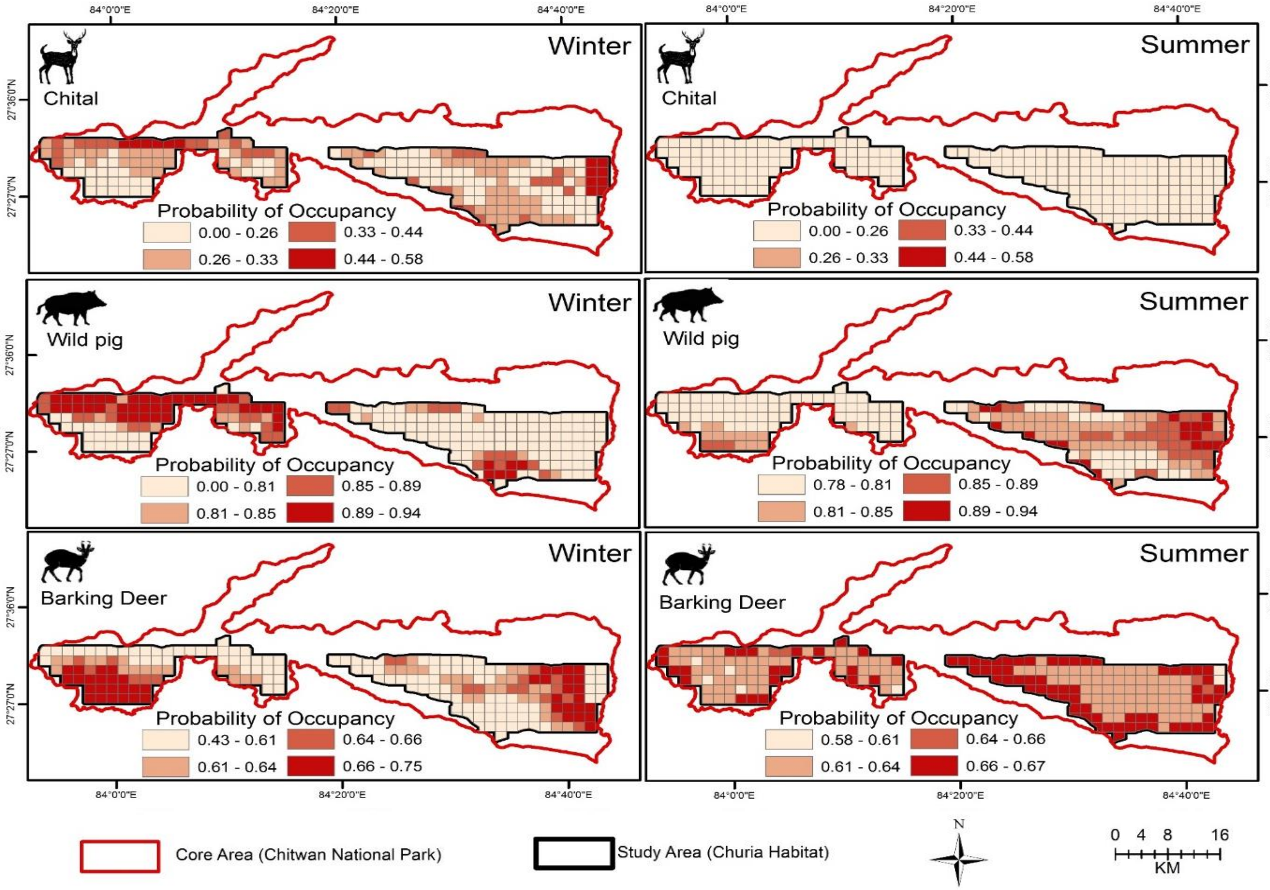

Figure 3.7: Chital, wild pig, and barking deer distribution pattern across the churia habitat in Chitwan National Park, Nepal. Grid cells shading shows the seasonal pattern based on estimated probabilities of occupancy in the winter (left panel) to the derived probabilities of occupancy in summer season (right panel). Lamda values indicate decrease in occupancy estimates for chital (λ=0.65), while stable occupancy estimates for barking deer (λ=1.00), and increase in occupancy estimates for wild pig (λ=1.11) across the seasons (winter to summer) in churia habitat.

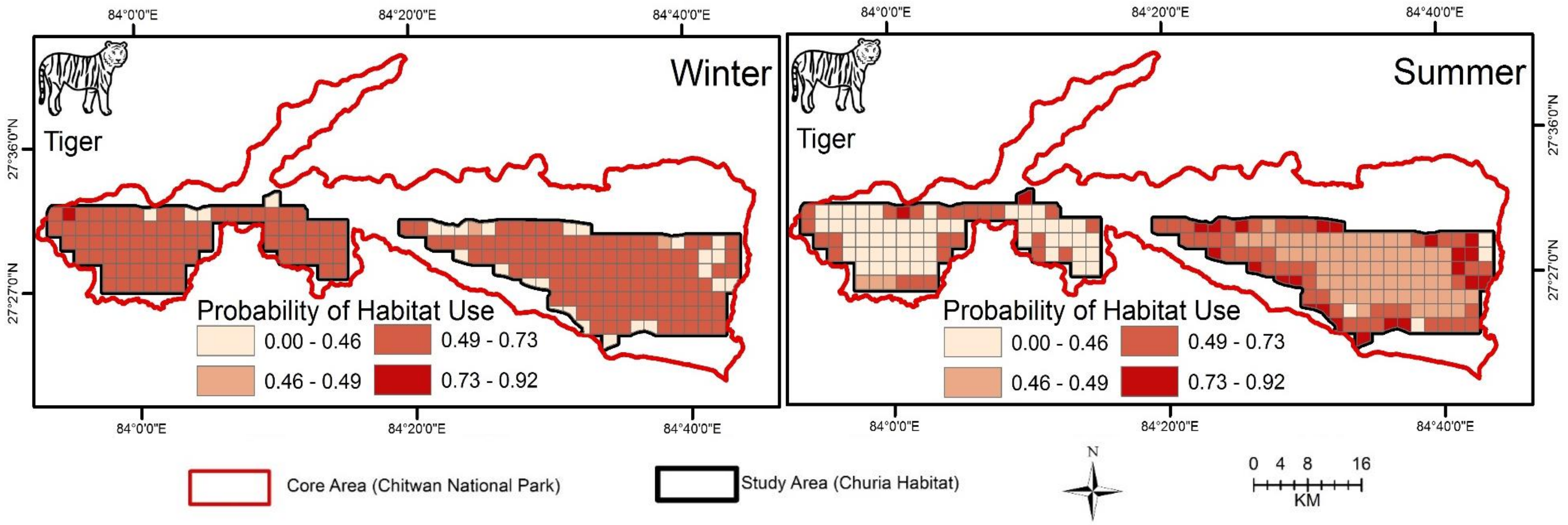

Figure 3.8: Tiger habitat use patterns across the churia habitat in Chitwan National Park, Nepal. Grid cells show the seasonal pattern based on estimated probabilities of habitat use in winter (left panel), and based on the derived probabilities of habitat use in summer season (right panel). Lamda values indicate decrease in habitat use estimates for tiger (λ=0.73) across the seasons (winter to summer) in churia habitat.

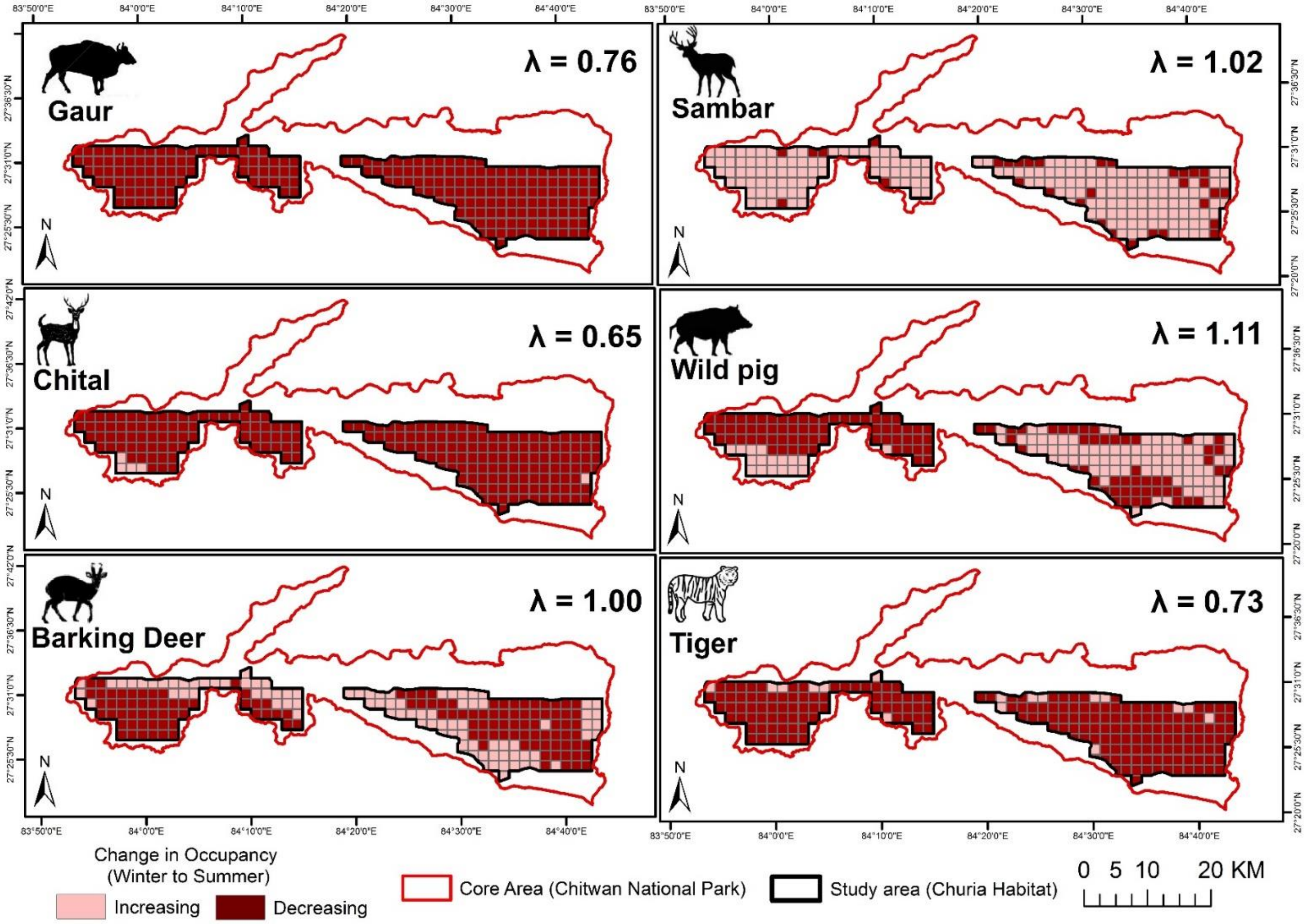

Figure 3.9: Change in occupancy and/or habitat use (winter to summer) pattern of prey and tiger based on lamda (λ) estimates across the grid cell in the Churia habitat.

Chapter 4

Genetic diversity, genetic structure and gene flow of tigers in Terai Arc Landscape, Nepal

ABSTRACT

I examined Nepal's tiger population across the foothills of the Himalaya Mountain for genetic variation, genetic structure, and gene flow between potential sub-populations. I opportunistically collected 700 scat samples from four protected areas and five hypothesized corridors across the Terai Arc Landscape. Historical land-use change in the Terai Arc was extracted from Anthrome data sets to relate land-use change to potential barriers and subsequent hypothesized bottleneck event on the landscape. I used standard genetic metrics (e.g. allelic diversity, heterozygosity) to estimate genetic variation in the tiger population. Using program Structure (non-spatial) and TESS (spatial), I defined the putative genetic clusters present in the landscape. Migrant analysis was carried out in Geneclass and Bayesass for estimating contemporary gene flow. I tested for a recent population bottleneck with heterozygosity excess test using program Bottleneck. Of the 700 scat samples, 396 were tiger-positive (57% success). Screening eight microsatellite loci, I identified 78 individual tigers. I found large-scale landuse changes across the Terai Arc Landscape due to conversion of forest into agriculture in last two centuries and I identified areas of suspected barriers. I found low levels of genetic variation (expected heterozygosity = 0.61) and moderate genetic differentiation ($F_{ST} = 0.14$) across the landscape, indicative of sub-population structure and potential isolation of sub-populations. I detected three genetic clusters across the landscape consistent with three demographic sub-populations respectively occurring in the Chitwan-Parsa, Bardia, and Suklaphanta protected areas. I detected 10 migrants across all study sites, confirming there is still some dispersal-mediated gene flow across the landscape. I found evidence of a bottleneck signature, especially around lowland forest in the Terai, likely caused by large-scale land-use change in last two centuries, which could explain the low levels of genetic variation detected at the sub-population level. These findings are highly relevant to tiger conservation, indicating that efforts to protect source sites and to improve connectivity are needed to augment gene flow and maintain genetic diversity across the landscape.

Keywords: Tiger, genetic variation, non-invasive, terai arc, structure, bottleneck, gene flow

INTRODUCTION

Reduced genetic diversity and reduction in habitat area are potential influential factors leading to the extirpation of populations (Lacy 1997) and extinction of species (Burkey 1989, Soule et al. 1992, Avise 1996). In the face of habitat fragmentation and isolation, maintaining the optimum level of genetic connectivity among fragmented patches is a challenging management task (Mills and Allendorf 1996, Baudry and Burel 1998). Yet, gene flow among isolated populations is necessary to avert the negative consequences of genetic drift and inbreeding (Wright 1932, Harrison and Hastings 1996, Crnokrak and Roff 1999, Keller and Waller 2002, Dutta et al. 2013) and it plays an important role in persistence of natural populations (Slatkin 1985). Gene flow is particularly critical for carnivores, which often occur at naturally low densities (Carbone and Gittleman 2002), thus increasing their risk of extinction due to a greater susceptibility to stochastic events (Caughley 1994, Frankham et al. 2002).

The tiger (*Panthera tigris*), an apex predator, is in a precarious state. The tiger range has declined by more than 90% in past two decades and now occupies only 7% of its former range (Sanderson et al. 2006). The few remaining wild tigers (est. 3,200) are concentrated within 76 global Tiger Conservation Landscapes (TCLs) across a wide range of tiger habitats types (Sanderson et al. 2006). Besides poaching, habitat loss and fragmentation remain the largest threats to the extant tiger populations (GTRP 2010), and threats are mounting rather than diminishing in these TCLs (Sanderson et al. 2006, Seidensticker 2010, Seidensticker et al. 2010).

The Terai Duar and Savannah Grasslands Ecoregion (Wikramanayake 2002), along the foothills of the Himalayas, holds a rich assemblage of carnivores (Wikramanayake et al. 2010) in Nepal and northwest India. The Terai Arc Landscape (also referred to as the Terai Arc) occupies a significant portion of this ecoregion, containing 12 core tiger clusters connected by contiguous forest blocks (Wikramanayake et al. 2004, Jhala et al. 2011). Five protected areas are spread in a somewhat linear configuration across primarily forested habitat, with varying degrees of connectivity among them, and providing core habitat for Nepal's only tiger populations ($\widehat{N}$=198) (Dhakal et al. 2014). For species of conservation concern like tigers in Nepal, habitat connectivity is especially important (Wikramanayake et al. 2011) because external factors such as human development projects, resettlement of villages and encroachment into protected areas (GTI 2013), make the human-dominated landscape a difficult barrier for tiger to cross. Development of migration corridors and restoration of critical bottlenecks for dispersal are crucial for maintaining genetic variation (Wilson and Willis 1975, Beier and Noss 1998). Corridors that facilitate dispersal can allow gene flow in wide-ranging, low-density predators like tigers (Reddy et al. 2012a, Sharma et al. 2013a).

Mondol et al. (2009b) showed that Indian tigers are the most diverse globally and represent half of the extant genetic diversity in the species. Multiple studies in India have shown moderate to high levels of genetic variation that maintain fine-scale genetic sub-divisions (Mondol et al. 2009b, Sharma et al. 2009, Reddy et al. 2012a, Joshi et al. 2013, Sharma et al. 2013b) and varying levels of gene flow between the tiger sub-populations (Sharma et al. 2013a) living in fragmented landscapes. Wikramanayake et al. (2004) identified three possible sub-populations of tigers across the Terai Arc, Nepal based on landscape classification (i.e., by identification of potential landscape barriers to dispersal) based on long-term field data on tiger detections and habitat requirements. The existing habitat connectivity and corridors were delineated assuming that tigers dispersed recently among sub-populations and thus share a common gene-pool. However, there is no genetic study to support this presumed sub-structuring of the tiger population across the Terai Arc, Nepal. Against this background, I investigated genetic subdivision of the hypothesized tiger sub-populations which are now geographically separated and largely confined to protected areas, with possible ecological and genetic connectivity based on persistence habitat corridors of questionable effectiveness.

Barber-Meyer *et al.* (2013) showed that 36% of the Terai Arc is occupied by tigers and that major clusters occur within the protected areas. Few tiger signs have been detected outside of protected areas (Gurung 2002, Wikramanayake et al. 2010); however, telemetry studies have shown that tigers in the Terai have dispersed as far as 30 km (Smith 1993), including dispersal through human-dominated areas within the landscape (Joshi et al. 2013, Sharma et al. 2013a). Camera-trap data also have confirmed the presence of tigers in corridors (Wikramanayake et al. 2010, 2011). Thus, a landscape-level genetic approach to conservation is needed to assess whether dispersal and subsequent breeding (genetically effective migration) of tigers occurs across the fragmented habitat. Existing methods (e.g., camera-trapping and telemetry studies) require long-term data sets to demonstrate dispersal events, and are ineffective for estimating numbers of genetic migrants. Noninvasive genetic techniques therefore, could prove useful tools to study landscape connectivity and dispersal (Joshi et al. 2013) across the Terai Arc.

The Terai Arc has suffered significant land-use change in the recent past (Acharya and Dangi 2009), which might impede dispersal and gene flow across the landscape. If dispersal is not possible, I expect to find significant genetic clusters within the tiger population caused by large-scale habitat fragmentation and disruption of gene flow across the landscape.

I examined landuse change through time, as well as used past tiger research, in order to identify potential landscape barriers and dispersal corridors, combined with noninvasive genetic sampling and analysis techniques using tiger fecal (scat) samples collected over the Terai Arc, as source of DNA for this study. I used multilocus microsatellite DNA data to assess the level of genetic diversity and connectivity, identifying the tiger sub-population structure across the Terai Arc. My objectives were thus to: 1) assess genetic diversity of tigers, 2) provide an assessment of genetic differentiation and recent gene flow among sub-populations, and 3) detect evidence of population bottleneck signatures in the tiger population of the Terai Arc, Nepal.

STUDY AREA

This study was conducted across the Terai Arc in Nepal- 23,199-km^2 landscape that stretches along southern lowland areas of the country (Figure 4.1). The Terai Arc has a sub-tropical monsoonal climate and mixed deciduous vegetation ranging from successional alluvial floodplain grassland communities to climax Sal (*Shorea robusta*) forests. This global priority landscape (Wikramanayake et al. 1998) includes five protected areas: Suklaphanta, Bardia, Banke, Chitwan and Parsa. Nepal's protected areas also are connected ecologically with several protected areas across the border with India (Jhala et al. 2011). Of the five protected areas; Banke and Bardia, and Chitwan and Parsa, have contiguous habitat and thus I hypothesized that their tigers could be combined as sub populations. Therefore, I hypothesized there would be three genetic clusters, or potential sub-populations of tigers (Suklaphanta, Bardia-Banke, and Chitwan-Parsa) spatially segregated somewhat linearly across the landscape, with the Bardia and Suklaphanta populations being more similar due to closer proximity to each other than to Chitwan. Demographically, from past camera-trapping studies, Chitwan-Parsa has the largest abundance, while Suklaphanta has the lowest abundance of tigers in the landscape.

Besides tigers, leopards (*Panthera pardus*), dholes (*Cuon alpinus*) and spotted hyenas (*Hyena hyena*) are the top carnivores found in the Terai Arc. Illegal encroachment and infrastructure development are threats to the tiger habitat in the landscape, and direct persecution of tigers by humans remains a challenge for their persistence in this human-dominated landscape (248 people km^{-2}).

METHODS

Forest-Agriculture Landuse Change Detection

I analyzed land-use change across the Terai Arc over the past 400 years based on Anthrome 2.0 datasets (Ellis et al. 2010). Anthrome data sets characterize global anthropogenic transformation at the century level (i.e., every 100 years) for the terrestrial biosphere in a discrete time frame for the years 1700-2000. I clipped the coarse data sets (~10 km pixels) for the landscape using ArcGIS 10.1 (Esri, Redlands, USA) and calculated the amount of area under different land-use classes across different time frames (1700-1800-1900-2000). I reclassified the 13 land-use classes from Ellis et al. (2010) into two classes (forest and agriculture-settlement) to analyze the changes in forest areas to agriculture or vice versa over the time frame. This analysis was done to identify potential barriers to tiger dispersal based on historical changes in forest conditions, to hypothesize where bottleneck events might occur across the landscape.

Fecal DNA Survey

I used the non-invasive molecular scatology technique (Reed and Tollit 1997, Wultsch et al. 2014) to collect tiger fecal samples as a source of DNA for the study. I collected tiger fecal samples from both the protected areas and corridors outside protected areas across the Terai Arc. I divided the landscape into 98 grid cells across the landscape, each measuring 15 X 15 km (225 km^2) as sampling units (Figure 4.2). First, I collected samples from grid cells (*n* = 30) within the four protected areas (Parsa, Chitwan, Bardia and Suklaphanta). Second, I collected samples from grid cells (n = 10) focusing on two hypothesized corridors. Within each grid cell, I opportunistically searched for tiger fecal (scat) samples across human trails, fire lines, and animal trails. I identified tiger scats in the field based on their physical appearance and associated indirect signs like pugmarks and scratches (Karanth and Sunquist 1992, Ramakrishnan et al. 1999). Upon encountering scat samples, I scratched off a few grams from upper and side surfaces of the scat (Mondol et al. 2009a). I stored the samples in 2-ml vials in 1:4 ratios filled with dimethyl sulphoxide saline solution (DETs buffer, Seutin et al. 1991, Frantzen et al. 1998, Wultsch et al. 2014). I kept a few grams (200-300 g) of samples from the widest portion of the scats for future molecular diet study, and the remainder of the sample was left in the original location to avoid possible changes in tiger behavior due to the territoriality nature of the species. To avoid double collection of the same scats in subsequent sampling sessions, I either marked the scat with a small red dot using nail polish (in the case of dried samples) or pushed a twig inside the substrate at the side of scat (in case of wet samples) after collecting the genetic and diet samples. I recorded other ancillary information, such as GPS location, time and date of collection, morphology of the scat samples, habitat type, and other indirect signs observed. All samples were sent to the laboratory at the Center for Molecular Dynamics, Nepal (CMDN) for further processing within two weeks from the date of collection.

