

DISSERTATION

CONSERVING TIGERS BEYOND PROTECTED AREA BOUNDARIES:
THE SPATIAL ECOLOGY OF TIGERS AND THEIR PREY IN FARMLANDS IN
NORTH INDIA

Submitted by

Rekha Warriar

Graduate Degree Program in Ecology

In partial fulfillment of the requirements

For the Degree of Doctor of Philosophy

Colorado State University

Fort Collins, Colorado

Summer 2019

Doctoral Committee:

Advisor: Barry Noon

Larissa Bailey
Kevin Crooks
Tara Teel

Copyright by Rekha Warriier 2019

All Rights Reserved

ABSTRACT

CONSERVING TIGERS BEYOND PROTECTED AREA BOUNDARIES: THE SPATIAL ECOLOGY OF TIGERS AND THEIR PREY IN FARMLANDS IN NORTH INDIA

Terrestrial, large mammalian carnivores have experienced dramatic declines in their ranges worldwide, and today largely occur within landscapes dominated and modified by humans. Within these landscapes, large carnivore conservation has largely been focused on protected areas, a practice predicated on the rarely tested assumption that the surrounding human modified land (matrix) has little or no carnivore conservation value. While protected areas are critical to the persistence of carnivore populations, neglecting the human modified matrix has two consequences: 1) it leaves matrix areas that provide important resources such as dispersal routes, seasonal prey, and breeding areas, vulnerable to further modification and loss on account of land-use change, and 2) it treats carnivore presence within the matrix as anomalous occurrences, resulting in a misinterpretation of carnivore resources needs and the drivers of human-carnivore conflicts. To effectively address these challenges, conservation efforts need to be expanded beyond the boundary of protected areas. This requires an understanding of the spatial ecology of carnivores and their prey in the human dominated matrix. In addition, it requires an understanding of the scale and nature of the interactions of these species with humans.

There exists a large body of literature on the ecology of carnivores and their herbivorous prey species. Most of these studies however, have been conducted within protected areas free of

human disturbance. Consequently, very little is currently known about the ecology of these species within human modified areas. To address this knowledge gap, between Dec 2015 and Aug 2016, I conducted a study examining the spatial ecology of tigers (*Panthera tigris*), their herbivorous prey species, and their interactions with humans within matrix areas of the Central Terai Landscape (CTL) in India. The CTL, a tiger conservation landscape of global significance, is also one of the most densely human-populated areas within the tigers' distributional range in India. Within the CTL, I selected a 1200 sq. km agricultural corridor region separating two protected areas (Dudhwa tiger reserve and Pilibhit tiger reserve) as my intensive study site. The study area is comprised of the perennial Sharada River flowing through its center, sugarcane farmlands, riparian grassland and forest areas, dense human settlements, and associated infrastructure like roads and canals. Within this study area, I examined the environmental and anthropogenic factors driving space use by tigers and their prey. I recorded detections of these species within 94 grid cells, each measuring 1.6 X 1.6 km, and distributed in a spatially balance random fashion across the study area. I recorded detections using three different survey methods; Farmer Surveys, Sign surveys, and Camera surveys. To determine the influence of vegetative cover on species space use, I repeated these surveys in the winter (Dec-Feb), summer (Mar-May) and monsoon (Jun-Aug) seasons. These seasons approximately coincide with the planting and harvest cycle of sugarcane, the most dominant agricultural crop in the study area. Winter, when the sugarcane crop is ready for harvest, marks a period of very high resource and cover availability for tigers and their prey. The crop is completely harvested by the end of the summer season, consequently, this season is characterized by very low cover availability in the study area. Finally, the monsoon season is characterized again by increasing cover availability and the flooding of many portions of the study area, a result of the Sharada River breaching its banks. In

addition to estimating space use patterns, I was also interested in determining the relationship between habitat use patterns of different species and their interactions with humans. Specifically, I was interested in determining how human perceptions of the spatial distribution of tiger and prey species, and peoples' interactions with them, matched the estimated distribution patterns of these species within the study area. To achieve this, I conducted detailed interviews, within a subset of surveyed cells, with farmers who practiced agriculture within these sample units. Based on these interview surveys, I estimated how individual farmers perceived conflicts with different species found in the study area and also determined their attitudes towards species and their conservation.

In Chapter 1, I present findings from fitting dynamic occupancy models to detection data on tigers. I examined the influence of resource availability and anthropogenic disturbance on the spatial and seasonal patterns of space use by tigers. I found that, in the winter season, the study area experienced high use by tigers, and the probability that a cell was used by tigers was driven primarily by the availability of cover, the length of drainage features, the extent of human presence and the distance of the cell to a protected area boundary. Between survey seasons, the probability that a used cell will transition to not used by tigers was most strongly related to the distance of the cell from a protected area boundary and the availability of permanent water. No new cells were to be used by tigers in the summer and monsoon season. Collectively, my results suggest that in the winter season tigers use the study area extensively and occur up to six kilometers beyond the boundary of protected areas. Space use by tigers in the matrix is driven primarily by the avoidance of humans as evidenced by their selection of areas with high cover and minimal human presence (e.g., small or few villages). These results, in conjunction with my field observations, suggest that tiger presence in the matrix areas is not an irregular or

unpredictable occurrence. Rather, these areas serve not only as dispersal routes and seasonal habitats, but also provide prey resources and breeding areas for tigers. Consequently, my results suggest an urgent need to expand the scope of conservation efforts in tiger landscapes to include the agricultural matrix. For the CTL, these efforts should include the establishment of eco-sensitive zones that extend up to 6 km beyond protected area boundaries and the inclusion of land-sharing based agricultural practices within those areas where tiger conservation is a priority.

In Chapter 2, I modeled the space use patterns of multiple herbivorous tiger prey species focusing specifically on three species – hog deer (*Axis porcinus*), wild boar (*Sus scrofa*) and nilgai (*Boselaphus tragocamelus*). I determined the environmental correlates that explain the spatio-temporal distribution patterns of these species within farmlands by fitting dynamic occupancy models to their detection data. I found that the three herbivore species use areas within farmlands that are structurally similar to their known native habitats. Unlike tigers, the three herbivore species did not demonstrate strong seasonality in their use of matrix areas. All three species used farmlands with high probability throughout the study period. Farmlands however, do not offer habitats to the majority of mammalian herbivore species found in the CTL. Species associated with forested habitats such as chital (*Axis axis*), and species associated with native tall grassland habitats such as swamp deer (*Cervus duvaucelli*) were detected on only two of the 94 sites surveyed with camera traps. Blackbuck (*Antilope cervicapra*), a species thought to occur largely within unprotected grassland habitats in the study area, were also never detected in farmlands. In addition, I found that human perceptions about herbivore species richness within farmlands, and their perceptions about species' distributions and conflict potential, differed significantly from my estimates of the distribution of these species. In particular, farmers perceived wild boar to be the most widely distributed herbivore species in the area, although the

species was not more widespread than nilgai and hog deer. In addition, community members perceived chital and swamp deer to be more widely distributed than was estimated based on the detections of these species using camera traps. My results suggest that current agricultural practices significantly fragment the landscape for most mammalian herbivores in the CTL even as they provide habitats for a few herbivore species. I found that studies based on interviews of community members and self-reported conflict surveys are not a reliable means to estimate the distribution and diversity of species within farmlands.

In Chapter 3, I present an analytical framework for jointly modeling the spatial distribution of a species and its spatial interaction probabilities with humans. This framework provides estimates of the probability with which conflict with a species is reported at sites where the species is present (true-positive conflict reporting) or absent (false-positive conflict reporting). I fit the model to wild boar detection data in the CTL and self-reported conflicts with the species by farmers. Results demonstrated that farmers falsely reported conflicts with wild boar with a probability of nearly 63 %. Wild boar use agricultural landscapes with a probability of 27 % in the CTL, and at sites where the species occurs, farmers report conflict with the species with a probability of 87 %. In addition, using a simulation study I provide practical recommendations for designing studies aimed at jointly estimating species space use and human-wildlife interaction probabilities. By allowing the estimation of conflict reporting probabilities to be conditional on species occupancy, my model represents an important step towards estimating the risk associated with farmers sharing space with other wildlife species. As human populations expand and encroach further into wildlife habitats, understanding these risks will be key to implementing effective conservation measures.

ACKNOWLEDGEMENTS

This study was made possible by the support and encouragement offered by a number of people and organizations. I would like to start by thanking my advisor Dr. Barry Noon, for his support and encouragement through the course of my doctoral work. My Ph.D committee comprising of Dr. Larissa Bailey, Dr. Kevin Crooks and Dr. Tara Teel provided invaluable guidance and technical support. I am grateful to, the Uttar Pradesh Forest Department who provided the necessary permits for this research. In particular, I am thankful for the support provided by Mr Sanjaya Singh (CCF, Dudhwa Tiger Reserve), Mr Mahaveer Koujalagi (DFO, DUDhwa Tiger Reserve) and Mr Sanjaya Biswal (DFO, South Kheri). In addition, I would like to extend my sincere gratitude to the wildlife wardens, rangers and forest guards of Dudhwa Tiger Reserve for the help they extended during the study.

The research would not have been possible without the support offered by the members of the WWF-India, TAL-UP landscape office. I extend my gratitude to Dr Mudit Gupta, for facilitating this research. In addition Mr. Dabeer Hasan, Dr Kamlesh Maurya and Mr Rohit Ravi provided invaluable support for this work. Support in field was provided by my excellent and resourceful team comprised of Mr. Rambharose, Mr. Mukhtiar Singh, Raja and Mr. Radheshyam. In addition, I would like to thank. Shwetha Nair and Ms. Shivai Upadhyayula who helped with data collection at various stages.

The research would not have been possible without the help of the farmers and land owners who permitted us to conduct surveys on their property and also ensured the safety of camera traps deployed on their lands. I would also like to acknowledge here the community members of the landscape for their generosity and warm hospitality. The dissertation project was

funded by WWF-India, the Center for Collaborative Conservation at Colorado State University and the Rufford Foundation. I am grateful for the support provided by Dr. Pranav Chanchani who kindly made available 30 camera traps that were central to data collection. He also provided extensive inputs on logistics and study design through the course of the research.

I am thankful for the opportunity to study and learn new skills at CSU, and the wonderful opportunities to interact with the FWCB and GDPE community. In particular, I would like to thank Dr. Ken Wilson and Dr. Kathryn Stoner, for enabling my graduate studies here at CSU. I will always cherish the time I shared with my fellow Noon-lab members, Vincent Landau, Valerie Steen, Jason Tack, Jess Shyvers, Rick Scherer, Pranav Chanchani and Helen Sofaer.

Many people contributed towards making Fort Collins a home away from home for me. Foremost among them are Paige and Barry Noon, who offered me a loving home and family (and adorable dogs Marley & Bodhi) to come back to at the end of a long day at school. I learnt my most valuable lessons, including how to live with large hearted generosity by watching them live and share their lives. I hope to emulate their example in my own life. I would like to thank my wonderful partner Danny Martin, for his love, support and his infectious love of nature.

I dedicate this dissertation to my parents, and my brother. I am where I am today, on account of the love and support of my parents who have patiently endured my long absences from home. I thank them for encouraging me to pursue my passions. Finally, I would never have discovered the great outdoors, if my brother Balram had not convinced me to hike the Western Ghats with him.

TABLE OF CONTENTS

ABSTRACT.....	ii
ACKNOWLEDGEMENTS.....	vii
CHAPTER ONE: FARMALNDS OFFER SEASONAL HABITATS TO TIGERS IN A FRAGMENTED & HUMAN-DOMINATED LANDSCAPE IN INDIA	1
Introduction.....	1
Methods.....	4
Results.....	13
Discussion.....	20
LITERATURE CITED.....	25
CHAPTER TWO: ECOLOGICAL DRIVERS OF HERBIVORE SPACE USE & HUMAN- HERBIVORE INTERACTIONS IN FARMLANDS IN THE CENTRAL TERAJ LANDSCAPE, INDIA	28
Introduction.....	28
Methods.....	32
Results.....	42
Discussion.....	48
LITERATURE CITED.....	56
CHAPTER THREE: A FRAMEWORK FOR ESTIMATING HUMAN-WILDLIFE INTERACTION PROBABILITIES CONDITIONAL ON SPECIES OCCUPANCY.....	59
Introduction.....	59
Methods.....	63
Results.....	71
Discussion.....	75
LITERATURE CITED.....	79
APPENDIX 1.1.....	82
APPENDIX 1.2.....	85
APPENDIX 1.3.....	90
APPENDIX 1.4.....	94
APPENDIX 2.1.....	96
APPENDIX 2.2.....	99
APPENDIX 3.1.....	104

CHAPTER ONE

FARMLANDS OFFER SEASONAL HABITATS TO TIGERS IN A HUMAN-DOMINATED & FRAGMENTED LANDSCAPE IN INDIA

Introduction

Designation of protected areas (PA) is the preferred means for species conservation efforts worldwide (Gray et al., 2016). The global PA network has been instrumental in stemming the declines of many species, particularly large carnivore species such as tigers (*Panthera tigris*) and lions (*Panthera leo*) by affording protection to critical breeding habitats and protecting their populations from illegal harvest. As human pressures on land increase, and climate change shifts the spatial distribution of suitable habitats, the narrow focus on PA-based conservation measures is unlikely to be adequate to ensure the persistence of large carnivores into the future (Stephens et al., 2015). For example, to ensure the long-term persistence of large carnivores, the expansion of the worldwide network of PAs has been identified as a vital goal (Di Minin et al., 2016). This is a daunting task, especially in countries where human population growth places competing demands on land (Crist et al., 2017). Moreover, as a result of their wide-ranging movements and dispersal needs, large carnivore species face many risks within the surrounding landscape matrix and beyond PA boundaries. The loss of functional connectivity between isolated populations within PAs and human-carnivore conflicts are two significant challenges that arise because of an increase in human population and urbanization within the matrix (Ripple et al., 2014). Ensuring the persistence of large carnivores into the future requires the expansion of conservation measures beyond PAs. To develop a more comprehensive conservation strategy requires a more

detailed understanding of how large carnivores use the human dominated matrix (Di Minin et al., 2016).

Much of what is known about the spatial ecology of large carnivores stems from well-studied populations within PAs (Ghosal et al., 2013; Stephens, 2015). As a result, there exists major gaps in our understanding of the ecology of large carnivores in matrix areas, especially from agricultural landscapes (Ferreira et al., 2018). This knowledge gap impacts carnivore conservation efforts in multiple ways by: 1) hindering our ability to proactively protect lands outside PAs that may serve as critical habitats or corridors, 2) confounding our understanding of the drivers of human-carnivore conflicts and impacting our ability to devise long-term conflict prevention and mitigation measures, 3) precluding the inclusion of carnivores in the discourse on how agricultural production can be reconciled with biodiversity conservation (Phalan et al., 2011), and 4) not allowing us to fully understand the functional role of carnivores in human dominated landscapes (Brackowski et al., 2018).

We conducted a study examining the use of farmland areas by tigers to address some of these knowledge gaps. Expanding conservation actions beyond PA boundaries is especially vital to the long-term persistence of tiger populations. Nearly 70% of the global tiger population occurs within India (Jhala et al., 2015), the second most populous nation in the world. Unfortunately, the existing network of PAs in India encompass only a fraction of the landscape necessary to sustain viable tiger populations. For example, the average size of a tiger reserve in India is 300 km² (Karanth and Nepal, 2012), whereas the median home range of a single adult male tiger is 160 km² (Chundawat et al., 2016). While most PA's supporting tiger populations in India are widely separated from each other, to date they continue to remain functionally connected via the movement of tigers through a matrix of unprotected, agricultural and,

community owned lands (Thatte et al., 2018). Besides dispersal movements, areas adjacent to PA's with dense vegetative cover and wild prey also offer seasonal habitats to tigers in many landscapes (Athreya et al., 2014; Karanth, 2016) and may increase the effective size of neighboring PAs.

Matrix areas surrounding protected parks worldwide, and particularly in India, are experiencing accelerated human population growth rates and land-use alterations (DeFries et al., 2007) (Wittemyer et al., 2008). The presence of tigers amidst dense human populations increases the probability of negative human-tiger interactions, leading to livestock, human, and tiger casualties (Goodrich, 2010). However, conversion of matrix habitats to land-use types more resistant to tiger use and movement reduces matrix permeability and results in a net loss of carnivore habitat (Crooks et al., 2011). Existing conservation initiatives focused solely on PA management in Indian tiger landscapes do not comprehensively address these challenges.

We documented the space use probabilities of tigers in the agricultural corridor between two protected areas in the Central Terai Landscape (CTL) in northern India. Our objective was to determine the spatio-temporal patterns of matrix use by tigers and the underlying environmental drivers of this use. This information is needed to inform land conservation measures such as the need for and size of eco-sensitive zones (ESZ) around PAs. In India, ESZs are mandatory buffer zones, extending up to 10 km around protected areas as per the directive issued by the Ministry of Environment and Forests (Banerjee et al., 2010). Land-use alterations and developmental activities are regulated within ESZs with the explicit intention of reducing adverse human impacts on native wildlife. While these zones constrain land conversion, the ESZ notification also includes provisions to promote sustainable agricultural practices within its boundaries. In addition, information on matrix use when viewed in conjunction with locations of human-tiger

conflicts can help clarify the circumstances under which humans and tigers may safely overlap without conflicts. This information is critical to determining long-term conflict prevention measures.

Estimating habitat use probabilities requires detecting tigers when, and where, they use the surrounding matrix. Unfortunately, conventional, non-invasive species detections methods such as camera trapping and sign-encounter surveys are characterized by low detection probabilities for tigers because of the species cryptic behaviors and low densities. We therefore used a novel sampling strategy to generate detection/ non-detection data for tigers in our study area by combining camera trapping and sign surveys with interview surveys of farmers engaged in agricultural within the matrix (Zeller et al., 2011). While interview surveys are cost-effective and potentially associated with higher detection probabilities for elusive species, they are prone to false-positive detection errors which can bias estimates of habitat use and its drivers (Pillay et al., 2011). To address these potential biases, we applied dynamic occupancy models that corrected for false positive detection errors (Miller et al., 2013). We discuss the implications of our results for tiger conservation in the CTL and in broadening our understanding of the importance of the human dominated agricultural matrix in sustaining populations of tigers in north India.

Methods

Study Area

Our study was conducted within the Central Terai Landscape (CTL) in the state of Uttar Pradesh in north India. The study area was a 1550 km² agricultural region lying between two tiger reserves-Dudhwa Tiger Reserve (Dudhwa National Park and Kishanpur Wildlife Sanctuary) and Pilibhit Tiger Reserve (PTR) and bounded on the north by the India-Nepal international

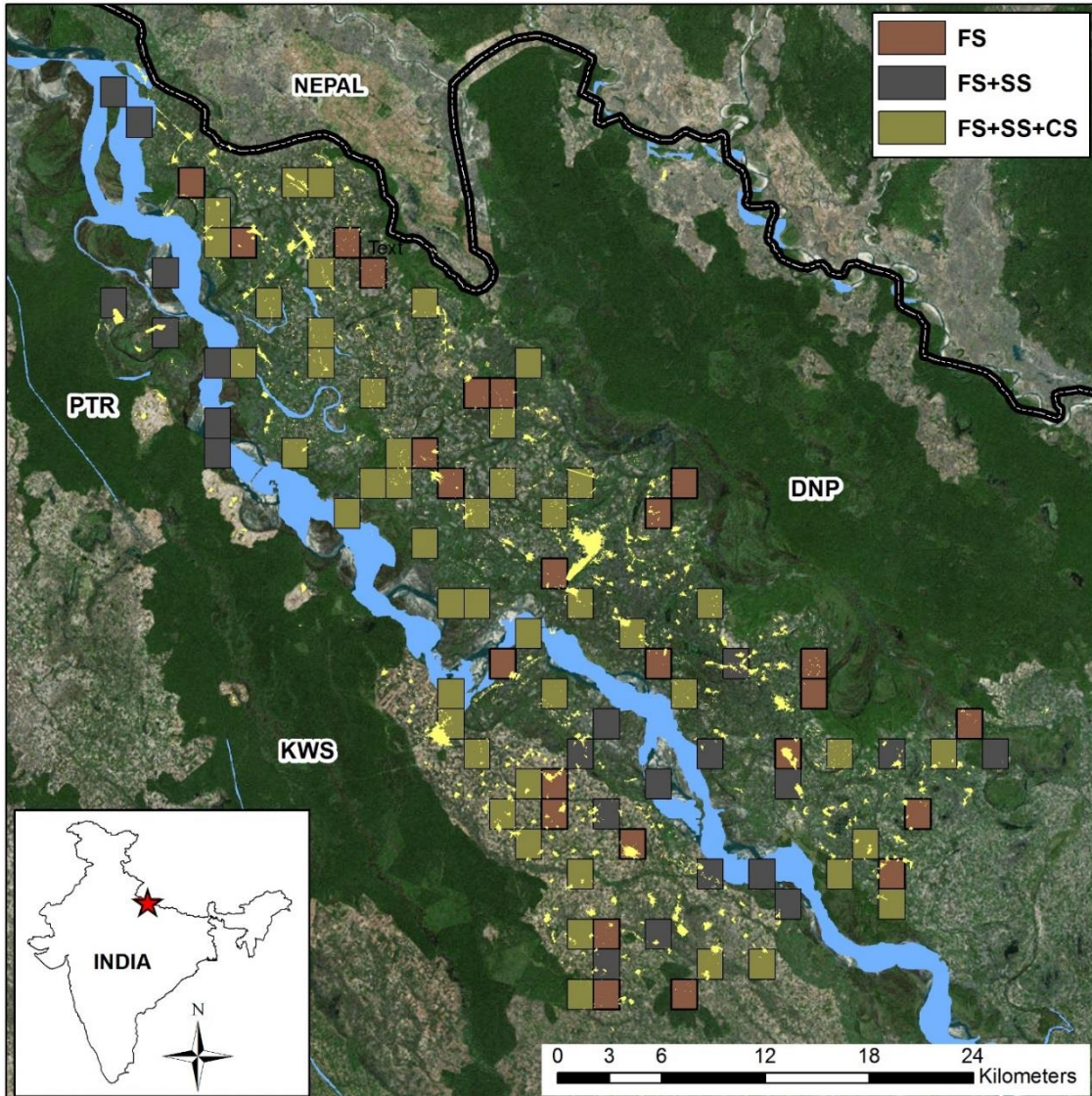


Figure 1.1: Study area and sampling design. The study area was the agricultural matrix separating Pilibhit Tiger Reserve (PTR), Kishanpur Wildlife Sanctuary (KWS) and Dudhwa National Park (DNP). In the winter season, a total of 94 randomly selected 2.6 km² cells were surveyed. A subset of these cells was surveyed in the summer (91 cells) and monsoon seasons (85 cells). Cell colors indicate the survey methods applied during each sampling season (FS-Farmer surveys; SS-Sign surveys; CS-Camera surveys). The black and white dashed line represents the international border between India and Nepal and features in blue represent water bodies associated with the Sharada River system.

border (Figure 1.1). The area is comprised primarily of extensive sugarcane agriculture, dense human settlements, and remnant patches of riparian habitats associated with the Sharada River. These riparian habitats lie within the jurisdiction of the North and South Kheri Forest Division and are designated as multiple-use forests allowing harvest of forest resources. The remaining

land within the study area is comprised of privately-owned agricultural land, village clusters, and small towns; the average human population density is 500/km² (Chandramouli, 2011). The area is subject to humid sub-tropical climatic conditions with four dominant seasons: summer (April-June), monsoon (July-September), post-monsoon (October-November), and winter (December-March). During the monsoon season substantial portions of the area experienced flooding (Midha and Mathur, 2014). Besides tigers, the landscape supports multiple species of threatened fauna such as the greater one-horned rhinoceros (*Rhinoceros unicornis*), swamp deer (*Cervus duvaucelli duvaucelli*), hog deer (*Axis porcinus*) and Asian elephants (*Elephas maximus*).

Study Design & Field Methods:

We estimated the space-use patterns of tigers and other large mammals within the study area using a spatially balanced sample of 94 randomly selected 1.6 km x 1.6 km cells (Figure 1.1), chosen using Generalized Random Tessellation Stratified (Stevens and Olsen, 2004). We were interested in how tigers use privately-owned lands and multiple-use areas, so we excluded areas that overlapped protected areas from our sampling frame. To determine how tiger space-use changed with available crop and vegetative cover, we conducted repeated surveys over three survey seasons defined according to the growth and harvest cycle of sugarcane, the dominant crop in the matrix. Seasons were defined as: winter/high cover, summer/low cover and monsoon/moderate cover. Survey seasons coincided with the prevailing climatological seasons, characterized by marked differences in vegetation growth and cover, temperature, and precipitation (Table 1.1).

Each season, we employed three different survey methods: farmer surveys (FS), animal sign surveys (SS) and camera surveys (CS; Table 1.1). Farmer surveys (FS) involved

independent interviews of 1-12 farmers directly encountered while walking a random path within each cell.

Table 1.1. Survey season characteristics, sampling effort and tiger detections for three survey methods: farmer surveys (FS), sign surveys (SS) and camera surveys (CS).

Season (Survey months)	Max temperature, Mean precipitation, Cover	Number of cells surveyed (Min–Max surveys/cell); Number of cells with tiger detections		
		FS	SS	CS
Winter (15 Dec.–15 Feb.)	22°, 19.1mm, Very High	94 (1–12); 58	69 (1–4); 13	47 (9-39); 4
Summer (15 Mar.–15 May)	38°, 5.8mm, Low	91 (1–12); 55	56 (1–6); 3	43 (8-39); 3
Monsoon (15 Jul.–15 Aug.)	33.8°, 277.4mm, High	85 (1–10); 22	26 (1)*; 1	32 (4-36); 2

**In the monsoon season sign surveys (SS) were conducted only on a single occasion due to inclement weather conditions*

Each farmer was shown images and given verbal descriptions of large mammals and their signs (e.g., tracks, scat, etc.) and asked if they had observed/detected these species on their lands within the past month. Farmer surveys yielded *uncertain* species detections, allowing for the potential of false-positives. Farmers could incorrectly report the presence of a species due to multiple factors including species misidentification, memory lapses, or location errors

Sign Surveys (SS) were conducted in a random subset (69 cells) of cells. Two independent observers walked separate random paths (>500 m) searching for sign (spoor, scat, direct sightings) of wild mammals within the cell. Surveys were repeated 1-6 times per season. We assumed unambiguous sign identification represented *certain* detections for tigers (that is, no false positives); however, sign identification was less reliable for species such as hog deer and wild boar (*Sus scrofa*). Since most cells were either agricultural land or river beds, substrate quality for sign detection was consistently high except during the monsoon season.

Camera Surveys (CS) were conducted in a random subset of the sign survey cells (47). We placed a single motion activated Cuddeback Attack 5.0-megapixel Trail Camera (Cuddeback Digital, Green Bay, Wisconsin, USA) within a cell for 30-40 days during a given season. Detections of large mammals generated over this period formed an additional source of certain detections for all species (i.e., no species misidentification). Within a cell, camera placement targeted areas with higher likelihood of animal movements such as natural drainages. In subsequent analyses, we treated each five-day period the camera was active as a survey occasion. In each season, we first deployed camera traps in cells, followed by sign surveys. Efforts were made to conduct farmer surveys towards the end of each season to limit tiger detections to the given season. Because the timing of survey methods were not coincident, and we could not safely assume closure across the survey season, our models estimated cell *use* and not cell *occupancy*.