DNA Extraction, Species Identification and Sex Identification

DNA was extracted from scat samples using the commercially available DNA stool kit (QIAGEN Inc.) following the manufacture’s instruction with slight modification. I kept one negative control (water) in each batch of samples to monitor contamination during DNA extraction. To avoid contamination at PCR reactions, DNA extraction was carried out in a separate room. All scat samples first were screened for species identification using species-specific primers developed earlier (Bhagavatula and Singh 2006). The tiger positive-samples were further processed for sex identification (Pilgrim et al. 2005) and then processed for individual identification using an assay of 10 polymorphic microsatellite loci (Table 4.1).

Microsatellite Primer Selection

I screened 17 loci which were identified for domestic cat (Menotti-Raymond et al. 1999) and also used in previous studies of tigers (Bhagavatula and Singh 2006, Mondol et al. 2009a, Mishra et al. 2014). I selected the 10 loci based on expected heterozygosity and variation in allelic diversity (Table 4.1).

Polymerase Chain Reaction (PCR) Standardization and Genotyping

PCR standardization was carried out with field-collected samples. Amplification was carried out in 7 µl reaction volumes containing 3.5 µl Qiagen Mastermix and 0.07 µl of Q solution, forward and reverse primers for all microsatellite loci mixed to the final standard concentration; (i.e., 0.4 µM FCA205, 0.2µM FCA391, 0.07µM PttD5, 0.14µM FCA232, 0.07µM FCA304, 0.30µM F85, 0.14µM FCA441, 0.07µM PttA2, 0.09µM FCA043 and 0.49µM F53), 2.50µl of DNA extract. The PCR conditions for microsatellites included an initial denaturation (95˚C for 15 min); initial touchdown PCR was performed for 10 cycles with denaturation at 94 ˚C for 30s, annealing initially at 62˚C and reduced by 0.5˚C in each cycle for 90 seconds and extension at 72˚C for 60s; followed by 25 cycles of denaturation at 94˚C for 30s, annealing at 57˚C for 90s and extension at 72˚C for 60s followed by a final extension at 72˚C for 10 min and cooled to 4˚C for 10 min in an MJ Research PTC-225 Thermal Cycler. 0.7µl of amplified product was added into 0.3µl of LIZ-500 size standard and then the assay was run in an automated ABI 310 genetic analyzer (Applied Biosystems). Microsatellite alleles were scored in GENEMAPPER-4.1 (Applied Biosystems). To finalize the consensus genotypes, a multi-tube approach was used in which at least three identical homozygote PCR results were required for calling homozygote genotypes, and each allele had to be observed in two independent PCR reactions to record a heterozygous genotype (Wultsch et al. 2014).

DATA ANALYSIS

PCR Amplification, Genotype Accuracy and Error Rates

I used results from last two PCR runs for calculating PCR amplification rates, genotype accuracy, and error rates (Wultsch et al. 2014). For PCR success, I calculated percentage of PCR success across all the tiger-positive samples. Genotype accuracy was calculated based the percentage of successful PCR results, which matched the finalized consensus genotype. Genotype errors (allelic dropout and false allele) were estimated based on the protocols used by Broquet and Petit (2004). Allelic dropout (ADO, in which one allele of a heterozygous individual is not amplified during a PCR) was estimated only for heterozygous genotypes as the ratio of the number of errors detected by the total number of cases in which an error could be an issue, while false allele (FA, PCR-generated incorrect alleles resulting from slippage artefact during the first cycles of the reactions) was estimated across all the consensus genotypes. I estimated the frequencies of null alleles (alleles that failed to amplify during PCR) using program Microchecker (Van Oosterhout et al. 2004).

Individual Tiger Identification with Genetic Data

I estimated the probability of apparent identity for unrelated individuals ($P_{(ID)}$) and siblings ($P_{(ID)sib}$) (Waits et al. 2001). I used the minimum criteria of $P_{(ID)sib} < 0.010$ (Mills et al. 2000, Waits et al. 2001) for selecting the minimum number of loci required for individual identification. I used program GenAlEx version 6.5 (Peakall and Smouse 2012) to determine the minimum number of individual tigers in the consensus genotype data sets. Any repeated matching genotypes were regarded as recaptures of individual tigers.

Genetic Differentiation

I quantified genetic diversity using the metrics of observed heterozygosity (H_o) and expected heterozygosity (H_e) using GenAlEx 6.5, and allelic richness using the rarefaction method in HP-RARE, version 1.0 (Kalinowski 2005). I tested for global and population-level deviations from Hardy-Weinberg equilibrium (HWE) and linkage disequilibrium (LDE) (Lewontin and Kojima 1960) using the program Arlequin, version 3.5 (Excoffier and Lischer 2010) and applied Bonferonni corrections to adjust probability levels taken as statistically significant at account for multiple comparisons (Rice 1989). I used Arlequin with 10,000 permutations to test the statistical significance of the pairwise F_{ST} value (Weir and Cockerham 1984) between the three populations in the Terai Arc. I used an AMOVA (Analysis of the Molecular Variance), implemented in Arlequin, for estimating the amount of variation within and across individuals and populations. I measured D_{EST} (Jost 2008) as the improved metrics for genetic distances between the populations. This estimator outperforms F_{ST} as an accurate and unbiased metric of the level of differentiation between populations when sample size is high and number of loci is low (Jost 2008). I calculated the harmonic mean of D_{EST} across the loci for each population using the web-based program SMOGD (Crawford 2010) with 1000 bootstrap replicates.

Genetic Subdivision

Firstly, I used multivariate techniques using Principal Coordinate Analysis (PCoA) to find and plot major patterns within the multivariate data sets (sampled tiger populations with multiple loci). This was done in program GenAlEx 6.5. This uses the a I used individual-based Bayesian clustering methods implemented in programs Structure (non-spatially explicit), version 2.3.4 (Pritchard et al. 2000) and TESS (spatially explicit), version 2.3 (Durand et al. 2009) for inferring genetic subdivision across the tiger population in the Terai Arc. In program Structure, I allowed the value of *k*, representing the potential number of clusters (sub-populations) to vary between 1 and 5 and performed 10 independent runs for each value of *k*. I ran the analysis with admixed models with correlated frequencies using a burn-in of 500,000 Markov Chain Monte Carlo (MCMC) steps followed by additional 1,000,000 iterations. I ran the analysis with and without prior information on the sampling sites for comparing consistency in results. The most appropriate value of *k* was obtained based on the method described by Evanno et al. (2005) using the web-based program Structure Harvester (Earl and vonHoldt 2012). The optimal *k* value from Structure Harvester was used in the program Clumpp (Jakobsson & Rosenberg 2007) for estimating the mean k of the permuted matrices across replicates.

TESS, the spatially explicit clustering program, builds individual neighborhoods using the Voronoi tessellation (Voronoï 1908). TESS uses the spatial information along with multi-locus genotypic data from individuals to define population structure without using predefined population information.

I ran the admixture models within both programs, as Bayesian clustering methods with admixture models are more robust in identifying diverging sub-populations (Falush et al. 2007, François and Durand 2010). In program TESS, I ran both admixture Gaussian modelsconvolution Gaussian model (BYM) and conditional auto-regressive (CAR), with 100,000 burn-in runs followed by 20,000 iterations for $k = 2$ to 10 with 100 replications per k. I used the average of the 10% of the lowest Deviance Information Criteria (DIC) values for each $k_{\max}$. I used DIC values for estimating the number of optimal $k_{\max}$ (genetic sub-populations) (Spiegelhalter et al. 2002).

Estimation of Contemporary Gene flow

To examine whether the individuals sampled originated in the location from which they were sampled, I implemented assignment/exclusion tests using program Geneclass2 (Piry et al. 2004). I used the Bayesian approach with resampling (Paetkau et al. 2004) with 10,000 individuals and an alpha value of 0.05. I also carried out assignment tests in program Structure incorporating the geographical sampling sites as prior information (LOCPRIOR) without changing the other parameter settings as described above. I used the stringent criterion of $q > 0.9$ for assigning individuals as residents to potential sub-populations. Values below 0.9 were considered representative of individuals with admixed ancestry.

Presence of strong genetic differentiation caused by isolation-by-distance (IBD) has been shown to bias gene flow estimates. I first tested for evidence of IBD in the population using the web-based software IBDWS (Jensen et al. 2005). The program checks for correlation between the geographical distances and genetic distance (F_{ST}). Tigers are known to disperse through different habitat types, avoiding human settlements (Smith et al. 2011); hence, the geographical Euclidian distances through forested blocks do not necessarily translate to true connectivity between the sites (Sharma et al. 2013b).

To measure the genetically effective dispersal (i.e., gene flow) of tigers, I used Geneclass2 for detection of first-generation migrants in the Terai Arc. First-generation migrants were selected using the "detection of migrant" functions to detect individuals that were sampled in one population, but likely originated in another sampling location as determined by their genetic similarity to that population. I used the likelihood ratio (L_{home}/ L_{max}) test statistic to identify migrants. The method uses the Bayesian criteria of Rannala & Mountain (1997) along with the MCMC resampling method (Paetkau et al. 2004) to determine the critical value of L_{home}/ L_{max} beyond which a sample is treated as a migrant. I used $\alpha=0.05$ as the critical value for detection of migrants. I did a similar analysis with program Structure for detection of migrants. Since I did not have prior knowledge about migration of individuals between potential sub-populations, I used the default setting.

I used program Bayesass, version 1.3 (Wilson and Rannala 2003) to estimate rates of recent immigration over the last several generations among the sub-populations. This Bayesian approach uses multilocus genotype data and relaxes the key assumptions of populations being in HWE or migration-drift equilibrium. I assumed recent flow over the past 5-7 generations (25-30 years) (Sharma et al. 2013b), given a generation time of 5 years for tigers (Smith and McDougal 1991). I ran multiple runs of the program Bayesass with 3×10^7 MCMC iterations and a 10^7 burn-in with different seed numbers and delta values to confirm to final parameters and ensured convergence of the final parameters. I regarded both immigration and emigration rates between populations as contemporary migrations. I also reported the number of recent migrants detected.

I used program ML-Relate (Kalinowski et al. 2006) to calculate maximum likelihood estimates of pairwise relatedness and relationship categories (unrelated (U), half-siblings (HS), full-siblings (FS) and parent-offspring (PO)) between individuals among the three sub-populations. I utilized the relationship between the dispersed migrants from the population and degree of relatedness between individuals at different sites to assess other measures of contemporary gene flow.

Detection of Bottlenecks

I used two qualitative approaches to test for the genetic signature of a severe demographic contraction in the tiger population across the Terai Arc. First, I calculated the M-ratio (Garza and Williamson 2001) using program Arlequin, version 3.5, which compares the number of alleles (*k*) with the allelic size range (*r*). A bottleneck signature inferred in a population when rare alleles are lost and k is reduced faster than r. M-ratio values less than the threshold of 0.68 imply the presence of a bottleneck signature in the population (Garza and Williamson 2001). Second, I used the Cornuet and Luikart (1996) approach in program Bottleneck (Piry et al. 1999) for comparing the bottleneck signature in each population. This method tests for the departure from mutation-drift equilibrium based on heterozygosity excess or deficiency (H_{eq}). Simulations were performed under three mutation models: infinite allele model (IAM), single stepwise model (SSM) and two-phase model (TPM) to obtain the distribution of H_{eq}, and the simulation values then were compared to the real data values. For the TPM, I used the generic values of 0.95 and 0.12 for frequency of single-step mutations and variance, respectively (Piry et al. 1999). A Wilcoxon sign-rank test was used to test the significance of heterozygosity excess or deficiencies across loci. I also used a qualitative approach with the mode-shift test to detect population bottlenecks. A recently bottlenecked population shows a mode-shift in the distribution of allele frequencies, such that alleles with very low frequency (less than 0.1) are less abundant than alleles that occur frequently. Any deviation from a normal L-shaped distribution that arises in the population is taken as an indicative of a bottleneck signature in a population.

RESULTS

Land-use Change

Results of the land-use change analysis showed a dramatic decline in forest and increase in agricultural area by 62% over the last 300 years across the Terai Arc (Figure 4.3). The major decline in forested area occurred between the 19th and 20th centuries with a 47% decrease. There has been a 97% increase in agriculture and settlement areas over the past 200 years in the Terai Arc (Figure 4.4). Within the Terai Arc, a major break in the contiguous forest landscape occurred around 100 km east of Chitwan National Park due to a large-scale resettlement and development project. For the protected areas, Chitwan Valley suffered the largest and most dramatic decline in forested area. Therefore I predicted that the Chitwan-Parsa tiger population would be a isolated sub-population and I expected to infer a bottleneck signature between Chitwan-Parsa and the other hypothesized sub-populations (Bardia and Suklaphanta). .

Tiger Identification

We (field assistants and I) collected a total of 770 putative tiger scat samples from four protected areas and three corridors within the Terai Arc, Nepal. I identified 396 tiger-positive samples. Locus FCA205 did not work well, because the locus did not amplify with majority of samples. The rest of the loci were polymorphic except PttA2. Therefore, I removed loci FCA205 and PttA2 from subsequent analysis. PCR amplification success across all tiger-positive samples was 84% ranging from 66% to 94% per locus (Table 4.2). I used an assay of 8 highly polymorphic microsatellites to individually identify 78 tigers, with a P_{ID} of 1.5E-06 and $P_{ID(sibs)}$ of 3.2E-03 (Figure 4.5) with an overall genotyping success of 40% (Table 4.3). DNA from none of the samples from the corridors amplified sufficiently well for individual identification, due to low DNA quality. I genotyped only one tiger from Parsa Wildlife Reserve. I added the tiger from Parsa to the Chitwan dataset since the habitat is contiguous to Chitwan National Park. The genotyped Parsa tiger sample was collected at 15 km from the eastern most boundary of Chitwan National Park within the Parsa wildlife reserve.

Genetic Structuring

Genetic variation metrics for the overall tiger population were 0.54 mean H_o, observed heterozygosity, and 0.61 mean H_e, expected heterozygosity, and 6.0 mean number of alleles per locus, respectively. Levels of genetic variability varied between the protected areas, with the highest genetic diversity found in Chitwan, and the lowest in the Suklaphanta population (Table 4.4). The average local inbreeding coefficient (F_{IS}) was high in the smaller Suklaphanta population relative to other sites in Terai Arc (Table 4.4).

Results of AMOVA analysis showed that genetic variation among the sites was 13.7%, while 86.3% was the residual variation among individuals within the sites (Table 4.5). After pooling all individuals from the entire landscape, two of the eight loci (PttD5 and F85) were found to be significantly out of HWE after the Bonferonni corrections. Based on the population-level analysis, four loci in Chitwan, two loci in Bardia and three loci in Suklaphanta were significantly out of HWE (Table 4.4). No locus was consistently out of HWE across the populations. After Bonferonni corrections, one locus (F85) in Chitwan and one locus (F53) in Suklaphanta were significantly out of HWE.

The mean F_{ST} value (level of differentiation) for the Terai Arc was found to be moderate ($F_{ST} = 0.14 \pm 0.07$). The pairwise (between protected areas) F_{ST} and D_{EST} values were found to be moderate to low and significant (Table 6, $p < 0.05$). Comparatively low F_{ST} and D_{EST} were found between the Bardia and Suklaphanta populations and high between the Suklaphanta and Chitwan populations (Table 4.6).

I first implemented the principal coordinate analysis (PCoA) in GenAlx 6.3. The PCoA showed that individual tigers formed three overlapping, but distinct clusters respectively occurring in Chitwan, Bardia, and Suklaphanta (Figure 4.6). Results of the Bayesian genetic clustering algorithms using program Structure indicated three discrete, admixed, core demographic-scale populations across the Terai Arc. The individual-based Structure admixed models showed higher statistical support at $k = 3$ and $k = 4$ based on the Ln P(k), and $k = 3$ based on delta k method. Further four clusters showed a high standard deviation relative to $k = 3$ (Figure 4.7). Hence, I interpreted $k = 3$ as the most likely value for the analysis, especially since it aligns with the prior knowledge of the spatial distribution of tiger demographic populations and landuse analysis (Figure 4.8).

Results of the non-spatially explicit clustering analysis were corroborated with those spatially explicit analyses from Program TESS (Figure 4.8). Based on the DIC model selection criteria, graphs tended to plateau at k=3, and the standard deviation increased with an increasing value of $k_{\max}$ (Figure 4.9). The hard-clustering algorithm for individual membership with BYM admixture models did not change with $k_{\max} \geq 3$, while in the CAR admixture model, there were inconsistent results with $k_{\max} > 3$. Hence, I concluded that k=3 (Figure 4.10) was the best supported inferred number of genetic clusters for the tiger populations across Terai Arc. With $k = 3$, there are Chitwan (1), Bardia (2) and Suklaphanta (3) sub-populations within the Terai Arc.

The inferred degree of admixture within populations was found to be variable across the three clusters: Chitwan (91%, 7% and 2%); Bardia (13%, 72% and 15%); and Suklaphanta (2%, 7% and 91%) respectively. Within inferred populations, sites (protected areas) are spatially separated from each other (Chitwan-Bardia: 314 km; Bardia-Suklaphanta: 136 km; and Suklaphanta-Chitwan: 450 km) with variable forest connectivity between them. I found similar results (*k*=3) with no prior information regarding the origin of the samples.

Detection of Migrants

Results of the individual assignment/exclusion test using program Geneclass2 revealed that 63 of the 78 samples were correctly assigned (highest probability) to their sampling location, with a correct assignment index of 81%. The remaining samples were either identified as admixed individuals with their ancestry from either of the populations or detected as first-generation migrants, meaning that the individuals migrated from another population recently. Similarly, Structure revealed 57 of 78 individuals were correctly assigned to their sampling locations (Figure 4.8).

No significant correlation ($r = 0.47$, $p = 0.66$) between geographical distance and genetic distance was observed using the web-based isolation-by-distance program, IBDWS. This at cue suggests absence of isolation-by-distance and true meta-population structure for tigers in the Terai Arc. Indirect estimates of equilibrium gene flow based on Wright's F_{ST} estimate ($F_{ST} = 0.14 \pm 0.07$) revealed that there are approximately two genetically effective migrants per generation. I identified a total of ten migrants in the current study across the Terai Arc based on an individual-based likelihood tests. Structure identified five migrants, while Geneclass2 identified ten total migrants across the landscape (Table 4.7). Five individuals were common to results of both analyses. Three migrants in Bardia were assigned to Chitwan as their source population, while two migrants in Bardia were assigned to Suklaphanta. Two migrants were detected in Chitwan with their origin in Bardia. Three migrants were detected in Suklaphanta, with their source population in Bardia. Program Structure identified one individual in Chitwan and four in Bardia with admixed ancestry. Except for two female migrants detected in each Bardia and Suklaphanta, all the others migrants were males. No migrants were detected between Suklaphanta and Chitwan sub-populations.

The Bayesass analysis yielded that migration (m_c) was symmetric, except for Suklaphanta. High immigration rate was suggested from the Suklaphanta to Bardia sub-population ($m_c = 0.13$). The Bardia sub-population appears to be receiving the migrants from both Chitwan and Suklaphanta, with a total migration rate of a 0.17 (Table 4.8). The 95% Confidence intervals overlapped for migration rates for the pair of populations in both directions, suggesting roughly symmetric bidirectional gene flow between sub-population, except between Bardia and Suklaphanta, which appear to have only uni-directional flow from Suklaphanta to Bardia. Net emigration rate was highest for Suklaphanta, as it contributes the most migrants to the other protected areas (Figure 4.11). Net emigration rate for Bardia was negative, suggesting it receives more migrants than it contributes to other populations. Identified second generation migrant analysis revealed more recent gene-flow in the landscape. Bayesass detected eight-second generation migrants, with the majority of them (6) migrating from Suklaphanta to Bardia. Two migrants from Bardia were detected in Suklaphanta.

The average relatedness value between pairs of identified individuals was 0.115, and 72% of individuals observed were unrelated (Table 4.9). The Chitwan-Suklaphanta populations were least related; while in Bardia-Suklaphanta, and Bardia-Chitwan, many individuals were related to each other as half -sibs, full-sibs and parent-offspring. Suklaphanta had the lowest percentage of unrelated animals (69%), while Bardia National Park had the highest (73%). Suklaphanta also has the highest percent of closely related individuals (7% half sibs, 12% full sibs, and 12% parent-offspring).

Detection of Bottlenecks

The average M ratio describing potential bottlenecks for all sites was 0.29 (0.07), which is below the threshold value of 0.68 (Garza and Williamson 2001) (Figure 4.12), which suggests that the tiger population suffered a bottleneck event that caused a severe decline in the population size in the recent past. These results were supported among all sub-populations. Program Bottleneck detected heterozygote excess, with 5 to 6 loci, depending upon the mutation models. However, results of the two-tailed Wilcoxon signed ranked test ($p = 0.03$) showed that the signature of a bottleneck event was significant only for the Chitwan population under Infinite Allele Mutational (IAM) model (Table 4.10). The mode-shift test showed the normal "L"-shaped allele distribution in Bardia, only showing the presence of a large proportion of alleles at low frequencies, indicating a genetic bottleneck in Chitwan and Suklaphanta but not Bardia.

DISCUSSION

Globally, consequences of high rates anthropogenic transformation of landscapes (Ellis et al. 2010) play a major role in extinction of wild mammal populations (Ceballos and Ehrlich 2002). For highly vagile predators like tigers, these transformations of land-use have caused significant loss of habitat across the historical distribution, with severe population declines and even local extirpations in the last few generations (Sanderson et al. 2006). Most wild tiger populations are now confined to protected areas (Walston et al. 2010). The situation in the Terai Arc is no different from the world scenario. Poaching and habitat loss are major threats to the extant tiger population (GTRP 2010) and to the remaining 13,500 km^2 of potential habitat in Nepal (Barber-Meyer et al. 2013). Against this background, results of my genetic study of tigers is important for understanding current levels of genetic diversity and connectivity in order to prioritize conservation efforts in the Terai Arc.