Statistical Analyses

Our goal was to estimate factors influencing the probability and the relative frequency of cell use by tigers and the dynamics of use across seasons. We estimated model parameters (Table 1.2) by fitting dynamic occupancy models that account for false-positive errors. The false-positive model (Miller et al., 2013; MacKenzie et al., 2017) extends the traditional dynamic occupancy model (MacKenzie et al., 2003) to allow for the estimation of false positive detection rates by exploiting data from both certain and uncertain detection methods. In our study, FS, the more extensively applied survey method, was the source of uncertain detections whereas CS and SS were assumed to be the source of certain tiger detections.

Table 1.2. Name, notation, and definitions for parameters in the false positive dynamic occupancy model.

Parameter (Symbol)	Definition
Probability of use in winter (Ψ_w)	Probability that a cell was used by tigers in the first season of the study (winter).

Extinction probability (ϵ_t)	Probability that a used cell in season t will not be used in the subsequent season $t + 1$.
Colonization probability (γ_t)	Probability that an unused cell in season t will be used in the subsequent season $t + 1$.
False positive detection probability, p_{10}^{FS}	Probability that a species will be incorrectly detected during a given survey in an unused cell. This probability is nonzero for farmer surveys (FS) only. The probability was fixed to zero for sign and camera trap surveys ($p_{10}^{SS} = p_{10}^{CS} = 0$).
True detection probability, p_{11}^{FS} , p_{11}^{SS} , p_{11}^{CS}	Probability of detecting tigers on a survey occasion given the cell was used by tigers during the survey season. True detection probability varied among the three survey types (FS, SS, CS).
b^{FS} , b^{SS} , b^{CS}	Probability that a detection can be designated as certain given that a cell was used by tigers and the species was detected. This probability was fixed to zero for farmer surveys ($b^{FS} = 0$) and to 1 for camera and sign surveys ($b^{SS} = b^{CS} = 1$)
Derived Parameter	
Probability of tiger use in summer (Ψ_s) and monsoon (Ψ_m) seasons.	Probability that a cell was used by tigers in the summer (s) and monsoon (m) season, respectively. These quantities are calculated using estimates of winter use probabilities and associated extinction and colonization probabilities (Eq. 1)

Note the first entry of the detection probability subscript designates the detection state (1=detected), while the second entry designates the true occupancy (use) state: 0 if the cell was truly not used by tigers and 1 if the cell was truly used.

We selected candidate covariates and generated hypotheses explaining possible drivers of habitat use of tigers by applying the *landscape of coexistence* concept (Oriol-Cotterill et al., 2015). The concept posits that spatio-temporal patterns of carnivore occurrence in human altered landscapes are governed largely by carnivore behaviors that minimize exposure to anthropogenic risks and maximize access to resources. We selected covariates that represented the spatial distribution of risks (human presence) and resources (prey, water and cover) across the three survey seasons (Appendix 1.1: Table S1). Prior to model-building, we tested for multicollinearity among covariates based on their variance inflation factors (Zuur et al., 2010) and removed covariates with a value greater than 5.

Our *a-priori* hypotheses and expected relationships between model parameters and covariates are summarized in Table 1.3. Specifically, we modeled the probability of initial tiger use within a cell (*winter*, Ψ_w) as a function of six covariates: median NDVI values (NDVI_W), prey availability index (Prey_W; Appendix 1.2), distance to protected areas (PA), length of natural drainages (Drain), % tree canopy cover (Tree) and proportion of a cell dominated by human settlements (Sett). Changes in cell use between seasons were modeled via two dynamic processes, local extinction and colonization. Local extinction probability (ε_t) is the probability that a cell used in one season (t) is not used in the subsequent season ($t+1$). We expected local extinction probabilities to vary across seasons and cells primarily as a function of two covariates: water availability (Water) and cover availability in the subsequent season (NDVI_S, NDVI_M). Local colonization probability (γ_t) is the probability that an unused cell in season t will be used in the subsequent season ($t+1$). Local colonization probability was modeled as a function of three covariates; median NDVI values in the subsequent season (NDVI_S, NDVI_M), prey availability in the subsequent season (Prey_S, Prey_M) and change in prey availability between successive seasons (Prey_WS, Prey_SM).

We modeled two types of detection probabilities: true detection probability (p_{11}), or the probability of detecting species' use when the cell was truly used and false positive detection probability (p_{10}), the probability of reporting species' use when the cell was not used. True detection probability (p_{11}) was modeled as a function of survey method (Method), season (Season), an index of season-specific cover availability (NDVI_W, NDV_S, NDVI_M), and the proportion of settlement within a cell (Sett). Survey effort (spatial coverage) of FS was higher than CS and SS--therefore, we expected detection probabilities for all seasons to be highest for FS and lowest for CS ($p_{11}^{FS} > p_{11}^{SS} > p_{11}^{CS}$). Since false positive detections were possible for farmer

surveys (p_{10}^{FS}) we modeled this parameter as a function of season and distance to protected area boundary (PA). We expected farmers living further from PA boundaries to be less familiar with tiger signs and hence more likely to falsely report the species. We hypothesized that the probability of false positive reporting of tigers would be highest in the winter since farmers in the region believe that tigers occur extensively in the matrix in the winter season.

We evaluated the above hypotheses using the false-positive, robust design occupancy models in Program MARK (White and Burnham, 1999). Models within a set were ranked according to Akaike's Information Criteria (AIC; Burnham and Anderson, 2003). Employing a sequential approach to model building, we compared alternative models to identify the best-supported covariate structure (lowest AIC) for detection probabilities (p_{11}^{FS} , p_{11}^{SS} , p_{11}^{CS} and p_{10}^{FS}) while retaining a global structure (i.e. all covariate of interest) on initial tiger use (Ψ_w) and associated vital rates (local extinction and colonization). We first considered 10 alternative model structures on p_{11} (Appendix 1.3: Table S4) while allowing false-positive detections to vary by season and distance to protected area, p_{10}^{FS} (Season+PA). The true detection probability structures included univariate and additive combinations of the covariates Season, Method, linear and quadratic relationship with cover (NDVI_W, NDVI_S, NDVI_M) and proportion of settlement within a cell (Sett). In addition, we fit an intercept only model where true detection was assumed constant across surveys. Retaining the best-supported p_{11} structure, we considered four alternative model structures for false-positive detections, p_{10}^{FS} . These models included univariate and additive combinations of Season and distance to protected areas (PA) and an intercept only model.

Retaining the best-supported detection structures and a global covariate structure on the dynamic rate parameters, we explored covariates hypothesized to affect tiger space-use in our

initial winter survey season (Ψ_w ; Appendix 1.3: Table S5). We considered 22 alternative models including individual or additive combinations for the covariates on Ψ_w (Drain, Sett, NDVI_W, Tree, Prey_W and PA). We retained the best-supported covariate structure for initial use probabilities, and subsequently explored specified covariate combinations for local extinction (ε_t) and colonization (γ_t) probabilities (Appendix 1.3: Table S6-S7). We tested 23 alternative covariate models for local extinction probability (ε_t), fitting individual and additive combinations for Season, Water and PA. In addition, we fit models with a seasonal interaction term to determine if the relationship between local extinction probability and the specified covariates differed for winter-summer and the summer-monsoon transitions (i.e. different slopes and intercepts). Finally, after retaining the best-supported structure for local extinction probability, we tested 22 alternative models for local colonization probability (γ_t). These models included the covariates of interest for γ_t (Season, NDVI_S, NDVI_M, Prey_S, Prey_M, Prey_WS, Prey_SM) either individually or in additive combinations. We also fit interactive models with season and all covariates of interest. We hypothesized farmland tiger use would be highest in the winter and decline in subsequent seasons, and we expected colonization probability to be close to 0 between seasons. We therefore fit a model where we fixed the colonization probability at 0 during the study.

In each of the above steps, we fit intercept-only models and in the final model set included a model where all parameters were modeled without covariates. For comparison, we fit a version of the best-supported model in the model-set by assuming no false-positive errors ($p_{10} = 0$ for all survey types; Appendix 1.4: Table S8). Finally, using parameter estimates from the best supported model, we derived estimates of the probability of tiger use for summer and monsoon seasons using the recursive equation (Eq.1; (MacKenzie et al., 2017)). Specifically, we

used estimates of tiger use and associated vital rates in one season (t) to estimate tiger use in the subsequent season ($t+1$).

$$\Psi_{t+1} = \Psi_t * (1 - \varepsilon_t) + (1 - \Psi_t) * \gamma_t \quad \text{Eq. 1}$$

Results

Survey effort, species detections and naïve use estimates

We interviewed 1495 farmers, conducted 322 sign surveys and obtained photo-captures of tigers and prey species over 3449 trap nights. Using camera surveys, we detected 15 mammal species including tigers and locally rare species such as the Indian wolf (*Canis lupus pallipes*) and fishing cat (*Prionailurus viverrinus*). Tigers were detected in all seasons using all survey methods. Detections were highest in the winter season for all three methods and the lowest in the monsoon season (Table 1.1). We obtained 11 tiger photo-captures belonging to at least seven individuals, including a female with a cub. We compared these photographs to the tiger ID database maintained for nearby protected areas. Two individuals were previously photo-captured within Dudhwa National Park (DNP) and the tigress with the cub had been photo-captured within Kishanpur Wildlife Sanctuary in 2013. Within the study area, two of the seven individuals were captured in single cell adjoining the DNP boundary and the other five individuals were captured at cells ranging from 0.5 – 3 km from a protected area boundary. Tiger sign was detected in multiple cells ranging from 0 – 8 km from PA boundaries.

Covariate relationships and parameter estimates

We fit a total of 79 models (Appendix 1.4, Table S8) estimating the effects of covariates on the parameters of interest, including intercept-only models and a version of the best supported model that assumed no false positive detections ($p_{10} = 0$ for all survey methods). Variation in true detection probability (p_{11}) was best explained by an additive combination of season and

method (Appendix 1.3: Table S4). As hypothesized, the estimated true detection probability (p_{11}) was highest for farmer surveys (FS) followed by sign surveys (SS) and camera surveys (CS, Figure 1.2). For all survey types, true detection probability was highest during the winter season and declined in the summer and monsoon season.

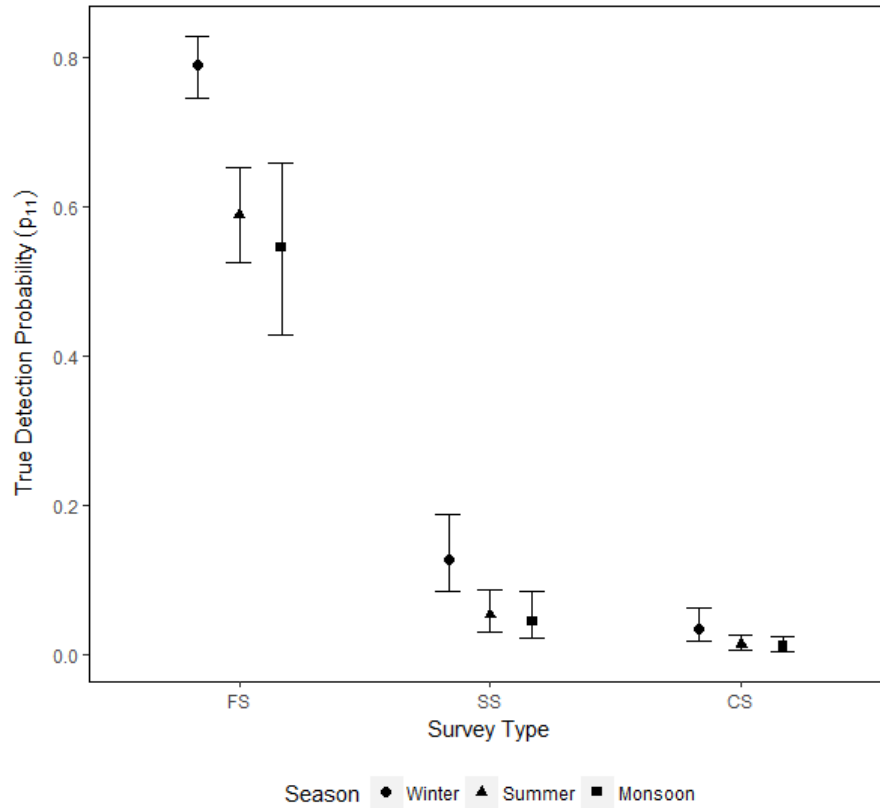


Figure 1.2: True detection probability estimates (p_{11}) by season and method, Farmer surveys (FS), Sign surveys (SS) and Camera surveys (CS) with associated confidence intervals. Estimates are based on the best supported model in the overall model-set (Appendix 1.4, Table S4).

The best supported model for false positive detection probability for farmer surveys (p_{10}^{FS}) included the covariates season (Season) and distance to protected areas (PA). As expected the probability of a false positive detection increased with increasing distance to a PA boundary (Table 1.3) and was highest in the winter and lowest in the monsoon season. On average, the probability of a false positive tiger detection from a farmer survey was 0.09 in the winter (SE 0.02), 0.06 in the summer (SE 0.01) and 0.01 in the monsoon season (SE 0.01).

Initial probability of tiger use in the winter (Ψ_w) was a function of distance to protected areas (PA), length of drainages within a cell (Drain), proportion of the cell area occupied by settlements (Sett) and a quadratic relationship with median NDVI values in winter (NDVI_W). This model had nearly three times more weight than the next best supported model, which included the additional covariate mean % tree cover (Tree). Our hypotheses regarding the relationship between initial tiger use and distance to protected areas, and the availability of cover, drainages, settlement were supported by the top models (Tables 1.3, Appendix 1.3: Table S5, Figure 1.3).

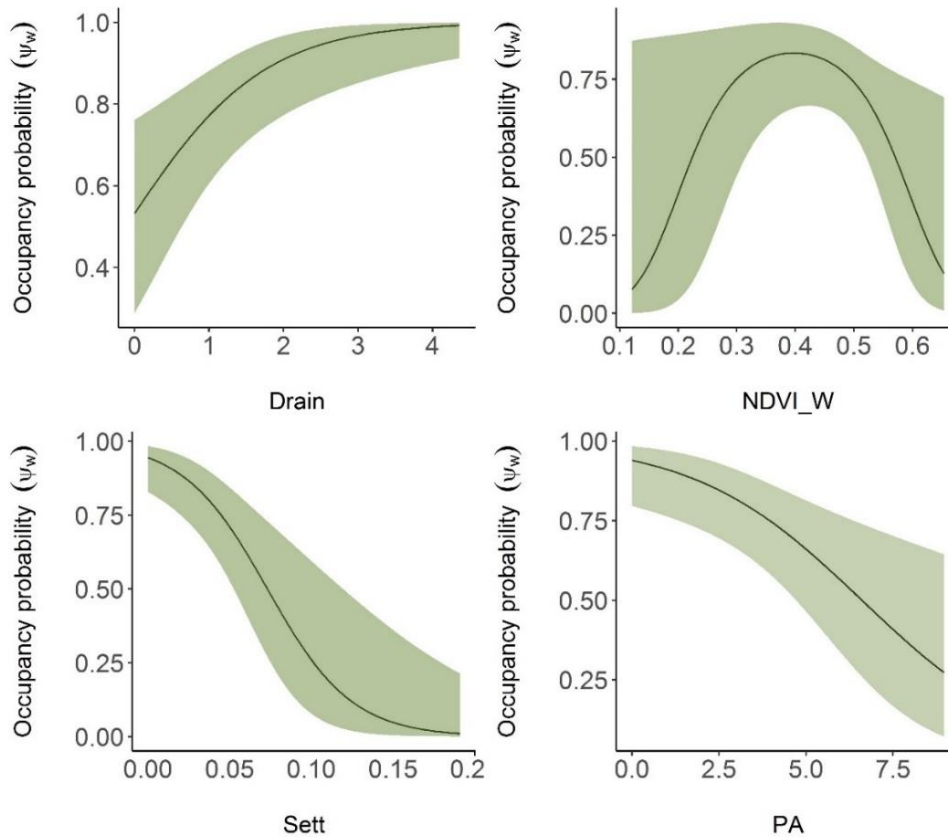


Figure 1.3: Covariate relationships with probability of tiger use in winter Ψ_w and associated confidence intervals (gray shaded area). Relationships are based on coefficient estimates from the best supported model in the overall model set using mean values for covariates that are not graphed. Drain: Total length of drainages within cell (km); NDVI_W: Mean cell specific NDVI in winter; Sett: Proportion of cell area under human settlements PA: Cell distance to nearest protected area boundary (km)

Table1.3: Covariates and their *a-priori* hypothesized and estimated relationships with model parameters

Hypothesis	Covariate	$\beta_{\text{hypothesized}}^a$	$\hat{\beta}_{\text{estimated}}^b$ (SE)
Seasonal tiger use and false-positive detection probability for farmer surveys will be higher in cells proximate to protected area boundaries (Karanth, 2016).	PA: Minimum Euclidean distance (km) between cell center and protected area boundary.	$\Psi_w (-)$ $\varepsilon_t (+)$ $p_{10}^{FS} (+)$	$\Psi_w_{PA}: -0.42$ (0.14) $\varepsilon_t_{PA}: 0.60$ (0.21) $p_{10}^{FS}_{PA}: 0.002$ (0.07)
Winter tiger use and true detection probability using farmer surveys (FS), sign surveys (SS) and camera surveys (CS) will increase in a linear or quadratic manner with cover availability. Local extinction probability will decline with increase in cover availability.	NDVI_W, NDVI_S, NDVI_M: Cell-specific median NDVI values for each season (index of cover availability)	$\Psi_w (+ / \text{quadratic})$ $\varepsilon_t (-); \gamma_t (+)$ $p_{11}^{FS}, p_{11}^{SS}, p_{11}^{CS} (+ / \text{quadratic})$	$\Psi_w_{NDVI_W}: 42.72$ (20.77); $\Psi_w_{NDVI_W^2}: -53.78$ (24.72)
Winter tiger use should be higher in cells with more extensive drainages	Drain: Total length of drainages within cell	$\Psi_w (+)$	$\Psi_w_{Drain}: 1.09$ (0.36)
Winter tiger use should be higher in cells with greater canopy cover (Joshi et al. 2013)	Tree: Mean tree canopy cover within cell	$\Psi_w (+)$	
Winter tiger use and detection probability for all surveys methods (FS, SS and CS) will be lower in cells with more extensive settlement areas (Oriol-Cotteril et al.2015b).	Sett: Proportion of cell area under human settlements	$\Psi_w (-)$ $p_{11}^{FS}, p_{11}^{SS}, p_{11}^{CS} (-)$	$\Psi_w_{Sett}: -38.82$ (11.14)
The availability of permanent water sources will positively influence use in the summer (dry) season (i.e. lower local extinction probability) and negatively in the monsoon season (flooding).	Water: Availability of permanent water sources within cells	ε_t (winter-summer, -) ε_t (summer-monsoon, +)	$\varepsilon_t_{Water}: 0.04$ (0.02)

The availability of wild prey will positively influence spatio-temporal space use patterns (Athreya et al., 2014; Gehr et al., 2017).	Prey_W, Prey_S, Prey_M Cell-specific prey availability index for each season.	$\Psi_w (+)$ $\gamma_t (+)$
Probability of use should be higher for cells that experience a net increase in prey availability between seasons	Prey_WS, Prey_SM Cell-specific index of change in prey availability between seasons	$\gamma_t (+)$

^aHypothesized direction of relationship between covariates and model parameters (Ψ_w , probability of cell use in winter; ε_t , probability that a cell used in season t will not be used in season $t+1$; γ_t , probability that an unused cell in season t will be used in season $t+1$; p_{10}^{FS} , probability that a surveyed farmer will report a tiger as present in a cell that is truly unused; probability of detecting tigers using farmer surveys (p_{11}^{FS}), sign surveys (p_{11}^{SS}) and camera surveys (p_{11}^{CS})).

^bEstimated relationship between model parameters and covariate based on best supported model in the overall model set

Winter use probability decreased with distance from PAs and proportion of settlements in the cell. Tiger use increased with increasing length of drainages (Drain) within a cell and had a quadratic relationship with winter cover availability (NDVI_W) (Table 1.3, Figure 1.3). Contrary to our *a priori* expectations, models that included prey availability as a covariate were not strongly supported.

The probability of local extinction (ϵ_t) was best explained by models that included seasonal variation (Season), water availability (Water) and distance to protected areas (PA) (Appendix 1.3: Table S6). While there was considerable model uncertainty, the season covariate was included in seven of the top-supported models, with a cumulative model weight of 80%. The covariates Water and PA were also important and were included in six of the top models. Consistent with our predictions, local extinction probability increased with increasing distance to PAs (Table 1.3, Figure 1.4). Contrary to our expectations, availability of permanent water sources within a cell increased the probability of extinction in both the winter-summer and summer-monsoon transitions. Local extinction probability was higher in the summer-monsoon transition as compared to the winter-summer transition (Table 1.3, Figure 1.4).

The best-supported colonization probability structure suggested that no new cells were used in the summer and monsoon seasons (Appendix 1.3: Table S7). This model was 2.5 times more likely than the next best-supported model and suggests that tiger use of the matrix is highest during the winter, with declining use throughout the remainder of the year (Figure 1.5). The model assuming no false-positive detections performed poorly ($\Delta \text{AICc} = 132.58$) compared to the best-supported model (Appendix 1.4: Table S8) and overestimated mean tiger use probabilities for all seasons (Figure 1.5). The intercept only model was the least supported model in our overall model-set ($\Delta \text{AICc} = 291.07$)

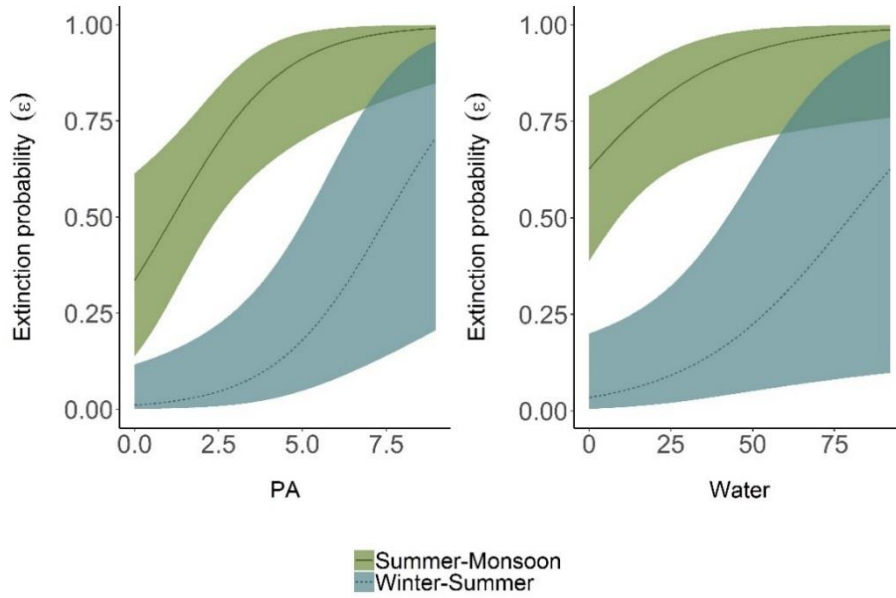


Figure 1.4: Covariate relationships with probability of local extinction (ϵ_i) between winter-summer and summer-monsoon seasons. Relationships are based on coefficient estimates from the best-supported model in the overall model-set using mean values for covariates that are not graphed. PA: Distance of cell to nearest protected area boundary; Water: Mean index of water availability within a cell. Values range from no water (0) to presence of permanent water sources (100).

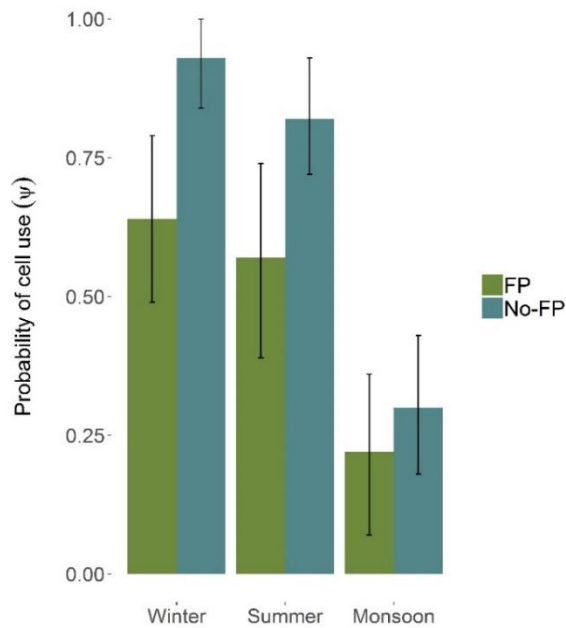


Figure 1.5: Mean season-specific cell use probabilities for tigers with 95% confidence intervals based on the best-supported model allowing false-positive detections (FP) and a model assuming no false -positive errors (No-FP).

Discussion

We quantified space-use patterns of tigers in agricultural areas of the CTL, one of the most densely human populated landscapes in the tiger's range in India. Using dynamic occupancy models that corrected for false-positive detections, we demonstrated that tigers use agricultural areas extensively, albeit seasonally. In the human dominated matrix, tigers selected habitat features such as hiding/resting cover while avoiding areas with large human settlements. Farmlands areas in the landscape experienced high use by tigers for up to eight kilometers from the PA boundaries (Figure 1.3). Use probability was particularly high in the winter season when cover provided by sugarcane crops and riparian grasslands was most extensive. In addition, we found that the presence of extensive natural drainages was associated with habitat use by tigers. These drainages may function both as a source of temporary cover and as movement routes, for tiger and prey species, to travel between patches of native habitats. Contrary to our expectations and findings from recent studies on other large carnivore species (Gehr et al., 2017), the availability of wild prey, as measured in our study, was not a strong predictor of local tiger habitat use probabilities. We believe, however, that tigers using agricultural areas subsist on wild prey since reports of livestock depredation in the matrix are very rare (Chatterjee et al., 2018).

Space-use probabilities declined from the winter (high use) season as reflected in low local colonization probabilities (γ_t) and high local extinction probabilities (ε_t , Figures 1.4-1.5). Cells with more perennial water sources and further away from protected areas experienced higher local extinction probabilities. This may be a result of increasing human disturbances near perennial water sources in the summer and the likelihood that these areas are inundated during the monsoon season. Our results also highlight the prevalence of false-positive errors in interview-based detection data. This probability varied both spatially and across seasons

suggesting that caution must be exercised in the interpretation of occupancy and use probabilities estimated using citizen science data. We recommend that studies involving interview-based detection data incorporate at least one other survey method that is free of false-positive errors, at least at a subset of the sample sites.

In their recent review, Ferreira et al. (2018) note the conspicuous absence of studies examining the use of agroecosystems by large carnivores and the causal factors underlying this use. We believe our study is the first to comprehensively document the seasonal space-use patterns of tigers within an agricultural matrix. During our study, we obtained photos of multiple tigers, including a tigress with a cub, previously photographed within the boundaries of Kishanpur Wildlife Sanctuary during a camera trap-based population study in 2013. The presence of tigresses with cubs had been reported on multiple occasions both within the study area and in the larger landscape. In 2016, camera-trapping in protected areas in the landscape documented the first known successful dispersal of a tiger from Kishanpur Wildlife Sanctuary into Dudhwa National Park (personal communication, WWF-India). Our results and these observations together suggest that the matrix areas of the CTL, despite high human densities, serve not only as dispersal routes but also breeding areas for tigers.

Preserving the functional role of the matrix requires immediate efforts to regulate land-use change. Human populations are projected to increase across most tiger landscapes in India including the CTL. The consequent increase in the rates of urbanization is predicted to significantly impact tiger persistence probabilities (Sanderson et al., 2019). In the CTL, cells with > 15 % of area under human settlements were not used by tigers (Figure 1.3). This suggests that even minor increases in the extent of human settlement in the matrix may cause sharp declines in the net available habitat for tigers. As a first step towards regulating land-use change

in the CTL, we recommend the establishment of an ESZ around protected areas that extends at least eight kilometers beyond the boundaries of existing PAs. In addition, promoting land sharing based conservation measures such as incentivizing the cultivation of cover crops, the restoration of native riparian grassland habitats currently threatened by livestock grazing, and establishment of long-term conservation easements can help enhance the role the matrix plays in sustaining tigers populations in India (Kinnaird and O'Brien, 2012). Such measures stand to benefit other species besides tigers given the diverse community of mammals that were detected using the matrix during this study.

In addition, our study provides a much needed spatio-temporal context to better understand human-tiger conflicts both within the CTL and in other tiger landscapes. When viewed in conjunction with known records of conflicts in the CTL (Chatterjee et al., 2018), our study demonstrates that conflicts (livestock depredation and human attacks) occur in only a subset of locations and time periods where tigers and humans overlap (i.e. conflict free co-occurrence of humans and tigers is the norm rather than the exception in the CTL). Even though tigers use areas up to six kilometers beyond PA boundaries in the winter and summer season, most conflicts occur at or near PA boundaries in the winter (Chatterjee et al., 2018). This pattern of co-occurrence has been shown to be true in other landscapes that harbor large carnivores (Athreya et al., 2013). The presence of tigers in agricultural areas may also impose a landscape of fear on other human adapted, wild herbivore (e.g. wild boar, nilgai) and carnivore (e.g. leopard, Indian wolf and golden jackals) species that are involved in conflicts with local communities (Thinley et al., 2018). For example, detections of jackals using camera traps were lower at sites where we detected tigers. Accounting for such trophic interactions may help us better understand patterns of human-wildlife conflict in landscapes with large carnivores.

Space-use patterns of large carnivores within human dominated areas are also strongly influenced by social factors such as degree of tolerance within human communities. In India, culturally mediated tolerance for tigers, in combination with strict wildlife protection laws, mean that tigers may not be subject to the same risks as other large carnivores such as wolves that use human dominated areas. A recent study in Sumatra, for example, found that community tolerance towards tigers is influenced not only by spiritual factors but also by the risk of an actual attack (Struebig et al., 2018). We speculate that the high tolerance of human communities towards tigers in the CTL and elsewhere in India may in part be attributed to the long history of largely conflict free sharing of space with these species. We recommend that future efforts to understand community attitudes towards large carnivores and the spatial patterns of conflicts with these species should be conducted in conjunction with studies such as ours to gain a more nuanced perspective on the socio-ecological factors that facilitate the persistence of large carnivores in human dominated landscapes.

The loss of unprotected critical habitats is predicted to exacerbate the rate of decline of many large carnivore populations (Di Minin et al., 2016). Results from this study add to the body of literature that expands our current understanding of the role of unprotected habitats to include annual croplands (Ferreira et al., 2018). In India, as in many tropical nations that harbor large carnivores, agroecosystems support many small land holders or subsistence agriculture, and are subject to high vulnerability as a consequence of climate change (Morton, 2007). While the role of large carnivores in buffering the impacts of climate change on species communities has been explored (Ripple et al., 2014), little is known about the diverse impacts that climate change is likely to have on large carnivore populations themselves. Our results suggest that in agricultural landscapes with large carnivore populations, climate change impacts on large carnivore

persistence may be mediated by its effects on subsistence agriculture. We recommend that within agricultural landscapes, large carnivore conservation should integrate existing PA based measures with broader land sharing approaches. Such an approach, while acknowledging the primacy of native habitats in the conservation process, would also treat agricultural lands and practices as integral to the success of large carnivore conservation efforts.

LITERATURE CITED

- Athreya, V., Navya, R., Punjabi, G.A., Linnell, J.D.C., Odden, M., Khetarpal, S., Karanth, K.U., 2014. Movement and activity pattern of a collared tigress in a human-dominated landscape in central India. *Trop. Conserv. Sci.* 7, 75–86.
- Athreya, V., Odden, M., Linnell, J.D.C., Krishnaswamy, J., Karanth, U., 2013. Big cats in our backyards: persistence of large carnivores in a human dominated landscape in India. *PLoS One* 8, e57872.
- Banerjee, K., Jhala, Y. V, Pathak, B., 2010. Demographic structure and abundance of Asiatic lions *Panthera leo persica* in Girnar Wildlife Sanctuary, Gujarat, India. *Oryx* 44, 248–251.
- Braczkowski, A.R., O'Bryan, C.J., Stringer, M.J., Watson, J.E., Possingham, H.P., Beyer, H.L., 2018. Leopards provide public health benefits in Mumbai, India. *Front. Ecol. Environ.* 16, 176–182.
- Burnham, K.P., Anderson, D.R., 2003. Model selection and multimodel inference: a practical information-theoretic approach. Springer Science & Business Media.
- Chandramouli, C., 2011. Census of India 2011. Provisional Population Totals. New Delhi.
- Chatterjee, M., Krishnendu, B., Pandey, P., Singhai, S., Ashraf, N.V., Kaul, R., 2018. Living with the Wild; Mitigating Conflict between Humans and Big Cat species in Uttar Pradesh. Conservation Action Series No. 20. National Capital Region.
- Chundawat, R.S., Sharma, K., Gogate, N., Malik, P.K., Vanak, A.T., 2016. Size matters: Scale mismatch between space use patterns of tigers and protected area size in a Tropical Dry Forest. *Biol. Conserv.* 197, 146–153.
- Crist, E., Mora, C., Engelman, R., 2017. The interaction of human population, food production, and biodiversity protection. *Science* 356, 260–264. <https://doi.org/10.1126/science.aal2011>
- Crooks, K.R., Burdett, C.L., Theobald, D.M., Rondinini, C., Boitani, L., 2011. Global patterns of fragmentation and connectivity of mammalian carnivore habitat. *Philos. Trans. R. Soc. London B Biol. Sci.* 366, 2642–2651.
- DeFries, R., Hansen, A., Turner, B.L., Reid, R., Liu, J., 2007. Land use change around protected areas: management to balance human needs and ecological function. *Ecol. Appl.* 17, 1031–1038.
- Di Minin, E., Slotow, R., Hunter, L.T.B., Pouzols, F.M., Toivonen, T., Verburg, P.H., Leader-Williams, N., Petracca, L., Moilanen, A., 2016a. Global priorities for national carnivore conservation under land use change. *Sci. Rep.* 6, 23814.
- Ferreira, A.S., Peres, C.A., Bogoni, J.A., Cassano, C.R., 2018. Use of agroecosystem matrix habitats by mammalian carnivores (Carnivora): a global-scale analysis. *Mamm. Rev.* 48, 312–327.

- Gehr, B., Hofer, E.J., Muff, S., Ryser, A., Vimercati, E., Vogt, K., Keller, L.F., 2017. A landscape of coexistence for a large predator in a human dominated landscape. *Oikos* 126, 1389–1399.
- Ghosal, S., Athreya, V.R., Linnell, J.D.C., Vedeld, P.O., 2013. An ontological crisis? A review of large felid conservation in India. *Biodivers. Conserv.* 22, 2665–2681.
- Goodrich, J.M., 2010. Human–tiger conflict: a review and call for comprehensive plans. *Integr. Zool.* 5, 300–312.
- Gray, C.L., Hill, S.L.L., Newbold, T., Hudson, L.N., Börger, L., Contu, S., Hoskins, A.J., Ferrier, S., Purvis, A., Scharlemann, J.P.W., 2016. Local biodiversity is higher inside than outside terrestrial protected areas worldwide. *Nat. Commun.* 7, 12306.
- Jhala, Y. V, Gopal, R., Qureshi, Q., 2015. The status of tigers in India 2014.
- Karant, K.K., 2016. Wildlife in the matrix: spatio-temporal patterns of herbivore occurrence in Karnataka, India. *Environ. Manage.* 57, 189–206.
- Karant, K.K., Nepal, S.K., 2012. Local residents perception of benefits and losses from protected areas in India and Nepal. *Environ. Manage.* 49, 372–386.
- Kinnaird, M.F., O’Brien, T.G., 2012. Effects of Private-Land Use, Livestock Management, and Human Tolerance on Diversity, Distribution, and Abundance of Large African Mammals. *Conserv. Biol.* 26, 1026–1039.
- MacKenzie, D.I., Nichols, J.D., Hines, J.E., Knutson, M.G., Franklin, A.B., 2003. Estimating site occupancy, colonization, and local extinction when a species is detected imperfectly. *Ecology* 84, 2200–2207.
- MacKenzie, D.I., Nichols, J.D., Royle, J.A., Pollock, K.H., Bailey, L., Hines, J.E., 2017. *Occupancy estimation and modeling: inferring patterns and dynamics of species occurrence.* Elsevier.
- Midha, N., Mathur, P.K., 2014. Channel characteristics and planform dynamics in the Indian Terai, Sharda River. *Environ. Manage.* 53, 120–134.
- Miller, D.A.W., Nichols, J.D., Gude, J.A., Rich, L.N., Podruzny, K.M., Hines, J.E., Mitchell, M.S., 2013. Determining occurrence dynamics when false positives occur: estimating the range dynamics of wolves from public survey data. *PLoS One* 8, e65808.
- Morton, J.F., 2007. The impact of climate change on smallholder and subsistence agriculture. *Proc. Natl. Acad. Sci. U. S. A.* 104, 19680–5.
- Oriol-Cotterill, A., Valeix, M., Frank, L.G., Riginos, C., Macdonald, D.W., 2015. Landscapes of coexistence for terrestrial carnivores: the ecological consequences of being downgraded from ultimate to penultimate predator by humans. *Oikos* 124, 1263–1273.
- Phalan, B., Onial, M., Balmford, A., Green, R.E., 2011. Reconciling food production and biodiversity conservation: land sharing and land sparing compared. *Science* 333, 1289–91.

- Pillay, R., Johnsingh, A.J.T., Raghunath, R., Madhusudan, M.D., 2011. Patterns of spatiotemporal change in large mammal distribution and abundance in the southern Western Ghats, India. *Biol. Conserv.* 144, 1567–1576.
- Ripple, W.J., Estes, J.A., Beschta, R.L., Wilmers, C.C., Ritchie, E.G., Hebblewhite, M., Berger, J., Elmhagen, B., Letnic, M., Nelson, M.P., Schmitz, O.J., Smith, D.W., Wallach, A.D., Wirsing, A.J., 2014. Status and Ecological Effects of the World’s Largest Carnivores. *Science* (80-.). 343, 1241484.
- Sanderson, E.W., Moy, J., Rose, C., Fisher, K., Jones, B., Balk, D., Clyne, P., Miquelle, D., Walston, J., 2019. Implications of the shared socioeconomic pathways for tiger (*Panthera tigris*) conservation. *Biol. Conserv.* 231, 13–23.
- Stephens, P.A., 2015. Land sparing, land sharing, and the fate of Africa’s lions. *Proc. Natl. Acad. Sci.* 112, 14753–14754.
- Stevens, D.L., Olsen, A.R., 2004. Spatially balanced sampling of natural resources. *J. Am. Stat. Assoc.* 99, 262–278.
- Struebig, M.J., Linkie, M., Deere, N.J., Martyr, D.J., Millyanawati, B., Faulkner, S.C., Le Comber, S.C., Mangunjaya, F.M., Leader-Williams, N., McKay, J.E., St. John, F.A. V., 2018. Addressing human-tiger conflict using socio-ecological information on tolerance and risk. *Nat. Commun.* 9, 3455.
- Thatte, P., Joshi, A., Vaidyanathan, S., Landguth, E., Ramakrishnan, U., 2018. Maintaining tiger connectivity and minimizing extinction into the next century: Insights from landscape genetics and spatially-explicit simulations. *Biol. Conserv.* 218, 181–191.
- Thinley, P., Rajaratnam, R., Lassoie, J.P., Morreale, S.J., Curtis, P.D., Vernes, K., Leki, L., Phuntsho, S., Dorji, T., Dorji, P., 2018. The ecological benefit of tigers (*Panthera tigris*) to farmers in reducing crop and livestock losses in the eastern Himalayas: Implications for conservation of large apex predators. *Biol. Conserv.* 219, 119–125.
- White, G.C., Burnham, K.P., 1999. Program MARK: survival estimation from populations of marked animals. *Bird study* 46, S120–S139.
- Wittemyer, G., Elsen, P., Bean, W.T., Burton, A.C.O., Brashares, J.S., 2008. Accelerated human population growth at protected area edges. *Science* (80-.). 321, 123–126.
- Zeller, K.A., Nijhawan, S., Salom-Pérez, R., Potosme, S.H., Hines, J.E., 2011. Integrating occupancy modeling and interview data for corridor identification: A case study for jaguars in Nicaragua. *Biol. Conserv.* 144, 892–901.
- Zuur, A.F., Ieno, E.N., Elphick, C.S., 2010. A protocol for data exploration to avoid common statistical problems. *Methods Ecol. Evol.* 1, 3–14.

CHAPTER TWO

ECOLOGICAL DRIVERS OF HERBIVORE SPACE USE & HUMAN-HERBIVORE INTERACTIONS IN FARMLANDS IN THE CENTRAL TERAJ LANDSCAPE, INDIA

Introduction

Wild, terrestrial mammalian herbivores belong to a diverse taxonomic group comprised of numerous species spanning multiple taxonomic families. This group includes charismatic species such as the African elephant (*Loxodonta africana*) and one-horned rhinoceros (*Rhinoceros unicornis*), and lesser known species such as the recently discovered saola (*Pseudoryx nghetinhensis*). As primary consumers, wild herbivores mediate both the bottom-up, and top-down forces that shape the structure and function of the ecosystems (Paine, 2000). For humans who share landscapes with these species, they are not only an important source of protein, but also a significant source of conflict because of potential competition with livestock and agricultural production. Most species of wild herbivores have experienced world-wide population declines with nearly 60% of the largest of these species (body mass ≥ 100 kg) currently threatened with extinction (Ripple et al., 2015). In many ecosystems, ongoing declines in herbivore populations have triggered the collapse of predator populations (Wolf and Ripple, 2016) and alteration of ecosystem functions (Pringle et al., 2007). The abundance and distribution of wild mammalian herbivores are the nexus of many contemporary conservation challenges.

Globally, declines in large herbivore populations have been precipitated by over-hunting, habitat loss and competition with livestock (Ripple et al., 2015). An insidious threat facing these

species is the conversion of critical habitats surrounding existing protected areas (PAs) to agricultural expansion and other anthropogenic land-uses (Gordon, 2009). Agricultural expansion around PAs affect herbivore populations in multiple ways. For species tolerant of anthropogenic disturbance, some agricultural practices often provide resource rich habitats (Abbas et al., 2011). The presence of herbivores within agricultural areas however, often leads to conflicts with local communities, resulting in eventual wildlife conflicts and persecution. Beyond population-level consequences for crop-raiding species, sustained human-herbivore conflicts undermine local livelihoods and erode community support for conservation overall (Treves et al., 2006). In addition, for species sensitive to anthropogenic disturbances, agricultural areas may create barriers to movements resulting in isolation of populations within PAs and precluding herbivore access to key seasonal resources (Hobbs et al., 2008).

Agriculture land use is projected to expand and intensify in African and Asian nations accompanied by a rapid increase in human populations (Laurance et al., 2014; Wilcove et al., 2013). These nations together harbor > 80 % of global mammalian herbivore diversity (Ahrestani and Sankaran, 2016). Agriculture expansion is expected to particularly affect herbivore populations in Asian nations, where a large majority of herbivore species are currently threatened with extinction (Ripple et al., 2015). Among Asian nations, India, with its dense and increasing human population, exemplifies many of the challenges facing large herbivore conservation globally. India currently harbors 39 species of wild mammalian herbivores, a large proportion of which are endemic to south Asia. Mirroring global trends, many of these Indian species are currently threatened with extinction (Ahrestani and Sankaran, 2016). PAs in India are embedded within largely agricultural landscapes and herbivore populations in many PAs are threatened by hunting and competition with livestock (Harihar et al., 2014). In addition, across most Indian

landscapes, crop depredation by wild herbivores is the most pervasive form of human-wildlife conflict. Today 22 of the 29 states in India offer compensations for crop losses, and in the period between 2012 and 2013 these payments totaled over 5 million USD (Karanth et al., 2018). While compensations offer a means to temporarily mitigate the adverse effects of wildlife conflicts, they are not a panacea since little evidence exists to suggest that they result in improved, long-term conservation outcomes (Naughton-Treves et al., 2003).

Addressing the twin challenges of habitat loss and human - herbivore conflict resulting from agricultural expansion requires an understanding of the spatial ecology of herbivores within agricultural areas as well as their patterns of interactions with humans. Even as studies on the use of agricultural lands by wild mammals, particularly carnivores, has gained traction in recent years (Ferreira et al., 2018; Chapter 1), little to no information exists about the ecology of wild herbivores in these human modified areas. In India, much of our limited understanding of how wild mammalian herbivores use farmlands stems from studies examining human-herbivore interactions, the spatio-temporal patterns of crop depredation, and species distribution models based on key informant surveys (Sankaran and Ahrestani, 2016). Undoubtedly, these studies provide important insights into how local communities perceive the impacts of herbivore species on their lives. Where community perceptions of different species, their abundances, and their potential for undesired effects are highly uncertain, conflict surveys have the potential to paint a biased picture of the true underlying distribution patterns of these species (Naughton-Treves, 1997). When these biases are accounted for, leveraging the ecological knowledge of local community members can be an efficient way to sample human dominated areas, where conventional species detection methods such as camera traps, animal signs may be characterized by low detection probabilities and other logistical constraints (Pillay et al., 2014).

In our research, we examined the differential impacts of agriculture on a diverse assemblage of herbivore species in the Central Terai Landscape (CTL) in northern India. The alluvial tall grassland and riparian forest habitats of the CTL support multiple mammalian herbivores including several threatened and endangered species such as hog deer (*Axis porcinus*), swamp deer (*Cervus duvaucelli*) and one horned rhinoceros (*Rhinoceros unicornis*). Previous studies have shown that compared to many similar landscapes, herbivore densities within PAs of the CTL are very low, undermining tiger population recovery efforts (Chanchani et al., 2014). The key objective of our study was to determine the environmental factors associated with spatio-temporal variation in the distribution patterns of mammalian herbivores that occur within agricultural areas in the CTL. In addition, we determined the perceptions of local human communities to herbivore use and conflicts in this area. Specifically, we were interested in the relationship between community perceptions of the spatial occurrence patterns of herbivore species, perceived patterns of conflicts, and the estimated distribution of these species relative to the reported areas of conflict.

To address these objectives, we collected species detection data under a novel sample design, employing two different species detection methods; camera traps and rapid farmer interviews. We applied dynamic occupancy models that corrected for positive and false-negative detection errors (Miller et al., 2013) to estimate the environmental factors underlying the space use patterns of multiple herbivore species and to determine the probability with which farmers report a species from a site where it is truly absent (false-positive detection probability). In addition, we generated a map showing the location of human-wildlife conflicts in the CTL by conducting detailed interviews of farmers. From this dataset we investigated the relationship between reported levels of conflict with a species and its estimated site level use probability.

Methods

Study Area

The Central Terai Landscape (CTL) lies within the state of Uttar Pradesh in northern India. Remnant fragments of the Terai ecosystem occur within this landscape separated by extensive areas of human habitation and agriculture. Protected areas (PAs) and multiple-use forests encompassing these fragments support a globally significant population of tigers (Chanchaniet al. 2014). In addition, the landscape also supports populations of eleven species of wild mammalian herbivores (Appendix 2.1, Table S9). While most of these species occur predominantly within PAs, a small population of the endemic antelope species, blackbuck (*Antelope cervicapra*), is believed to occur exclusively within matrix areas. Our study was conducted in a 1500 sq.km agricultural area in the CTL that forms a movement corridor for tigers and swamp deer between Pilibhit Tiger Reserve (PTR) and Dudhwa Tiger Reserve (DTR; Fig. 2.1). The CTL has a sub-tropical climate comprising of four seasons: summer (April-June), monsoon (July-September), post-monsoon (October-November), and winter (December-March). Sugarcane is the dominant agricultural crop in the matrix between PAs and has an eight-month growing cycle beginning with planting in March and harvest starting in December. In addition to sugarcane, wheat and rice are also cultivated in the winter and post monsoon season, respectively. The Sharada River flows through the center of the study area and the river system, along with its extensive network of drainages, supports riparian grassland and forest habitats that lie within the jurisdiction of the North and South Kheri Forest Divisions. These areas experience various forms of resource extraction including timber harvest, livestock grazing, and the collection of non-timber forest produce.

Species detection/non-detection surveys

Using Generalized Random Tessellation Stratified (GRTS; Stevens & Olsen 2004), we randomly selected 94, 1.6 km x 1.6 km cells (Fig. 2.1). Our sampling frame excluded any cells that overlapped protected areas, since we were primarily interested in determining herbivore space use on privately-owned and multiple-use lands.

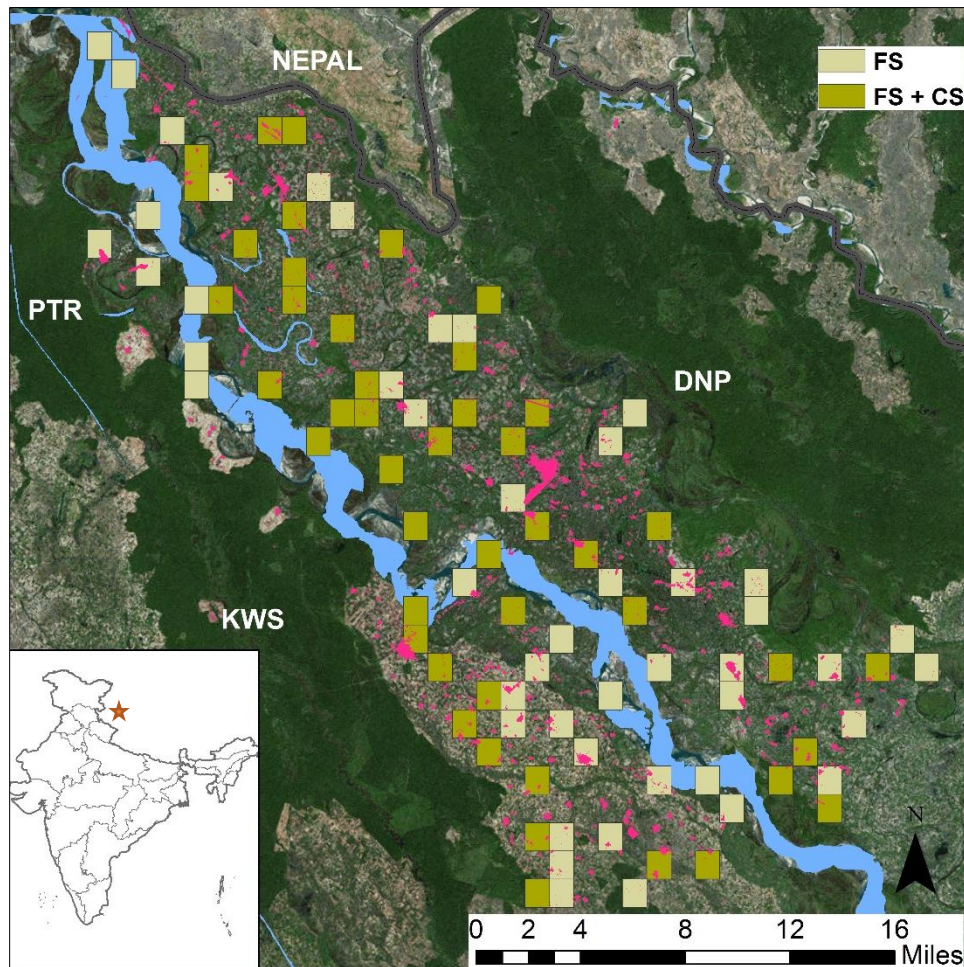


Figure 2.1: Study area and sampling design. Pink polygons indicate human settlements and the Sharad River and its associated drainages are shown in blue. The study area separates Dudhwa National Park (DNP) from Pilibhit Tiger Reserve (PTR) and Kishanpur Wildlife Sanctuary (KWS). Interview surveys to assess human-wildlife conflicts in the study area were conducted within the dark green cells and included both farmer surveys (FS) and camera surveys (CS). The dimension of each cell is 1.6 X 1.6 km.

Within the selected cells we sampled for herbivore species using two different survey methods; farmer surveys (FS) and camera surveys (CS). FS were conducted in all cells and involved rapid interviews with 1-12 farmers per cell to document the presence of multiple mammalian species on their lands within a given season. Each farmer was shown images of large mammals along with verbal descriptions of each species and their signs (e.g. tracks, scat, etc.) and asked if they observed these species on their lands within the past month. By surveying farmers within their fields, we limited the possibility of their misunderstanding the spatial extent of the cell being surveyed. CS were conducted in a randomly selected subset of the cells where FS were conducted (Fig. 2.1).

For CS, we placed a single motion-activated Cuddeback Attack 5.0-megapixel Trail Camera (Cuddeback Digital, Green Bay, Wisconsin, USA) within the cell for a period of 30-40 days. For each camera location, we collected data on the presence of guard dogs, fences and the number of homes within a 100 m radius of the camera trap. We also noted the presence of water, sugarcane, and wheat/ rice crop near the camera trap. In the final analysis, we treated each five-day period as an independent survey occasion.

In this study, farmer surveys (FS) were considered a source of uncertain detections, that is, farmers may report a herbivore species as present at a site that is truly unoccupied (false-positive error) or fail to report a species that is present (false-negative error). False-positive errors could arise for a variety of reasons including, mis-identifying a species, misunderstanding the spatial extent of the cell for which information is being sought, or memory lapses. In contrast, CS were considered a source of certain data—that is, CS were assumed to be free of false-positive errors. We repeated both surveys (FS and CS) in each of the three sampled

seasons (Appendix 2.1, Table S10). In each season, sampling entailed first deploying camera traps followed by farmer surveys which were conducted towards the end of each season.

To understand the influence of cover availability on site use, we repeated these surveys over three survey seasons. The seasons were defined according to the growth and harvest cycle of sugarcane, the dominant crop in the matrix; winter/high cover, summer/low cover and monsoon/moderate cover. Our survey seasons also coincided with the prevailing climatological seasons in the area and were characterized by marked differences in vegetation growth, cover, temperature, and precipitation (Appendix 2.1, Table S10). The seasons also roughly demarcate periods of forage availability for prey species both within and outside PAs. The native grassland patches within PAs in the CTL are at their tallest and most unpalatable state during the winter months. Towards the end of January, grassland habitats are burnt to stimulate fresh grass production (Moe and Wegge, 1997). These grassland areas are generally low-lying and become inundated during the monsoon season. Outside PAs, wheat is planted in early winter, whereas rice is planted in late summer and post-monsoon season.

Conflict surveys

To characterize community perceptions of human-herbivore conflicts in the landscape, we conducted 350 semi-structured interviews with farmers. We restricted these interviews to a random set of farmers practicing agriculture within cells where we applied both types of species detection surveys (FS and CS; Fig.2.1). We asked farmers to list the ongoing livelihood challenges they face as agriculturalists living in the area. Farmers who reported crop losses as a challenge were asked to list the species they believed to be responsible, the crops most vulnerable, and extent of damage annually. They were also asked about the measures they

employed to address wildlife conflicts—for example, the use of guard dogs, fences, or night guarding.