Examining historical land-use change could explain the present structuring of animals in the landscape into sub-populations (Dinerstein and McCracken 1990, Dutta et al. 2013, Sharma-et al. 2013b). Variation in microsatellite data shows the effects of how the forested Terai landscape was separated into somewhat isolated, distinct clusters across the foothills of Himalayas (Mondol et al. 2013). Tigers used to roam in the vast expense of Terai forests in Nepal and India. Beginning in the mid-1840s, core tiger habitat was protected by the Rana rulers for their exclusive royal hunting, thus discouraging people from settling and conducting agriculture. Tigers were persecuted in large numbers during organized royal hunts. However, recovery was relatively quick following this time, likely due to immigration from adjacent areas. Rampant malaria also hindered people from settling in the Terai region and clearing the forest (Dinerstein 2003). By the late 20th century, however, extensive land clearing occurred and hunting was high, fragmenting the tiger habitat and contracting their range to the Chitwan Valley in central Nepal (Blanford 1898, Dinerstein and McCracken 1990) and to Bardia and Suklaphanta in the west, as well as to a few large blocks of forest in the east. High human population density and extensive deforestation for agricultural practices (Thapa and Weber 1990) led to inadequate cover and low prey availability for tigers, and they became extirpated in the eastern Terai region by the 1970s (Smith et al. 1999, Gurung 2002). With eradication of malaria and the government policy of extending settlements along the border with India, large swaths of forest landscape were disturbed (Nagendra et al. 2005, Panta et al. 2008). In a nutshell, these events reflects Ellis et al. (2010) transformation of the forested biomes in Terai Arc, likely causing a decline in population size and genetic diversity and subsequent sub-structuring of tiger population in Nepal, perhaps through population bottlenecks. Historical patterns and intensity of forest fragmentation imposed similar effects upon jaguars in Brazil (Haag et al. 2010) and Amur leopards in the Russian Far East (Sugimoto et al. 2014), causing significant loss of genetic variation. In contrast, tigers (Mondol et al. 2013, Sharma et al. 2013b) and leopards (Dutta et al. 2013) in India have high degrees of genetic variation, and no genetic bottlenecks were detected despite habitat fragmentation.

Tigers in the Terai Arc, Nepal displayed moderate levels of genetic variation (He= 0.61) across the landscape perhaps due to moderate population size and/or gene flow. Genetic variation within populations was similar and relatively moderate (H_e~ 0.57), although these values were below those at the landscape level; thus showing no signs of genetic variation loss at the higher scale. My estimates of genetic variation were lower in comparison to overall genetic diversity of the tiger subspecies (*Panthera tigris*) (H_e=0.72, Luo et al. 2004) and Bengal tigers (*Panthera tigris tigris*) in the Indian Subcontinent (H_e=0.70, Mondol et al 2012), however, they were higher than other sub-species of tigers (Ave H_e=0.53, Sumatran, Indochinese, Malayan and Siberian, Luo et al. 2004). Landscape-wide genetic variation in tigers across the major Tiger Conservation Landscapes in India are as low as H_e=0.58 in the southeastern Ghats (Reddy et al. 2012b), H_e=0.67 in the northeast landscape (Borthakur et al. 2013), H_e=0.76 in the western Ghats (Reddy et al. 2012a), and He=0.81 in the central Indian landscape (Sharma et al. 2013b). Nevertheless, direct comparisons should be made with caution since these studies employed different genetic markers. Overall, my results suggest low to moderate levels of genetic diversity based on 8 polymorphic loci across the tiger population in Terai Arc, Nepal. Lower levels of genetic diversity were detected in this population compared to other, high-diversity areas in the Satpura-Maikal landscape (Sharma et al. 2013b) of India.

The average inbreeding coefficient (F_{IS}) across the sub population in Terai Arc suggests a weak inbreeding that statistically non-significant ($p = 0.42$). At the sub-population level, Suklaphanta showed a weak sign of local inbreeding ($F_{IS} = 0.16$), which was marginally non-significant statistically ($p = 0.06$). This suggests the importance of connectivity in averting inbreeding depression in the small Suklaphanta sub-population (John et al. 2014). Spatially, Suklaphanta is now surrounded by human settlements, but retains dispersal potential through the northern sections of the Terai Arc. Additionally, the creation of the Pilibhit Tiger Reserve in the south strengthens the possibility of future connectivity via dispersal through the Lagga Bagga in India (Dr A.J.T Johnsingh: Personal Communication, WWF India). Currently the net migration estimates suggest that more tigers are leaving Suklaphanta than coming in.

My population based test for assessing the level of genetic sub-division reveals moderate levels of differentiation across the landscape ($F_{ST} = 0.14$) (Wright 1978). Interestingly, the level of genetic differentiation was lower between protected areas that were further separated spatially (Chitwan-Bardia~310 km) and higher between protected areas that were closer (Suklaphanta-Bardia~ 96 km). The observed genetic division cannot be explained by the geographical distances between the populations as indicated by the isolation-by-distance analysis. This outcome can more likely be explained by high gene flow prior to the fragmentation process and stronger barrier between the closer populations preventing dispersal. Alternatively, lag time in achieving equilibrium F_{ST} (~200 generations) could explain the observed effect as an artefact prior to the effect of massive habitat fragmentation being incorporated into the metrics.

My results suggest three distinct clusters (sub-populations) within the landscape. In a situation of similar probabilities for different *k*, the *k* with lower probabilities is often suggested and one which captures the major structure in the data (Pritchard et al. 2000). My admixed models and concurrent results from both spatial and non-spatial algorithms in programs Structure and TESS, suggested three (*k* = 3) clusters or tiger sub-populations in the landscape confirming to my apriori hypothesis. The field data suggest demographic contiguity in and around the protected areas (Barber-Meyer et al. 2013). However, in the absence of tiger samples from Indian side of the Tiger Arc, my story is half told in explaining the overall genetic structure of tigers in the entire landscape, since tigers could travel through the contiguous protected areas of India into Nepal.

There was disagreement between results of the different tests that I used to detect population bottlenecks. The M ratio test revealed a population bottleneck in all populations, in contrast to the heterozygous excess test showing a bottleneck only in the Chitwan population. Each test has been found to be effective at detecting bottlenecks, but each works under a different scenario. Peery et al. (2012) suggested that in spite of correctly assuming the mutation models (IAM, SSM or TPM), statistical power to detect a bottleneck with the two methods might depend upon the pre-bottleneck genetic variation. Heterozygosity may be less powerful than the M ratio test when pre-bottleneck genetic diversity is high (Peery et al. 2012). On the other hand, the heterozygosity excess may work best when the pre-bottleneck population was smaller or when the bottleneck was milder and more recent (Williamson-Natesan 2005).

If a bottleneck event happened in the recent past (a few generations before the 1950s), its effect on population-based metrics like F_{ST} is yet to become fully apparent, because the effect of historical gene flow have a lag time of ~200 generations to become fully equilibrated. Hence, it is possible that F_{ST} is a weak metric for measuring recent differentiation (Landguth et al. 2010). Landguth et al. (2010) also recommended using distance-based metrics with Mantel tests (isolation by distance) to detect changes in the landscape in recent times (1- 15 generations).

However, I found no significant correlation between genetic and geographical distances for explaining observed divisions in the landscape. Thus, the individual-based approach incorporated in programs TESS and Structure better reflect recent changes in landscape, and their effects on allelic variation than does the population-based F_{ST} approach.

Results of Assignment tests as evidence of contemporary gene-flow of tigers between sub-populations suggest that tigers can and do disperse across the Terai Arc of Nepal. Tigers are known to disperse wide distances (~200 km) based on long-term camera-trap data (Patil et al. 2011). The detection of tiger dispersal (First generation migrants) between protected areas, which range from 314 km (Chitwan and Bardia) and 136 km (Bardia and Suklaphanta) apart may not be a surprise given that dispersal has been recorded as far as 600 km in the central Indian landscapes (Joshi et al. 2013). Results of the Bayesass analysis showed high estimates of recent migration of tigers among the sub-populations. High net immigration rates along with high numbers of second generation migrants also were detected in Bardia. Comparisons with recent migrants from Structure and Geneclass2 revealed six more second generation migrants in the past few generations in Bardia, migrating from Suklaphanta. In the medium and large sub-populations (Bardia and Chitwan), I found evidence of 2-3 male tiger dispersals per generation, which if they breed is likely to avert the detrimental effects of inbreeding depression and flatten the slopes of extinctions curves accordingly (John et al. 2014). The Suklaphanta population, while small, holds the highest density of tigers, likely owing to high prey density (Dhakal et al. 2014) and could explain why Suklaphanta is the source of many migrants to other areas (Wikramanayake et al. 2011). However, it could be argued that, due to small size of the reserve and high tiger density, there might be no space for dispersing male tigers to established territories within the reserve, hence it is not possible to receive migrants from surrounding areas. The high percentage of related individuals (32%), low genetic variation, and slight but weak evidence of inbreeding relative to other protected areas in the landscape suggest the need to increase migration of tigers into the Suklaphanta population to avert inbreeding depression and increase genetic variation of the population. For example, leopards in the Russian Far East suffered significant loss in genetic variation due to lack of connectivity to a source population and continue to suffer loss of genetic variation (Sugimoto et al. 2014). The designation of 727 km^2 of Pilibhit Forest Division as a Tiger Reserve by the Government of India is an important step toward increasing connectivity between the western Terai Arc in India with Suklaphanta in Nepal (Dr. Dipankar Gosh: personal communication, WWF India). I did not find migrants from Chitwan into Suklaphanta and vice versa in any of the migrant detection tests, except that a few pairs of individuals are apparently related, suggesting that their dispersal to Suklaphanta from Chitwan will be more a stepping-stone process (Fabbri et al. 2014).

I showed the presence of three genetically admixed sub-populations across the Terai Arc, Nepal based on spatial (TESS) and non-spatial (Structure) techniques, suggesting that tigers have been able to move between the populations and breed at least in the recent past. Contemporary gene flow measures of tigers were estimated in the Terai Arc based on both likelihood and Bayesian approaches. Improved connectivity between the protected areas facilitated by male dispersal appears able to avert the negative consequences of inbreeding depression following the bottleneck event in the landscape. Thus, there is a need to maintain connectivity. In the recent times, connectivity in the landscape was improved by protection of large forest blocks in the landscape after the nationalization of forests in 1960s (Thapa et al. 2013) and improved governance and management of forest resources (Nagendra et al. 2008). The launch of the community forest program in the "Terai forest" (Acharya 2002, Dinerstein 2003) in the early

1980s has been successful in building more forest habitat at the edges and buffers of the large forest blocks for dispersal of tigers in the landscape. Steps undertaken by the Government of Nepal (GoN) are positive in restoring connectivity across the Terai Arc and include adopting the successful community-based approach of forest management (Wikramanayake et al. 2010). The GoN's declaration of a key corridor forest as a protected forest area is a milestone (Shrestha et al. 2014). Results of my study indicate that the landscape is currently functional with respect to dispersal of tigers among the protected areas, but there is evidence of genetic structure indicating that sub-populations exist and isolation is ongoing. In the face of a growing human population, economic development post insurgency, political unrest, and developmental road projects, genetic connectivity seems likely to erode (GTI 2013) and impede gene flow of tigers in the landscape, lowering their persistence in the long run (John et al. 2014). Securing source sites and functional corridors requires careful planning and prevention of developmental activities to enhance gene flow across landscape to ensure that tiger populations exist for generations to come.

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TABLES AND FIGURES

Table 4.1: Genetic variability of 17 candidate microsatellite loci screened and “*” indicates locus used in this study. N_A, number of alleles; H_O, observed heterozygosity. Sources of microsatellite markers are indicated in the footnote.

Locus	**Allele Size Range (bp)**	**Repeat type**	**Ho**	**N_A**	**Source**
FCA205*	102-116	DI	0.78	5	1
FCA232*	100-108	DI	0.44	3	1
FCA272	115-127	Di	0.667	6	1
FCA304*	122-140	Di	0.622	5	1
FCA391*	122-154	Tetra	0.64	6	2
FCA441*	78-118	Tetra	0.57	4	2
FCA453	69-89	Tetra	0.43	5	2
FCA742	160-184	Tetra	0.55	6	1
F41	100-172	Tetra	0.429	4	2
F42	152-180	Tetra	0.43	5	2
F53*	(165 - 181)	Tetra	0.778	5	1
F85*	155-167	Tetra	0.6	4	1
PttD5*	200-224	Tetra	0.61	4	2
PttA2	188 - 198	DI	0.51	4	2
Pun82	105-123	DI	0.483	5	4
FCA043*	111-117	DI	0.52	6	1
FCA008	128-140	DI	0.55	4	1

1: Menotti-Raymond et al. (1999).

2:Mondol et al.(2009a).

3: Sharma et al.(2008).

4: Janecka et al. (2008).

Table 4.2: Summary of PCR amplification success, genotyping accuracy and genotyping error rates for 8 microsatellite loci for all processed tiger-positive samples (*n* = 401) in three protected areas: Chitwan National Park, Bardia National Park and Suklaphanta Wildlife Reserve across the Terai Arc Landscape. PCR, % polymerase chain reaction amplification success; GA, % genotyping accuracy; ADO, % allelic dropout; FA, % false alleles. NP: National Park; WR: Wildlife Reserve

S.No	**Locus**	**All Samples (*n*=401)**				**Chitwan NP (*n*=257)**				**Bardia NP (*n*=78)**				**Suklaphanta WR (*n*=66)**			
		PCR	GA	ADO	FA	PCR	GA	ADO	FA	PCR	GA	ADO	FA	PCR	GA	ADO	FA
1	FCA391	75.67	88.59	0.16	10.52	87.58	89.47	0.47	12.60	57.50	89.86	0.00	8.82	81.94	86.44	0.00	10.14
2	PttD5	88.43	88.82	1.12	10.48	91.69	91.99	1.04	8.01	83.33	83.84	2.33	15.63	90.28	90.63	0.00	7.81
3	FCA232	87.50	77.02	2.06	23.34	82.79	80.17	0.62	25.51	82.50	65.59	5.56	28.57	97.22	85.29	0.00	15.94
4	FCA304	94.00	87.46	0.00	10.94	93.95	90.25	0.00	8.66	90.83	79.38	0.00	18.37	97.22	92.75	0.00	5.80
5	FCA043	93.59	80.26	2.72	17.79	95.22	88.97	0.00	11.03	92.50	80.61	0.00	18.09	93.06	71.21	8.16	24.24
6	F53	65.84	84.62	0.27	13.09	69.75	81.90	0.80	18.10	33.33	79.41	0.00	18.18	94.44	92.54	0.00	2.99
7	F85	73.86	73.42	7.94	19.01	75.48	85.07	0.00	15.32	89.17	57.14	0.00	34.41	56.94	78.05	23.81	7.32
8	FCA441	94.85	74.73	5.40	21.69	94.27	85.76	0.63	14.24	91.67	71.28	4.94	27.66	98.61	67.16	10.64	23.19
	Mean	84.22	81.87	2.46	15.86	86.34	86.70	0.45	14.18	77.60	75.89	1.60	21.22	88.72	83.01	5.33	12.18
	SD	10.97	6.33	2.85	5.25	9.53	4.19	0.40	5.68	21.21	10.58	2.39	8.29	13.90	9.82	8.62	8.04

Table 4.3: Summary of genotype success showing percentage of species identification, sex identification, and genotyping success with putative tiger fecal samples (*n* = 770) in Terai Arc Landscape. Species identification was based on the total number of samples processed; sex identification was based on the total number of tiger positive samples; and genotyping success was based on the number of positive samples for species and sex identification.

Name of Protected Areas	**Total Samples Processed**	**Species Identification** **% (# samples)**	**Sex Identification** **% (# samples)**	**Genotyping Success** **% (# samples)**
Chitwan National Park	420	57 (239)	99(237)	61(145)
Bardia National Park	116	72(84)	80(67)	65(43)
Suklaphanta Wildlife Reserve	79	75(59)	66(39)	58(23)
Parsa Wildlife Reserve	85	8(7)	75(5)	13(1)
Corridors	70	6(4)	50(2)	0(0)
Overall Success	770	51(393)	89(350)	53(212)

Table 4.4: Genetic diversity estimates across 8 microsatellite loci for tigers in three protected areas: Chitwan National Park, Bardia National Park and Suklaphanta Wildlife Reserve across the Terai Arc Landscape. N_A, number of alleles; A_R, allelic richness using the rarefaction method; H_O, observed heterozygosity ; H_E, expected heterozygosity; P_{HW}, P values for exact tests of Hardy-Weinberg equilibrium (level of significance,α= 0.05); *n* = sample size. * represent locus out of HWE after Bonferonni correction at *P*=0.002.

Locus	**Chitwan National Park (*n*=37)**							**Bardia National Park (*n*=25)**							**Suklaphanta Wildlife Reserve (*n*=16)**						
	N_A	A_R	H_o	H_E	P_{HW}	F_{null}	F_{IS}	N_A	A_R	H_o	H_E	P_{HW}	F_{null}	F_{IS}	N_A	A_R	H_o	H_E	P_{HW}	F_{IS}	F_{null}
FCA391	4.00	3.96	0.78	0.69	0.67	-0.07	-0.11	3.00	2.95	0.26	0.42	0.00	0.15	0.39	3.00	2.78	0.31	0.51	0.10	0.41	0.21
PttD5	4.00	2.66	0.32	0.30	0.01	-0.02	-0.07	4.00	3.75	0.54	0.53	0.93	0.00	-0.01	3.00	2.99	0.63	0.54	0.05	-0.12	-0.03
FCA232	3.00	2.89	0.74	0.55	0.04	-0.24	-0.35	5.00	3.84	0.39	0.40	0.79	-0.07	0.03	3.00	2.56	0.13	0.12	1.00	-0.02	-0.06
FCA304	5.00	3.62	0.65	0.51	0.11	-0.21	-0.27	5.00	3.75	0.52	0.44	0.61	-0.10	-0.16	2.00	2.00	0.19	0.48	0.03	0.63	0.28
FCA043	4.00	3.87	0.51	0.61	0.01	0.08	0.17	5.00	4.28	0.57	0.53	0.56	-0.05	-0.04	4.00	3.77	0.38	0.54	0.07	0.33	-0.04
F53	5.00	4.26	0.67	0.67	0.42	0.01	0.02	5.00	4.91	0.56	0.75	0.03	0.12	0.29	5.00	5.00	0.67	0.73	0.00*	0.13	0.14
F85	6.00	4.83	0.42	0.64	0.00*	0.18	0.36	4.00	3.50	0.63	0.61	0.90	-0.02	0.00	3.00	3.00	0.73	0.64	0.91	-0.12	0.04
FCA441	4.00	3.30	0.57	0.58	0.89	0.01	0.03	4.00	3.99	0.92	0.72	0.54	-0.12	-0.26	3.00	3.00	0.64	0.62	0.89	0.00	-0.05
Average	**4.00**	**3.67**	**0.58**	**0.57**			**-0.03**	**4.00**	**3.87**	**0.57**	**0.55**			**0.03**	**3.00**	**3.14**	**0.46**	**0.52**		**0.16**	
SE	**0.32**	**0.72**	**0.06**	**0.04**			**0.08**	**0.26**	**0.57**	**0.04**	**0.05**			**0.07**	**0.31**	**0.90**	**0.08**	**0.06**		**0.09**	

Table 4.5: Summary results from analysis of molecular variance (AMOVA) for tigers detected across three populations across the Terai Arc Landscape implemented in program ARLEQUIN 3.5 (Excoffier and Lischer 2010). df = degree of freedom, *P* value (α=0.05).

Source of Variation	**df**	**Sum of Squares**	**Variance Component**	**Percentage of Variation**	***P* Value**
Among Populations	2	32.155	0.28998	13.72	<0.00
Within Populations	153	279.031	1.82373	86.28	<0.00
Total	155	311.186	2.11371		

Table 4.6: Pairwise measure of the level of differentiation based on F_{ST} (Weir and Cockerham 1984) and D_{EST} (in parentheses) values (Jost 2008) (below the diagonal); the estimated number of migrants per generation (Nm, Wright 1969) and the geographical distances in km (in parentheses) (above the diagonal). Italic font indicates significant differences at $P<0.05$ for F_{ST} values based on 10,000 permutations.

	Chitwan	**Bardia**	**Suklaphanta**
Chitwan		2.88 (314)	0.94 (450)
Bardia	0.*08* (0.07)		1.54 (136)
Suklaphanta	0.*21* (0.21)	0.*14* (0.12)	

Table 4.7: Migrants across the landscape directly detected using programs Structure and Geneclass2; "*" indicates that individuals were identified as migrants by both Structure and Geneclass2.

ID No	**Sampling Location**	**GeneClass F_0 log ratio (L_home)/(L_Max)]**	**P Value**	**STRUCTURE migrant probability (probability of being from assumed population)**	**Assigned Population**	**Sex**
CHIT001*	Chitwan National Park	2.536	0.0001	0.029	BARDIA	Male
CHIT011	Chitwan National Park	0.385	0.0101	0.937	BARDIA	Male
BRD001*	Bardia National Park	2.768	0.0041	0.137	CHITWAN	Male
BRD002*	Bardia National Park	2.01	0.023	0.21	CHITWAN	Male
BRD003	Bardia National Park	1.07	0.0353	0.841	CHITWAN	Male
BRD024*	Bardia National Park	2.673	0.0093	0.226	SUKLAPHANTA	Female
BRD025*	Bardia National Park	2.395	0.0154	0.238	SUKLAPHANTA	Female
SUK004	Suklaphanta Wildlife Reserve	0.763	0.0203	0.88	BARDIA	Female
SUK005	Suklaphanta Wildlife Reserve	0.225	0.0188	0.85	BARDIA	Female
SUK018	Suklaphanta Wildlife Reserve	0.039	0.0317	0.977	BARDIA	Female
10 individuals						Five male; five female

Table 4.8: Summary of pair-wise migration rate (immigration and emigration) between three populations estimated in Program Bayesass (Wilson and Rannala 2003). Estimated net migration rates (immigration-emigration) were estimated as 0.02 for Chitwan, -0.08 for Suklaphanta, and +0.10 for Bardia.

	Protected Areas	**Migrating from**		
		Chitwan	**Bardia**	**Suklaphanta**
Migrating into	**Chitwan**	0.98	0.03	0.01
	Bardia	0.04	0.83	0.13
	Suklaphanta	0.02	0.04	0.96

Table 4.9: Percentage of relatedness relationships for individual tigers within the three populations (U: Unrelated; HS: Half-Siblings; FS: Full-Siblings; and PO: Parent-Offspring) calculated using Program ML-Relate (Kalinowski et al. 2006).

Protected Areas	U	HS	FS	PO
Chitwan	73.12	8.71	7.96	10.21
Bardia	75.00	7.00	6.00	12.00
Suklaphanta	68.60	6.61	11.57	12.40

Table 4.10: Results from program Bottleneck showing the expected and actual numbers of loci with heterozygosity excess under the respective mutation models, and significance of heterozygosity excess: IAM: Infinite Allele Model; TPM: Two-Phase Mutation Model; SMM: Stepwise-Mutation Model. Assuming any mutation model, a Wilcoxon test results with $P<0.05$ signifies significant heterozygous excess, suggesting that a bottleneck event occurred in Chitwan only.

Population	**Heterozygote excess**	**IAM**	**TPM**	**SMM**
Chitwan	Expected	4.53	4.71	4.77
	Actual	6	5	3
	Wilcoxon Test results	0.02	0.62	0.80
Bardia	Expected	4.59	4.72	4.74
	Actual	5	3	3
	Wilcoxon Test results	0.23	0.87	0.87
Suklaphanta	Expected	4.33	4.67	4.65
	Actual	7	6	6
	Wilcoxon Test results	0.09	0.23	0.23

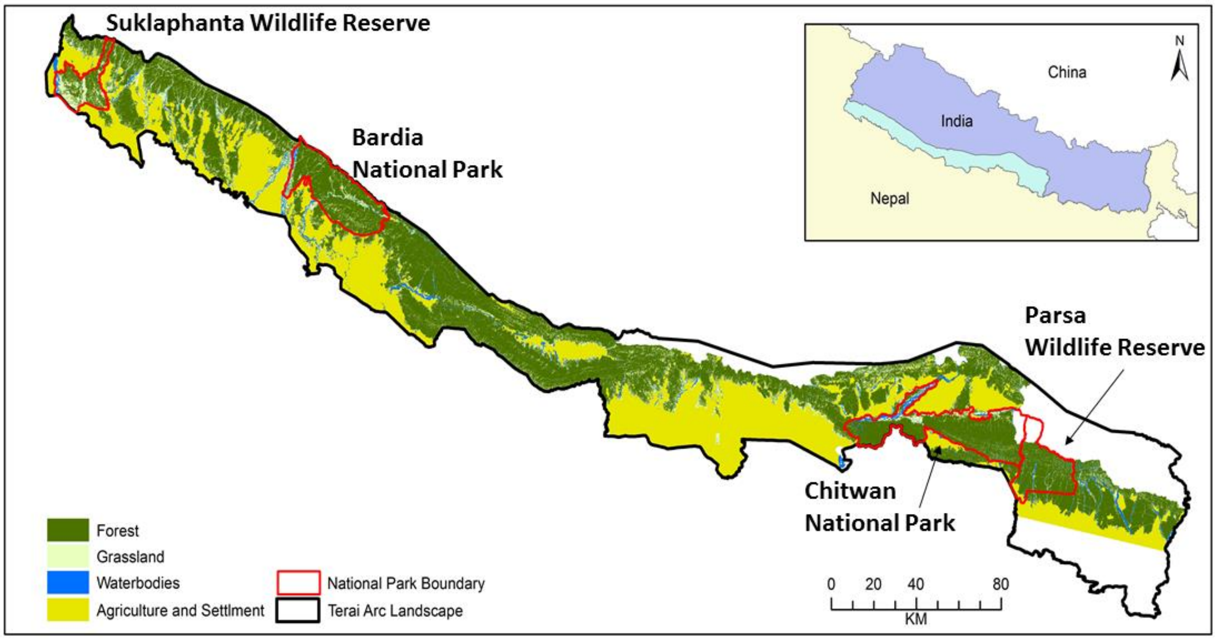

Figure 4.1: Protected areas within the Terai Arc Landscape, Nepal. Protected areas of interest include, from East to West, Parsa Wildlife Reserve, Chitwan National Park, Banke National Park, Bardia National Park, and Suklaphanta Wildlife Reserve.

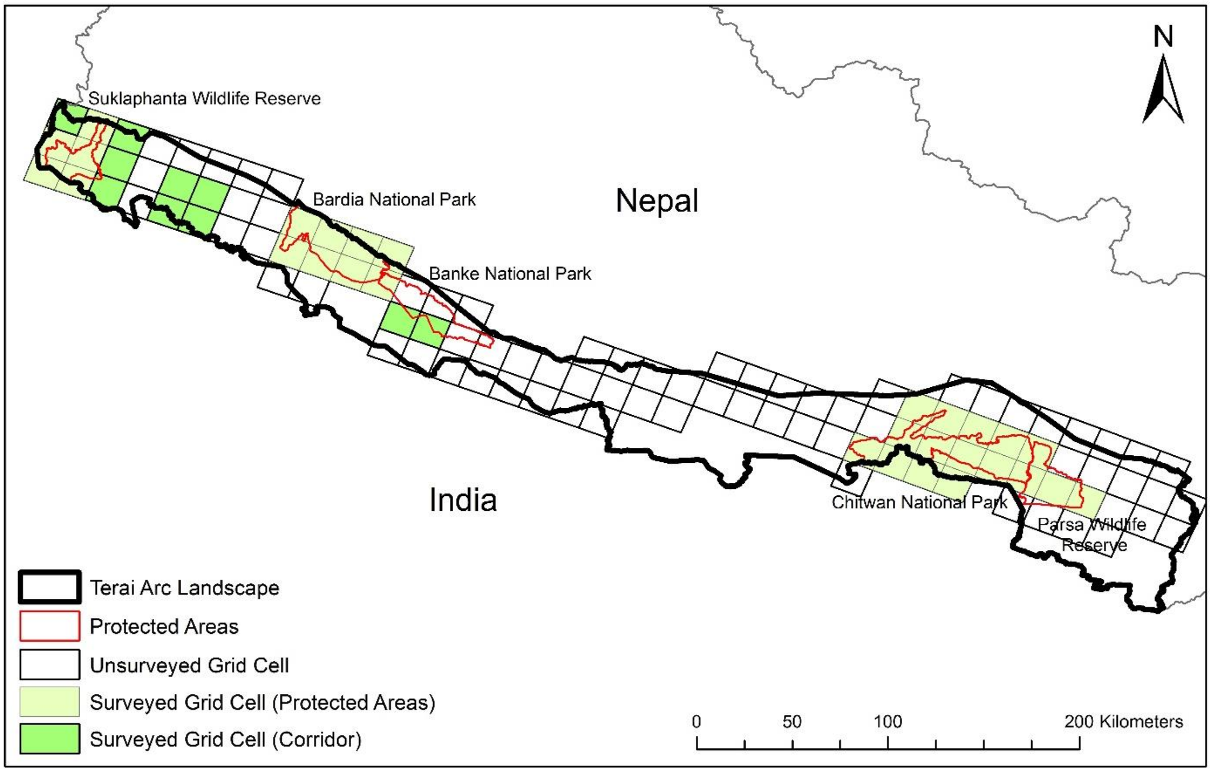

Figure 4.2: Sampling grids cells (15km by 15 km) used for collection of scat samples across the Terai Arc Landscape. A total of 40 grid cells, corresponding to 9,000 km^2 of area were searched for scats (n = 770 scats collected)

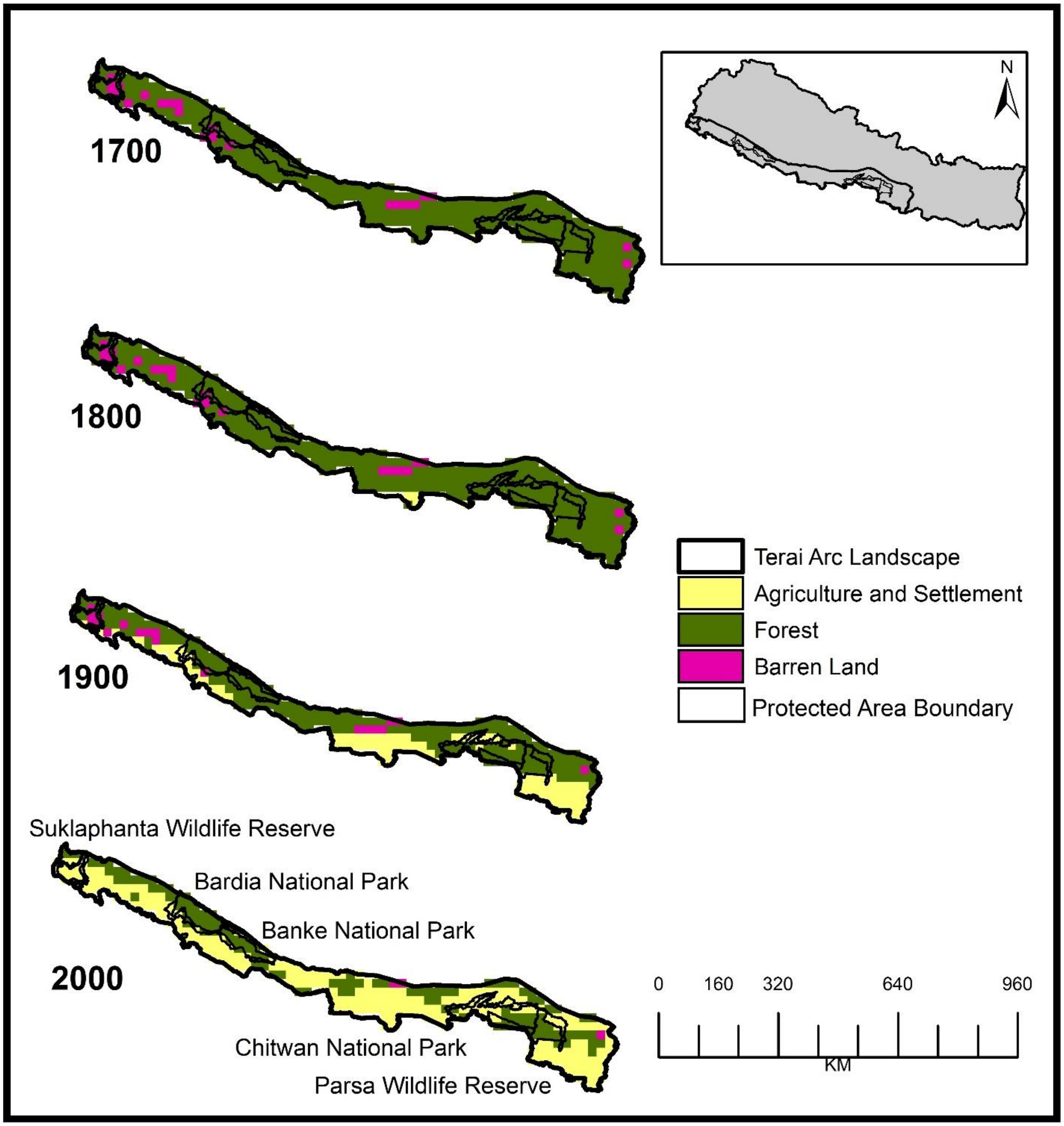

Figure 4.3: Land-use Change (forest into agriculture and settlement) in the Terai Arc using Anthrome 2.0 datasets at resolution of ~10 km pixel size (Ellis et al. 2010) in ArcGIS 10.1.

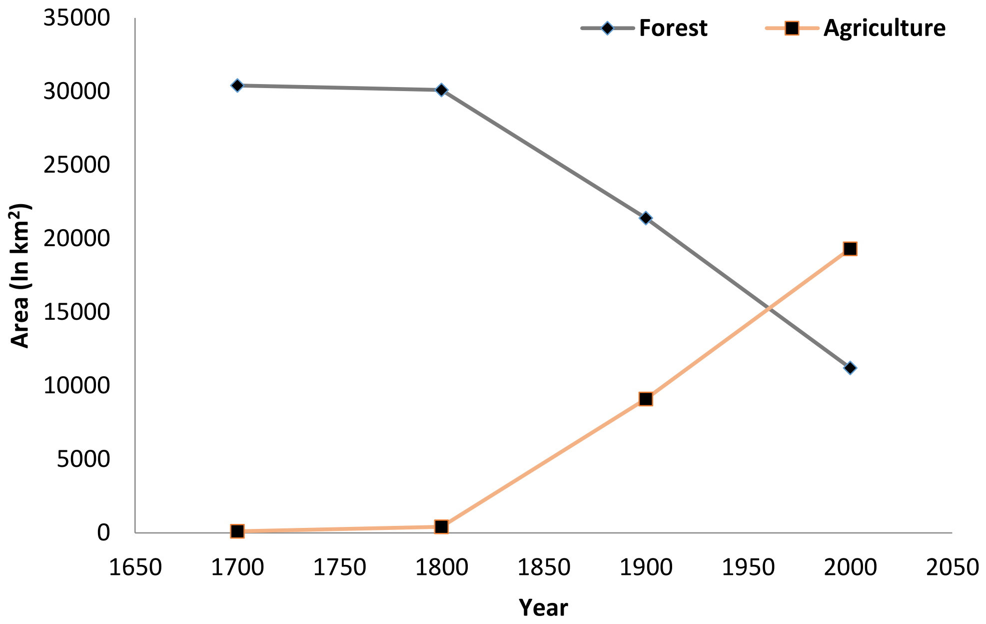

Figure 4.4: Century-wide land-use change detected in the Terai Arc using Anthrome 2.0 datasets (Ellis et al. 2010)

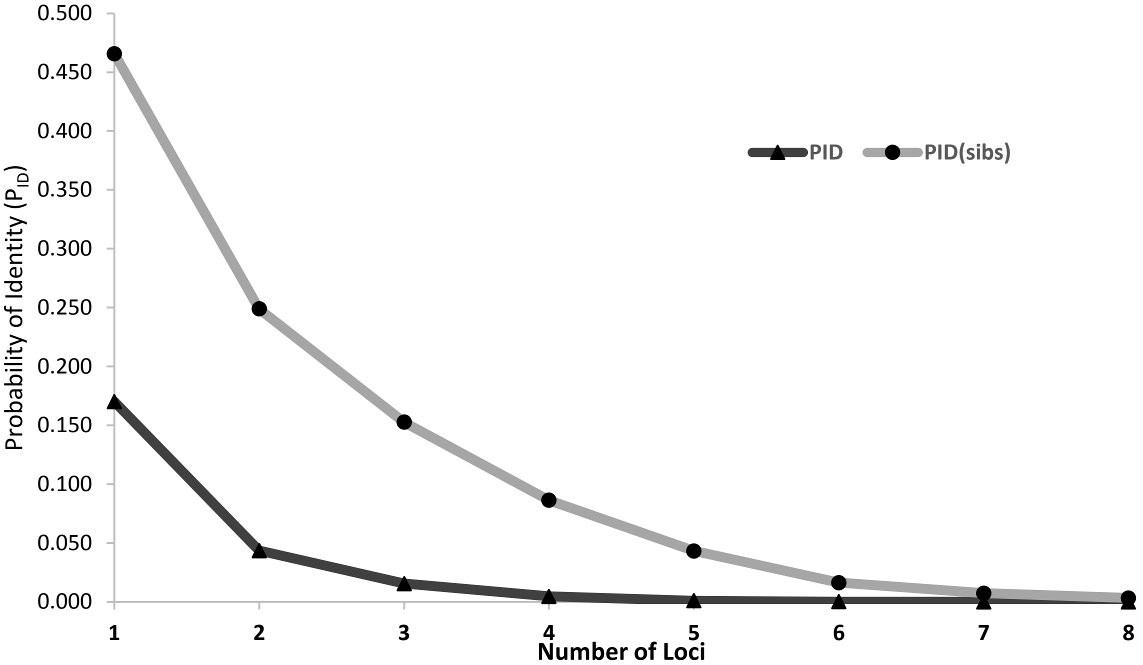

Figure 4.5: The effect of number of microsatellite loci screened on the probability-of-identity for siblings [$P_{ID(sibs)}$] and unrelated individuals [P_{ID}] for tiger samples. P(ID)sibs < 0.010 was used as criterion for individual identification (Waits et al 2001). This criterion represents the probability that two related individuals would have same genotype as one in one hundred when two samples are drawn at random. The order of the loci (1-8) is as follows: FCA391, PttD5, FCA232, FCA304, FCA043, F53, F85, and FCA441.

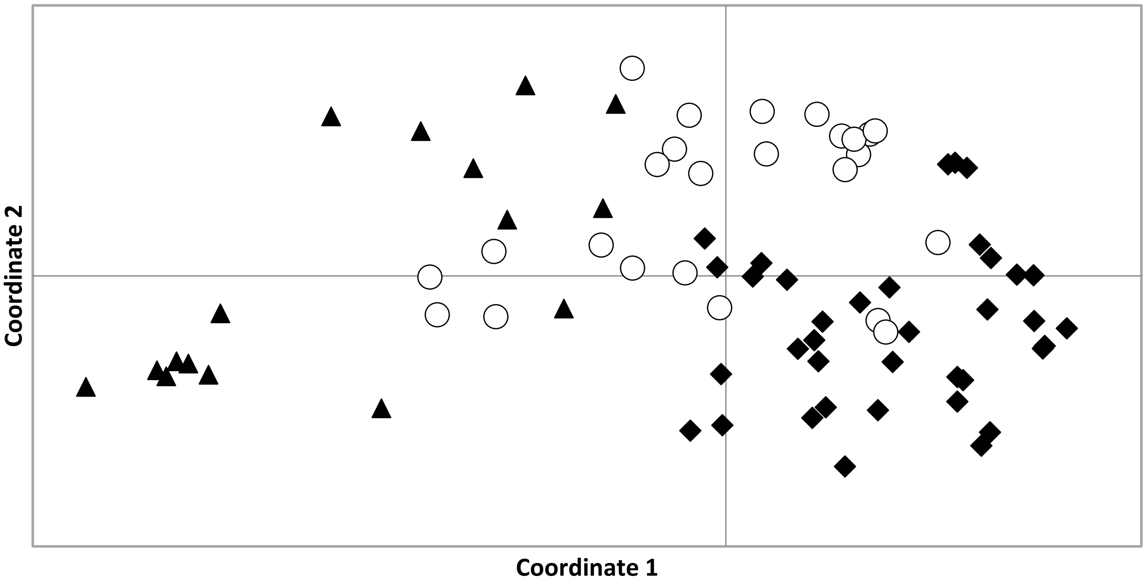

Figure 4.6: Principal Coordinate Analysis of genotypes obtained from “■” Chitwan National Park, “○” Bardia National Park, and “▲” Suklaphanta Wildlife Reserve, implemented in program GenAlEx.

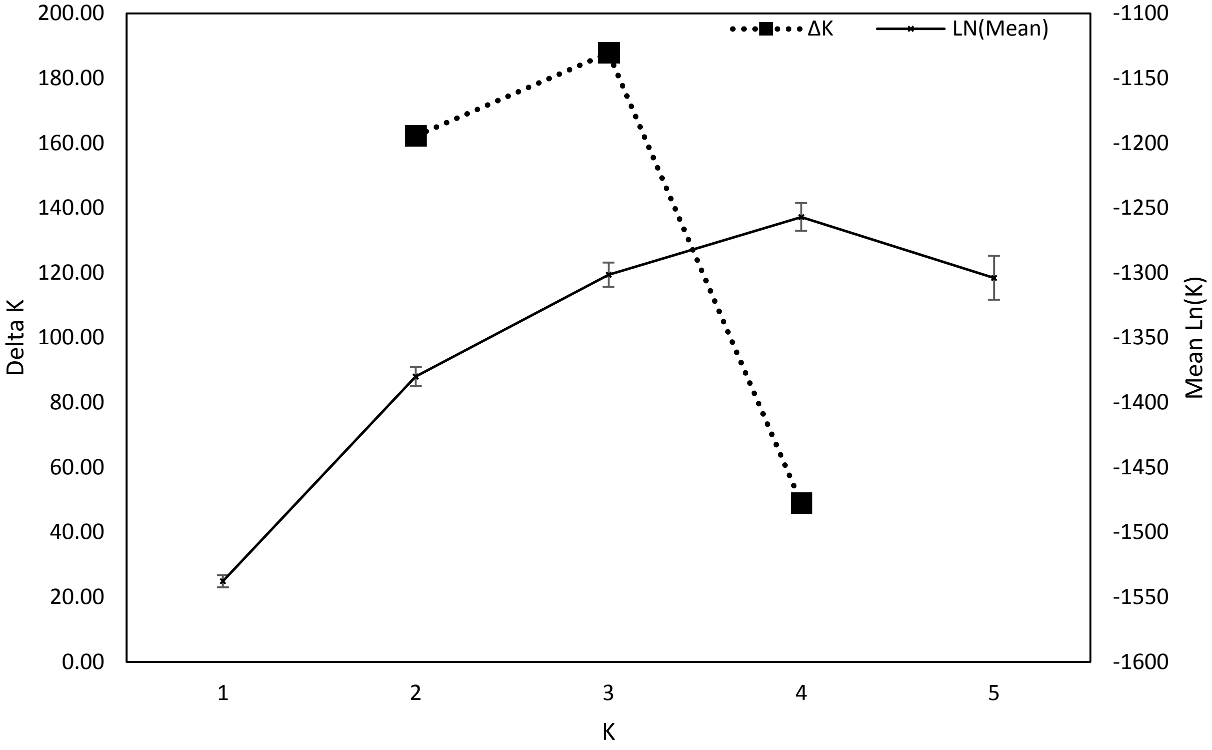

Figure 4.7: Magnitude of ΔK (rate of change in the log probability of K) and Ln P(K) (posterior probability of the data) as a function of K (number of sub-populations) detected three and four genetic clusters in the sampled population following Evanno et al. (2005).