Analysis

Seasonal use probabilities.

We estimated, by fitting dynamic occupancy models that correct for false-positive errors (Miller et al. 2013), season-specific use probabilities for the three wild herbivore species (hog deer, wild boar and nilgai) for which we had adequate camera detections. These models extract information from uncertain (FS) and certain (CS) survey data to estimate initial use, vital rates associated with seasonal use dynamics (extinction and colonization probability), and detection probability parameters. Model parameters, associated notations and their descriptions are summarized in Table 2.1.

Table 2.1: Definitions and notations for model parameters

Parameter (Notation)	Definition
Probability of use in winter (Ψ_w)	Probability that a cell was used by a species in the first season of the study.
Extinction probability (ε_t)	Probability that a cell that is used in one season will not be used in the subsequent season.
Colonization probability (γ_t)	Probability that an unused cell will be used in the subsequent season.
False positive detection probability, $p_{10,FS}$	Probability that an unused cell will be incorrectly classified as used. This probability is nonzero for farmer surveys (FS) only. The probability was zero for camera trap surveys.
Detection probability for FS and CS $p_{11,FS}$, $p_{11,CS}$	Probability of detecting a species on a survey occasion given the cell was used by the species during the survey season
Derived Parameters	
Probability of use in summer (Ψ_s) and monsoon (Ψ_m) seasons.	Probability that a cell was used in the summer and monsoon season, respectively. These quantities are calculated using estimates of winter use probabilities and associated extinction and colonization probabilities

For each species, we estimated parameters as functions of covariates that were *a-priori* hypothesized to influence their habitat use dynamics and detection probabilities. We selected covariates that together represented the availability of vegetative cover, native habitats, and anthropogenic disturbances within the study area. In addition, we measured the minimum Euclidean distance between a cell and the nearest PA boundary and the mean elevation of each cell. We tested for multicollinearity among covariates based on their variance inflation factor (Zuur et al. 2010) and retained covariates with a value less than 5 for possible inclusion in the occupancy models (Appendix 2.2, Table S11).

We modeled the initial probability of use (Ψ_w)—the probability of use in winter—for each species as a function of 5 covariates: cell-specific median NDVI values in the winter (NDVI_W), distance of cell to protected area boundary (PA), proportion of cell under native habitats (Nat), proportion of cell under human settlements (Sett) and mean elevation of the cell (Elev). We expected use probabilities for all species to decline with increasing distance to PA boundaries (Karanth, 2016). In the winter season, standing sugarcane crop and native riparian grassland habitats are the principal source of vegetative cover in the matrix. Wild boar and hog deer are known to regularly occur within sugarcane stands and dense stands of riparian grasslands. We therefore expected use probabilities for these species to be higher in cells with dense cover reflected by a positive or quadratic relationship between initial occupancy and our index for cell specific winter cover availability (NDVI_W). In contrast, we expected use probabilities to decline with the availability of denser cover for nilgai which uses more open habitats (Dinerstein, 1979). We expected cells with a higher proportion of their area under native vegetation (Nat) to have higher use probabilities for all three species. Conversely, we predicted use probabilities to decline for all species as the area covered by human settlements (Sett)

increased within a cell. While elevation does not vary dramatically across the study area, the presence of multiple drainage features lends some topographic variation to the site. Low-lying areas are typically characterized by marshy conditions, higher probability of inundation during monsoon, and are populated by either by native vegetation or sugarcane cultivation. We therefore expected use probabilities to be higher for wild boar and hog deer in cells with lower mean elevation (Elev) and lower for nilgai.

Local extinction (ε_t) and colonization probabilities (γ_t) influence temporal habitat use dynamics. Extinction probability (ε_t) reflects the probability that a cell used in season t , will become unused in season $t+1$. Conversely, colonization probability (γ_t) describes the probability that an unused cell in season t will become used in the subsequent season ($t+1$). The study area experiences a net loss of cover in the summer season following the harvest of sugarcane. In the monsoon season, flooding inundates many parts of the study area, resulting in a decline in available habitats. Moreover, the availability of palatable forage within native grasslands inside PAs in the CTL is at its lowest in the winter season. Forage availability increases steadily through the summer and monsoon season following the burning of grasslands. We therefore predicted that herbivore use of matrix areas would be high during the winter season and progressively decline through the summer and monsoon seasons.

False-positive dynamic occupancy models allow for the estimation of two detection probabilities: the probability of detecting a species given the cell is occupied (used) by the species (p_{11} , true detection probability) and the probability of reporting a species as present when the cell is unoccupied (unused) by the species (p_{10} , false-positive detection probability). For this study, we estimated true detection probabilities for both farmer surveys ($p_{11,FS}$) and camera surveys ($p_{11,CS}$) and false-positive detection probabilities (p_{10}) for the farmer surveys

(FS). We modeled these parameters as functions of covariates hypothesized *a-priori* to influence the detection process. We expected false-positive detection probabilities for all species to decline with increasing distance to protected areas (PA). Since farmers in the area believe that wild mammals are most prevalent in the study area during the winter season and ‘return’ to the forest in the monsoon season, we predicted that false-positive probabilities for all species would be highest in the winter season and lowest in the monsoon season.

The probability of detecting a species given it used a cell can be influenced by the abundance of the species within the cell (Royle and Nichols, 2003) . We modeled true detection probabilities for farmer surveys ($p_{11,FS}$) and camera surveys ($p_{11,CS}$) for all species as functions of covariates predicted to influence species abundance at the scale of the cell. We predicted that detection probabilities for both FS and CS would be higher for all species in cells closer to park boundaries (PA) and with small settlement areas (Sett). In addition, we tested the additive effects of five local level covariates (Home, Dog/Fence, Wheat, Cane, Water) on detection probabilities using CS. We expected detection probabilities with camera traps to be higher at camera locations proximate to water features and sugarcane or wheat cultivation. Similarly, we predicted detection probabilities to be lower at camera locations with higher anthropogenic disturbance (Home) and the presence of crop protection measures (Dog/Fence). Finally, we predicted that true detection probabilities with both surveys methods would be highest in the winter season and lowest in the monsoon seasons reflecting our expectations of the change in abundance of the species within the study area across seasons.

We tested these hypotheses in Program MARK (White and Burnham 1999) using the false-positive robust design occupancy model. We built models using a step-wise approach and compared them based on Akaike’s Information Criteria (AIC; Burnham and Anderson, 2003).

The step-wise approach involved comparing alternative models for a given parameter to identify the best supported covariate structure (lowest AIC) while holding a global covariate structure constant (all covariates of interest) on all other parameters. Once the best structure was identified for the parameter under consideration, we retained this structure and proceeded to identify the best covariate structure for the next model parameter. We first identified the best-supported covariate structure from among nine competing models for our true detection probability parameters ($p_{11,FS}, p_{11,CS}$). In these models, we included the cell level covariates (PA, Sett), the local level covariates (Home, Dog/Fence, Wheat, Cane, Water), the effect of survey season (Season), and survey method (Method) in various additive and interactive combinations (Appendix 2.2, Table S12). Retaining the best supported structure on p_{11} we considered three alternative model structures for false-positive detection probability ($p_{10,FS}$) that included both univariate and additive combinations of the covariates distance to protected area boundary (PA) and survey season (Season). Next, we considered models for initial use in the winter season (Ψ_w) where the covariates of interest (PA, Sett, Nat, NDVI_W, Elev) were included in select additive combinations (Appendix 2.2, Table S13), while retaining a global structure on the vital rate parameters (ϵ_t, γ_t). Retaining the best fit structure on the detection and occupancy parameters, we fit seven models to explore the effects of season on extinction and colonization probabilities (Appendix 2.2, Table S14). We explicitly tested whether herbivore use changed among seasons by fitting models where either extinction and/or colonization probability were fixed to zero (i.e., models with no extinction and/or models with no colonization among seasons).

At each step we also fit intercept-only models. Our final model-set included a version of the best-supported model in the model-set assuming no false-positive errors ($p_{10,FS} = 0$ for all survey types). Finally, using parameter estimates from the best supported model, we derived

estimates of the probability of cell use by herbivores for summer (Ψ_s) and monsoon (Ψ_m) seasons (MacKenzie et al., 2017).

Perceived conflicts

We summarized data from social surveys to determine the frequencies with which respondents reported experiencing different livelihood challenges, the frequency with which different species were reported as causing conflict, and the conflict prevention measures employed. We generated these summaries both at the scale of the study area and for individual cells where respondents practiced agriculture.

Relationship between species use probabilities and perceived levels of conflicts

For each species, we estimated conditional use probabilities for the winter season at cells where we conducted camera surveys. Conditional use probability, or the probability that the cell was used given the sampling effort, is 100 % for cells where the camera detected the species. For all cells where the species was never detected using CS, we estimated conditional use probabilities using eq. 1 (MacKenzie et al., 2017). We estimated use probabilities for each cell ($\hat{\Psi}_i$) using coefficient estimates from the best-supported model and associated covariates. We estimated use ($\hat{\Psi}_w$) and detection probabilities (\hat{p}_i) for each cell using covariate values and coefficient estimates from the best-supported model.

$$\tilde{\Psi}_{i,condl} = \frac{\tilde{\Psi}_i (1-\hat{p}_i)^J}{(1-\tilde{\Psi}_i) + \tilde{\Psi}_i (1-\hat{p}_i)^J} \quad \text{eq. 1}$$

In addition, within each cell we calculated the proportion of interviewed farmers who reported experiencing conflicts with wild boar, nilgai or hog deer. We were interested in estimating the relationship between the frequencies with which species are reported as conflict causing with the use probabilities of these species. We therefore estimated the Pearson's

correlation between each species conditional use probability at a site and the proportion of respondents who report the species as problematic.

Results

Of the 11 herbivore species found in the CTL, five were detected within agricultural areas with camera traps including chital, wild boar, nilgai, hog deer and swamp deer. Naïve estimates of the proportion of cells used for these species varied substantially between FS and CS and were higher for all species using FS across the three survey seasons (Table 2.2).

Discrepancies between naïve use estimates based on FS and CS were highest for chital, wild boar and swamp deer

Table 2.2: Naïve proportion of cells used by different herbivore species based on farmer surveys (FS) and camera surveys (CS)

Species	Winter		Summer		Monsoon	
	FS	CS	FS	CS	FS	CS
Chital	0.64	0.04	0.40	0.02	0.30	0.06
Hog deer	0.75	0.40	0.59	0.39	0.46	0.28
Swamp deer	0.40	0.02	0.26	0	0.19	0.09
Nilgai	0.96	0.46	0.83	0.25	0.76	0.21
Wild boar	0.82	0.19	0.76	0.19	0.72	0.18

Detection Probability

Models where detection probabilities varied by method and season had the highest support for all three species (Appendix 2.2, Table S12). Detection probabilities via FS were 3-5 times those for CS and were highest in the winter and lowest in the summer season (Table 2.3).

Detection probabilities associated with FS were highest for nilgai and lowest for wild boar.

Contrary to our expectations, the local scale covariates (Home, Dog/Fence, Water, Cane, Wheat) influenced the detection probabilities of wild boar and nilgai, but not hog deer.

As expected, proximity to water and the presence of sugarcane positively affected wild boar detection probabilities using camera traps whereas presence of wheat crop was associated with lower detection probability (Table 2.4). These covariates had the opposite effect on the detection probabilities of nilgai. Detection probability for the species was higher at camera locations proximate to wheat crop and lower at locations with water and sugarcane crop. As hypothesized, anthropogenic disturbance, indexed by the number of homes within a 100 m radius of a camera trap, negatively influenced the detection probabilities of both nilgai and wild boar. Unexpectedly, the presence of crop protection measures such as fencing, and guard dogs were associated with higher detection probabilities for both wild boar and nilgai (Table 2.4).

Table 2.3: Species and season specific true detection probabilities (standard errors) for Farmer Surveys (FS) and Camera Surveys (CS)

Species	Hog deer		Nilgai		Wild boar	
	FS	CS	FS	CS	FS	CS
Winter	0.84 (0.02)	0.27 (0.03)	0.92 (0.01)	0.32 (0.03)	0.59 (0.03)	0.14 (0.02)
Summer	0.64 (0.03)	0.11 (0.02)	0.85 (0.02)	0.18 (0.02)	0.45 (0.03)	0.09 (0.02)
Monsoon	0.73 (0.04)	0.15 (0.03)	0.87 (0.02)	0.20 (0.03)	0.52 (0.03)	0.11 (0.02)

Table 2.4: Effects of local scale covariates on specific detection probabilities associated with camera surveys. Beta coefficients and standard errors are based on best supported models

Species	Home	Dog/Fence	Water	Sugarcane	Wheat
Hog deer	-	-	-	-	-
Nilgai	-1.47 (0.34)	0.99 (0.47)	-0.9 (0.25)	-0.21 (0.32)	0.13 (0.26)
Wild boar	-0.13 (0.35)	0.89 (0.64)	1.37 (0.38)	0.16 (0.43)	-0.84 (0.44)

The cell level covariates (PA and Sett) only influenced the detection probabilities of wild boar. Consistent with our hypothesis, detection probabilities for the species declined with increasing distance to protected areas ($\beta_{PA} = -0.21$, SE 0.03) and increasing area of settlements within a cell (β_{Sett} ; -5.5, SE 1.67). False-positive detection probabilities varied by season for hog deer and nilgai and were highest in the winter but declined in the summer and monsoon season (Fig.2.2). False-positive probabilities for wild boar declined with increasing distance to PA boundaries (PA; -0.37, SE 0.08). False-positive probabilities averaged across sites was highest for wild boar and lowest for hog deer (Fig.2.2).

Use Probability

Among candidate models for winter hog deer habitat use, a model that included elevation (Elev), a linear relationship with cover (NDVI_W), distance to protected areas (PA), availability of native habitats (Nat) and proportion of cell area under settlements (Sett) had the highest support (Appendix 2.2, Table S13). Individual covariate effects on use probabilities estimated with this model were consistent with our expectations. Hog deer use increased with increasing cover availability, with increasing proportion of native habitats (Nat), and elevation (Elev; Table 5). Use probabilities for hog deer decreased with increasing distance to protected areas (PA) and increasing proportion of settlements within a cell (Sett). For nilgai, the best supported model for winter use probabilities included a quadratic relationship with cover availability of cover (NDVI_W + NDVI_W²) and the availability of native habitats (Nat) (Appendix 2.2, Table S13). As hypothesized, nilgai habitat use peaked at low cover availability and was lowest at intermediate and high cover availability (Table 2.5).

None of the covariates considered were included in the best-supported model for wild boar winter use probabilities (Table 2.5, Appendix 2.2, table S13). However, univariate models

that included a linear relationship with cover (NDVI_W) and the proportion of the cell area under human settlements (Sett) were the second and third best supported models. Contrary to our hypotheses, wild boar use probabilities declined with increasing cover availability and increased with increasing settlement area within a cell (Table 2.5).

Table 2.5: Covariate coefficients and standard errors associated with species-specific initial use probability (Ψ_w) based on best-supported models

	Hog deer	Nilgai	Wild boar
Intercept	-59.65 (15.87)	95.75 (16.13)	0.12 (0.27)
PA	-0.23 (0.16)		
Sett	-25.38 (11.55)		8.72 (7.17)*
NDVI_W	51.01 (16.41)	-732.75 (125.41)	-8.02 (6.5)**
NDVI_W^2		1383.68 (244.58)	
Nat	1.73 (1.67)	4.89 (3.08)	
Elev	312.24 (85.15)		

Estimates based on model with second () and third (**) highest support (Appendix 2.2).*

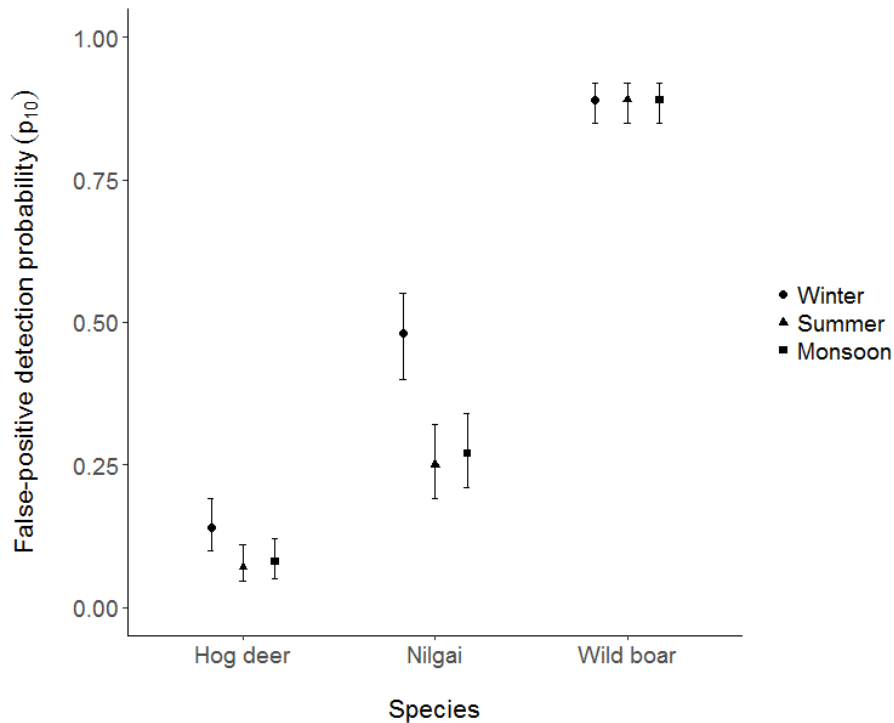


Figure 2.2: Species and season specific false-positive detection probability estimates using farmer surveys (FS).

Vital rates

Our hypothesis that use of farmlands by herbivores would decline following the winter season was supported only for hog deer (Appendix 2.2, table S14). A model where colonization probabilities were fixed at 0 had the highest support for the species (Table 2.6). Extinction probabilities for the species was marginally higher in the summer-monsoon transition compared to the winter-summer transition, resulting in a steep decline habitat use probabilities by hog deer in the monsoon season. As per the best-supported model, the number of sites used by nilgai declined slightly during the winter-summer transition, following which habitat use remained static in the summer and monsoon (Table 2.6, Appendix 2.2, Table S14). Wild boar was the only species characterized by an increase in the number of sites used in the summer season. Based on the best-supported model, the habitat use probabilities for wild boar increased in the summer season before declining in the monsoon season (Table 2.6, Fig 2.3, Appendix 2.2, Table S14).

Table 2.6: Local extinction and colonization probabilities based on best-supported models for each species.

Species	Extinction probability (Winter-Summer)	Colonization probability (Winter-Summer)	Extinction probability (Summer-Monsoon)	Colonization probability (Summer-Monsoon)
Hog deer	0.05 (0.04)	0	0.21 (0.07)	0
Nilgai	0.25 (0.06)	0.20 (0.08)	0	0
Wild boar	0.14 (0.05)	0.37 (0.09)	0.14 (0.05)	0.05 (0.06)

Socio-economic characteristics of interviewed farmers and perceived conflicts.

We interviewed a total of 351 farmers across 46 grid cells. All but three interviewed farmers were male, and the median age of respondents was 45. Flooding and crop depredation by wildlife were the two most frequently reported challenges. Seventy-one percent of interviewed farmers reported flooding as a significant challenge, whereas crop raiding by wild herbivores was reported by 57 % of the farmers. Other challenges reported less frequently (<5%) included

poverty, non-profitability of agriculture, unemployment and livestock depredation. All instances of livestock depredation recorded were attributed to the Indian wolf (*Canis lupus pallipes*) and jackals (*Canis aureus*).

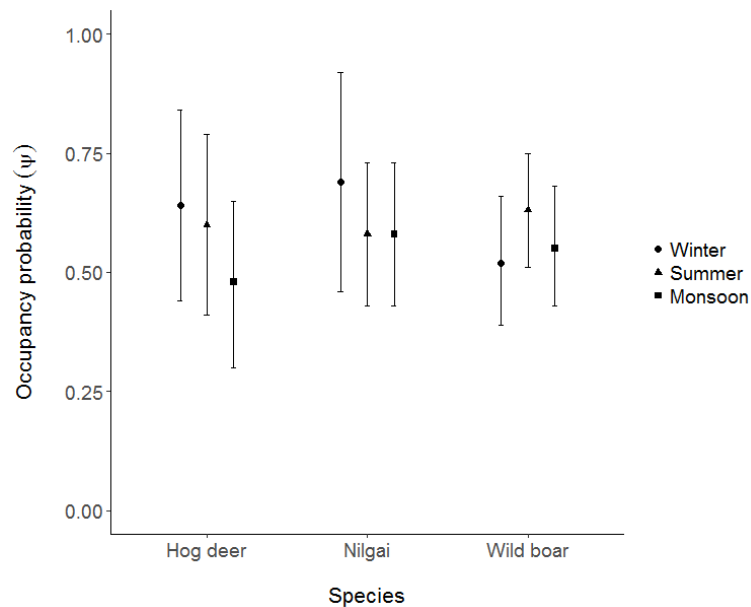


Figure 2.3: Species-specific seasonal occupancy probabilities based on mean values of covariates

Wild boar was the most frequently reported conflict-causing species during the survey period. Similarly, nilgai and hog deer were the second and fifth most commonly reported conflict-causing species (Fig. 2.4). Most interviewed farmers (82 %) reported using some form of crop protection measure including fencing, watch dogs, guarding, and chemicals repellents. On average, farmers reported spending approximately 60 USD annually and 8 hours per day on crop protection.

Relationship between species use probabilities and perceived levels of conflicts

For wild boar and hog deer we found no correlation between their use probabilities and the reported conflict frequency ($\rho = 0.08$ for wild boar and $\rho = 0.14$ for hog deer). There was moderate correlation between these variables for nilgai ($\rho = 0.60$).

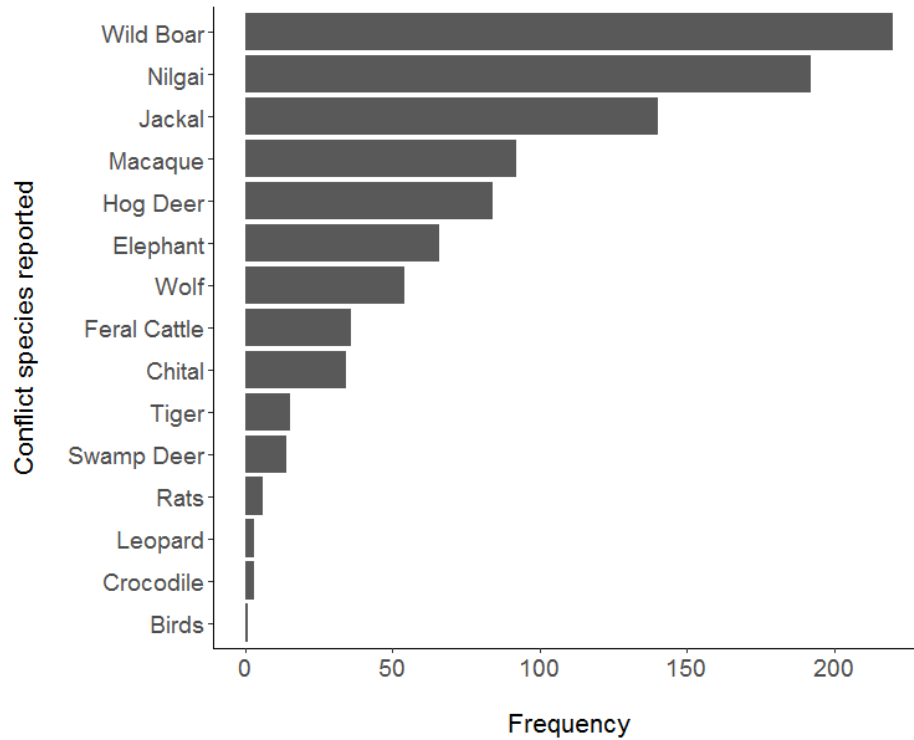


Figure 2.4: Number of farmers (frequency) which reported conflicts with species across the study area

Discussion

We found that farmlands were used by only a subset of mammalian herbivore species found in the CTL. Six of the 11 species found in the CTL were never detected within agricultural areas. Notable among these is the black buck, whose populations are thought to exist primarily within unprotected grassland and agricultural areas in the larger Terai landscape (Dinerstein, 1979). The two largest herbivore species found in the CTL, one-horned rhinoceros and Asian elephants, were also not detected using the study area. There have been sporadic reports of one-horned rhinoceros moving through agricultural areas of the CTL, particularly in the northern sections of the study area. Elephants on the other hand, have only been reported using farmlands proximate to the southern boundary of Dudhwa National Park (DNP). Herbivore species that are largely restricted to forested habitats such as the four-horned antelope, barking deer and sambar deer (Appendix 2.1, Table S9) were also never detected using farmlands. Even though chital are

the most numerous wild herbivore within PAs in the CTL (Chanchani et al., 2014), nilgai, hog deer and wild boar were the most widely distributed species in farmlands (Fig. 2.3). Using camera traps, swamp deer and chital were only detected at two sites, both adjoining PA boundaries.

Nilgai, hog deer and wild boar, the three most widely distributed species in the landscape, used agricultural areas with high probability across all three seasons. This result is consistent with a hog deer study conducted within native habitats in Nepal which showed that the species tends to show high habitat fidelity and low movement rates across seasons, including during periods of low cover availability (Moe and Wegge, 1997). This contrasts with tiger habitat use of the matrix which peaked during the winter and dropped significantly during the other two seasons (Chapter 1). The summer season was characterized by a decline in detection probabilities for all three species. We believe this decline may be indicative of a decline in the abundance of these species within agricultural areas suggesting movement of individuals of all three species into PAs. All else equal, abundance variation within a cell will lead to substantial variation in detection probability (Royle and Nichols, 2003). Movement into PAs may be triggered by an increase in forage availability within PAs in the summer season associated with the management practice of burning of grasslands in late winter. A study conducted in Nepal, for example, documented an increase in the density of hog deer within burnt grasslands in the summer season (Moe and Wegge, 1997). The decline in detection probabilities in the summer season may also result from a behavioral response to decreased cover during this season.

Use probabilities of hog deer and nilgai were influenced primarily by the distribution of native habitat and agricultural crop cover (Table 2.5, Appendix 2.2, Table S13). Proportion of cell area under native habitats was positively associated with use probabilities for both species.

These native habitats are comprised of riparian vegetation that are currently threatened by uncontrolled livestock grazing. Dense sugarcane crop cover was associated with higher use probabilities for hog deer and lower use probabilities for nilgai consistent with what is known about the ecology of these species. Dense sugarcane stands structurally resemble native alluvial tall grasslands, the primary native habitats of hog deer, whereas nilgai show strong associations with open savanna habitats (Bagchi et al., 2004; Dinerstein, 1979). Avoidance of dense sugarcane stands by nilgai was evident even at finer spatial scales. Detection probabilities for nilgai was lower at camera locations proximate to dense sugarcane crop and higher near low cover crops such as wheat.