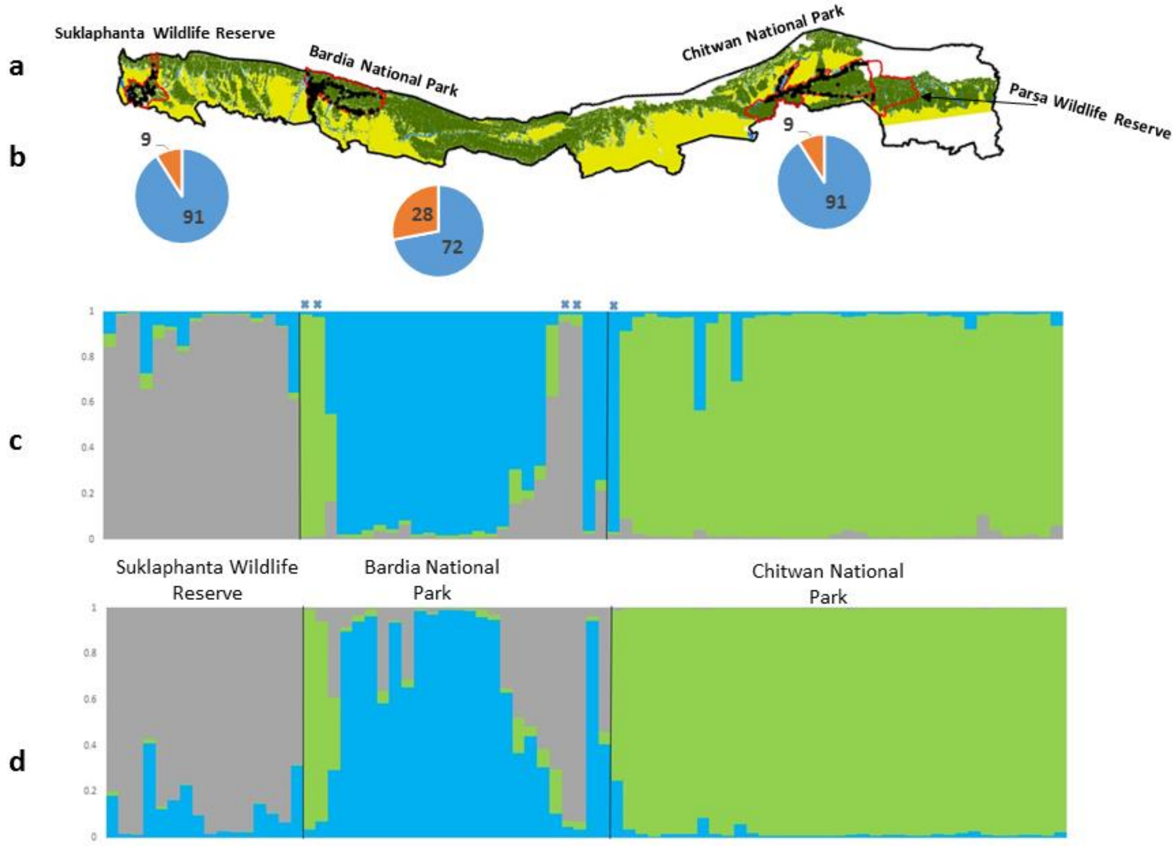

Figure 4.8: Map of the Terai Arc Landscape (a) showing the protected areas (starting from left: Suklaphanta Wildlife Reserve, Bardia National Park, Chitwan National Park, and Parsa Wildlife Reserve) along with the spatial location of identified tiger-positive samples (black dots); and (b) pie charts showing the percentage of admixture proportion (orange) of identified genetic clusters in the populations, and blue represents the percentage of residents assigned to the populations. (c) The Structure (non-spatially explicit) bar plot with each bar representing an individual tiger identified (n = 78) in three populations across the Terai Arc Landscape revealing three (*k*=3) admixed sub-populations along with five migrants (marked as “*’) identified across the population. (d) Bar plot showing three identified sub-populations from spatially explicit assignment Program TESS.

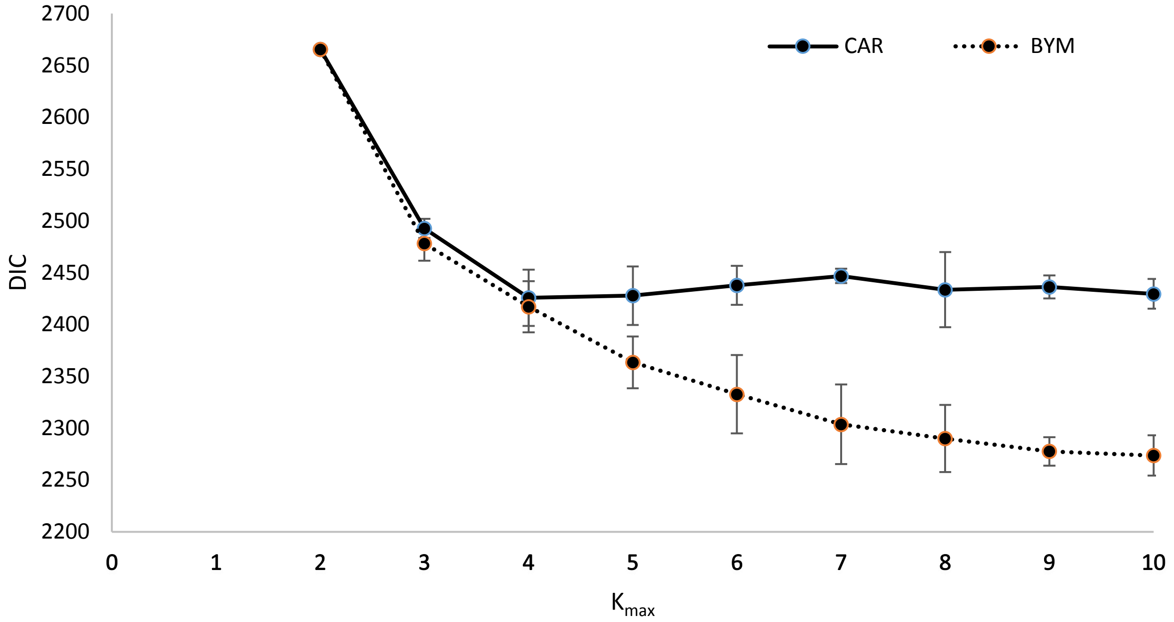

Figure 4.9: Optimal number of genetic clusters (K_{max}) based on DIC (Deviance Information Criteria) for admixture models (CAR and BYM). Both models selected three genetic clusters across the landscape. Error bars represent standard deviations.

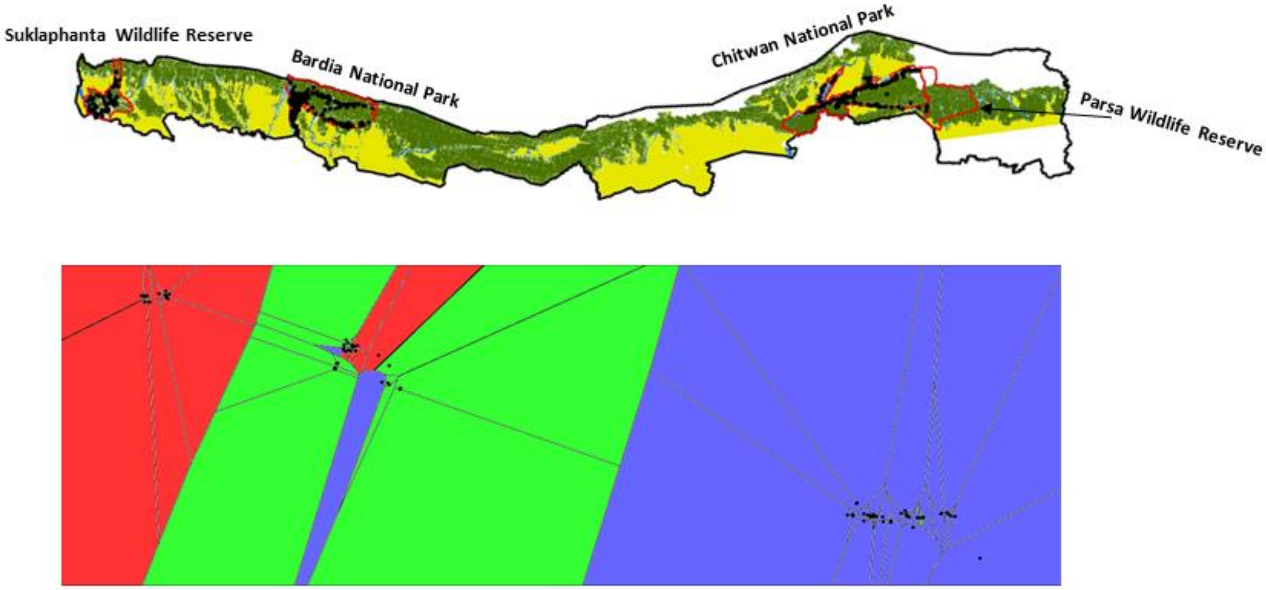

Figure 4.10: Hard-clustering plots at $k_{\max}$=3 showing three genetic populations with predicted membership and location of each sampled individual (black dots). Colors (red, green, blue) coded Voronoi cells (black lines) from program TESS represent the predicted membership of that individual in the respective genetic sub-populations. Similar color combinations were evident in all predicted members in all runs.

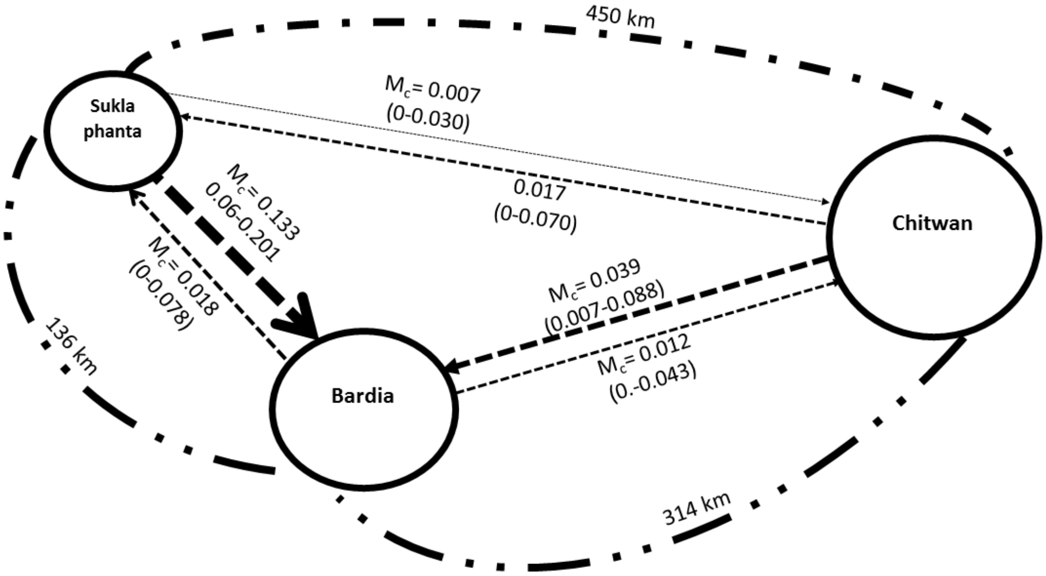

Figure 4.11: Contemporary gene flow pattern inferred in Terai Arc Landscape based on migration rates (M_c) estimated in Bayesass (Wilson and Rannala 2003). Broken lines indicate direction of migration, and line thickness represents the magnitude of estimates along with the migration rates. Figures within parentheses represent 95% CI for migration rates (M_c). Size of the circle represents the estimated size of breeding population. Broken lines around the periphery represent the spatial distances between the populations.

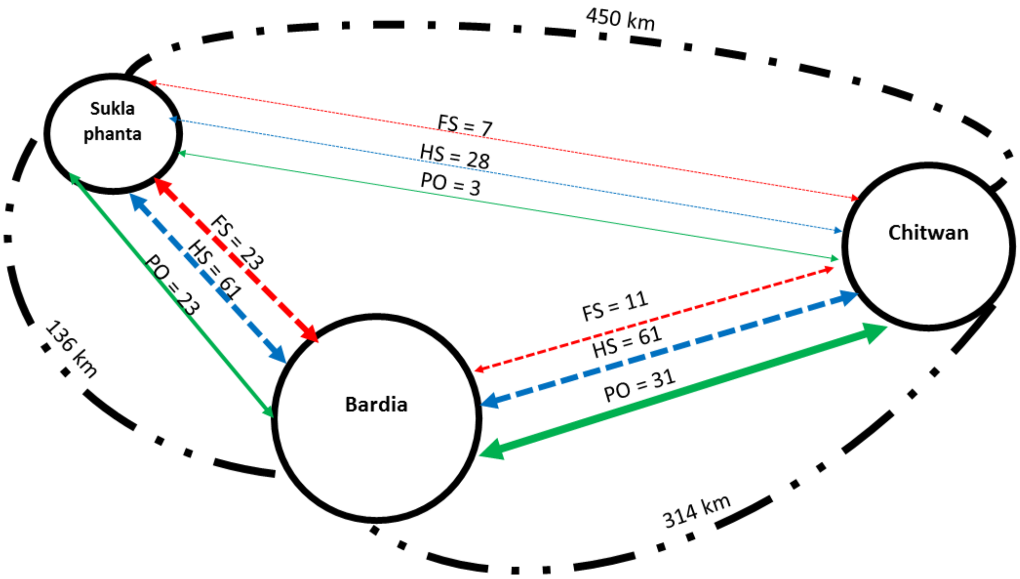

Figure 4.12: Pairs of individuals related between the sub-populations indicated by broken lines identified using Program ML-Relate (Kalinowski et al. 2006). Size of the broken line indicates the magnitude of relatedness with particular relationship (FS: Full-Siblings; HS: Half-Siblings; PO: Parent-Offspring). Size of the circle represents unrelated pairs in the sub populations. Broken lines around the periphery represent the spatial distances between the populations.

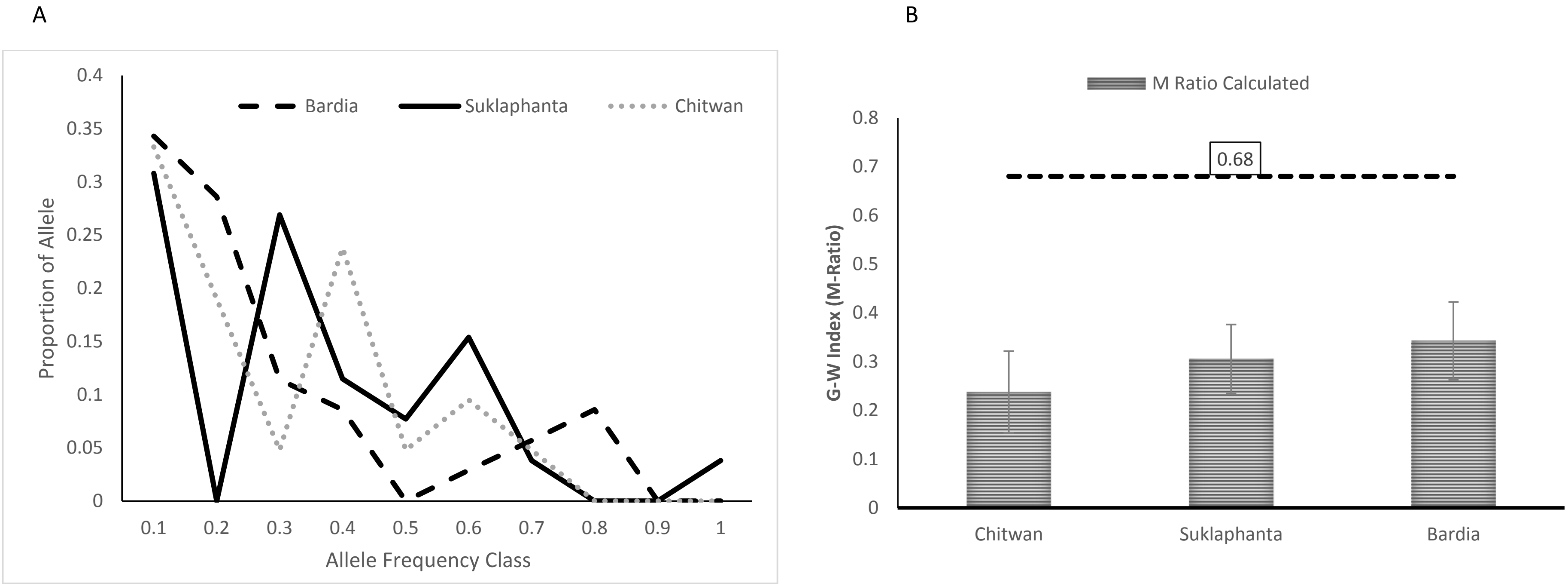

Figure 4.13: (A) Qualitative "L- shaped mode-shift" test in the Bardia and Suklaphanta populations suggesting negative bottleneck event (left); The x-axis shows 10- allele frequency class (0.1 to 1.0) from Program Bottleneck. Garza-Williamson (G-W) Index (M-Ratio test)(B): The broken horizontal line shows the threshold value of the M ratio at 0.68 (Garza and Williamson 2001) (Left). The observed M ratio (M = 0.28) values is less than the 0.68 threshold, suggesting that all three populations have undergone a bottleneck event in the recent past.

Chapter 5

Comparison of abundance and density estimates from non-invasive sources: genetic and camera-trap capture-recapture analyses

ABSTRACT

I compared the abundance and density of tigers estimated using two non-invasive sampling techniques: camera-trapping and fecal DNA sampling. For cameras: I pooled the 2009 camera-trap data from the core tiger population across the lowland areas of Chitwan National Park. I sampled 359.2 km^2 of the core area with 187 camera-trap locations, spending 2,821 trap-nights of effort. I obtained 264 identifiable photographs and identified a total of 41 individual tigers. For genetics, I sampled 325 km^2 of the core area along three spatial routes, walking a total of 1,173 km, collecting a total of 420 tiger fecal samples in 2011. I identified 36 tigers using the assay of 8 multilocus genotypes and captured them 42 times. I analyzed both data types separately for estimating density and jointly in an integrated model using both traditional and spatial capture-recapture frameworks. Using Program MARK and the model-averaged results, my abundance (SE) estimates were 46 (SE 1.86) and 44 (SE 9.83) individuals from camera and genetic data, respectively. Density estimates (tigers per 100 km^2) via traditional buffer strip methods using half of the Mean Maximum Distance Moved (½ MMDM) as the buffer surrounding survey grids were 4.01 (SE 0.64) for camera data and 3.49 (SE 1.04) for genetic data. Spatially explicit capture-recapture models resulted in lower density estimates both in the likelihood based program DENSITY at 2.6 (SE 0.6) for camera-trap data and 2.6 (SE 0.9) for genetic data, while the Bayesian based program SPACECAP estimates were 2.4 (SE 0.3) for camera-trap data and 2.2 (SE 0.5) for genetic data. Using a spatially explicit, integrated model that combines data from both cameras and genetics, density estimates were 1.5 (SE 0.2) tigers per 100 km^2 for camera-trap data and 1.9 (SE 0.4) tigers per 100 km^2 for genetic data. I found that the addition of camera-trap data improved precision in genetic capture-recapture estimates, but not visa-versa, likely due to low numbers of recaptures in the genetic data. While a non-invasive genetic approach can be used as a stand-alone capture-recapture method, it may be necessary to increase sample size to obtain more recaptures. Camera-trap data may provide more precise estimates, but genetic data return more information on other aspects of genetic health, recent demographic history and connectivity. Combining data sets in an integrated modeling framework aided in pinpointing strengths and weaknesses in data sets, thereby improving modeling inference.

Keywords: *Panthera tigris*, camera-trapping, fecal survey, density, abundance, lowland, integrated analysis

INTRODUCTION

Knowing population abundance or density of wildlife populations is central to their conservation and management (Williams et al. 2002, Nichols 2014). For rare and cryptic animals, the answer to “how many?” is often unknown (Sunarto et al. 2013b). Making an objective decision on the conservation status of an animal, especially for rare and cryptic species, requires precise estimates using robust analytical techniques, which must take into account imperfect ability to detect animals. Noninvasive sampling techniques that may use, for example, conventional traps, automated cameras, fecal DNA, and hair snares have been used within a capture-recapture (CR) framework (Otis et al. 1978) for estimating population parameters such as abundance and density. There has been widespread use of traditional, non-spatial techniques to assess populations of elusive and sparsely distributed animals, especially large carnivores such as tigers (*Panthera tigris tigris*: Karanth 1995, 1998), leopards (*Panthera pardus*: Thapa et al. 2014), snow leopards (*Panthera uncia*: Jackson et al. 2006), jaguars (*Panthera onca*: Silver et al. 2004), and pumas (*Puma unicolor*: Kelly et al. 2008). Because of the shortcomings of these traditional CR models, spatially explicit capture-recapture (SECR or SCR) models have been developed that more directly incorporate how animals are detected by a trap array, conditioned on the ecological processes governing their distribution and movement in space into the detection process (Efford 2004, Royle and Young 2008, Efford et al. 2009, Gardner et al. 2010).

Camera-trapping has proven an efficient tool for monitoring rare and cryptic animals, including tigers (Karanth and Nichols 2002, McCallum 2013), and in determining the conservation status of species at risk (O'Connell et al. 2011). Multiple studies have shown the utility of non-invasive approaches using camera-trapping for estimating population size (Karanth 1995, Karanth and Nichols 1998, Karki et al. 2013, Sunarto et al. 2013a), occupancy (Linkie et al. 2007, Steinmetz et al. 2013), habitat use (Di Bitetti et al. 2006, Tobler et al. 2009), and studying carnivore communities (Ahumada et al. 2011, Tempa et al. 2013). In addition, noninvasive genetic sampling has become a powerful tool for studying and monitoring elusive and low-density species, including using genetic sampling in a capture-recapture framework (Taberlet et al. 1999, Lukacs and Burnham 2005). Additionally, non-invasive genetic sampling using scats can provide useful insight into genetic diversity and fitness, and also into the feeding ecology of the species under study (Farrell et al. 2000, Sollmann et al. 2013a). Both camera and genetic techniques provide an avenue for researchers to collect in-depth population monitoring information (Mills et al. 2000) and provide a growing analytical framework in which to advance my sampling and analytic methodologies (Efford 2004, Royle and Young 2008, Royle et al. 2009a, Gardner et al. 2010, Obbard et al. 2010, Gopalaswamy et al. 2012a, Sollmann et al. 2013b, Rich et al. 2014), complementing and extending my efforts for better understanding species biology. Recently, there has been growing interest in providing improved estimates of population parameters from a single or multiple sources or reanalysis of data using the recently developed spatial, capture-recapture models (Mohamed et al. 2013, Rich et al. 2014, Thapa et al. 2014) to better inform conservation of rare and cryptic species. Gopalaswamy et al. (2012a) and Sollmann et al. (2013b) also demonstrated that data from two different sources (cameras and genetics) can be combined so long as they share at least one of the same variables in the model in order to provide more precise estimates of density of carnivore populations.

The Terai Arc Landscape (also referred as the Terai Arc) represents a meta-population of tigers across the foothills of the Himalayas in Nepal and northwest India (Wikramanayake et al. 2004, 2010). Population monitoring of tigers using camera-trapping has been conducted at the multiple sites across the Terai Arc in Nepal (Wegge et al. 2004, Barlow et al. 2009, Karki et al.

2013, Thapa et al. 2014) and India (Harihar et al. 2011, Jhala et al. 2011). Recently, a few studies (Mondol et al. 2009a, Gopalaswamy et al. 2012a) used molecular genetic techniques for estimating population abundance and density of tigers in India, but no such studies exist using a non-invasive genetics approach in Nepal, and across the Terai Arc.

In this study I had three objectives. First I estimated abundance of tigers with genetic data using the conventional CR framework to compare with population estimates from the camera-trap survey carried out in the same areas but in a different time period. Second, I estimated tiger density separately from both data sources using traditional adhoc non-spatial approaches that determine the survey area and convert the abundance into density estimates by buffering the survey grid, versus the newer spatial SECR/SCR approaches that take into account heterogeneity in detection probability arising from different exposure of individuals to the trap array, thereby more explicitly linking spatial trap arrangement into the estimation process. Third, I used integrated models to estimate density by combining data from multiples sources (camera-traps and genetics) to produce improved, survey-specific density estimates, and to examine whether they had higher precision in a single spatially explicit model. This study demonstrates how genetic data can be used in population monitoring of an endangered, elusive, flagship species.

STUDY AREA

This study was carried out in Chitwan National Park (CNP, 27°30′N, 84°20′E) located in central Nepal. The park covers an area of 932 km^2 in the sub-tropical lowland forest of the inner Terai. The sampling area covers the core area of the lowland forest south of the Rapti and Narayani Rivers and covers an area measuring 421.2 km^2 (Figure 5.1). CNP is part of the Tiger Conservation Unit (TCU) that is contiguous with the Valmiki Tiger Reserve, India, to the south, and the Parsa Wildlife Reserve, Nepal to the east (Dinerstein et al. 2007). CNP represents a source population of tigers in the eastern part of the Terai Arc. The major habitat types of CNP and surrounding areas include: grassland (176 km^2), forest (2,957 km^2), and settlement and agricultural areas (1,312 km^2). CNP has three distinct seasons: winter, summer, and the monsoon season (Dinerstein 2003). The mean annual rainfall is 2,437 mm per year, with highest rainfall during the months of July-September (Karki et al. 2013). Average ambient temperature varies from a minimum of 11°C in winter to a maximum of 38°C in summer season. Tigers (*Panthera tigris tigris*), leopards (*Panthera pardus fusca*), and wild dogs (*Cuon alpinus*) are the top carnivores, and the large ungulates include big pachyderms such as the one-horned rhinoceros (*Rhinoceros unicornis*) and elephant (*Elephus maximus*). Gaur (*Bos gaurus*), sambar (*Rus unicolor*), chital (*Axis axis*), barking deer (*Muntiacus muntjac*), wild boar (*Sus scorfa*), hog deer (*Axis porcinus*), and primates are the potential carnivore prey found in CNP. More details on the CNP are suitable elsewhere (Dinerstein 2003, Gurung et al. 2008, Bhattarai and Kindlmann 2012, Karki et al. 2013, Subedi et al. 2013).

METHODS

Camera-trap Survey

I selected a subset of data from the 2009 camera-trap survey (DNPWC 2009) representing 359.2 km^2 of the core area of Chitwan National Park. Within the core area, we (my field assistants and I) followed standard procedures for conducting camera-trap surveys (Karanth and Nichols 1998, Karki et al. 2013). I divided the lowland area into 8 blocks, each measuring an average of 38 km^2 (SD 10.18), for conducting the camera-trap survey based on previous informal records and regular site-specific tiger monitoring conducted by CNP staff. First, I did an extensive survey of the blocks to identify strategic locations for installing camera-traps. Based on indirect sign and current movements of animals, I chose 187 locations with an average of 24 locations per block (SD = 4.0). To maximize capture probability, I positioned my camera-trap locations within habitat features known as tiger travel routes, such as forest roads, dry stream beds, and human and animal trails (Karanth and Nichols 1998, Karanth and Nichols 2002). The average inter-trap distance between two consecutive locations was approximately 1.5 km (SE 0.41). I used a combination of 2 passive remote cameras (Moultrie Feeders and Stealth Cam) at each location that were activated by animal movement and placed one on either side of the trail (Karanth and Nichols 2002). I collected other ancillary information, such as date, time, and spatial location of the camera-traps for use in my analyses. I simultaneously worked in three blocks at a time, and each location was sampled for 24 hours for 16 consecutive days in each block. After 16 days, the cameras were moved to the next block until all survey blocks were completed. My camera-trap survey was conducted in the winter season from December 2008 to March 2009.

Fecal DNA Survey

The fecal DNA survey was carried out in 324.9 km^2 of the core area of the national park. I used the Mondol et al. (2009a) field-sampling design for collection of fecal samples with modifications. Due to the linear orientation of the study area, I divided the core area of the national park into three blocks: Sauraha, Madi, and Tiger Tops. I selected three spatial routes, embedded within the earlier camera-trap survey, covering an average length of 65.13 (SD 9.20) km within each block, ensuring that all the scats in the areas have high probability of detection (Barlow et al. 2009, Karki et al. 2013). The spatial routes consisted of firelines, motorable roads, and human and animal trails, which have high probability of use by tigers (Karanth and Nichols

2002). Three observers walked across each spatial route searching for scat samples. Three observers sampled each route continuously for six days, rested on seventh day and returned back to the starting location of the route to begin the search over again. Each sampling occasion, therefore, spanned six days, ensuring that scats were fresh, less than seven days old (Andheria et al. 2007, Mondol et al. 2009a). The total sampling period was 42 days, consisting of six sampling occasions and sampling effort was 1172.5 km of routes walked. I conducted the survey in winter season in December 2011.

Upon encountering scats in the field, I scratched a few grams from upper and side surfaces to obtain samples (Mondol et al. 2009a). I stored the samples in 2-ml vials at a 1:4 ratio filled with dimethyl sulphoxide saline solution (DETs buffer, Seutin et al. 1991, Frantzen et al. 1998, Wultsch et al. 2014). I also took a 200-300-g sample from the widest portion of the scats for future molecular diet study, and the rest of the scat was left in the original location to avoid possible change in behavior due to the territorial nature of tigers. To avoid double-collection of the same scats in subsequent sampling sessions, I either marked the scat with a small red dot by nail polish (in case of dried samples) or pushed a twig inside the substrate at the side of the scat (in case of wet scats) after collecting the samples.

DNA was extracted from scat samples using a commercially available DNA stool kit (Qiagen Inc.) and following the manufacturer’s instructions with slight modifications. I kept one negative control (water) in each batch of samples to monitor for contamination during DNA extraction. To avoid contamination from fecal samples, DNA extraction was carried out in a separate room for PCR replication. All scat samples were first screened for species identification using species-specific primers developed by Bhagavatula and Singh (2006).

Microsatellite Primer Selection

I screened variation at 19 loci that were developed for domestic cats (Menotti-Raymond et al. 1999) and used in previous studies of tigers (Bhagavatula and Singh 2006, Mondol et al. 2009a). I optimized use of the primers that were in use on the Indian side of the Terai Arc (Dr. S.P. Goyal: Personal Communication, Wildlife Institute of India) so that my data will be comparable to India's in the future. I selected 10 loci based on expected heterozygosity and variation in allelic diversity (See Chapter 4, Table 4.1).

PCR Standardization and Genotyping

All PCR standardization was carried out with field-collected samples. For all standardizations, amplification was carried out in 7-µl reaction volumes containing 3.5 µl Qiagen Mastermix and 0.07 µl of Q solution, forward and reverse primers for all the microsatellite loci mixed to final standard concentration: 0.4 µM FCA205, 0.2µM FCA391, 0.07µM PttD5, 0.14µM FCA232, 0.07µM FCA304, 0.30µM F85, 0.14µM FCA441, 0.07µM PttA2, 0.09µM FCA043 and 0.49µM F53 and 2.50µl of DNA extract. The PCR conditions for microsatellites were as follow: The temperature regime included an initial denaturation step (95˚C for 15 min); initial touchdown PCR was performed for 10 cycles with denaturation (94 ˚C for 30s), annealing (62˚C for 90s) reduced by 0.5◦C in each succeeding cycle and extension (72˚C for 60s); followed by 25 cycles of denaturation (94˚C for 30s), annealing (57˚C for 90s) and extension (72˚C for 60s) followed by a final extension (72˚C for 10 min), and cooling to 4˚C in an MJ Research PTC-225 thermal cycler. 0.7µl of amplified product was added to 0.3µl of LIZ-500 size standard and then the genotyping assay was run in an automated ABI 310 genetic analyzer (Applied Biosystems). Microsatellite alleles were scored using GENEMAPPER-4.1 (Applied Biosystems). To finalize the consensus genotypes, a multitube approach was used where at least three identical homozygote PCR results were required for definitely scoring homozygote genotypes, and each allele had to be observed in two independent PCRs in order to score a heterozygous genotype (Wultsch et al. 2014).

DATA ANALYSIS

Individual Tiger Identification with Camera-Trap Data

Two investigators independently identified photos to build consensus on individual tiger identity. Individual tigers were identified based on their stripe patterns on their flanks, limbs, tails and forequarters, and given unique identification numbers, as done in other studies (Karanth and Nichols 2002, Karki et al. 2013, Sunarto et al. 2013a). I chose subsets of data from both surveys, representing the core of the core area of CNP (Chapter 2), to meet my study objectives for comparing the datasets from two sources: camera-trap data and fecal DNA markers under a common capture and recapture framework (Otis et al. 1978).

PCR Amplification, Genotype Accuracy and Error Rates

I used data from the last two PCR runs for standardizing data collection across the runs for all loci across all the tiger-positive samples to calculate PCR amplification rates, genotype accuracy, and error rates (Wultsch et al. 2014). For PCR success, I calculated percentage of PCR success across all the tiger-positive samples. Genotype accuracy was calculated based on percentage of successful PCR runs whose results matched the finalized consensus genotype. Genotype errors (allelic dropout and false alleles) were estimated based on the protocols used by Broquet and Petit (2004). Allelic dropout was calculated only on heterozygous genotypes as the ratio of allelic dropout at a locus to the total number of heterozygotes genotypes, while the false allele rate was calculated across all the consensus genotypes.

Individual Tiger Identification with Genetic Data

I checked for probability of identity for unrelated individuals ($P_{(ID)}$) and siblings ($P_{(ID)sib}$) (Waits et al. 2001). I used the minimum criteria of $P_{(ID)sib} < 0.010$ (Mills et al. 2000, Waits et al. 2001) for selecting the minimum number of loci required for individual identification. I used program GenAlEx, version 6.5 (Peakall and Smouse 2012) to determine the minimum number of individual tigers in the consensus genotype data sets. Any repeatedly matching genotypes were interpreted as recaptures of individual tigers.

Population Estimation

I used traditional capture-recapture analytical techniques (Otis et al. 1978, White et al. 1982) for estimating population size of large felids from both camera-trap (Karanth 1995) and genetic data (Mondol et al. 2009a). I developed detection histories for each individual tiger from both data sources and assigned individuals to the appropriate encounter occasions (16 days for camera-trap and six, 6-day periods for genetic data). I used the closure test in Program CAPTURE (Rexstad and Burnham 1991) under the assumption of the demographic closure for the tiger population during the105-day, and 42-day, sampling for camera-trap and genetic surveys, respectively.

I used the closed population models (Otis et al. 1978) implemented in Program CAPTURE for estimation of overall capture probability ($\hat{P}$) and abundance ($\hat{N}$), using several different models that can incorporate effects of ecological and sampling-related factors (for details, refer to (Karanth 1995, Karanth and Nichols 1998, Karanth and Nichols 2002). I also used the Huggins Closed Capture with Heterogeneity Model (Huggins 1991) implemented in Program MARK (White and Burnham 1999) to estimate abundance. These models use a maximum likelihood framework, and I fit 8 models of Otis et al (1978), which allow capture probabilities to vary over time (p(t)=c(t)), by individual's heterogeneity (p(h)=c(h)), due to a behavioral response (initial capture being different from recapture probabilities, p(.).c(.)) along with null model (with no variation in capture probabilities, p(.)=c(.)), and combinations of the above factors. Model input included the one time winter season capture histories with 16 and 6 encounter occasions for camera and genetic data sets, respectively. I ranked models using sample size-adjusted Akaike's Information Criterion (AIC) (Akaike 1973) and considered all models with ΔAICc <2 as competing models (Burnham and Anderson 2002).

Density Estimation

Unlike camera-trapping where detectors are stationary, genetic data can be collected anywhere along the survey routes. While this aspect does not present a problem for traditional capture-recapture analysis methods, the newer spatially explicit models determine detectability based on stationary detectors. Therefore I needed to assign scat samples collected to a specific discrete detector in space. Therefore, I compared the use of suitable "detectors" at two different scales, the grid versus the segment level. At the grid level, I divided the study area into 1-km^2 grid cells and used the mid-points of the grid cells to represent the stationary trap location. All DNA collected within that 1 km^2 grid cell was assigned the location of the center of that cell (Russell et al. 2012). At the route-based level, I used every 1-km linear segment as the "trapping device" that accumulated DNA evidence, and the location was represented by the mid-point of each 1-km-long linear segment (Gopalaswamy et al. 2012a). I checked for spatial autocorrelation (Legendre 1993) between grids or segments (1 km^2/ 1 km) on tiger detections based on Moron's I statistic in ArcGIS 10.1 (using the default options). I used both traditional (non-spatial) and Spatially Explicit Capture Recapture (SECR-Maximum Likelihood and SCR-Bayesian) approaches with genetic datasets to compare between grid versus segment level "trapping devices”. I consider density estimates to be different when their 95% CI do not overlap (Payton et al. 2003) between the trapping devices.

Using the abundance estimates from Programs CAPTURE and MARK to convert it into densities, I used the traditional ½ MMDM (Karanth 1995, Karanth and Nichols 1998) and full MMDM (Soisalo and Cavalcanti 2006) approaches to calculate the buffer strip surrounding my camera-traps and genetic locations to determine the effective trap area (ETA). The ½ MMDM and full MMDM were calculated from photographed and genotyped individuals trapped in more than one location, buffered each camera-trap, and dissolved the overlapping areas to calculate the ETA. I clipped the non-habitat areas from the buffer area to calculate final ETA. I then divided the population estimates from CR (capture-recapture) analysis by total ETA to determine density. I used the delta method to calculate the variance in density estimates (Karanth and Nichols 1998).

I used SECR models using the maximum likelihood (SECR-ML) and the Bayesian (SCR-B) approach for estimating densities including heterogeneity in capture probabilities among individuals in a population (Borchers and Efford 2008, Royle and Young 2008, Royle et al. 2009b, Royle et al. 2013). I used the SECR-ML implemented in program DENSITY (Efford et al. 2004) and SCR-B implemented in program SPACECAP (Gopalaswamy et al. 2012b) for both the data sets.

In Program DENSITY version 5.0, I first modeled to select the appropriate detection (observational) process as half-normal, hazard rate, or negative exponential. Using the selected detection function, I then allowed g_0 (the capture probability at the hypothetical center of an individual’s home-range) and sigma (a function of the scale of animal movement) to vary using 2-class, finite mixture (h2) to represent heterogeneity, and/or a behavioral response (b). Thus, a half-normal detection function model with 2-class finite mixture of g_0 and constant sigma would be represented as HN g_0(h2) sig(.). I used the estimated log likelihood and root-pooled spatial variance (RPSV) of varying integration buffers for determining the appropriate buffer size. I ranked all the models using sample size-adjusted Akaike's Information Criterion (AICc) and considered all models with $\Delta AIC_c < 2$ as competing models. I used model-averaging techniques to determine final density estimates (Burnham and Anderson 2002). I report the unconditional variance estimates for the model-averaged estimates. I carried out the analysis both with and without using habitat mask. I used a habitat mask due to presence of distinct blocks of habitat (3,262 km^2) and non-habitat (3,158 km^2). I removed the non-habitat (settlements and agricultural areas: 3,158 km^2) and assumed uniformity of tiger activity centers over the remaining blocks judged to be suitable (Royle et al. 2013). I considered parameters to be different when their 95% CI did not overlap (Payton et al. 2003, Sollmann et al. 2013b) between two data sources.

For the SCR-B approach, for both data sets, I used program SPACECAP version 1.1.0 implemented in R package version 3.1.0 (Team 2013) for estimating tiger density. I buffered 15 km around the sampling area to represent the probable extent of tiger home-range centers (Gopalaswamy et al. 2012a, Sollmann et al. 2013b). I generated a grid of hypothetical home-range centers with equally spaced points (n = 7,524), each 1 km apart. This resulted in an area of 3,262 km^2 of tiger habitat (n = 3,779) over which these activity centers were uniformly distributed. I carried out the analysis both with and without using the habitat mask. For the habitat mask, I removed the 3,158 km^2 area of settlements (town, city, villages, and agriculture areas) from the hypothetical state space. I used three standard input data files (animal capture locations and dates, trap deployment dates and locations, and the hypothetical activity centers) and assumed a half-normal detection function. I performed 250,000 iterations for the camera data set and 150,000 iterations for the genetic data set, of which the initial 50,000 were discarded as the burn-in period, and I used an augmentation value of 250 individuals (more than five times the expected number of animals). I evaluated the results using the Geweke diagnostic (Geweke 1992) and z-score statistics of $|z-\text{score}|$ more than 1.6 implying lack of convergence (Gopalaswamy et al. 2012b). I considered densities to be different from each other when their 95% CI did not overlap (Payton et al. 2003, Sollmann et al. 2013b) between two data sources. I produced the pixelated density map showing the estimated tiger densities per pixel of size 1 km^2 pixel size using ArcGIS 10.1.

Density Estimation using Integrated Model

I modified an integrated spatial capture-recapture (SCR) model to estimate density using data from two sources: camera-traps and fecal DNA. The integrated approach originally was described by Gopalaswamy et al. (2012a) and later modified by Sollmann et al. (2013b). I extended this approach to allow density estimation in two separate years, demonstrating the utility of integrated SCR models to incorporate previously incomparable data sets. For the camera model, I used the SCR_0 model (Royle et al. 2013) and accounted for sampling effort as the number of days that the station was functional for the camera-trap survey. I also used the SCR_0 observation model for the fecal genotype model. To account for individual detection along scat-collection transects, I imposed a 1-km^2 grid cell matrix over the landscape and treated each 1-km^2 grid cell as a trap (J) that was visited multiple occasions (K). I calculated length of transect within each grid cell to account for varying survey effort, with grid cells not containing transects represented by zero search effort. The two data sets were collected using different protocols in two different years. To combine data sets in a single model, I assumed that individual tiger movement was similar across both surveys, which allows modeling movement around an activity center (sigma) as a shared parameter between the two datasets. This hierarchical approach allowed us to implement the same process model representing individual movement across years, and different observation models for each survey method in each year. Thus, there is one estimate for the scaling parameter, sigma, but survey-specific estimates for detection (lambda), the data augmentation parameter (psi), and density (D). Details on model formulation are described by Gopalaswamy et al. (2012a) and Sollmann et al. (2013b)

To obtain an estimate of abundance, I used a data augmentation approach (Royle and Young 2008), assuming that some individuals were not detected during surveys but belonged to the population, and therefore had a capture history consisting of all zeros. I set a state space (S) of 6,420 km^2, and a maximum number of individuals within the state space (M) at 250 individuals. This includes individuals detected, and possible individuals not detected, and I associated a latent indicator variable, z_i, for each possible data-augmented individual to estimate the probability that an augmented capture history of zeros represents a real individual that was not detected. The abundance estimate (N) is the sum over all possible individuals (M) for which the indicator variable (z) is not equal to zero. Density, D, is a derived parameter obtained by dividing the estimate of total number of individuals (N) by the area of the state space (S).

In addition to the joint model for the combined data sets, I also ran the SCR$_0$ model separately for each dataset to estimate density independently from camera-trap and scat surveys. Thus, for the two separate models, the scaling parameter, sigma, is estimated independently using only survey-specific data. I implemented all three models using the Bayesian analysis package rjags (Su and Yajima 2012) using the R platform (Team 2013). I ran each model with three Markov Chain Monte Carlo (MCMC) chains with 200,000 iterations, a burn-in of 100,000 and a thinning rate of 1. I assessed MCMC convergence by visually inspecting the trace plots for each parameter, and using the Gelman-Rubin statistic (Gelman et al. 2004), $\hat{R}$, which compares between- and within-chain variation analogous to an ANOVA (Zar 2009). I used an $\hat{R}$ value less than 1.1 to indicate convergence (Gelman and Hill 2006). For all parameters, I report the posterior mean, standard deviation, and 95% Credible Interval (CI). I consider the estimates to be different if the 95% CI do not overlap (Sollmann et al. 2013b). I assessed improvements to precision using coefficients of variation (CV = SE/mean), with lower CV indicating better precision (Sollmann et al. 2013b).

RESULTS

Sampling Effort and Individual Tiger Captured

We amassed 2,821 trap-nights and obtained 264 identifiable photographs comprising 145 right-flanks and 119 left-flanks tiger photographs from the core area (lowland forest) of the Chitwan National Park. Two interpreters matched 100% on all the capture events (*n*=103) and identified 41individuals visually assessed to be 1 year or older (12 males, 16 females, 13 unknown sex) and built the capture history based on the identified tigers (Table 5.1).

In order to compare and validate my DNA-based results conducted in 2011 with earlier results from the camera-trap survey conducted in 2009, I chose the subsets of data from lowland forest representing the core areas of Chitwan National Park. The subsets of data represent 91% and 69% of the total identified with fecal DNA marked (M_{t+1}=34) and camera-trap survey observation (M_{t+1}=59) in Chitwan National Park.

Sampling Effort and Individual Tiger Identified with Genetic Data

We (My field assistants and I) spent 1172.5 km of route-walk and collected 420 scat samples from Chitwan National Park. Using the species-specific PCR primers, I identified 57% samples to be tigers, and 53% samples (positive samples, *n*=240) yielded genotype information. Locus FCA205 did not work well with the samples. The rest of the loci were polymorphic except PttA2. I removed FCA205 and PttA2 from subsequent analysis. PCR amplification success across all tiger-positive samples was 70.1% ranging from 51% to 84% per locus (See Chapter 4, Table 4.1). Using probability-of-identify for unrelated individuals ($P_{(ID)}$) and siblings ($P_{ID(sibs)}$) information and a criteria of <0.010, genotypes at a minimum of six loci were needed to identify individuals tigers with high statistical confidence. Within lowland core area of the national park, I identified 31 tigers with an 8-loci assay (multiplex-1) for the Chitwan scat samples with cumulative $P_{(ID)}$ and $P_{ID(sibs)}$ of 1.1×10^{-5} and 5.8×10^{-3} respectively using Program GenAlEx (See Chapter 4, Figure 4.2). I built the detection history on the identified individuals with 42 capture events (Table 5.1) based on 8 loci.