Anthropogenic disturbances negatively impacted use probabilities of hog deer and were positively associated with wild boar use. Stillfried et al. (2017) demonstrated that wild boar show considerable behavioral plasticity when using human dominated areas and modulate exposure to anthropogenic risks by avoiding areas near homes. We documented a similar pattern where at larger spatial scales wild boar used areas with large settlements; however, at finer spatial scales (near camera traps) their detection probabilities declined with increasing number of homes. The relative insensitivity of nilgai use to anthropogenic disturbances may reflect the fact that the species is not hunted by local communities due to religious taboos (Johnson et al., 2018) and that settlement areas offer few foraging opportunities to the species. However, like wild boar, the species may occur at lower densities near homes reducing its detection probability.

Multiple studies have demonstrated that crop depredation by wild herbivores is higher near the boundaries of PAs (Linkie et al., 2007; Naughton-Treves, 1997). Similarly, we found support for a negative relationship between distance to PA boundary and use probability for hog deer (Table 2.6). Alluvial grassland areas that are critical hog deer habitats lie along the

boundaries of PAs in the CTL and are a potential reason why farmlands proximate to PA boundaries had higher hog deer use probabilities. The two most commonly reported crop-raiding species, nilgai and wild boar, however, did not show declines in their use probabilities with increasing distance to PA boundaries suggesting that PAs may not be an important source of individuals for these species. Finally, the presence of two crop guarding measures (fences and guard dogs) was associated with higher detection probabilities for both nilgai and wild boar. Other studies have found that guard animals and fencing significantly reduce crop losses (Karanth et al., 2013; Linkie et al., 2007). Our result may be indicative of the fact that farmers who experience high levels of crop depredation by these species are more likely to invest in these forms of crop protection measures (Karanth and Kudalkar, 2017).

Species using novel and human dominated habitats are often characterized by behaviors such as increased vigilance, altered grouping patterns, and avoidance that reduce their exposure to anthropogenic risks (Stillfried et al., 2017). Based on our camera trap data, we did not detect any age or sex bias in the use of agricultural areas by hog deer, nilgai and wild boar. However, our sample sizes did not allow for powerful tests of potential differences. In the case of hog deer and nilgai, we detected females with young fawns suggesting that these species may breed within agricultural areas. Grouping patterns of these species were also not markedly different from those seen within native habitats. Hog deer were typically detected in groups of two which is consistent with their grouping patterns within native habitats (Dhungel and O’Gara, 1991). Nilgai are known to segregate into loose groups by sex, with females and fawns grouping together and males occurring either solitarily or in small bachelor herds (Bagchi et al., 2008). Nilgai detected using camera traps within farmlands were either females with yearling and fawns or solitary adult males. This contradicts findings by Bayani and Watve (2016) who found that crop

raiding nilgai tended to be largely female, with males and young calves occurring less frequently within farmlands. Alternatively, wild boar were never detected in groups and most camera trap captures were of solitary individuals.

Our results provide an important ecological basis for understanding farmland use and depredation patterns. In the CTL, herbivore use of agricultural areas is consistent with their habitat use patterns within native habitats. The availability of cover was a strong determinant of both nilgai and hog deer use patterns. For example, nilgai prefer areas with native habitats and areas with low cover. This suggests that depredation by nilgai is more likely in areas where low cover crops such as wheat and rice are grown in the proximity of native habitats. Conversely, depredation potential for wild boar may be higher in areas with dense patches of sugarcane cultivation located adjacent to large settlements. In addition, for both nilgai and hog deer, the presence of native habitats within a cell positively affected their use probabilities. These patches of riparian grassland habitats are currently threatened by intense domestic livestock grazing pressures. Competition for forage with domestic livestock may cause increased crop depredation by hog deer and nilgai in farmlands proximate to these native habitat patches. In addition, with increasing urbanization in the CTL, we speculate that the area will experience an increase in crop depredation by species such as nilgai and wild boar and a decline in overall habitat availability for hog deer.

Use estimates from FS resulted in positively biased estimates of herbivore species' diversity and the distribution of individual species within farmlands. There were significant disparities between the naïve proportion of sites occupied by different species estimated using FS and CS (Table 2.3). While naïve estimates of use were higher using FS for all species, these disparities were especially large for chital, swamp deer and wild boar (Table 2.3). Chital and

swamp deer were reported as present by farmers in 65 and 40 % of the study area respectively however, they were detected with camera traps only at two sites proximate to PAs. We believe that disparities in naïve use estimates reflect the fact that farmer perceptions of the spatial distribution of herbivore species overestimates their true distributions. This is reflected in the high false-positive probabilities with which farmers report the presence of hog deer, nilgai and wild boar. At sites not used by wild boar, there was an 80 % probability of farmers falsely reporting the presence of the species (Fig. 2.2). False-positive probabilities were lower for nilgai and lowest for hog deer. Based on these results, we speculate that farmers in the study area perceive wild boar as the most abundant herbivore species followed by nilgai and hog deer. Farmers perceptions of the abundance of conflict-causing species is often used as an index of their acceptance capacity or tolerance for that species (Zinn et al., 2008). These false-positive probabilities may therefore also indicate low community tolerance for wild boar and nilgai, consistent with studies from other areas in India (Karanth and Kudalkar, 2017).

Detection biases are also reflected in the frequencies with which conflicts with different species are reported. Across the study area, wild boar were reported with the highest frequency followed by nilgai and hog deer (Fig. 2.4). In addition, at the scale of the sampling unit, we found no relationship between the conditional probability that a cell was used by wild boar or hog deer and the proportion of interviewed farmers who report conflict with these species. This suggests that conflicts with wild boar and hog deer are potentially reported from cells where these species may not occur. Interestingly, we found a moderate correlation between nilgai use probabilities and the frequency with which farmers reported conflicts with the species. Perceived conflicts with a species may often be influenced by social, cultural and psychological factors, besides the direct impact of the species on a person's livelihood (Dickman, 2010). In the absence

of parallel studies on the behavior and ecology of conflict species, studies on perceived levels of conflicts may be of limited value in inferring the distribution of conflict causing species and in the subsequent formulation of conflict prevention measures.

The need to implement additional conservation measures to arrest the decline of these mammalian herbivorous species has been well-documented (Ripple et al., 2015). Our study found that agriculture, a rapidly expanding land use globally, adversely affects the populations of herbivore species in the CTL, either through the direct loss of habitats or by attracting individuals of these species to areas where they can experience higher mortality rates. The conversion of native riparian grasslands to agriculture has resulted in the loss of habitat for most mammalian herbivore species in the CTL. For example, agriculture has resulted in a loss of functional connectivity between Dudhwa National Park (DNP) and Pilibhit Tiger Reserve (PTR) for the endangered swamp deer and possibly in the local extirpation of the threatened black buck. Agricultural lands, however, continue to support populations of hog deer, nilgai and wild boar, species which are perceived by community members to cause significant crop damage.

Currently, interview-based data and data on human-wildlife conflicts are the primary sources for estimating herbivore use of agroecosystems. As a result of false positive detections, these data may vastly overestimate the extent to which agricultural areas are used by different herbivore species and their impacts on human communities. In the absence of rigorous verification of conflict claims, compensation schemes based on these data, while mitigating perceived conflicts, may do little to aid the long-term conservation of herbivores within these landscapes. We recommend that studies aimed at understanding human-herbivore conflicts within human dominated areas be paired with independent studies examining the behavior and spatial ecology of these species.

Like many landscapes in India, ongoing conservation initiatives in the CTL fall short of addressing conservation challenges plaguing wild herbivores in the human dominated matrix (Karanth et al., 2018). There is an urgent need to proactively conserve remaining native habitat patches and regulate the expansion of human settlements in the landscape. Additional studies are needed to understand both the movement ecology of herbivores within the matrix and to examine the effects of habitat management within PAs on seasonal habitat use patterns of these species both within and beyond PA boundaries. Perceived escalations in conflicts with species such as nilgai and wild boar have prompted contentious debates on the use of culling to reduce conflicts (Karanth et al., 2018). Given our results, we suggest that defensible population estimates of herbivore species within farmlands should be conducted prior to adopting lethal action as a conflict reduction measure. Finally, we recommend that conservation programs expend more efforts towards educating local community members about the rich diversity of wildlife species that occur within the CTL and working with them to identify effective measures to reduce crop depredation.

LITERATURE CITED

- Abbas, F., Morellet, N., Hewison, A.J.M., Merlet, J., Cargnelutti, B., Lourtet, B., Angibault, J.-M., Daufresne, T., Aulagnier, S., Verheyden, H., 2011. Landscape fragmentation generates spatial variation of diet composition and quality in a generalist herbivore. *Oecologia* 167, 401–411.
- Ahrestani, F.S., Sankaran, M. (Eds.), 2016. The Large herbivores of South and Southeast Asia, in: *The Ecology of Large Herbivore in South and South-East Asia*. Springer, pp. 1–13.
- Bagchi, S., Goyal, S.P., Sankar, K., 2004. Herbivore density and biomass in a semi-arid tropical dry deciduous forest of western India. *J. Trop. Ecol.* 20, 475–478.
- Bagchi, S., Prakash Goyal, S., Shankar, K., 2008. Social organisation and population structure of ungulates in a dry tropical forest in western India (Mammalia, Artiodactyla). *Mammalia* 72, 44–49.
- Bayani, A., Watve, M., 2016. Differences in behaviour of the nilgai (*Boselaphus tragocamelus*) during foraging in forest versus in agricultural land. *J. Trop. Ecol.* 32, 469–481.
- Burnham, K.P., Anderson, D.R., 2003. *Model selection and multimodel inference: a practical information-theoretic approach*. Springer Science & Business Media.
- Chanchani, P., Bista, A., Warriar, R., Nair, S., Sharma, R., Hasa, D., Gupta, M., 2014. *Status and Conservation of Tigers and their Prey in the Uttar Pradesh Terai*. New Delhi.
- Dhungel, S.K., O’Gara, B.W., 1991. Ecology of the hog deer in Royal Chitwan national Park, Nepal. *Wildl. Monogr.* 119, 3–40.
- Dickman, A.J., 2010. Complexities of conflict: the importance of considering social factors for effectively resolving human–wildlife conflict. *Anim. Conserv.* 13, 458–466.
- Dinerstein, E., 1979. An ecological survey of the Royal Karnali-Bardia Wildlife Reserve, Nepal. Part II: Habitat/animal interactions. *Biol. Conserv.* 16, 265–300.
- Ferreira, A.S., Peres, C.A., Bogoni, J.A., Cassano, C.R., 2018. Use of agroecosystem matrix habitats by mammalian carnivores (Carnivora): a global-scale analysis. *Mamm. Rev.* 48, 312–327.
- Gordon, I.J., 2009. What is the future for wild, large herbivores in human-modified agricultural landscapes? *Wildlife Biol.* 15, 1–9.
- Harihar, A., Pandav, B., MacMillan, D.C., 2014. Identifying realistic recovery targets and conservation actions for tigers in a human-dominated landscape using spatially explicit densities of wild prey and their determinants. *Divers. Distrib.* 20, 567–578.
- Hobbs, N.T., Galvin, K.A., Stokes, C.J., Lockett, J.M., Ash, A.J., Boone, R.B., Reid, R.S., Thornton, P.K., 2008. Fragmentation of rangelands: Implications for humans, animals, and

- landscapes. *Glob. Environ. Chang.* 18, 776–785.
- Johnson, M., Karanth, K., Weinthal, E., 2018. Compensation as a Policy for Mitigating Human-wildlife Conflict Around Four Protected Areas in Rajasthan, India. *Conserv. Soc.* 16, 305.
- Karanth, K.K., 2016. Wildlife in the matrix: spatio-temporal patterns of herbivore occurrence in Karnataka, India. *Environ. Manage.* 57, 189–206.
- Karanth, K.K., Gupta, S., Vanamamalai, A., 2018. Compensation payments, procedures and policies towards human-wildlife conflict management: Insights from India. *Biol. Conserv.* 227, 383–389.
- Karanth, K.K., Kudalkar, S., 2017. History, Location, and Species Matter: Insights for Human-Wildlife Conflict Mitigation From India. *Hum. Dimens. Wildl.* 22, 331–346.
- Laurance, W.F., Sayer, J., Cassman, K.G., 2014. Agricultural expansion and its impacts on tropical nature. *Trends Ecol. Evol.* 29, 107–116.
- Linkie, M., Dinata, Y., Nofrianto, A., Leader-Williams, N., 2007. Patterns and perceptions of wildlife crop raiding in and around Kerinci Seblat National Park, Sumatra. *Anim. Conserv.* 10, 127–135.
- MacKenzie, D.I., Nichols, J.D., Royle, J.A., Pollock, K.H., Bailey, L., Hines, J.E., 2017. *Occupancy estimation and modeling: inferring patterns and dynamics of species occurrence.* Elsevier.
- Miller, D.A.W., Nichols, J.D., Gude, J.A., Rich, L.N., Podruzny, K.M., Hines, J.E., Mitchell, M.S., 2013. Determining occurrence dynamics when false positives occur: estimating the range dynamics of wolves from public survey data. *PLoS One* 8, e65808.
- Moe, S.R., Wegge, P., 1997. The effects of cutting and burning on grass quality and axis deer (*Axis axis*) use of grassland in lowland Nepal. *J. Trop. Ecol.* 13, 279–292.
- Naughton-Treves, L., 1997. Farming the forest edge: Vulnerable places and people around Kibale national Park, Uganda. *Geogr. Rev.* 87, 27–46.
- Naughton-Treves, L., Grossberg, R., Treves, A., 2003. Paying for Tolerance: Rural Citizens' Attitudes toward Wolf Depredation and Compensation. *Conserv. Biol.* 17, 1500–1511.
- Paine, R.T., 2000. Phycology for the mammologist: Marine rocky shores and mammal-dominated communities- How different are the structuring processes? *J. Mammal.* 81, 637–648.
- Pringle, R.M., Young, T.P., Rubenstein, D.I., McCauley, D.J., 2007. Herbivore-initiated interaction cascades and their modulation by productivity in an African savanna. *Proc. Natl. Acad. Sci. U. S. A.* 104, 193–7.
- Ripple, W.J., Newsome, T.M., Wolf, C., Dirzo, R., Everatt, K.T., Galetti, M., Hayward, M.W., Kerley, G.I.H., Levi, T., Lindsey, P.A., Macdonald, D.W., Malhi, Y., Painter, L.E., Sandom, C.J., Terborgh, J., Van Valkenburgh, B., 2015. Collapse of the world's largest

- herbivores. *Sci. Adv.* 1, e1400103.
- Royle, J.A., Nichols, J.D., 2003. Estimating abundance from repeated presence-absence data or point counts. *Ecology* 84, 777–790.
- Sankaran, M., Ahrestani, Farhid. S, 2016. The ecology of large herbivores of South and Southeast Asia: Synthesis and future directions, in: Ahrestani, Farhid. S, Sankaran, M. (Eds.), *The Ecology of Large Herbivores in South and Southeast Asia*. pp. 237–249.
- Stillfried, M., Gras, P., Börner, K., Göritz, F., Painer, J., Röllig, K., Wenzler, M., Hofer, H., Ortmann, S., Kramer-Schadt, S., 2017. Secrets of Success in a Landscape of Fear: Urban Wild Boar Adjust Risk Perception and Tolerate Disturbance. *Front. Ecol. Evol.* 5, 157.
- Treves, A., Wallace, R.B., Naughton-Treves, L., Morales, A., 2006. Co-Managing Human–Wildlife Conflicts: A Review. *Hum. Dimens. Wildl.* 11, 383–396.
- Wilcove, D.S., Giam, X., Edwards, D.P., Fisher, B., Koh, L.P., 2013. Navjot’s nightmare revisited: logging, agriculture, and biodiversity in Southeast Asia. *Trends Ecol. Evol.* 28, 531–540.
- Wolf, C., Ripple, W.J., 2016. Prey depletion as a threat to the world’s large carnivores. *R. Soc. Open Sci.* 3, 160252.
- Zinn, H.C., Manfredo, M.J., Vaske, J.J., 2008. Human Dimensions of Wildlife Social psychological bases for Stakeholder acceptance Capacity.

CHAPTER THREE

A FRAMEWORK FOR ESTIMATING HUMANWILDLIFE INTERACTION PROBABILITIES CONDITIONAL ON SPECIES OCCUPANCY

Introduction

In many parts of the world, biodiversity conservation is undermined by habitat loss, fragmentation, and urbanization, all a consequence of rapid human population growth and unconstrained economic development (DeFries et al., 2007). Expanding human populations result in a net loss of habitat outside protected areas (PA) boundaries and increases the frequency of human-wildlife interactions (Nyhus, 2016). Human-wildlife conflicts (HWC) are a subset of these interactions that adversely affect species populations and human communities. Acting synergistically, habitat loss and HWC increase the isolation of PAs and eventually reduce the size of wildlife populations within them. Habitat loss beyond PA boundaries and HWC can significantly compromise the conservation of large mammal species characterized by their small population sizes and wide-ranging behaviors. The conservation of these imperiled species increasingly depends on extending conservation measures beyond PA boundaries with the goal of minimizing habitat loss and HWC. Consequently, there is growing interest in understanding the spatio-temporal habitat use patterns of species when they occur beyond PA boundaries and with the behavioral responses of wildlife that lead to HWC (Cushman et al., 2018). This understanding is essential in guiding spatial prioritization decisions pertaining to land-use planning and the implementation of conflict prevention measures within the matrix areas that surround PAs.

Space use patterns of species within matrix areas have been investigated by applying species distribution models to species occurrence or detection/non-detection data (Elith and Leathwick, 2009; Morelle and Lejeune, 2015). These approaches identify areas in the matrix that are “used” or “occupied” and assumed to represent suitable habitats. However, these models are subject to several sources of bias and may not serve as an adequate measure of the probability that species conflicts are likely to occur at those sites. For example, while large carnivores such as tigers (*Panthera tigris*), lions (*Panthera leo*) and wolves (*Canis lupus*) use human dominated areas extensively (Ferreira et al., 2018; Chapter 1), conflicts with these species are often clustered in space and time (Gazzola, Capitani, Mattioli, & Apollonio, 2008; Packer et al., 2019; Treves et al., 2004). Thus, in most landscapes, HWC typically occurs over a smaller, non-random subset of the area over which wildlife and humans co-occur.

Patterns of HWC have primarily been investigated using distribution models applied to spatial records of reported conflicts. Historical records of conflict locations (e.g. compensation records) or self-reporting of conflicts by affected human communities are typical sources of these data (Krafte Holland et al., 2018). These models allow us to infer the spatial and temporal drivers of conflicts across a landscape and help delineate areas at high risk for conflicts (Goswami et al., 2015; Miller, 2015). Such risk models, however, do not allow inference to the full distribution of the species across the landscape. Specifically, it is not possible to determine if the absence of conflicts at a site is simply the consequence of the absence of the species at the site, or if the species occurred at the site without conflict. Similarly, recording conflict at a site may not always imply that the species of interest was present at the site. This may occur when a conflict event is incorrectly attributed to a particular species. For example, a study collating instances of livestock depredation in Wisconsin found that out of the 575 cases where livestock

owners blamed wolves for depredation, only 60% of the cases were attributable to wolves following independent verification (Treves et al., 2002). Such false attribution of conflicts may be especially high for species for whom local community members have low tolerance (Suryawanshi et al., 2013). Moreover, in the absence of information on where the species occurs in the larger landscape, spatial models of conflict risk do not identify the ecological factors that precipitate HWC, thereby limiting their applicability in forecasting where new conflicts are likely to emerge (Treves et al., 2011).

Previous studies have attempted to link species distribution models with conflict risk models (e.g., Braunisch et al., 2011; de Souza et al., 2018). However, these studies do not explicitly link the probability of a species occurring at a site with conflict information—that is, estimating the probability of conflict occurring conditional on species occupancy. Failure to understand the link between species occupancy and conflict probability impacts species conservation efforts in multiple ways. For example, the willingness of human communities to coexist with a species is often linked to their perceptions of the risk that the species poses to their lives or livelihoods. This risk perception therefore inevitably determines the course of individual or management actions directed towards a species (Riley and Decker, 2000). In many cases, these perceptions of risks are often disproportionately higher than the real risks posed by the species. A study on community perceptions of risks from cougars (*Puma concolor*) found that a large proportion of respondents incorrectly believed that the risks from cougars were higher than those incurred when using airplanes, automobiles and tractors (Riley and Decker, 2000). Determining the probability of HWC conditional on species occupancy presents an effective way to understand and clearly communicate the risks associated with sharing landscapes with multiple wildlife species. In addition, for many species, our current understanding of their use of

human-dominated areas are based on conflict risk maps (Miller, 2015). Since the presence of a species in the midst of humans is implicitly linked to conflict in these risk maps, they obscure complex human-wildlife interactions that may be at play within the landscape. For example, a recent study by Laverty et al., (2019) found that pastoralist communities in Namibia experience both positive and negative interactions with wildlife that co-occur on their lands. In this study, negative interactions experienced by pastoralists were typically associated with HWC, whereas positive interactions included encounters that appealed to their aesthetic or spiritual sensibilities.

In the following, we develop a Bayesian hierarchical occupancy model to integrate data on species occurrence and perceived or actual conflicts. In doing so, we offer a generalized framework for estimating the spatio-temporal dynamics of species occupancy and the probability of conflict occurring at a site conditional on species presence. As a novel contribution, our model also allows the estimation of the probability that conflicts are reported at sites the species did not use or occupy. After introducing the model, we provide study design recommendations based on a simulation study. We also illustrate the practical utility of the model by applying it to data on wild boar (*Sus scrofa*) distribution and self-reported human-wild boar conflict data generated by interviewing farmers in north India. These data were collected from the matrix areas of the Central Terai Landscape (CTL; state of Uttar Pradesh), a globally significant tiger conservation region (Wikramanayake et al., 2011). Our objective in applying the model to these data was to identify the factors associated with real and perceived conflicts with wild boar in the CTL. We define real conflicts as any conflict report that is recorded from a site where the species occurs, whereas perceived conflicts are those that are reported from a site where the species does not occur. The spatial patterns of real conflicts may be driven by environmental factors that determine the distribution of conflict causing species and influence their foraging decisions and

behaviors. In contrast, perceived conflicts may be driven by the attitudes of community members towards the species, community beliefs about the species potential to cause damage, etc. (Dickman, 2010). Consequently, these two types of conflicts can be resolved only by the application of fundamentally different mitigation measures. Our goal was to determine what proportion of recorded conflicts with wild boar within the CTL are perceived, and how community attitudes towards species conservation drive the reporting of these perceived conflicts. In doing so, we illustrate how our model can help illuminate the complex socio-ecological drivers of observed patterns of conflicts with species.

Methods

Determining the spatio-temporal occurrence patterns of a species, and their environmental correlates, is a central pursuit in ecology and conservation biology. However, efforts to this end are often impeded by the observer's inability to perfectly detect the species of interest. Occupancy modeling (MacKenzie et al., 2002) approaches offer a means to explicitly address potential biases in estimating habitat use probabilities arising from imperfect detection. Detection histories generated based on repeated searches for the species within sampling units constitute the primary data for estimating detection and occurrence probabilities within an occupancy modeling framework. It is important to understand that occupancy, or use (that is, the sampling unit is not continuously occupied during the survey period) probability is a property of the sample unit.

Application of occupancy models is premised on a few critical assumptions (MacKenzie et al., 2002). Key among these is the assumption that a species is not incorrectly recorded as present within an unoccupied site (i.e. no false detections). Violation of this assumption results in a false-positive detection error and a positive bias in the estimate of occupancy (use). False-

positive detection errors can arise because of species mis-identification or when detections are assigned to an incorrect spatial or temporal survey unit. Recent studies have demonstrated that even low levels of false-positive detections can significantly bias inferences of site occupancy probability and occupancy dynamics (McClintock et al., 2010; Royle and Link, 2006).

Miller et al., (2011; 2013) proposed a general occupancy model that explicitly accommodates both false- negative and false-positive detection errors. The application of these models necessitates the collection of additional auxiliary data that allows the estimation of the false-positive detection rate. These additional data may be collected under three broad sampling designs: 1) site confirmation design, 2) calibration design and 3) observation confirmation design (Chambert et al., 2015; Miller et al., 2011). The site confirmation design assumes or generates information on the true underlying occurrence state of a subset of sampled sites (Clement, 2016) determining for certain if the species truly occurs at the site. Known occurrence can be achieved by using an additional survey method that is known to be free of false-positive errors at all or a subset of the survey sites (multiple detection methods approach). It can also be achieved by classifying a subset of observations at a site as certain at the time of sampling (multiple detection states approach). Our Bayesian hierarchical model builds on the site confirmation design using multiple detection methods to determine the spatial correlates of species occupancy and HWC probabilities.

Survey protocol

Data on conflicts with the species of interest are collected for $i = 1, 2, \dots, S$ sites or spatial units (sites). At each site within each of $t = 1, 2, \dots, T$ primary surveys periods (seasons), conflict data are collected over $j = 1, 2, \dots, J$ survey occasions. If interviews of community members are used to generate data on conflicts, each interview respondent may be treated as a survey occasion

(Karanth, 2016). Survey occasions may also include spatial units or temporal intervals over which conflict episodes are recorded at a site. Additional data pertaining to each survey occasion may also be collected. These surveys generate information on the number of occasions within a site where a conflict event with the species of interest was detected. Since the probability of conflict occurring at a site is conditional on the species occupying/using the site, species occupancy may be inferred from these conflict surveys. However, these surveys may be an unreliable source of information on site occupancy even if there is a small probability of a false positive detection.

Conversely, if conflicts are not recorded at a site during any of the survey occasions it is not possible to determine whether the site was occupied by the focal species. To estimate the true underlying state of the surveyed sites during each primary period, additional surveys for the species of interest are simultaneously conducted at all or a subset of the sites ($i = 1, 2, \dots, s; s \leq S$) using a method that is assumed to be free of false-positive errors. Certain detection methods could include, for example, the use of camera traps, acoustic recorders, or unambiguous sign surveys with surveys repeated $k = 1, 2, \dots, K$ times at each site within each primary period. For example, when using camera traps, if the species of interest is detected at a site, then it may be inferred with certainty that the site is occupied. Using the terminology associated with the site confirmation-multiple-detection methods design, we categorized the conflict surveys as a source of ambiguous data (i.e. they provide ambiguous information on whether or not the species occurs at a site) whereas the auxiliary surveys were assumed to provide unambiguous detection data.

Model

We adopted a Bayesian hierarchical modeling approach to predict the spatio-temporal dynamics of species occupancy and probability of HWC. The hierarchical model is comprised of two sub-components, a process model and an observation model. The process model describes

the ecological processes that give rise to the unobserved (latent) spatio-temporal site occupancy states and temporal dynamics. In the model, $z_{i,t}$ describes the occupancy state of a site ' i ' in season ' t ' for S sites surveyed over T primary seasons. A site in season ' t ' can be in one of two possible states, occupied ($z_{i,t} = 1$) or unoccupied ($z_{i,t} = 0$) by the target species. Within a given season, sites are assumed closed to changes in their occupancy state. If sites cannot be assumed closed within a survey season then Ψ estimates site use. The occupancy state of a site ' i ' in the first season ($z_{i,1}$) is treated as a Bernoulli random variable with occupancy probability equal to $\psi_{i,1}$. The parameter $\psi_{i,1}$ describes the probability a site is occupied at the start of the study and may be defined as a function of site-specific covariates. The occupancy state of a site $z_{i,t}$ may change between the T seasons as a result of stochastic processes or as a consequence of changing environmental conditions. A site occupied in one season may stay occupied in the subsequent season with probability $\phi_{i,t}$. Conversely, an unoccupied site may transition to an occupied state with probability $\gamma_{i,t}$. Both these parameters may be related to spatio-temporally varying covariates.

$$z_{i,1} \sim \text{Bernoulli } \Psi_{i,1}$$

$$z_{i,t} \sim \begin{cases} \text{Bernoulli } (\phi_{t-1}) & z_{i,t-1} = 1 \\ \text{Bernoulli } (\gamma_{t-1}) & z_{i,t-1} = 0 \end{cases}$$

eq. 1

At site i in season t , the number of occasions during which a conflict event is recorded is represented by $w_{i,t}$. Similarly, $y_{i,t}$ represents the number of detections of the species at site i in season t using the unambiguous survey method. For occupied sites, the number of occasions during which conflicts with a species is recorded ($w_{i,t} \geq 0 | z_{i,t} = 1$) is described by a binomial distribution with probability $p_{11i,t}$. Whereas, at unoccupied sites, the number of occasions where

conflict with the species of interest is reported ($w_{i,t} \geq 0 | z_{i,t} = 0$) follows a binomial probability distribution with probability $p_{10,i,t}$. Thus, p_{11} describes the probability with which conflicts with the focal species are recorded at a site occupied by the species. In contrast, p_{10} represents the probability with which conflicts with the focal species are recorded at a site unoccupied by the species. Similarly, using the unambiguous survey method (e.g., camera trap surveys), the total number of detections at an occupied site within a season given ' K ' survey occasions ($y_{i,t} \geq 0 | z_{i,t} = 1$) follows a binomial probability distribution with detection probability ' $r_{i,t}$ '.

$$y_{i,t} \sim \begin{cases} 0 & z_{i,t} = 0 \\ \text{Binom}(K_{i,t}, r_{i,t}) & z_{i,t} = 1 \end{cases}, \text{ for } i \in s \subseteq S$$

$$w_{i,t} \sim \begin{cases} \text{Binom}(J_{i,t}, p_{10,i,t}) & z_{i,t} = 0 \\ \text{Binom}(J_{i,t}, p_{11,i,t}) & z_{i,t} = 1 \end{cases}, \text{ for } i \in S$$

eq. 2

Across sites where conflicts have been reported, uncertainty lies only in whether or not the conflict has been correctly attributed to the focal species. This differentiates our model from other studies that have used an occupancy modeling framework to determine spatial HWC patterns (Goswami et al., 2015). In previous studies, the probability of detecting and reporting conflicts was assumed to be less than 1. Consequently, the state variable ψ denoted the probability with which HWC occurs at a site given imperfect reporting of conflicts. In contrast, in our model, ψ represents the probability that the species of interest occurs at a site and the detection probability parameters p_{11} and p_{10} represent the probability with which conflicts with the species are reported at sites given the species is truly present or absent.

Simulation study

We assessed the ability of our model to predict species occupancy (Ψ) for a simulated study involving three survey seasons and an assumed decline in occupancy across seasons. We simulated data for 100 sites that explored multiple scenarios involving alternative probabilities of falsely attributing conflicts to the focal species (p_{10}) and true detection probabilities associated with the unambiguous survey method (r). We considered three alternative possibilities for the probability that conflicts would be reported for the focal species at least once at a site unoccupied by the species (p_{10}^* ; 10% (low), 50% (medium), 80% (high)). We assumed that these probabilities remained constant across sites and seasons. For each level of p_{10}^* we considered three scenarios for the probability of detecting the species using the unambiguous method at least once at any site during each survey season (r^* ; 10 % (low), 50 % (medium) and 80 % (high)). For each level of p_{10}^* ; and r^* , we explored five alternate scenarios with respect to the proportion of sites where the unambiguous method is applied (5%, 20%, 50%, 75% and 100%). This resulted in a total of 45 alternative combinations of false positive reporting and survey effort for the unambiguous method. We also set the probability of conflicts being reported at least once during a survey season from a site where the species truly occurs (p_{11}^*) as 60%. For all scenarios we simulated site-specific occupancy probabilities as a function of a single covariate such that $\text{logit}(\Psi_i) = \beta_0 + \beta_1 * cov_i$. We assumed that, on average, the probability of a species occurring at a site is 25% and that occupancy probability declines with increasing values of the simulated, normally distributed covariate ($\beta_1 = -3$). We simulated data such that occupancy probabilities declined across seasons by assuming low season-specific survival and colonization probabilities ($\phi_1 = \phi_2 = 0.2$ and $\gamma_1 = \gamma_2 = 0.1$). For each scenario we fit our model to 100 simulated datasets and evaluated the precision with which the intercept (β_0) and slope (β_1)

parameter associated with occupancy probability were predicted. For all simulations, we used vague priors on all model parameters and generated 25,000 MCMC samples with a burn-in period of 5000 iterations. For all parameters modeled without covariates, we generated MCMC samples by sampling from their full conditional distributions via Gibb's sampling, whereas for parameters that were modeled as functions of covariates we used the Metropolis MCMC algorithm (Geyer, 1997; Appendix 3.1). All simulations were carried out in the R statistical computing environment (R Core Team, 2013).

Application

We demonstrate the practical utility of this modeling approach by applying a single season version of the model to data on conflicts and detection collected for wild boar from an agricultural corridor area separating two tiger reserves (Dudhwa Tiger Reserve and Pilibhit Tiger Reserve) in north India. Wild boar are an important tiger prey species (Hayward et al., 2012) and are widely regarded as an agricultural pest across their distributional range (Lewis et al., 2017). We explored how conflicts with wild boar are reported from sites occupied and unoccupied by the species. Specifically, we were interested in understanding how attitudes towards wildlife and situational factors associated with farmers influence the reporting of conflicts with wild boar. We surveyed 46 randomly selected sites for wild boar presence and simultaneously collected data on human-wild boar conflicts between December 2015 and February 2016. Sites were 1.6 km X 1.6 km grid cells selected in a spatially balanced manner using Generalized Random Tessellation Stratified (GRTS; Stevens and Olsen (2004)). We generated data on wild boar presence by placing a single motion-activated camera (Cuddeback Attack) within the cell for a period of 40 days. The camera-trap surveys are assumed to be a source of unambiguous data, free of false-positive errors. We interviewed farmers within a randomly selected subset (27 sites) of the sites

where camera-trapping was conducted. We interviewed 1-10 farmers resident within each site using a survey instrument designed to generate data on conflict perception, and various, social, economic and attitudinal variables. Using the survey instrument, we obtained data on whether or not the respondent was experiencing crop losses due to wildlife and what species were believed to be responsible. We asked each farmer to select their preferred conflict mitigation option from among three possible choices; 1) compensation for losses, 2) permission to take lethal action and 3) fencing of protected areas. We also assessed the attitudes of respondents towards the prevailing Indian government ban on hunting of all wildlife by asking them if they favored the removal of the ban. Responses to all queries were recorded on a binary (Yes/No) response scale. We interpreted attitudes towards mitigation measures and hunting to be indicative of the degree of farmer tolerance for the species in general. For example, we expected that farmers who had low tolerance towards wild boar to be more accepting of the removal of a ban on hunting.

We generated detection histories for wild boars using one or both survey methods for all sites. For the camera trap surveys, we treated each eight-day period as an occasion. For the farmer interview surveys, each farmer was treated as a unique survey occasion. We fit a model where we treated site-specific wild boar occupancy probability (Ψ_i) as a function of distance of the site to the nearest protected area boundary (PA). We evaluated how the probability of a farmer falsely reporting conflicts with wild boar at an unoccupied site (p_{10}) was related to their tolerance for wildlife as reflected by their attitudes towards the three conflict mitigation measures and their attitude towards hunting. We *a priori* predicted that farmers who favored compensation (Comp) as a conflict mitigation strategy and who favored the removal of the ban on hunting (Hunt) were more likely to falsely report conflicts (Johnson et al., 2018). We also expected younger, less experienced farmers (Age) to have a higher probability of falsely

reporting conflicts. We evaluated the probability of a farmer reporting conflicts from a site occupied by wild boar (p_{11}) as a function of their land holding size. We expected conflict reporting probabilities to decline with increasing farm size since smaller land holders may disproportionately experience the effects of significant crop depredation and therefore to be more likely to report the conflict. We *a priori* expected wild boar occupancy probabilities to decline with increasing distance to park boundaries. Finally, for comparison with covariate models, we fit models where parameters were estimated without covariates. We implemented our analysis in the R statistical computing environment (R Core Team, 2013). We specified vague priors on the model parameters and ran three chains with 50,000 MCMC samples each and used a burn-in period of 5000 iterations. We tested for chain convergence by calculating the Gelman-Rubin statistic for each parameter. We fit a total of six models and compared them based on their Deviance Information Criterion (DIC; Hooten and Hobbs, 2015).

Results

Simulation Results

Our model recovered the data generating parameter values under all 45 simulation scenarios. An increase in survey effort associated with the unambiguous method resulted in greater precision in posterior means of parameters associated with ψ (i.e. β_0 and β_1). This trend was evident both when there was an increase in the proportion of sites where the unambiguous method was applied and an increase in its associated detection probability (r^*). Loss in precision was highest in scenarios involving high levels of false-positive reporting ($p_{10}^* = 80\%$) and when the unambiguous method was associated with low detection probability ($r^* = 10\%$) or was applied in fewer than 50% of the sites (Fig. 3.1). Loss in precision was more pronounced for the slope parameter (β_1 ; Fig. 3.1b). In simulation scenarios involving medium ($p_{10}^* = 50\%$) and high

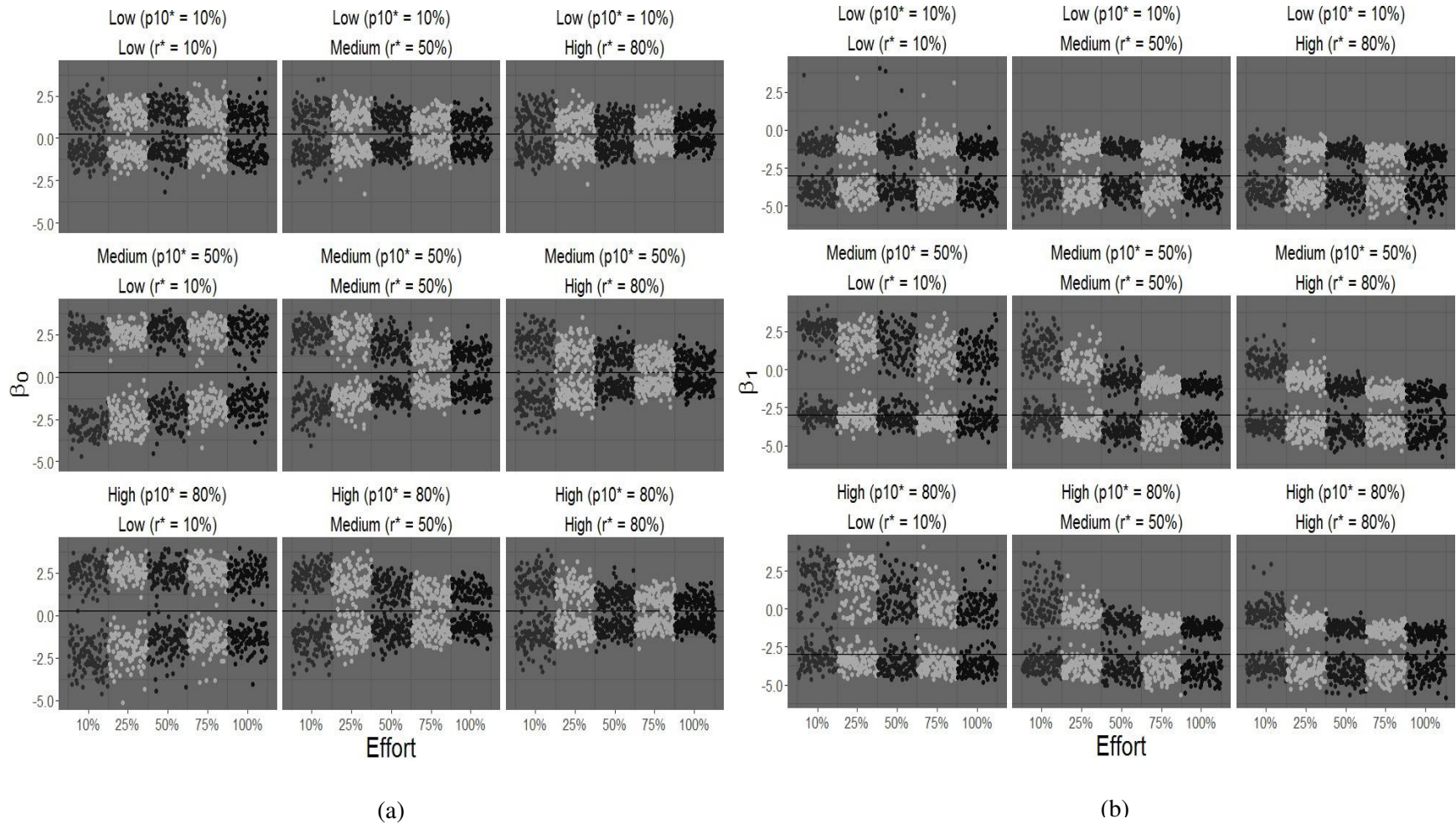


Figure 3.1: Simulation results: 95% credible intervals associated with predicted posterior mean probabilities for β_0 (a) and β_1 (b) across 45 scenarios. Data were simulated across a range of false-positive conflict reporting probabilities (p_{10}^*), true detection probabilities for the unambiguous method (r^*) and proportion of sites where the unambiguous method is applied (Effort). The true value of β_0 (intercept) and β_1 (slope) used to simulate data is indicated by the solid black line. Each dot indicates the upper/lower 95 % credible interval associated with estimates resulting from fitting the model to 100 simulated datasets across each scenario.

($p_{10}^* = 80\%$) levels of false positive reporting probabilities and low true detection probabilities ($r^* = 10\%$), we observed a positive bias in the β_1 estimates.

Application results

Using camera traps, we collected data on wild-boar occurrence over 286 trap weeks across 46 sites. Wild boar were detected at least once at nine sites across 19 trap weeks. Conflicts with wild boar were reported at least once at 26 of the 27 sites where we conducted interview surveys with farmers. Of the six candidate models, a model where the probability of falsely reporting conflicts with wild boars at an unoccupied site was a function of the attitudes of the survey respondent towards hunting (Hunt) had the highest support (Table 3.1).

Table 3.1 Candidate models and associated DIC values. ψ - probability site is occupied by wild boar; p_{11} - probability that conflict with wild boar is reported from a site occupied by the species; p_{10} probability that conflict with wild boar is reported from a site unoccupied by the species; r - probability that wild boar are detected using camera traps at a site occupied by the species

No.	Model	DIC
1	$\psi(.)p_{10}(\text{Hunt})p_{11}(.)r(.)$	518.9
2	$\psi(.)p_{10}(\text{Hunt})p_{11}(\text{LandOwned})r(.)$	522.02
3	$\psi(.)p_{10}(.)p_{11}(.)r(.)$	525.56
4	$\psi(.)p_{10}(\text{Compensation})p_{11}(.)r(.)$	526.25
5	$\psi(.)p_{10}(\text{Age})p_{11}(.)r(.)$	527.33
6	$\psi(\text{PA})p_{10}(\text{Hunt})p_{11}(\text{LandOwned})r(.)$	688.86
7	$\psi(\text{PA})p_{10}(.)p_{11}(.)r(.)$	691.23

Estimates of the probability that wild boar used the study area was 24% (Fig. 2). On average, there was an 87% probability that a farmer interviewed at random from a site used by wild boar would report experiencing conflicts with the species. Similarly, there was a 63% probability that a farmer would falsely report experiencing conflicts with wild boar from a site with no evidence of use by the species (Fig. 3.2). Farmers who favored the removal of the hunting ban had a higher probability of falsely reporting conflicts with wild boar (Fig. 3.3). The

probability of detecting wild boar using camera trap given the site was occupied was 33.6 % for each eight day survey occasion (Fig.3.2)

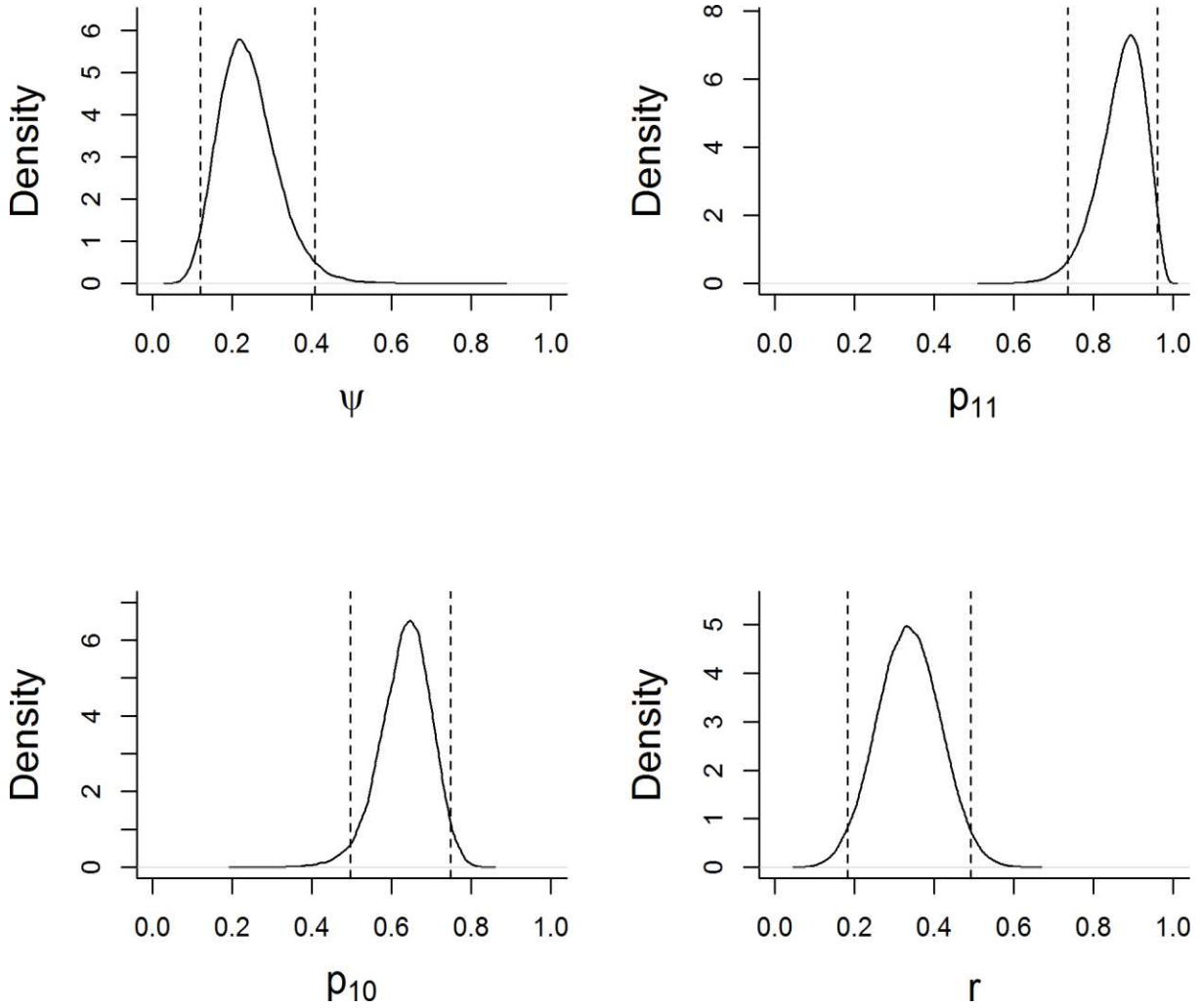


Figure 3.2: Marginal posterior distributions for model parameters based on the best supported model. Ψ - mean probability of wild boar occupancy; p_{11} - mean probability of conflict being reported from a site occupied by wild boar; p_{10} - mean probability of reporting conflicts from a site unoccupied by wild boar; r - mean probability of detecting wild boar using camera traps in an occupied site. Dotted lines indicate 95% credible intervals

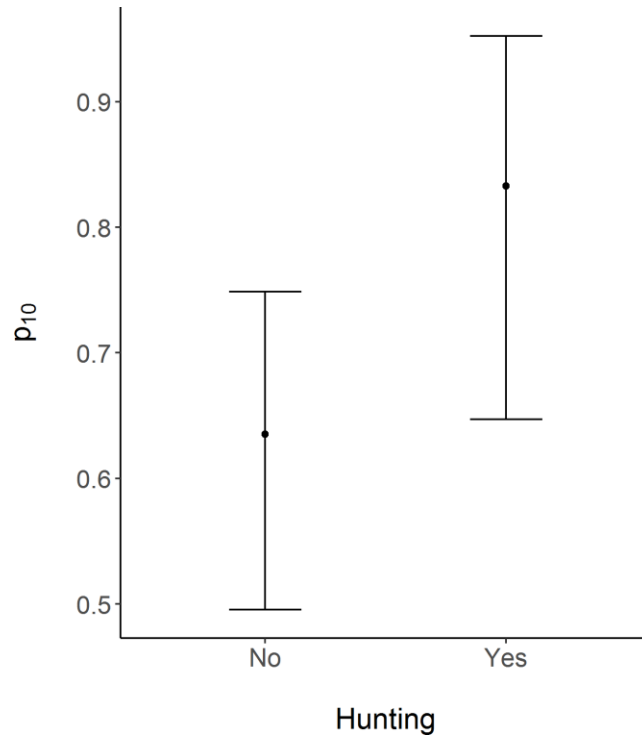


Figure 3.3: Mean probability of falsely reporting conflicts with wild boar by respondents who do (Yes) and do not (No) favor removal of the prevailing ban on hunting wildlife

Discussion

The model we developed allows for the joint modelling of the spatio-temporal dynamics of species habitat use and human-wildlife conflicts. Unlike previous efforts (Karanth et al., 2013), in our model formulation HWC reporting probabilities are estimated conditional on the presence or absence of the species at the site. This allows for the estimation of the probability that conflicts may be falsely recorded at an unoccupied site. Our model explicitly incorporates ecological processes (survival and colonization) that drive changes in species distribution across survey seasons. The simple data collection protocol and flexible modeling approach offers a cost-effective and efficient strategy to monitor species space-use and conflict over large spatial and temporal scales. This model requires the collection of additional auxiliary data at all or a subset of the sites over which conflict monitoring was conducted. Our simulation results suggest that using auxiliary survey methods that are free of false positive errors and that have a high

probability of detecting the species, yields unbiased coefficient estimates across all scenarios. The precision of estimated coefficients varies with the probability that conflict with the species of interest is falsely reported at an unoccupied site. Conflict monitoring programs surveying species with low human tolerance, or whose depredation patterns closely resemble those of other species (e.g. wolves and coyotes ; Treves et al., 2002) are likely situations where false reporting of conflicts may be high. In these situations, conducting auxiliary surveys at approximately 50% of the sites over which conflict is being monitored are needed to precisely estimate species occupancy probabilities (Fig 3.1). When false-positive probabilities are very low, the proportion of sites where the auxiliary method should be applied depends on how likely conflicts are at a site where the species occurs (p_{11}) and the probability that the auxiliary survey method can detect the species when it occurs (r).

Foraging decisions made by animals are the underlying driver of the observed patterns of many forms of HWC (Hill, 2015). Foraging decisions typically involve tradeoffs between risks in accessing a food item and the net profitability of the food item (Baruch-Mordo et al., 2013; Blackwell et al., 2016). Long-term conflict prevention therefore depends upon clearly understanding what factors are driving foraging decisions by species. For example, a study of livestock depredation patterns by wolves in the Tibetan plateau found that while wolves occurred over a large portion of the landscape, attacks on livestock were non-random, occurring more frequently in areas of low ruggedness (Suryawanshi et al., 2013). By allowing the estimation of conflict reporting probabilities conditional on the occurrence of the species at a site our modeling approach makes it possible to clearly determine the socio-ecological factors shaping the risk-benefit landscape that drives depredation decisions.

As our example illustrates, a further application of our model is in the integration of

social survey data on human perceptions of conflicts and the ecological drivers of species space-use patterns. In many cases, how affected communities perceive conflicts can be at odds with the actual patterns of conflicts. The perceived levels of conflicts are often shaped by multiple other factors besides the actual impacts of the species (Dickman, 2010). These factors include human social (e.g. age, religion), psychological (e.g. attitudes, beliefs), situational factors (e.g. economic status), and other unresolved human-wildlife conflicts that may manifest as reduced tolerance. In our analyses, we found that community members who supported the ability to hunt wild animals were more likely to falsely report experiencing conflicts with wild boar (Fig. 3.3). Wild boar occurs in the study area with a mean probability of 24%, yet farmers perceived it to be the most important agricultural pest, exemplified by the fact that conflicts with the species were reported from all the surveyed sites. In the absence of information on the actual distribution of wild boar, the conflict survey data alone would lead us to believe that the species was more widespread in the landscape than in actuality.

The inclusion of auxiliary, unambiguous detection data from a subset of sites where conflict surveys were conducted can clarify the spatial patterns of perceived and real conflicts. This information has important consequences for the formulation of conflict mitigation measures. Where significant disparities exist between perceived and real conflicts, efforts need to be expended to increase the tolerance or acceptance of the species by community members. In the CTL, conflict mitigation should employ a two-pronged approach that includes compensation for crop losses in conjunction with educational programs to improve community tolerance for species perceived to be sources of conflict.

Protected areas around the world are becoming increasingly isolated by expanding human populations and anthropogenic land-uses, particularly agriculture (Balmford et al., 2012;

Benton et al., 2003). The resulting acceleration in the loss of critical habitats outside protected areas and the increases in HWC pose important challenges to the conservation of species, particularly large-bodied, wide-ranging species (Ripple et al., 2014). Consequently, expanding conservation actions beyond protected area boundaries is an urgent need in most conservation landscapes (Stephens, 2015b). This entails not only retaining elements of the landscape that serve as critical wildlife habitats, or provide structural connectivity between habitat fragments, but also focusing on mitigating and preventing HWC related impacts on wildlife and the wellbeing of communities (Crespin and Simonetti, 2019; Cushman et al., 2018). Understanding the linkages between the probabilities with which humans and wildlife co-occur and the probabilities of HWC is essential for effective conservation planning measures beyond protected area boundaries. The model developed herein is an important step in this direction.