Closure Assumption and Abundance Estimate

Results of the closure test implemented in Program CAPTURE were consistent with the closed population assumption during the sampling period for the camera-trap (*n*= 105 days) and fecal (*n*= 42 days) surveys. Using the discriminate function analysis in Program CAPTURE, the model incorporating heterogeneity (M_h, 1.00) was the top model for the camera-trap dataset, while M_h models incorporating heterogeneity (M_h, 0.77) was the best fitted model next to the null model (M_o, 1.0) for the fecal dataset. The M_h (jackknife) estimator is the best fitted/robust model in capture-recapture studies for large felids, including tiger due to their social spacing mechanism (Karanth and Sunquist 2000) and due to differential exposure of individual tigers to detection on survey routes (Karanth and Nichols 2002b, Royle et al. 2009b). The average capture probability ($\hat{p}$) was 0.23, with an abundance estimate $\widehat{N}(SE)$ of 56 (SE 7.54) tigers (Table 5.2) for the camera-trap survey, while average capture probability ($\hat{p}$) was 0.28 with an abundance estimate

$\widehat{N}(SE)$ of 49(SE 6.39) tigers for fecal survey. In Program MARK, for the camera data set, the model supporting variation in the behavior and heterogeneity (M_{bh}) received highest support (w= 99%) for camera-trap data (Table 5.3). I used the top model with an abundance estimate ($\widehat{N}(SE)$) of 46 (1.9) tigers and capture probability $\hat{p}(SE)$ of 0.243 (SE 0.06). Five models supporting variation in behavior, constant (null model), time and heterogeneity accounted for 100% of the AIC weight for the fecal DNA data set (Table 5.3). I used model-averaging techniques with an abundance estimate $\widehat{N}$ (SE) of 44 (SE 9.8) tigers and capture probability $\hat{p}(SE)$ of 0.36 (SE 0.68). The point estimate from Program CAPTURE was higher than that from Program MARK for the camera-trap data; however, 95% CIs of the point estimates from both analytical platforms overlapped for the genetic data (Figure 5.2).

Density Estimates

I compared the density estimates between the choices of trapping devices (grid versus segment) and found no significant difference in density estimates for the choice of trapping devices, as more than 95% of the CI overlapped (Figure 5.3). I used the grid-based trapping device in further analyses for comparison with earlier studies (Sollmann et al. 2013b). In the test for spatial autocorrelation between the trapping devices (grids), tiger detection was highly clustered across the lowland areas (Z score > 3.84, *p*=0.00).

With camera-trap data sets, 24 individual tigers were captured more than once resulting in a MMDM of 9.4 km and an effective trapping area of 1,092 km^2 using the buffer-strip method (using ½ MMDM). The density estimates from traditional methods of dividing abundance by the ETA, were of 5.12 (SE 0.85) and 4.01 (SE 0.64) tigers per 100 km^2, from program CAPTURE and MARK, respectively (Table 5.4). I also used the full MMDM, resulting in an effective trapping area of 1,395 km^2 and density estimates 4.17 (SE 0.44) and 3.27 (SE 0.31) tigers per 100 km^2 with CAPTURE and MARK, respectively (Figure 5.4). Similarly with fecal DNA data sets, 14 individual tigers were captured more than once, resulting in a MMDM of 9.2 km and an effective trapping area of 1,254 km^2 using the buffer strip method (using ½ MMDM). The density estimates from traditional methods of dividing abundance by the ETA, were 3.90 (SE 0.83) and 3.49 (SE 1.04) tigers per 100 km^2, from programs CAPTURE and MARK, respectively. I also used the full MMDM, resulting in an effective trapping area of 1,798 km^2 and density estimates 2.72 (SE 0.52) and 2.43 (SE 0.64) tigers per 100 km^2 with CAPTURE and MARK, respectively (Figure 5.4).

Spatially explicit models produced much lower estimates than traditional ½ MMDM techniques, but comparable to those of the full MMDM methods. I selected the appropriate buffer sizes of 15,000 m and 24,000 m based on estimated log likelihood and RPSV for camera and fecal DNA data sets, respectively in Program DENSITY (Table 5.5). For the camera-trap data, the model supported the hazard rate detection function with detectability (at home-range center, g_o) and behavioral response in spatial scale (function of movement, s) both constant (null model) (Table 5.5). The model-averaged density estimate for the camera-trap dataset based on SECR-ML were 2.55 (SE 0.59) with habitat mask and 1.89 (SE 1.47) tigers per 100 km^2 without the habitat mask. Model selection in SECR-ML with fecal DNA data supported the hazard rate detection function with constant detectability (at home-range center, g_o) and behavioral response in spatial scale (function of movement, s) (Table 5.5). There was some support for behavioral response in detectability, as the models including that variable were within 2 ΔAIC_c of the top model. The model-averaged density estimate for the genetic dataset based on SECR-ML were

2.57(SE 0.88) tigers per 100 km^2 with habitat mask and 2.18 (SE 0.88) tigers per 100 km^2 without habitat mask.

Using the SCR-B analysis implemented in SPACECAP, all model parameters converged based on Geweke diagnostic statistics with z scores not more than 1.6 (Gopalaswamy et al. 2012b) for both data sets. For the camera-trap data, I obtained the posterior density estimates of 2.44(SE 0.30) tigers per 100 km^2 with habitat mask and 1.77 (SE 0.23) tigers per 100 km^2 (Table 5.6) without habitat mask. For the genetic data, I obtained the posterior density estimates of 2.23 (SE 0.46) tigers per 100 km^2 (Table 5.6) with habitat mask and 1.41 (SE 0.29) tigers per 100 km^2 without habitat mask. The resulting pixelated density maps show the relative animal densities over the animal home-range centers (Figure 5.5).

Density Estimation using Integrated Model

Tiger density from the independent models using camera-trap data yielded 1.73 (1.30 – 1.89) tigers per 100 km^2. Tiger density estimated from the genetic data was lower, 1.36 (0.88 – 2.03) tigers per 100 km^2, and 95% CIs from both methods overlapped (Table 5.7, Figure 5.6). The integrated model yielded similar results, but with lower point estimates for the camera-trap data: 1.48 (1.13 – 1.90) tigers per 100 km^2, and a higher point estimate using the genetics survey data: 1.89 (1.27 – 2.73) tigers per 100 km^2 (Figure 5.6, Table 5.7). The coefficient of variation for parameters using camera-trap data remained the same, with the exception of sigma, the shared parameter, which improved from 7% to 5%. The coefficients of variation for the parameters using the genetics survey data all improved, including a decrease in variability from 14% to 5% for the shared parameter, sigma, and a moderate decrease from 21% to 19% for abundance and density (Table 5.7).

DISCUSSION

This represents first genetic study to monitor the tiger population across the Terai Arc Landscape and to empirically estimate abundance and density based on genetic data for comparison to those of well-established camera-trap protocols and to combine information from both techniques in an integrated model for improving precision in density estimates (Royle and Young 2008, Royle et al. 2009b, Gopalaswamy et al. 2012a, Sollmann et al. 2013b). The main findings of this study were: 1) PCR amplification success was 86.3% and genotype accuracy was 86.7% for all tiger-positive samples ; 2) the core lowland forest area of CNP held and estimated 43-56 individuals, and the density estimate ranged from 2.27 to 2.44 tigers per 100 km^2; 3) differences the abundance and density estimates between two non-invasive data sources were very similar; 4) combining data from the two sources produced different and improved mean posterior estimates for both data sets; and 5) comparison of density estimates from all the density estimators from two non-invasive sources data collected at two different time-frames suggests a stable population over the two years (2009-2011).

Careful consideration is needed when conducing fecal sampling in order to reduce DNA degradation that can result from long delays from field collection to the processing of samples (Waits and Paetkau 2005). With my field-sampling design, I was able to collect scat samples less than 7 days old and quickly repeat sampling every 7 days, which allowed us to achieve a high sample size (*n* = 420) within a relatively short duration, while still fulfilling the closed population assumption. Improved field protocol, stringent laboratory conditions, an optimized panel of 8 polymorphic markers and sufficient PCR replicates (3 to 6) enabled us to reliably identify individuals from field-collected samples with varying DNA quality and quantity. My methods increased my PCR amplification rate, lowered genotyping errors, and more reliably obtained genotypes than in other recent non-invasive genetic sampling studies of felids based on a similar number of loci (61.2% for jaguars *P. onca*, Wultsch et al. 2014); 70% for Bengal tigers *P. tigris tigris*, Borthakur et al. 2011) and snow leopards *Panthera uncia*, Janecka et al. 2008). The criterion of $P_{(ID)sib} < 0.010$ (Mills et al. 2000, Waits et al. 2001) was high enough in my optimized panel of loci for resolving between related individuals with adequate statistical power.

My sampling efforts showed higher relative probability of capturing tigers present in the sampled area for cameras (81%) than for genetics (66%), but survey length was longer for cameras than genetics, 105 versus 42 days, respectively. Point estimates from both data sources do not represent the total estimated population size for CNP (GoN 2013, Karki et al. 2013), but represent estimates from the lowland forest in the core areas of Chitwan National Park. My results from both analytical platforms (CAPTURE and MARK) produced similar results, with higher estimates for cameras than for genetic data, but CIs overlapped. All of the models produced reasonably precise estimates of population abundance, with coefficients of variation (CV) < 22%. The lowest CV (< 13%) was produced by the M_h Jackknife estimator in Program CAPTURE, which has been shown to produce reasonable estimates of population size with tiger data in the past (Karanth and Nichols 1998, Mondol et al. 2009a). Abundance estimates from camera-trap versus genetic data were similar, suggesting a stable tiger population between the two sampling periods (2009 versus 2011) in the core lowland forest of CNP.

I did not perform a sensitivity analysis on the robustness of population parameter estimates (Mondol et al. 2009a) due to changes in recapture rates; however, the use of the maximum number of loci (8 loci in this study) produced stable estimates under the robust M_h-Jackknife estimator against the threshold of 6 loci based on $P_{ID(sibs)}$ (Waits et al. 2001). I note that the contribution of tiger cubs to the genetic sample size is likely negligible because I only included large scat sizes (Karanth and Sunquist 1995, Farrell et al. 2000) and did not include small scats that may have been from tiger cubs within the collected sample size. Thus, the likelihood of tiger cub captured and counted in population estimates is very low, and my estimates reflect population size accounting only for adult and sub-adult tigers (Karanth and Nichols 2002).

Of the four density estimators used in this study, tiger densities from SECR-ML and SCR-B models were similar (Gopalaswamy et al. 2012b), but much lower in comparison to buffer-strip method using ½ MMDM and FMMDM (Figure 5.4). Previous studies among carnivores also indicated that traditional ½ MMDM methods overestimate density compared to SECR methods (Obbard et al. 2010, Gerber et al. 2012, Karki et al. 2013, Sunarto et al. 2013a, Thapa et al. 2014), and this trend was similar for both of the data sets. Point estimates were similar, and the 95% confidence interval overlapped for both data sources, potentially suggesting stable density over the time period 2009-2011. However, SCR-B models were more precise (ave CV = 7%) than SECR-ML (ave CV = 28%), possibly due to a number of competing SECR-ML models and the inherent model uncertainties in the model-averaged estimates (Burnham and Anderson 2002, Borchers and Efford 2008).

Variability in distance moved to calculate MMDM was higher from camera-trap data than for the genetic data. This may result from the high recapture rates in camera data sets from numerous cameras, versus the highly clumped distribution of tiger scats. An advantage of SECR models is that they can incorporate issues related to spatial variability in detector locations, producing less biased and more precise density estimates (Royle et al. 2009b, Efford and Mowat 2014). Thus, understanding the potential pitfalls of traditional techniques, which may overestimate density with both the non-invasive sources, is crucial for managers to obtain reliable estimates and make objective assessments of the conservation status of a species at risk

(O'Connell et al. 2011, Gerber et al. 2012, Thapa et al. 2014). Therefore, the use of the SECR models may be more justified than traditional buffer-strip methods for both types of data sets.

Combining and sharing information between data sets may improve density estimates for tiger populations, particularly when one data set yields low detection rates, such as the genetics data set from this study, and when information from additional surveys can be added over time. As expected, sharing the spatial scalar parameter (sigma) between the two surveys, and allowing the basal encounter rate (λ) to differ between the surveys, generally improved precision for some survey-specific parameter estimates under a common SCR framework (Gopalaswamy et al. 2012a, Sollmann et al. 2013b). Thus, combining data from multiple surveys in which the scaling parameter remains unchanged but centers of activity can change, improved estimates in the integrated SCR model for the year where detection was very low and for the genetics survey technique (Gopalaswamy et al. 2012a, Sollmann et al. 2013b).

Gopalaswamy et al. (2012a) produced a single density estimate for tigers by combining two data sets collected in close temporal proximity, and Sollmann et al. (2013b) reported changes in the density estimates between time periods, which required open population models, an option unavailable to us as, I cannot match individuals identified in photographs to those identified later by fecal genotyping. However, by using the integrated SCR approach, I can easily compare differences in density estimates from one survey year to the next, even though two different survey methods were used, and effective trapping area, which would be expected to vary by year and method, is not known. In this study, the 95% CI for estimates for each survey type overlapped considerably, suggesting no detectable differences in tiger density between the two surveys conducted three years apart. This outcome has positive conservation implications, suggesting that the tiger population may be stable in the core lowland forest of Chitwan National

Park (Dhakal et al. 2014). However, three years may not be a suitable time-frame for estimating population growth for long-lived large carnivores. The true value of this integrated population model is it allows for updating the model with each additional year of data, using either survey method. As additional survey results are added every few years, the precision of estimates for each year should improve, and estimates from each year surveyed will be directly comparable. Thus, the updated model over a span of say, ten years may detect population growth trends that were not distinguishable over a three year span as precision improves and temporal scale becomes more appropriate in relation to the life-span of the target species.

In addition, through the use of an integrated SCR approach, survey efforts and costs for conservation each year can be stratified to address multiple objectives and immediate concerns. For example, fecal DNA genotyping is a powerful method for estimating population genetic diversity and assessing population health. However, fecal DNA genotyping is also expensive compared to camera-trapping surveys, and in my study did not improve information gained in the integration model compared to the independent camera-trapping model. In addition, genetic sampling can be species-specific, whereas camera deployment allows monitoring of a suite of predator as well as prey populations. But Fecal DNA data has a unique capability to analyses the genetic connectivity and historical demography, which camera trapping does not thus warrants their extended use. Thus, based on the integrated model for my study area, I would recommend the most survey years use camera-traps to monitor tiger density, and less frequent scat collection surveys could be used to monitor genetic diversity of the target tiger population every few survey periods. Because the density model used an integrated approach, the spatial capture-recapture data from the scat collection surveys can be readily substituted for the camera data in those years. This approach would reduce costs by using camera-trap surveys most years providing data to monitor general population parameters such as density, continually providing estimates comparable to baseline data to assess population trends, and maximize collection of data types and overall quality of data to meet population monitoring objectives.

Development of these advanced analytical frameworks employing spatially explicit capture-recapture (Royle and Young 2008, Royle et al. 2009a, Royle et al. 2009b, Royle et al. 2013) can give us more insight into the usefulness of both non-invasive data sources. Contingent upon a field design that permits CR analysis and a high degree of certainty in individual identification with fecal DNA samples, non-invasive genetic sampling likely can be improved by increasing sample size to obtain more recaptures, and this approach should be adopted instead of the adhoc survey techniques used in many genetic studies (Bhagavatula and Singh 2006, Roques et al. 2014). Additional analysis of genetic scat samples including prey content also can aid in obtaining additional information on the biology of the species (Farrell et al. 2000, Reddy et al. 2012a, Shehzad et al. 2012, Joshi et al. 2013, Sharma et al. 2013b).

This study highlights the potential use of a non-invasive genetic approach in population monitoring across the core area of Terai Arc Landscape and for comparing population estimates from camera-trapping to improve and complement the past efforts (GoN 2013, Karki et al. 2013, Thapa et al. 2014). Combining camera-trapping and genetic data can be beneficial in improving inference about population demographic parameters (Gopalaswamy et al. 2012a, Sollmann et al. 2013b). However, the choice of appropriate non-invasive techniques is contingent upon cost (laboratory), logistics, and expertise (Broquet et al. 2007). In the Terai Arc, successful population monitoring programs like the Tiger Census (Dhakal et al. 2014) and the Nepal Tiger Genome Project (NTGP 2014) can be integrated in analyses within an emerging SCR model framework (Efford 2004, Royle and Young 2008, Royle et al. 2009b, Gardner et al. 2010, Gopalaswamy et al. 2012a, Sollmann et al. 2013b). The new techniques are beneficial for improving estimates regarding the status of tiger populations to aid in achieving the goal of doubling the tiger population in Nepal (GTRP 2010).

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TABLES AND FIGURES

Table 5.1: Summary statistics for photographic and genetic capture-recapture data from the core lowland forest in Chitwan National Park, Nepal.

Survey Summary	**Cameras**	**Genetic**
Number of Stations	187	222
Sampling Days	105	42
Sampling Occasions	16	6
Survey Effort	2,821 trap-nights	1,172.5 km
Total number of individuals caught, M_{t+1}	41	31
Total number of captures	103	42
Number of individual animals caught once	17	17
Number of individual animals caught more than once	24	14
Survey Period	Jan-Mar, 2009	Nov-Dec, 2011

Table 5.2: Closure test and model selection (after Otis et al. 1978) for tiger population size estimation using genetic and photographic capture-recapture data from Chitwan National Park, Nepal in Program CAPTURE. DFS is the discriminant function score (model selection). The M_h shows the heterogeneity effect and the M_o shows the constant null model.

Data Type	**Closure Test**		**Individuals Caught (M_{t+1})**	**Total Captures (n)**	**Models**	**DFS**	**Capture Probability $\hat{p}$**	**Total Abundance $\hat{N}(SE)$**	**95% Confidence Interval (*CI*)**
	Z	***p***							
Camera	-0.527	0.30	41	103	M_h	1.00	0.23	56(7.54)	47-78
					M_o	0.86	0.30	43(1.83)	42-50
Genetic	-0.707	0.24	31	42	M_h	0.75	0.2857	49(6.39)	41-66
					M_o	0.87	0.2997	47(8.62)	37-73

Table 5.3: Summary of model selection results from tiger population estimates using photographic and genetic capture recapture data for tiger populations in program MARK. AICc represents Akaike's information criterion, corrected for the small sample size. The Δ AICc is the difference in AIC values between the top model and ith model in the set. Weight of support for each model is shown by the AICc weights (ω). $\widehat{N}$ represents the abundance estimate, while SE represents standard errors. The model averaged density estimates and standard errors are given in bold.

Data Type	**Model**	**AICc**	**Δ AICc**	**AICc Weights (ω)**	**Model Likelihood**	**Number of Parameters (k)**	**Abundance Estimate $\widehat{N}(SE)$**	**95% Confidence Interval**
Cameras	[M_{bh} (p(h).c(h)]	597.58	0	0.99	1	5	45.64(1.86)	44.27-53.75
	[M_o (p(.)=c(.)]	619.78	22.20	0.00	0	1	46.91(1.97)	44.87-53.71
	[M_b (p(.).c(.)]	620.44	22.86	0.00	0	2	45.42(1.56)	44.24-52.15
	[M_h (p(h)=c(h)]	621.80	24.21	0.00	0	2	46.91(1.97)	44.87-53.71
	[M_{ht} p(ht)=c(ht)]	624.94	27.36	0.00	0	31	51.25(3.84)	46.73-63.23
Genetic	[M_b (p(.).c(.)]	115.49	0.00	0.41	1.00	2	36.31(4.21)	32.86-53.44
	[M_o (p(.)=c(.)]	116.43	0.93	0.25	0.62	1	50.76(9.82)	39.14-81.24
	[M_t (p(t)=c(t)]	117.75	2.25	0.13	0.32	3	49.76(9.44)	38.67-79.23
	[M_{th}(p(th)=c(th)]	118.03	2.53	0.11	0.28	6	42.98(0.00)	42.97-42.97
	[M_h (p(h)=c(h)]	118.52	3.02	0.09	0.22	2	50.76(9.82)	39.14-81.24
					Model averaged results from top 5 models		**43.84(9.83)**	

Table 5.4: Traditional density estimates based on ½ MMDM and FMMDM with the estimated population size from Program CAPTURE and MARK. MMDM: mean maximum distance moved (MMDM for cameras: 9.4 km; MMDM for genetics: 9.2 km), MCP: Minimum Convex Polygon, M_{t+1}: number of animal captured, and ETA: Effective Trapping Area.

Data Type	**MCP (km^2)**	**M_{t+1}**	**Estimator**	**Abundance $\hat{N}$ (SE)**	**ETA**	**Buffer Type**	**Density $\hat{D}$ (SE)**
Camera	359.2	31	Capture	56.00 (7.54)	1,092	½ MMDM	5.12 (0.85)
Genetics	324.9	41	Capture	49.00 (6.39)	1,254		3.90 (0.83)
Camera	359.2	31	Mark	45.64 (1.86)	1,092		4.01(0.64)
Genetics	324.9	41	Mark	43.84 (9.83)	1,254		3.49 (1.04)
Camera	359.2	31	Capture	56.00 (7.54)	1,395	FMMDM	4.17 (0.44)
Genetics	324.9	41	Capture	49.00 (6.39)	1,798		2.72 (0.52)
Camera	359.2	31	Mark	45.64 (1.86)	1,395		3.27 (0.31)
Genetics	324.9	41	Mark	43.84 (9.83)	1,798		2.43 (0.64)

Table 5.5: Model selection results from tiger density estimates using photographic and genetic capture-recapture data from the lowland forest of Chitwan National Park, implemented in Program DENSITY using the hazard rate detection function. g_o is the capture probability at home-range center. s is the spatial scale parameter of the capture function. h_2 is the 2-class finite mixture probability for heterogeneity. Akaike's Information Criterion adjusted for small sample size is represented by AICc, w_i represents Akaike weight, $\widehat{D}$ is the estimated density (tigers per 100 km^2), and SE is the standard error. The model averaged density estimates and standard errors are given in bold.