LITERATURE CITED

- Baruch-Mordo, S., Webb, C. T., Breck, S. W., and Wilson, K. R. (2013). Use of patch selection models as a decision support tool to evaluate mitigation strategies of human–wildlife conflict. *Biological Conservation*, 160:263–271.
- Blackwell, B. F., DeVault, T. L., Fern´andez-Juricic, E., Gese, E. M., Gilbert-Norton, L., and Breck, S. W. (2016). No single solution: application of behavioural principles in mitigating human–wildlife conflict. *Animal Behaviour*, 120:245–254.
- Braunisch, V., Patthey, P., and Arlettaz, R. (2011). Spatially explicit modeling of conflict zones between wildlife and snow sports: prioritizing areas for winter refuges. *Ecological Applications*, 21(3):955–967.
- Chambert, T., Miller, D. A. W., and Nichols, J. D. (2015). Modeling false positive detections in species occurrence data under different study designs. *Ecology*, 96(2):332–339.
- Clement, M. J. (2016). Designing occupancy studies when false-positive detections occur. *Methods in Ecology and Evolution*.
- Cushman, S. A., Elliot, N. B., Bauer, D., Kesch, K., Bahaa-el din, L., Bothwell, H., Flyman, M., Mtare, G., Macdonald, D. W., and Loveridge, A. J. (2018). Prioritizing core areas, corridors and conflict hotspots for lion conservation in southern Africa. *PloS One*, 13(7):e0196213.
- De Souza, J. C., da Silva, R. M., Gon¸calves, M. P. R., Jardim, R. J. D., and Markwith, S. H. (2018). Habitat use, ranching, and human-wildlife conflict within a fragmented landscape in the Pantanal, Brazil. *Biological Conservation*, 217:349–357.
- DeFries, R., Hansen, A., Turner, B. L., Reid, R., and Liu, J. (2007). Land use change around protected areas: management to balance human needs and ecological function. *Ecological Applications*, 17(4):1031–1038.
- Dickman, A. J. (2010). Complexities of conflict: the importance of considering social factors for effectively resolving human–wildlife conflict. *Animal Conservation*, 13(5):458–466.
- Elith, J. and Leathwick, J. R. (2009). Species Distribution Models: Ecological explanation and prediction across space and time. *Annual Review of Ecology, Evolution, and Systematics*, 40(1):677–697.
- Ferreira, A. S., Peres, C. A., Bogoni, J. A., and Cassano, C. R. (2018). Use of agroecosystem matrix habitats by mammalian carnivores (Carnivora): a global-scale analysis. *Mammal Review*, 48(4):312–327.
- Gazzola, A., Capitani, C., Mattioli, L., and Apollonio, M. (2008). Livestock damage and wolf presence. *Journal of Zoology*, 274(3):261–269.

- Geyer, C. (1997). Introduction to markov Chain Monte Carlo. In Brooks, S., Gelman, A., Jones, G., and Meng, X. L., editors, Handbook of Markov chain Monte Carlo, pages 3–48. Chapman & Hall/CRC Boca Raton, Florida, USA.
- Goswami, V. R., Medhi, K., Nichols, J. D., and Oli, M. K. (2015). Mechanistic understanding of human-wildlife conflict through a novel application of dynamic occupancy models. *Conservation Biology*, 29(4):1100–1110.
- Hayward, M., Jedrzejewski, W., and Jedrzejewska, B. (2012). Prey preferences of the tiger *p anthera tigris*. *Journal of Zoology*, 286(3):221–231.
- Hill, C. M. (2018). Crop foraging, crop losses, and crop raiding. *Annual Review of Anthropology*, 47:377–394.
- Holland, K. K., Larson, L. R., and Powell, R. B. (2018). Characterizing conflict between humans and big cats panthera spp: A systematic review of research trends and management opportunities. *PloS one*, 13(9):e0203877.
- Hooten, M. B. and Hobbs, N. T. (2015). A guide to Bayesian model selection for ecologists. *Ecological Monographs*, 85(1):3–28.
- Johnson, M., Karanth, K., and Weinthal, E. (2018). Compensation as a policy for mitigating human-wildlife conflict around four protected areas in Rajasthan, India. *Conservation and Society*, 16(3):305.
- Karanth, K. K. (2016). Wildlife in the matrix: spatio-temporal patterns of herbivore occurrence in Kar- nataka, India. *Environmental management*, 57(1):189–206.
- Laverty, T. M., Teel, T. L., Thomas, R. E., Gawusab, A. A., and Berger, J. (2019). Using pastoral ideology to understand human–wildlife coexistence in arid agricultural landscapes. *Conservation Science and Practice*, page e35.
- Lewis, J. S., Farnsworth, M. L., Burdett, C. L., Theobald, D. M., Gray, M., and Miller, R. S. (2017). Biotic and abiotic factors predicting the global distribution and population density of an invasive large mammal. *Scientific Reports*, 7(1):44152.
- MacKenzie, D. I., Nichols, J. D., Hines, J. E., Knutson, M. G., and Franklin, A. B. (2003). Estimating site occupancy, colonization, and local extinction when a species is detected imperfectly. *Ecology*, 84(8):2200– 2207.
- McClintock, B. T., Bailey, L. L., Pollock, K. H., and Simons, T. R. (2010). Unmodeled observation error induces bias when inferring patterns and dynamics of species occurrence via aural detections. *Ecology*, 91(8):2446–2454.
- Miller, D. A., Nichols, J. D., McClintock, B. T., Grant, E. H. C., Bailey, L. L., and Weir, L. A. (2011). Improving occupancy estimation when two types of observational error occur: non-detection and species misidentification. *Ecology*, 92(7):1422–1428.
- Miller, D. A. W., Nichols, J. D., Gude, J. A., Rich, L. N., Podruzny, K. M., Hines, J. E., and Mitchell, M. S. (2013). Determining occurrence dynamics when false positives occur:

- estimating the range dynamics of wolves from public survey data. *PloS one*, 8(6):e65808.
- Miller, J. R. B. (2015). Mapping attack hotspots to mitigate human–carnivore conflict: approaches and applications of spatial predation risk modeling. *Biodiversity and Conservation*, 24(12):2887–2911.
- Morelle, K. and Lejeune, P. (2015). Seasonal variations of wild boar *Sus scrofa* distribution in agricultural landscapes: a species distribution modelling approach. *European Journal of Wildlife Research*, 61(1):45– 56.
- Nyhus, P. J. (2016). Human–Wildlife Conflict and Coexistence. *Annual Review of Environment and Resources*, 41(1):143–171.
- Packer, C., Shivakumar, S., Athreya, V., Craft, M. E., Dhanwatey, H., Dhanwatey, P., Gurung, B., Joshi, A., Kushnir, H., Linnell, J. D. C., and Fountain-Jones, N. M. (2019). Species-specific spatiotemporal patterns of leopard, lion and tiger attacks on humans. *Journal of Applied Ecology*, 56(3):585–593.
- Riley, S. J. and Decker, D. J. (2000). Risk perception as a factor in wildlife stakeholder acceptance capacity for cougars in Montana. *Human Dimensions of Wildlife*, 5(3):50–62.
- Royle, J. A. and Link, W. A. (2006). Generalized occupancy models allowing for false positive and false negative errors. *Ecology*, 87(4):835–841.
- Stevens, D. L. and Olsen, A. R. (2004). Spatially balanced sampling of natural resources. *Journal of the American Statistical Association*, 99(465):262–278.
- Suryawanshi, K. R., Bhatnagar, Y. V., Redpath, S., and Mishra, C. (2013). People, predators and perceptions: patterns of livestock depredation by snow leopards and wolves. *Journal of Applied Ecology*, 50(3):550–560.
- Treves, A., Jurewicz, R. R., Naughton-Treves, L., Rose, R. A., Willging, R. C., and Wydeven, A. P. (2002). Wolf depredation on domestic animals in Wisconsin, 1976-2000. *Wildlife Society Bulletin*, 30(1):231–241.
- Treves, A., Martin, K. A., Wydeven, A. P., and Wiedenhoeft, J. E. (2011). Forecasting Environmental Hazards and the Application of Risk Maps to Predator Attacks on Livestock. *BioScience*, 61(6):451–458.
- Treves, A., Naughton-Treves, L., Harper, E. K., Mlandenoff, D. J., Rose, R. A., Sickley, T. A., and Wydeven, A. P. (2004). Predicting Human-Carnivore Conflict: a Spatial Model Derived from 25 Years of Data on Wolf Predation on Livestock. *Conservation Biology*, 18(1):114–125.
- Wikramanayake, E., Dinerstein, E., Seidensticker, J., Lumpkin, S., Pandav, B., Shrestha, M., Mishra, H., Ballou, J., Johnsingh, A. J. T., Chestin, I., and Others (2011). A landscape-based conservation strategy to double the wild tiger population. *Conservation Letters*, 4(3):219–227

APPENDIX 1.1

Covariates used to model winter occupancy probability for tigers

Table S1: Description of covariates used in the false-positive dynamic occupancy model

Covariate	Type and source of covariate	Range
PA	Minimum Euclidean distance (km) between cell center and protected area boundaries.	0 - 8.97
NDVI_W,	A median NDVI layer for the study area was generated from NDVI data	0.12 - 0.65
NDVI_S,	for date ranges spanning each of the survey seasons using the Landsat-8,	0.07 - 0.39
NDVI_M	8-Day NDVI composite data set on the Google Earth Engine platform (Gorelick et al. 2017). These layers were then used to calculate cell and season specific median NDVI values for each season.	0.05 - 0.74
Drain	All visible drainages were digitized in Google Earth. The total length (km) of these features within each surveyed cell was calculated in R.	0 - 4.36
Prey_W	Index of prey availability within cells in winter (W), summer (S), and	0.88 - 1.70
Prey_S	monsoon (M). (Appendix S2)	1.01 - 1.99
Prey_M		1.07 - 1.66
Prey_WS	Calculated change in prey availability index between winter and summer	-0.39 - 0.42
Prey_SM	(WS) and summer and monsoon (SM). (Appendix S2)	-0.19 - 0.35
Water	Indicates seasonality in the occurrence of water. Values closer to 0 indicate highly seasonal water availability whereas values closer to 100 indicate permanent water sources. Layer was calculated by isolating the	0 - 92

	‘occurrence band’ from JRC Global Surface Water Metadata (Pekel et al. 2016)	
Tree	Percent of canopy cover within a cell, calculated from Hansen Global Forest Change Dataset v1.5 (2000-2017) (Hansen et al. 2013). Canopy cover for 2016 was calculated in Google Earth Engine platform by deducting areas of tree canopy loss (band = “lossyear”) experienced between the years 2000 and 2016 from the layer depicting tree canopy cover in 2000 (band= “treecover2000”). Mean percent tree cover values were calculated for each cell.	0.01 – 20.05
Sett	All settlements within the matrix were digitized in Google Earth. The proportion of each cell covered by settlement polygons was estimated in R.	0 - 0.19
Propnat*	Proportion of native habitat within a cell. Calculated using vegetation cover classification map for India (Roy et al. 2006). Pixels representing six different native vegetation types in the study site were reclassified as one land-use i.e.”native habitats”. Pixels representing this vegetation class were summed together to calculate the proportion of each cell covered by native vegetation.	0 - 1

The proportion of native habitats within a cell (Propnat) was used only to model the cell use probabilities of prey species to calculate the covariate (Prey_W, Prey_S, Prey_M; Appendix S2)

References

Gorelick N, Hancher M, Dixon M, Ilyushchenko S, Thau D, Moore R. 2017. Google Earth Engine: Planetary-scale geospatial analysis for everyone. *Remote Sensing of Environment* 202:18-27.

- Hansen MC, Potapov PV, Moore R, Hancher M, Turubanova SA, Tyukavina A, Thau D, Stehman SV, Goetz SJ, Loveland TR, Kommareddy A. 2013. High-resolution global maps of 21st-century forest cover change. *Science* 342:850-853.
- Pekel JF, Cottam A, Gorelick N, Belward AS. 2016. High-resolution mapping of global surface water and its long-term changes. *Nature* 540:418.
- Roy PS, Joshi PK, Singh S, Agarwal S, Yadav D, Jegannathan C. 2006. Biome mapping in India using vegetation type map derived using temporal satellite data and environmental parameters. *Ecological Modelling*. 197:148-58.

APPENDIX 1.2

Calculation of Prey availability index: Prey species occupancy models

Prey availability is an important driver of carnivore abundance and distribution patterns (Karanth et al. 2011). To test the effects of prey availability on tiger use probabilities we created a seasonal and cell-specific prey availability index. The index was calculated using detection data generated using farmer surveys (FS) and camera surveys (CS) for three prey species- hog deer (*Axis porcinus*), wild boar (*Sus scrofa*) and nilgai (*Boselaphus tragocamerlus*)- that commonly use the agricultural matrix. The following sections detail the steps involved in the calculation of this index.

Prey occupancy models:

Detection data for prey species generated using farmer surveys (FS) are prone to both false-positive and false-negative detection errors. To account for these errors in calculating an index of prey availability, we fit dynamic false positive occupancy models (Miller et al 2013) to detection/non-detection data from farmer surveys (FS) and camera surveys (CS). As with the models for tigers, FS is a source of uncertain detections for prey species (false-positive errors possible) and CS is a source of certain detections (no false-positive errors). For FS surveys, each farmer interviewed within a cell is treated as an occasion whereas for CS each 24-hour period is treated as an occasion. For each species, we used a step-wise approach and fit 7 candidate models (Table S2) that examined the relationship between select covariates of interest and the model parameters: initial probability of use (Ψ_w); vital rates (ε_t, γ_t); true detection probability (p_{11}) and false –positive detection probability (p_{10}).

Table S2: Set of candidate models tested for hog deer, nilgai and wild boar using a step-wise modeling approach

Step	Ψ_w	ε_t and γ_t	p_{10}	p_{11}
1	PA+Propnat+Sett	Season	Season	Season*Method
2	PA+Propnat+Sett	Intercept only (.)	Season	Season*Method
3	PA	Intercept only (.)	Season	Season*Method
4	Propnat	Best model between step 1 and 2	Season	Season*Method
5	Sett	Best model between step 1 and 2	Season	Season*Method
6	Intercept only (.)	Best model between step 1 and 2	Season	Season*Method
7	Intercept only (.)	Intercept only (.)	Intercept only (.)	Intercept only (.)

Specifically, we explored the relationship between the probability of winter cell use (Ψ_w) and three covariates of interest. We hypothesized that for all three species Ψ_w will scale positively with increasing proportion of native habitats (Propnat) and negatively with the proportion of cell under human settlements (Sett). In addition, we predicted that Ψ_w would decline with increasing distance from a protected area boundary (PA). We fit Ψ_w model structures with singular or additive combinations of these covariates. We tested whether vital rates (local colonization (γ_t) and local extinction (ε_t) probabilities) were similar or varied among seasons. The final model set and associated model selection results are included in Table S3.

Species-specific model results and covariate relationships

Based on AICc scores (Table S2), the best-supported model for hog deer was one where the probability of cell use in winter (Ψ_w) varied as an additive function of all three covariates under consideration (i.e. PA, Propnat, Sett). For nilgai, winter use probability was only a function of the proportion of native habitats within a cell (Propnat). Cell use was influenced only

by distance to protected areas (PA) for wild boar. For all three species the relationship between winter use (Ψ_w) and the covariates were consistent with our a priori expectations. Similarly, for all species except wild boar, models that included the effect of season (Season) on the vital rates (γ_t and ε_t) ranked better than models that assumed these probabilities were constant among seasons.

Composite prey availability index

For each species, we calculated model-averaged season- and cell-specific estimates of use (Ψ_w, Ψ_s, Ψ_m) using regression coefficients from the best supported models. We then calculated a seasonal prey availability index for each cell (Prey_W, Prey_S, Prey_M) by summing together season- and cell-specific use estimates for the three species. This index represents a combined measure of prey availability. This covariate can take on values between 0 and 3. Higher values indicate higher probabilities of availability of one or more prey species. We also calculated an index representing the change in cell specific prey availability between seasons (Prey_WS, Prey_SM). This was done by subtracting the cell specific prey availability index values for the following season ($t+1$) from the current season (t)

References

Karanth, K.U., Gopaldaswamy, A.M., Kumar, N.S., Vaidyanathan, S., Nichols, J.D. and MacKenzie, D.I., (2011). Monitoring carnivore populations at the landscape scale: occupancy modelling of tigers from sign surveys. *Journal of Applied Ecology*, 48(4), 1048-1056.

Table S3: Table of model results for hog deer, nilgai and wild boar. AICc- Akaike’s information criterion score, Δ AICc - Difference in adjusted Akaike’s information criterion (AIC) score between best supported model and any other model, ω – Model weight; K- Number of parameters; Deviance - Model deviance (-2ln(Model Likelihood))

Model	AICc	Δ AICc	ω	K	Deviance
Hog Deer					
Ψ_W (PA+Propnat+Sett) ε_t (Season) γ_t (Season) p_{10} (Season) p_{11} (Season*Method)	2355.84	0.00	0.90	17	2319.45
Ψ_W (PA) ε_t (Season) γ_t (Season) p_{10} (Season) p_{11} (Season*Method)	2361.61	5.76	0.05	15	2329.75
Ψ_W (Sett) ε_t (Season) γ_t (Season) p_{10} (Season) p_{11} (Season*Method)	2362.50	6.65	0.03	15	2330.64
Ψ_W (.) ε_t (Season) γ_t (Season) p_{10} (Season) p_{11} (Season*Method)	2366.13	10.28	0.00	12	2340.93
Ψ_W (Propnat) ε_t (Season) γ_t (Season) p_{10} (Season) p_{11} (Season*Method)	2366.30	10.45	0.00	13	2338.90
Ψ_W (.) ε_t (.) γ_t (.) p_{10} (Season) p_{11} (Season*Method)	2366.89	11.04	0.00	11	2343.89
Ψ_W (.) ε_t (.) γ_t (.) p_{10} (.) p_{11} (.)	2414.90	59.05	0.00	5	2404.67
Nilgai					
Ψ_W (Propnat) ε_t (Season) γ_t (Season) p_{10} (Season) p_{11} (Season*Method)	2951.97	0	0.30	15	2920.11
Ψ_W (Sett) ε_t (Season) γ_t (Season) p_{10} (Season) p_{11} (Season*Method)	2952.21	0.23	0.27	15	2920.35
Ψ_W (PA+Propnat+Sett) ε_t (Season) γ_t (Season) p_{10} (Season) p_{11} (Season*Method)	2953.24	1.26	0.16	17	2916.85

$\Psi_W(.) \varepsilon_t(\text{Season}) \gamma_t(\text{Season}) p_{10}(\text{Season}) p_{11}(\text{Season*Method})$	2953.67	1.69	0.13	14	2924.05
$\Psi_W(\text{PA}) \varepsilon_t(\text{Season}) \gamma_t(\text{Season}) p_{10}(\text{Season}) p_{11}(\text{Season*Method})$	2953.92	1.94	0.11	15	2922.06
$\Psi_W(.) \varepsilon_t(.) \gamma_t(.) p_{10}(\text{Season}) p_{11}(\text{Season*Method})$	2963.92	11.94	0.00	12	2938.73
$\Psi_W(.) \varepsilon_t(.) \gamma_t(.) p_{10}(.) p_{11}(.)$	3003.37	51.39	0	6	2991.05

Wild Boar

$\Psi_W(\text{PA}) \varepsilon_t(.) \gamma_t(.) p_{10}(\text{Season}) p_{11}(\text{Season*Method})$	2288.99	0	0.57	13	2261.59
$\Psi_W(\text{PA+Sett+Propnat}) \varepsilon_t(.) \gamma_t(.) p_{10}(\text{Season}) p_{11}(\text{Season*Method})$	2290.04	1.04	0.33	15	2258.18
$\Psi_W(.) \varepsilon_t(.) \gamma_t(.) p_{10}(\text{Season}) p_{11}(\text{Season*Method})$	2294.38	5.38	0.03	12	2269.18
$\Psi_W(\text{Sett}) \varepsilon_t(.) \gamma_t(.) p_{10}(\text{Season}) p_{11}(\text{Season*Method})$	2295.50	6.50	0.02	13	2268.10
$\Psi_W(\text{Propnat}) \varepsilon_t(.) \gamma_t(.) p_{10}(\text{Season}) p_{11}(\text{Season*Method})$	2295.99	6.99	0.01	13	2268.59
$\Psi_W(.) \varepsilon_t(\text{season}) \gamma_t(\text{Season}) p_{10}(\text{Season}) p_{11}(\text{Season*Method})$	2297.03	8.03	0.01	14	2267.41
$\Psi_W(.) \varepsilon_t(.) \gamma_t(.) p_{10}(.) p_{11}(.)$	2630.78	341.78	0	5	2620.55

APPENDIX 1.3

Model selection tables for model parameters (p_{10} , p_{11} , Ψ_w , ε_t , γ_t) for tigers.

Table S4: Model selection results for true detection probability (p_{11}) and false-positive detection (p_{10}) parameter structures. AICc- Akaike’s information criterion score, Δ AICc - Difference in adjusted Akaike’s information criterion (AIC) score between best supported model and any other model, ω – Model weight; K- Number of parameters; Deviance - Model deviance ($-2\ln(\text{Model Likelihood})$)

Model	AICc	Δ AICc	ω	K	Deviance
$p_{10}(\text{Season} + \text{PA}) p_{11}(\text{Season} + \text{Method})$	1577.33	0.00	0.65	33	1501.86
$p_{10}(\text{Season} + \text{PA}) p_{11}(\text{Season} + \text{Method} + \text{Sett})$	1579.21	1.88	0.25	34	1501.13
$p_{10}(\text{Season} + \text{PA}) p_{11}(\text{Season} * \text{Method})$	1582.37	5.04	0.05	37	1496.30
$p_{10}(\text{Season} + \text{PA}) p_{11}(\text{Season} + \text{Method} + \text{Sett} + \text{NDVI})$	1582.96	5.63	0.04	35	1502.23
$p_{10}(\text{Season} + \text{PA}) p_{11}(\text{Season} + \text{Method} + \text{Sett} + \text{NDVI}_W + \text{NDVI}_W^2)$	1594.40	17.07	0.00	36	1511.01
$p_{10}(\text{Season} + \text{PA}) p_{11}(\text{Method})$	1596.67	19.34	0.00	31	1526.37
$p_{10}(\text{Season} + \text{PA}) p_{11}(\text{Season} + \text{Method} + \text{NDVI})$	1634.09	56.76	0.00	34	1556.00
$p_{10}(\text{Season} + \text{PA}) p_{11}(\text{Season} + \text{Method} + \text{NDVI}_W + \text{NDVI}_W^2)$	1670.23	92.90	0.00	35	1589.51
$p_{10}(\text{Season}) p_{11}(\text{Season} + \text{Method})$	1715.05	137.72	0.00	32	1642.17
$p_{10}(\text{PA}) p_{11}(\text{Season} + \text{Method})$	1733.37	156.04	0.00	31	1663.07
$p_{10}(\cdot) p_{11}(\text{Season} + \text{Method})$	1737.25	159.92	0.00	30	1669.50
$p_{10}(\text{Season} + \text{PA}) p_{11}(\text{Season})$	1739.37	162.04	0.00	31	1669.07
$p_{10}(\text{Season} + \text{PA}) p_{11}(\cdot)$	1781.01	203.68	0.00	29	1715.79

Table S5: Model results for models evaluating covariate effects on initial use probability Ψ_w . The p_{11} , p_{10} , ε_t and γ_t structure used for all models: p_{11} (Season*Method); p_{10} $p_{10}(\text{Season} + \text{PA})$; ε_t (Season * (Water + PA+ NDVI_S/M)); γ_t (Season* (NDVI_S/M + Prey_S/M + PREY_WS/SM)). AICc- Akaike’s information criterion score, Δ AICc - Difference in adjusted Akaike’s information criterion (AIC) score between best supported model and any other model, ω – Model weight; K- Number of parameters; Deviance - Model deviance ($-2\ln(\text{Model Likelihood})$)

Model	AICc	Δ AICc	ω	K	Deviance
$\Psi_w(\text{PA} + \text{Drain} + \text{Sett} + \text{NDVI}_W + \text{NDVI}_W^2)$	1573.49	0.00	0.59	31	1503.19
$\Psi_w(\text{PA} + \text{Drain} + \text{Sett} + \text{Tree} + \text{NDVI}_W + \text{NDVI}_W^2)$	1575.63	2.14	0.20	32	1502.75

$\Psi_w(\text{PA} + \text{Drain} + \text{Sett} + \text{Tree})$	1577.10	3.61	0.10	30	1509.35
$\Psi_w(\text{PA} + \text{Drain} + \text{Sett} + \text{Prey}_W + \text{Tree} + \text{NDVI}_W + \text{NDVI}_W^2)$	1577.33	3.84	0.09	33	1501.86
$\Psi_w(\text{PA} + \text{Drain} + \text{Sett} + \text{Prey}_W + \text{Tree} + \text{NDVI}_W)$	1580.97	7.48	0.01	32	1508.09
$\Psi_w(\text{Drain} + \text{Sett} + \text{Tree} + \text{NDVI}_W + \text{NDVI}_W^2)$	1584.15	10.66	0.00	31	1513.85
$\Psi_w(\text{PA} + \text{Sett} + \text{NDVI}_W + \text{NDVI}_W^2)$	1585.26	11.77	0.00	30	1517.51
$\Psi_w(\text{PA} + \text{Drain} + \text{Prey}_W + \text{Tree} + \text{NDVI}_W + \text{NDVI}_W^2)$	1588.23	14.75	0.00	32	1515.36
$\Psi_w(\text{Drain} + \text{Prey}_W + \text{Tree} + \text{NDVI}_W + \text{NDVI}_W^2)$	1590.74	17.25	0.00	31	1520.44
$\Psi_w(\text{PA} + \text{Sett} + \text{Prey}_W)$	1590.74	17.26	0.00	29	1525.52
$\Psi_w(\text{PA} + \text{Drain} + \text{Tree} + \text{NDVI}_W + \text{NDVI}_W^2)$	1591.52	18.03	0.00	31	1521.22
$\Psi_w(\text{Sett} + \text{Prey}_W)$	1592.90	19.41	0.00	28	1530.19
$\Psi_w(\text{PA} + \text{Prey}_W)$	1594.70	21.22	0.00	28	1531.99
$\Psi_w(\text{Drain})$	1595.07	21.58	0.00	27	1534.84
$\Psi_w(\text{Prey}_W)$	1595.59	22.10	0.00	27	1535.36
$\Psi_w(\text{PA} + \text{Sett})$	1595.65	22.16	0.00	28	1532.93
$\Psi_w(\text{Drain} + \text{Tree} + \text{NDVI}_W + \text{NDVI}_W^2)$	1597.49	24.00	0.00	30	1529.74
$\Psi_w(\text{Sett})$	1600.67	27.19	0.00	27	1540.45
$\Psi_w(\text{PA})$	1607.90	34.41	0.00	27	1547.68
$\Psi_w(\text{Tree})$	1608.46	34.98	0.00	27	1548.24
$\Psi_w(\text{NDVI}_W + \text{NDVI}_W^2)$	1611.75	38.26	0.00	28	1549.04
$\Psi_w(.)$	1612.49	39.00	0.00	26	1554.74
$\Psi_w(\text{NDVI}_W)$	1613.21	39.72	0.00	27	1552.99

Table S6: Model results for models evaluating covariate effects on local extinction probability (ε_t). The p_{11} , p_{10} , Ψ_w and γ_t structure used for all models: p_{11} (Season*Method); p_{10} (Season + PA); Ψ_w (PA + Sett + NDVI_W + NDVI_W^2 + Drain); γ_t (Season* (NDVI_S/M + Prey_S/M + PREY_WS/SM)). AICc- Akaike's information criterion score, Δ AICc - Difference in adjusted Akaike's information criterion (AIC) score between best supported model and any other model, ω - Model weight; K- Number of parameters; Deviance - Model deviance (-2ln(Model Likelihood))