Data Type	**Model**	**AIC_c**	**ΔAIC_c**	**w_i**	**$\widehat{D}$ (SE)**
Camera-trap	g0[.]s[.]	1895.61	0	0.28	2.56±0.47
	g0[bh2]s[h2]	1896.35	0.74	0.19	2.65±0.56
	g0[b]s[.]	1897.08	1.47	0.13	2.72±0.55
	g0[.]s[bh2]	1897.55	1.94	0.11	2.99±0.75
	g0[.]s[b]	1898.01	2.4	0.08	2.61±0.59
	g0[bh2]s[bh2]	1898.77	3.16	0.06	2.93±0.84
	g0[h2]s[b]	1899.01	3.4	0.05	2.52±0.54
	g0[bh2]s[.]	1899.17	3.56	0.05	2.77±0.58
	Model averaged results from top 8 models				**2.55±0.59**
Genetic	g0[.]s[b]	671.01	0	0.42	2.68±0.81
	g0[b]s[b]	672.26	1.25	0.23	2.59±0.78
	g0[b]s[.]	673.44	2.43	0.13	2.91±0.90
	g0[.]s[.]	673.6	2.59	0.12	3.52±1.0
	g0[h2]s[b]	676.74	5.73	0.02	2.67±0.81
	Model averaged results from top 5 models				**2.57±0.88**

Table 5.6: The posterior summaries from the Bayesian spatially explicit capture recapture (SCR-B) models, and the tiger density estimates, implemented in Program SPACECAP for tigers from the lowland forest of Chitwan National Park for photographic and fecal datasets. Sigma (σ) represents the range parameter of the species while lambda (λ_0) is the intercept of the expected encounter frequency. Psi (Ψ) is the ratio of the number of animals present within the state space, S, to the maximum allowable number. Nsuper (N) is the number of activity centers in S. While, density (D, tigers per 100 km^2) is Ns divided by S. A Geweke statistic |z score| of greater than 1.6 implies lack of convergence.

Data Type	**Parameter**	**Posterior Mean**	**Posterior SD**	**95% Lower HPD Level**	**95% Upper HPD Level**	**Geweke's Statistics** **|z score|**
Camera-trap	σ	5072.14	345.02	4402.63	5752.74	0.1895
	λ_0	0.03	0.00	0.02	0.04	0.3647
	Ψ	0.27	0.04	0.19	0.36	-0.4854
	N	79.39	9.95	60.00	98.00	-0.5945
	D	0.02	0.00	0.02	0.03	
Genetic	σ	8442.86	1298.95	6218.87	11038.75	0.1223
	λ_0	0.01	0.00	0.00	0.01	0.7222
	b	2.96	0.35	2.30	3.65	-0.9012
	Ψ	0.26	0.06	0.15	0.38	-0.9543
	N	72.40	14.91	45.00	101.00	-0.9919
	D	2.23	0.46	1.44	3.17	
	$p1$	0.01	0.00	0.00	0.01	
	$p2$	0.11	0.03	0.06	0.17	

Table 5.7: Posterior summary statistics and tiger density estimates from independent and integrated SCR models from the lowland forest of Chitwan National Park, Nepal. Models were implemented in JAGS using the rjags package in R and convergence is indicated by Gelman-Rubin diagnostic parameters ≤ 1.1. Sigma (σ) is the scaling parameter representing movement of an individual around an activity center, lamda (λ_0) is expected encounter frequency at an activity center, psi (Ψ) is the proportion of estimated individuals to structural zeroes resulting from data augmentation,. N (N) is the number of activity centers in S, while, Density (D, tigers per 100 km^2) is N divided by S. Coefficients of variation were calculated by dividing the standard error of a posterior distribution of a parameter by the mean.

Data Type	**Parameter**	**Posterior Mean**	**Posterior SD**	**95% Lower HPD Level**	**95% Upper HPD Level**	$\hat{R}$	**CV**
Cameras	σ	4.70	0.31	4.14	5.35	1.0	0.07
	λ_0	0.04	0.01	0.03	0.05	1.0	0.25
	Ψ	0.45	0.07	0.32	0.60	1.0	0.16
	N	108.47	15.38	81.00	142.00	1.0	0.14
	D	1.73	0.25	1.30	1.89	1.0	0.14
Genetics	σ	8.05	1.16	6.21	10.74	1.0	0.14
	λ_0	0.009	0.002	0.005	0.015	1.0	0.22
	Ψ	0.36	0.08	0.22	0.54	1.0	0.22
	N	85.14	18.37	55.00	127.00	1.0	0.21
	D	1.36	0.29	0.88	2.03	1.0	0.21
Integrated Model	σ	5.48	0.31	4.91	6.11	1.0	0.05
	λ_{cameras}	0.03	0.006	0.02	0.05	1.0	0.20
	$\lambda_{\text{genetics}}$	0.01	0.003	0.009	0.02	1.0	0.30
	Ψ_{cameras}	0.39	0.06	0.28	0.51	1.0	0.15
	Ψ_{genetics}	0.49	0.10	0.32	0.72	1.0	0.20
	N_{cameras}	92.42	12.47	71.00	119.00	1.0	0.13
	N_{genetics}	118.45	22.79	81.00	171.00	1.0	0.19
	D_{Cameras}	1.48	0.20	1.14	1.90	1.0	0.14
	D_{Genetics}	1.89	0.36	1.27	2.73	1.0	0.19

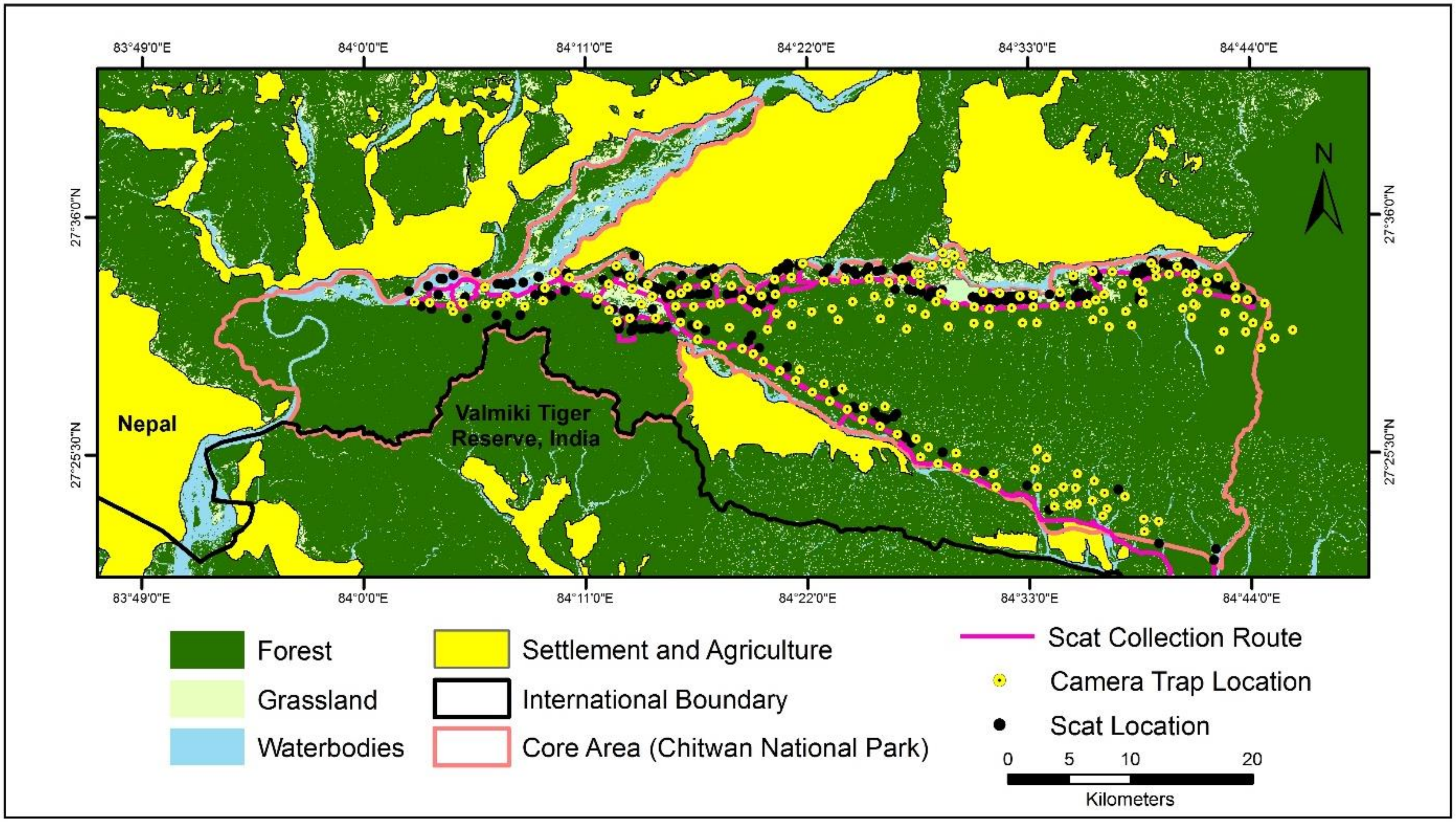


Figure 5.1: Study area showing camera-trap locations (black dots) and scat location (yellow dots) along with search routes (black lines) across the lowland forest in core area of Chitwan National Park.

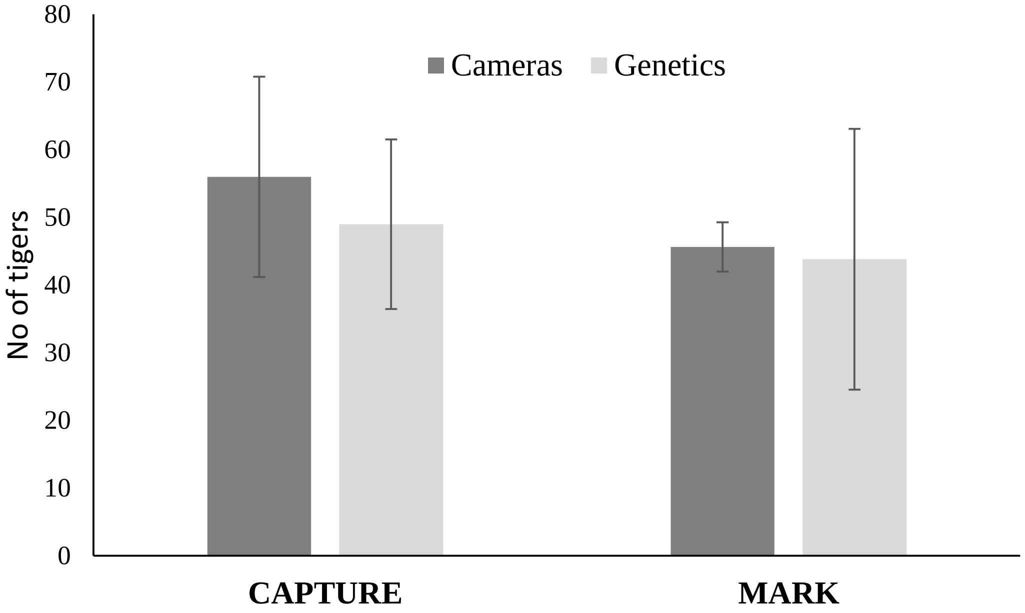


Figure 5.2: Comparative abundance estimates of tigers across the lowland forest in Chitwan National Park, Nepal using a photographic versus a genetic capture-recapture framework implemented in software Programs CAPTURE and MARK.

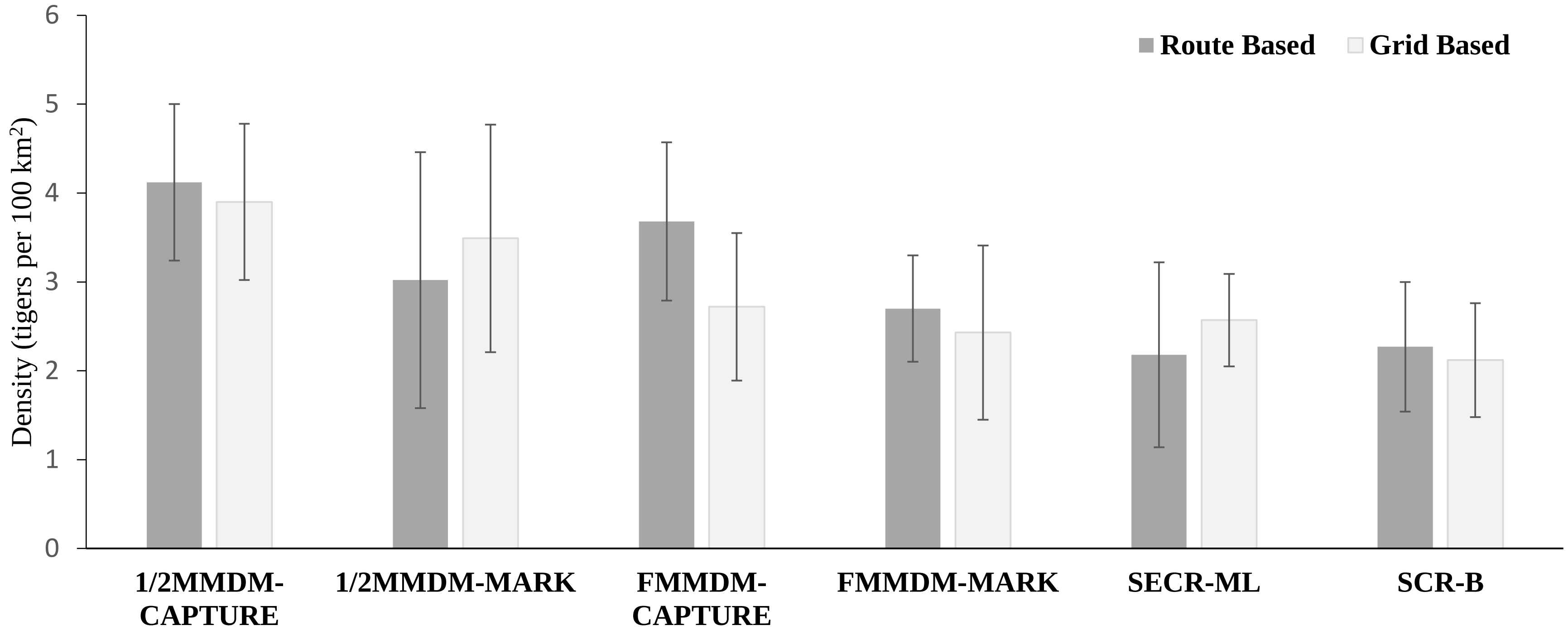


Figure 5.3: Comparative density estimates between the choices of "stationary trapping devices" (grid versus segment levels) with genetic data implemented with traditional (½MMDM and Full MMDM) models and spatially explicit maximum likelihood (SECR-ML) and Bayesian (SCR-B) models. Error bars represent 95% CIs. MMDM: Mean Maximum Distance Moved.

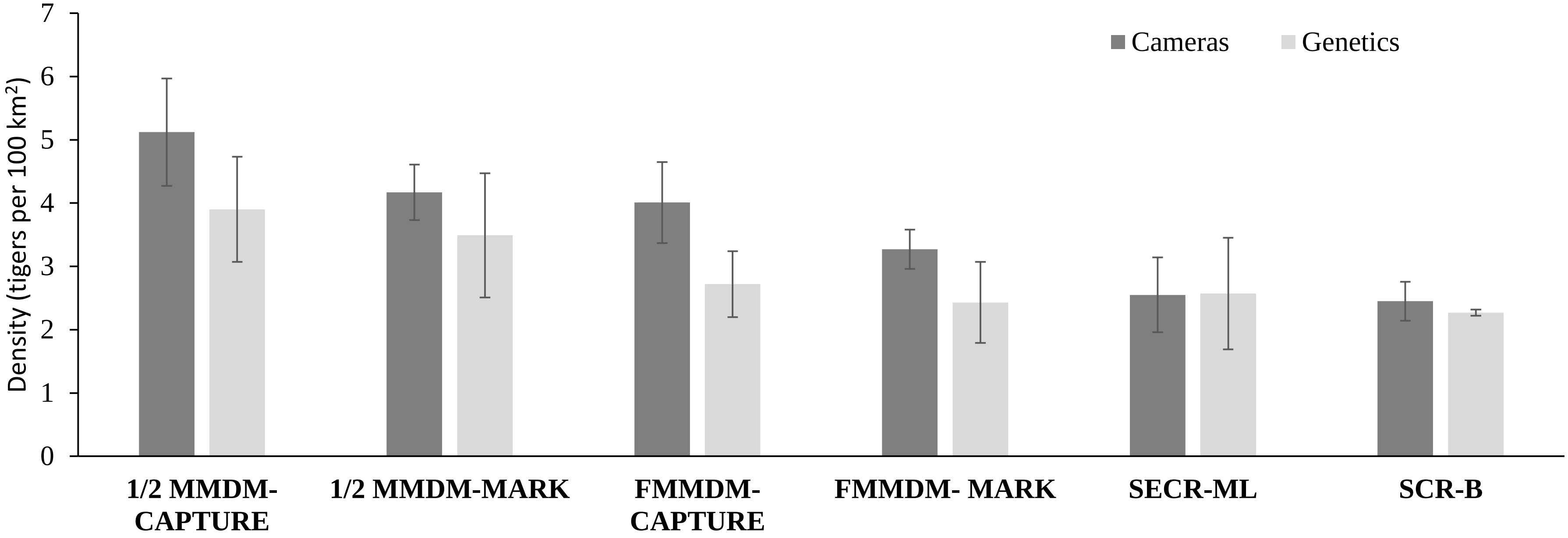
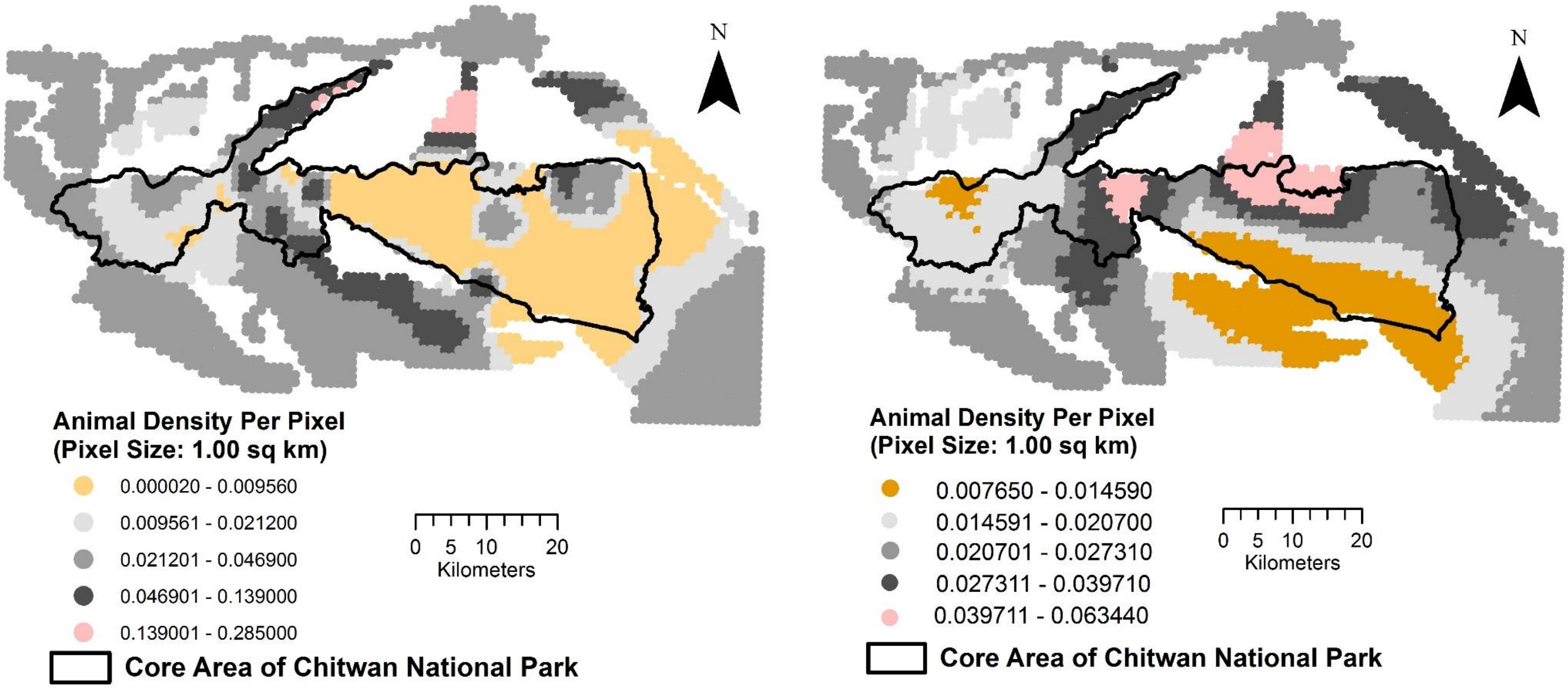


Figure 5.4: Comparative density estimates with photographic and genetic data implemented with traditional (½ MMDM and Full MMDM) models and spatially explicit maximum likelihood (SECR-ML) and Bayesian (SCR-B) models. Error bars represent 95% CIs. MMDM: Mean Maximum Distance Moved.



a) Based on camera-trap data

b) Based on genetic data

Figure 5.5: A pixelated density map showing the relative tiger densities per pixel of size 1 km^2 using (a) camera-trap data and (b) genetic data, prepared in ArcGIS 10.1.

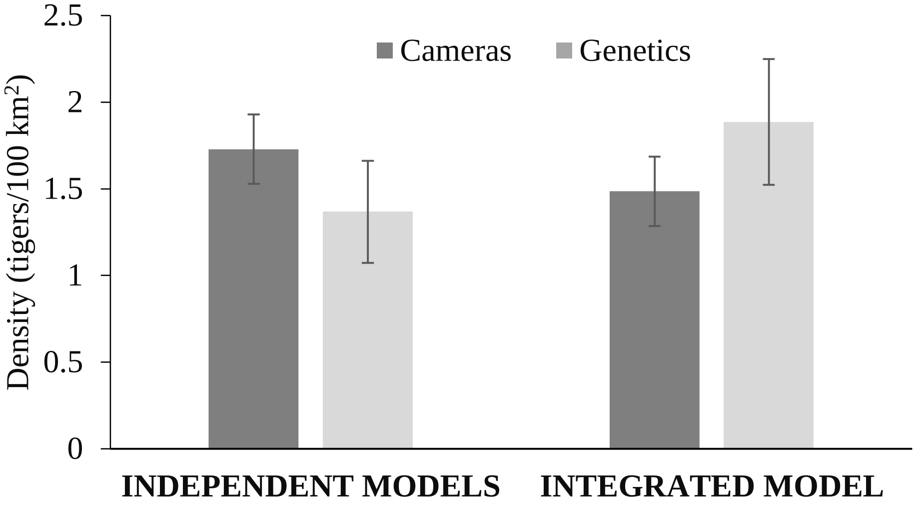


Figure 5.6: Comparative density estimates with photographic and genetic data implemented with the Integrated SECR models implemented in JAGS using the rjags package in R. The 95% Bayesian confidence interval overlaps more than half the margin of error for each density estimators between choices of array types. Independent models estimated density separately using independent camera and genetic. The integrated model combined both camera and genetic data sets with a shared parameter, sigma, estimating animal movement around an activity center.