Model	AICc	Δ AICc	ω	K	Deviance
ε_t (Season + Water + PA)	1567.31	0.00	0.14	27	1507.09
ε_t (Water + PA + NDVI_S/M)	1567.57	0.26	0.12	27	1507.35
ε_t (Season)	1567.79	0.47	0.11	25	1512.48
ε_t (Season + PA)	1567.93	0.61	0.10	26	1510.17
ε_t (Season + Water)	1568.34	1.03	0.08	26	1510.59
ε_t (Season * PA)	1568.99	1.68	0.06	27	1508.77
ε_t (Water + NDVI_S/M)	1569.10	1.78	0.06	26	1511.34
ε_t (Season *(Water + PA))	1569.41	2.10	0.05	29	1504.19
ε_t (Season + Water + PA + NDVI_S/M)	1569.48	2.16	0.05	28	1506.77
ε_t (PA + NDVI_S/M)	1569.77	2.46	0.04	26	1512.02
ε_t (Season * Water)	1570.12	2.80	0.03	27	1509.89
ε_t (NDVI_S/M)	1570.12	2.80	0.03	25	1514.81
ε_t (Season * NDVI S/M)	1570.20	2.88	0.03	26	1512.44
ε_t (Season + NDVI_S/M + PA)	1570.37	3.06	0.03	27	1510.15
ε_t (Season + Water + PA)	1570.63	3.32	0.03	27	1510.41
ε_t (Season * (NDVI S/M)	1572.24	4.93	0.01	27	1512.02
ε_t (Season * (NDVI_S/M + PA))	1572.71	5.40	0.01	29	1507.49
ε_t (Water+ PA)	1573.11	5.80	0.01	26	1515.36
ε_t (Season * (Water + PA + NDVI_S/M))	1573.49	6.17	0.01	31	1503.19
ε_t (PA)	1573.91	6.59	0.01	25	1518.60
ε_t (Season * (NDVI_S/M + Water))	1574.31	7.00	0.00	29	1509.09
ε_t (.)	1574.62	7.30	0.00	24	1521.74
ε_t (Water)	1575.55	8.23	0.00	25	1520.24

Table S7: Results for models evaluating covariate effects on local colonization probability (γ_t). The p_{11} , p_{10} , Ψ_w and ε_t structure used for all models: p_{11} (Season*Method); p_{10} (Season + PA); Ψ_w (PA + Sett + NDVI_W + NDVI_W^2 + Drain); ε_t (Season + PA +vWater). AICc- Akaike's information criterion score, Δ AICc - Difference in adjusted Akaike's information criterion (AIC) score between best supported model and any other model, ω – Model weight; K- Number of parameters; Deviance - Model deviance ($-2\ln(\text{Model Likelihood})$)

Model	AICc	Δ AICc	ω	K	Deviance
$\gamma_t (= 0)$	1565.52	0.00	0.38	19	1524.50
γ_t (Season *(NDVI_S/M +Prey_S/M+ Prey_WS/SM))	1567.31	1.79	0.15	27	1507.09
γ_t (NDVI_S/M + Prey_WS/SM)	1568.33	2.80	0.09	22	1520.25
γ_t (Season + Prey_WS/SM)	1568.78	3.26	0.07	22	1520.70
γ_t (Prey_S/M)	1569.04	3.51	0.06	21	1523.33
γ_t (NDVI_S/M + Prey_S/M)	1570.03	4.50	0.04	22	1521.95
γ_t (Season* (NDVI_S/M + Prey_S/M + PREY_WS/SM))	1570.12	4.60	0.04	25	1514.81
γ_t (NDVI_S/M)	1570.21	4.68	0.04	21	1524.50
γ_t (NDVI_S/M + Prey_S/M + Prey_WS/SM)	1570.72	5.19	0.03	23	1520.25
γ_t (Season + NDVI_S/M + Prey_S/M)	1570.72	5.19	0.03	23	1520.25
γ_t (Season + NDVI_S/M + Prey_WS/SM)	1570.72	5.19	0.03	23	1520.25
γ_t (Season + NDVI_S/M)	1572.21	6.69	0.01	22	1524.13
γ_t (Season + Prey_S/M)	1572.58	7.05	0.01	22	1524.50
γ_t (Season * (NDVI_S/M + Prey_S/M))	1573.06	7.54	0.01	25	1517.76
γ_t (Season + NDVI_S/M + Prey_S/M + Prey_WS/SM)	1573.12	7.60	0.01	24	1520.25
γ_t (Season * Prey_S/M)	1663.79	98.27	0.00	23	1613.32
γ_t (.)	1679.89	114.37	0.00	20	1636.53
γ_t (Prey_WS/SM)	1681.95	116.43	0.00	21	1636.24
γ_t (Season)	1682.22	116.69	0.00	21	1636.50
γ_t (Season * Prey_WS/SM)	1683.02	117.50	0.00	23	1632.55
γ_t (Season * (NDVI_S/M + Prey_WS/SM))	1685.03	119.51	0.00	25	1629.72
γ_t (Season * NDVI_S/M)	1685.19	119.67	0.00	23	1634.72

APPENDIX 1.4

Composite table of models fit to detection and non-detection tiger data using 3 methods over 3 seasons.

Applying the step-wise model building process, we fit a total of 79 models. The following table includes 22 of the best supported models that together account for 90 % of the overall model weights. In addition, a version of the best supported model where the false positive probability is fixed at 0 (No false positives model) and a model without covariates (Intercept only model) are included for comparison.

Table S8: Model selection results showing best supported models across all parameter model sets. Key: Ψ_w (Best fit)- Ψ_w (PA+ Drain + Sett + NDVI_W^2); ε_t (Best fit)- ε_t (Season + Water + PA); p(Best fit)- p_{10} (Season +PA) p_{11} (Season+Method). AICc- Akaike's information criterion score, Δ AICc - Difference in adjusted Akaike's information criterion (AIC) score between best supported model and any other model, ω – Model weight; K- Number of parameters; Deviance - Model deviance ($-2\ln(\text{Model Likelihood})$)

Model	AICc	Δ AICc	ω	K	Deviance
Ψ_w (Best fit) ε_t (Best fit) γ_t ($= 0$) p(Best fit)	1565.52	0.00	0.19	19	1524.50
Ψ_w (Best fit) ε_t (Best fit) γ_t (Season * NDVI_S/M +Prey_S/M +PREY_WS/SM) p(Best fit)	1567.31	1.79	0.08	27	1507.09
Ψ_w (Best fit) ε_t (Water +PA +NDVI_S/M) γ_t (Season *NDVI_S/M +Prey_S/M +PREY_WS/SM) p(Best fit)	1567.57	2.05	0.07	27	1507.35
Ψ_w (Best fit) ε_t (Season) γ_t (Season *NDVI_S/M +Prey_S/M +PREY_WS/SM) p(Best fit)	1567.79	2.26	0.06	25	1512.48
Ψ_w (Best fit) ε_t (Season + PA) γ_t (Season *NDVI_S/M +Prey_S/M +PREY_WS/SM) p(Best fit)	1567.93	2.40	0.06	26	1510.17
Ψ_w (Best fit) ε_t (Best fit) γ_t (NDVI_S/M +Prey_WS/SM) p(Best fit)	1568.33	2.80	0.05	22	1520.25
Ψ_w (Best fit) ε_t (Season + Water) γ_t (Season *NDVI_S/M +Prey_S/M +PREY_WS/SM) p(Best fit)	1568.34	2.82	0.05	26	1510.59
Ψ_w (Best fit) ε_t (Best fit) γ_t (Season +PREY_WS/SM) p(Best fit)	1568.78	3.26	0.04	22	1520.70
Ψ_w (Best fit) ε_t (Season *PA) γ_t (Season *NDVI_S/M +Prey_S/M +PREY_WS/SM) p(Best fit)	1568.99	3.47	0.03	27	1508.77

$\Psi_W(\text{Best fit}) \varepsilon_t(\text{Best fit}) \gamma_t(\text{PREY_S/M}) p(\text{Best fit})$	1569.04	3.51	0.03	21	1523.33
$\Psi_W(\text{Best fit}) \varepsilon_t(\text{Water}+\text{NDVI_S/M}) \gamma_t(\text{Season} * \text{NDVI_S/M} + \text{Prey_S/M} + \text{PREY_WS/SM}) p(\text{Best fit})$	1569.10	3.57	0.03	26	1511.34
$\Psi_W(\text{Best fit}) \varepsilon_t(\text{Season} * \text{Water} + \text{PA}) \gamma_t(\text{Season} * \text{NDVI_S/M} + \text{Prey_S/M} + \text{PREY_WS/SM}) p(\text{Best fit})$	1569.41	3.89	0.03	29	1504.19
$\Psi_W(\text{Best fit}) \varepsilon_t(\text{Season} + \text{Water} + \text{PA} + \text{NDVI_S/M}) \gamma_t(\text{Season} * \text{NDVI_S/M} + \text{Prey_S/M} + \text{PREY_WS/SM}) p(\text{Best fit})$	1569.48	3.95	0.03	28	1506.77
$\Psi_W(\text{Best fit}) \varepsilon_t(\text{PA} + \text{NDVI_S/M}) \gamma_t(\text{Season} * \text{NDVI_S/M} + \text{Prey_S/M} + \text{PREY_WS/SM}) p(\text{Best fit})$	1569.77	4.25	0.02	26	1512.02
$\Psi_W(\text{Best fit}) \varepsilon_t(\text{Best fit}) \gamma_t(\text{NDVI_S/M} + \text{Prey_S/M}) p(\text{Best fit})$	1570.03	4.50	0.02	22	1521.95
$\Psi_W(\text{Best fit}) \varepsilon_t(\text{ISeason} * \text{Water}) \gamma_t(\text{Season} * \text{NDVI_S/M} + \text{Prey_S/M} + \text{PREY_WS/SM}) p(\text{Best fit})$	1570.12	4.59	0.02	27	1509.89
$\Psi_W(\text{Best fit}) \varepsilon_t(\text{NDVI_S/M}) \gamma_t(\text{Season} * \text{NDVI_S/M} + \text{Prey_S/M} + \text{PREY_WS/SM}) p(\text{Best fit})$	1570.12	4.60	0.02	25	1514.81
$\Psi_W(\text{Best fit}) \varepsilon_t(\text{Season} * \text{NDVI_S/M}) \gamma_t(\text{Season} * \text{NDVI_S/M} + \text{Prey_S/M} + \text{PREY_WS/SM}) p(\text{Best fit})$	1570.20	4.67	0.02	26	1512.44
$\Psi_W(\text{Best fit}) \varepsilon_t(\text{Best fit}) \gamma_t(\text{NDVI_S/M}) p(\text{Best fit})$	1570.21	4.68	0.02	21	1524.50
$\Psi_W(\text{Best fit}) \varepsilon_t(\text{Season} + \text{NDVI_S/M} + \text{PA}) \gamma_t(\text{Season} * \text{NDVI_S/M} + \text{Prey_S/M} + \text{PREY_WS/SM}) p(\text{Best fit})$	1570.37	4.85	0.02	27	1510.15
$\Psi_W(\text{Best fit}) \varepsilon_t(\text{Season} + \text{Water} + \text{PA}) \gamma_t(\text{Season} * \text{NDVI_S/M} + \text{Prey_S/M} + \text{PREY_WS/SM}) p(\text{Best fit})$	1570.63	5.11	0.02	27	1510.41
$\Psi_W(\text{Best fit}) \varepsilon_t(\text{Best fit}) \gamma_t(== 0) p10(=0) p11(\text{Season} + \text{Method})^g$	1698.11	132.58	0.00	14	1668.47
$\Psi_W(.) \varepsilon_t(.) \gamma_t(.) p10(.) p11(.)^h$	1856.59	291.07	0.00	5	1846.369

APPENDIX 2.1

Table S9: Mammalian herbivore species found in the Central Terai Landscape.

Species	Habitat Type	IUCN Status	Endemic
Family: Cervidae			
Chital (<i>Axis axis</i>)	F, G, S	LC	South Asia
Swamp deer (<i>Rucervus duvaucelli</i>)	G, W	V	India, Nepal
Sambar (<i>Rusa unicolor</i>)	F, S, Sh, G	V	South and South-east Asia
Hog deer (<i>Axis porcinus</i>)	Sv, Sh, G, W	E	South Asia
Barking deer (<i>Muntiacus muntjac</i>)	F	LC	South and South-east Asia
Family: Bovidae			
Four-horned antelope (<i>Tetracerus quadricornis</i>)	F, S	V	India, Nepal
Black buck (<i>Antelope cervicapra</i>)	G, D, F	NT	India
Nilgai (<i>Boselaphus tragocamelus</i>)	G, S, F	LC	India, Nepal, Pakistan
Family: Suidae			
Wild boar (<i>Sus scrofa</i>)	F, G, Sv, Sh, W	LC	Asia, Europe
Family: Rhinocerotidae			
One-horned rhinoceros (<i>Rhinoceros unicornis</i>)	W, F, G	V	India, Nepal
Family: Elephantidae			
Asian elephant (<i>Elephas maximus</i>)	F, G, Sh	E	South and South-east Asia

IUCN Status: LC- Least concern; NT- near threatened; V- Vulnerable; E- Endangered

Habitat Type: F- Forest; G-Grassland; S-Savanna; Sh-Shrubland; W- Wetland

Table S10: Season characteristics and season-specific survey effort

SEASON	Max temperature, Precipitation, Cover	FS Grids surveyed (farmers interviewed)	CS Grids surveyed (maximum days)
Winter (15 Dec.–15 Feb.)	22 C, 19.1mm, High	94 (565)	47 (40)
Summer (15 Mar.–15 May)	38 C, 5.8mm, Low	91 (514)	43 (40)
Monsoon (15 Jul.–15 Aug.)	33.8 C, 277.4mm, Moderate	85 (416)	32 (37)

Table S11: Description of covariates used to model winter use probabilities using false-positive dynamic occupancy models for nilgai, wild boar and hog deer.

Covariate	Type and source of covariate	Range
PA	Minimum Euclidean distance (km) between cell center and protected area boundaries.	0 - 8.97
NDVI_W,	A median NDVI layer for the study area was generated from NDVI data for date ranges spanning the winter season using the Landsat-8, 8-Day NDVI composite data set on the Google Earth Engine platform (Gorelick et al. 2017).	0.12 - 0.65
Elev	SRTM Digital Elevation data (Jaarvis et al., 2008) at 90 mtr resolution was used to calculate mean cell-specific elevation values measured in kilometers	0.14 – 0.17
Sett	All settlements within the matrix were digitized in Google Earth. The proportion of each cell covered by settlement polygons was estimated in R.	0 - 0.19
Nat	Proportion of native habitat within a cell. Calculated using vegetation cover classification map for India (Roy et al. 2006). Pixels representing six different native vegetation types in the study site were reclassified as one land-use i.e.”native habitats”. Pixels representing this vegetation class were summed together to calculate the proportion of each cell covered by native vegetation.	0 - 1

References

- Gorelick N, Hancher M, Dixon M, Ilyushchenko S, Thau D, Moore R. 2017. Google Earth Engine: Planetary-scale geospatial analysis for everyone. *Remote Sensing of Environment* 202:18-27.
- Roy PS, Joshi PK, Singh S, Agarwal S, Yadav D, Jegannathan C. 2006. Biome mapping in India using vegetation type map derived using temporal satellite data and environmental parameters. *Ecological Modelling*. 197:148-58.
- Jarvis A, Reuter HI, Nelson A, Guevara E. 2008. Hole-filled SRTM for the globe Version 4, available from the CGIAR-CSI SRTM 90m Database: <http://srtm.csi.cgiar.org>.

APPENDIX 2.2

Model sets for true detection, false-positive detection, initial occupancy, local extinction and local colonization probabilities for hog deer, nilgai and wild boar.

Table S12: True and false-positive detection probability models Key:AICc- Akaike’s information criterion score, Δ AICc - Difference in adjusted Akaike’s information criterion (AIC) score between best supported model and any other model, ω – Model weight; K- Number of parameters; Deviance - Model deviance (-2ln(Model Likelihood)). Models for p_{11} and p_{10} with highest support are shown in bold

Models for $\Psi_w, \varepsilon, \gamma$: Hog deer: Ψ_w (PA + Sett + NDVI_W + NDVI_W ^2 + Elev + Nat) ε (S) γ (S)

Nilgai: Ψ_w (PA + Sett + NDVI_W + NDVI_W ^2 + Elev + Nat) ε (S) γ (S)

Wild boar: Ψ_w (PA + Sett + NDVI_W + NDVI_W ^2 + Elev + Nat) ε (S) γ (S)

Model	AICc	Δ AICc	ω	K	Deviance
Hog deer					
p_{11} (S + M) p_{10} (S)	1905.26	0	0.28	18	1866.57
p_{11} (S + M) p_{10} (S + PA)	1905.49	0.24	0.25	19	1864.5
p_{11} (S + M + Sett + PA) p_{10} (S + PA)	1907.51	2.26	0.09	21	1861.85
p_{11} (S + M) p_{10} (PA)	1907.55	2.3	0.09	17	1871.16
p_{11} (S + M *Resource) p_{10} (S + PA)	1907.67	2.41	0.08	22	1859.64
p_{11} (S + M) p_{10} (Intercept)	1907.68	2.43	0.08	16	1873.56
p_{11} (S + M * Crop Protection) p_{10} (S + PA)	1908.03	2.77	0.07	21	1862.36
p_{11} (S + M *(Crop Protection + Resource)) p_{10} (S + PA)	1910.31	5.05	0.02	24	1857.49
p_{11} (S + PA + Sett +M*(Crop Protection + Resource)) p_{10} (S + PA)	1913.16	7.9	0	26	1855.47
p_{11} (M) p_{10} (S + PA)	1948.73	43.47	0	17	1912.34
p_{11} (S) p_{10} (S + PA)	2279.56	374.31	0	18	2240.88
p_{11} (Intercept) p_{10} (S + PA)	2310.07	404.81	0	16	2275.95
Nilgai					
p_{11} (S + M *(Crop Protection + Resource)) + p_{10} (S)	2090.87	0	0.67	23	2040.45

p_{11} (S + M *(Crop Protection + Resource)) p_{10} (S + PA)	2093.14	2.05	0.23	24	2040.32
p_{11} (S + PA + Sett + M*(Crop Protection + Resource)) p_{10} (S + PA)	2094.59	3.49	0.11	26	2036.91
p_{11} (S + M *(Crop Protection)) p_{10} (S + PA)	2101.26	10.16	0	21	2055.59
p_{11} (S + M *(Crop Protection + Resource)) p_{10} (Intercept)	2106.76	15.67	0	21	2061.1
p_{11} (S + M *(Crop Protection + Resource)) p_{10} (PA)	2108.92	17.83	0	22	2060.89
p_{11} (S + M + Sett + PA) p_{10} (S + PA)	2116.38	25.28	0	21	2070.71
p_{11} (S + M *(Resource)) p_{10} (S + PA)	2117.48	26.39	0	22	2069.45
p_{11} (S + M) p_{10} (S +PA)	2120.23	29.13	0	19	2079.23
p_{11} (M) p_{10} (S +PA)	2131.98	40.89	0	17	2095.59
p_{11} (Intercept) p_{10} (S +PA)	2441.23	350.14	0	16	2407.12
p_{11} (S) p_{10} (S +PA)	2442.03	350.93	0	18	2403.35
Wild boar					
p_{11} (S + PA + Sett + M *(Crop Protection + Resource)) p_{10} (PA)	2024.96	0	0.82	24	1972.14
p_{11} (S + PA + Sett + M*(Crop Protection + Resource)) p_{10} (S + PA)	2028.24	3.28	0.16	26	1970.55
p_{11} (S + M + Sett + PA) p_{10} (S + PA)	2033.72	8.76	0.01	21	1988.06
p_{11} (S + PA + Sett + M*(Crop Protection + Resource)) p_{10} (S)	2043.44	18.48	0	25	1988.2
p_{11} (S + PA + Sett + M*(Crop Protection + Resource)) p_{10} (Intercept)	2044.39	19.43	0	23	1993.97
p_{11} (S + M + Resource) p_{10} (S + PA)	2067.82	42.86	0	22	2019.79
p_{11} (S + M *(Crop Protection + Resource)) p_{10} (S + PA)	2070.87	45.91	0	24	2018.05
p_{11} (S + M*(Crop Protection)) p_{10} (S + PA)	2076.1	51.13	0	21	2030.43
p_{11} (S + M) p_{10} (S + PA)	2077.25	52.29	0	19	2036.25
p_{11} (M) p_{10} (S + PA)	2085.95	60.99	0	17	2049.56
p_{11} (S) p_{10} (S + PA)	2158.22	133.26	0	18	2119.54
p_{11} (Intercept) p_{10} (S + PA)	2165.36	140.39	0	16	2131.24

Table S13: Models of initial occupancy probability (Ψ_w) for hog deer, nilgai and wild boar. Key: AICc- Akaike's information criterion score, Δ AICc - Difference in adjusted Akaike's information criterion (AIC) score between best supported model and any other model, ω – Model weight; K- Number of parameters; Deviance - Model deviance (-2ln(Model Likelihood)). PA – Distance of cell to protected area; Sett – Proportion of cell under human settlements; NDVI_W – Cell specific median NDVI values in winter; Elev – Mean elevation; Nat – Proportion of cell area under native habitats.

Models for p_{11} , p_{10} , ε , γ

Hog deer: p_{11} (S + M) p_{10} (S) ε (S) γ (S)

Nilgai: p_{11} (S + M + Crop Protection + Resource) p_{10} (S) ε (S) γ (S)

Wild boar: p_{11} (S + M + PA + Sett + Crop Protection + Resource) p_{10} (PA) ε (S) γ (S)

Model	AICc	Δ AICc	ω	K	Deviance
Hog deer					
Ψ_w (PA + Sett + NDVI_W + Elev + Nat)	1902.97	0	0.747	17	1866.58
Ψ_w (PA + Sett + NDVI_W + NDVI_W ^2 + Elev + Nat)	1905.26	2.29	0.238	18	1866.57
Ψ_w (NDVI_W + NDVI_W ^2 + Elev + Nat)	1910.89	7.92	0.01	16	1876.78
Ψ_w (PA + Sett)	1942.29	39.32	0	14	1912.67
Ψ_w (NDVI_W + NDVI_W^2 + Nat)	1944.67	41.7	0	15	1912.81
Ψ_w (NDVI_W + NDVI_W^2)	1944.76	41.79	0	14	1915.14
Ψ_w (PA)	1945.9	42.93	0	11	1922.9
Ψ_w (NDVI_W)	1946.27	43.29	0	13	1918.87
Ψ_w (Sett)	1946.59	43.62	0	11	1923.58
Ψ_w (Intercept)	1959.08	56.11	0	12	1933.88
Ψ_w (Nat)	1959.29	56.32	0	13	1931.89
Nilgai					
Ψ_w (NDVI_W + NDVI_W^2 + Nat)	2087.26	0	0.56	20	2043.94
Ψ_w (NDVI_W + NDVI_W^2)	2087.74	0.48	0.30	19	2046.75
Ψ_w (NDVI_W + NDVI_W ^2 + Elev + Nat)	2088.34	1.08	0.23	21	2042.68
Ψ_w (PA + Sett + NDVI_W + NDVI_W ^2 + Elev + Nat)	2090.87	3.61	0.06	23	2040.45
Ψ_w (PA + Sett)	2096.57	9.31	0	19	2055.58
Ψ_w (Sett)	2097.37	10.11	0	18	2058.68
Ψ_w (Nat)	2098.09	10.83	0	18	2059.40
Ψ_w (PA)	2099.11	11.85	0	18	2060.43
Ψ_w (NDVI_W)	2099.41	12.15	0	18	2060.73
Ψ_w (Intercept)	2099.81	12.55	0	17	2063.42
Wild boar					
Ψ_w (Intercept)	2022.66	0	0.21	18	1983.98
Ψ_w (NDVI_W)	2023.31	0.64	0.15	19	1982.32
Ψ_w (Sett)	2023.35	0.684	0.14	19	1982.36

Ψ_w (NDVI_W+ NDVI_W^2)	2024.03	1.36	0.14	20	1980.71
Ψ_w (NDVI_W+ NDVI_W ^2 + Elev + Nat)	2024.4	1.74	0.08	22	1976.37
Ψ_w (Nat)	2024.49	1.82	0.083	19	1983.49
Ψ_w (PA)	2024.75	2.08	0.07	19	1983.76
Ψ_w (PA + Sett + NDVI_W+ NDVI_W ^2 + Elev + Nat)	2024.97	2.3	0.06	24	1972.15
Ψ_w (PA + Sett)	2025.41	2.74	0.05	20	1982.08
Ψ_w (NDVI_W + NDVI_W^2 + Nat)	2026.37	3.7	0.03	21	1980.7

Table S14: Models for local extinction and colonization probabilities for hog deer, wild boar and nilgai Key:AICc- Akaike's information criterion score, Δ AICc - Difference in adjusted Akaike's information criterion (AIC) score between best supported model and any other model, ω – Model weight; K- Number of parameters; Deviance - Model deviance (-2ln(Model Likelihood));

Models for p_{11} , p_{10} and Ψ_w

Hog deer: Ψ_w (PA + Sett + NDVI_W+ NDVI_W ^2 + Elev + Nat) p_{11} (S + M) p_{10} (S)

Nilgai: Ψ_w (NDVI_W + NDVI_W^2 + Nat) p_{11} (S + M + Crop Protection + Resource) p_{10} (S)

Wild boar: Ψ_w (Intercept) p_{11} (S + M + PA + Sett + Crop Protection + Resource) p_{10} (PA)

Model	AICc	Δ AICc	ω	K	Deviance
Hog deer					
ϵ (S) γ (S1=S2=0)	1898.44	0	0.52	15	1866.58
ϵ (S) γ (Intercept)	1900.69	2.26	0.16	16	1866.58
ϵ (S) γ (S2=0)	1900.69	2.26	0.16	16	1866.58
ϵ (S) γ (S)	1902.97	4.53	0.05	17	1866.58
ϵ (Intercept) γ (S)	1903.93	5.49	0.03	16	1869.816
ϵ (S2=0) γ (S2=0)	1921.74	23.29	0	15	1889.878
ϵ (S1=S2=0) γ (S1=S2=0)	1932.67	34.23	0	13	1905.27
NOFP	2161.15	262.71	0	12	2135.95
Nilgai					
ϵ (S2=0) γ (S2=0)	2080.33	0	0.72	17	2043.94
ϵ (S) γ (S2=0)	2082.62	2.29	0.23	18	2043.94
ϵ (S) γ (S)	2087.26	6.93	0.02	20	2043.94
ϵ (S2=0) γ (Intercept)	2087.65	7.32	0.01	19	2046.65
ϵ (Intercept) γ (S)	2092.44	12.11	0	19	2051.45

ε (S2=0) γ (S1=S2=0)	2096.12	15.79	0	16	2062.01
ε (S1=S2=0) γ (S1=S2=0)	2158.36	78.03	0	15	2126.5
NOFP	2482.84	402.51	0	15	2450.98
Wild Boar					
ε (Intercept) γ (S)	2020.41	0	0.44	17	1984.02
ε (S) γ (S2=0)	2021.16	0.76	0.3	17	1984.77
ε (S) γ (S)	2022.66	2.25	0.14	18	1983.98
ε (Intercept) γ (Intercept)	2023.99	3.58	0.07	16	1989.87
ε (S) γ (Intercept)	2026.15	5.74	0.02	17	1989.76
ε (S2=0) γ (S2=0)	2028.4	7.99	0	16	1994.28
NOFP	2037.61	17.2	0	15	2005.75
ε (S1=S2=0) gam (S1=S2-0)	2044.02	23.61	0	14	2014.4

Models with highest support are shown in bold. NOFP: A version of the model with the highest support in the model set for each species that does not include false-positive errors ($p_{10,FS}$ set to 0)

APPENDIX 3.1

Posterior distribution and marginal probability distribution for all model parameters

Posterior Distribution

$$[\mathbf{Z}, \boldsymbol{\beta}, \boldsymbol{\phi}, \boldsymbol{\gamma}, r, p_{11}, p_{10} | \mathbf{Y}, \mathbf{W}] \propto \prod_{t=1}^T \prod_{i=1}^S [y_{i,t} | r]^{z_{i,t}} \cdot 1_{y_{i,t}=0}^{1-z_{i,t}} \cdot [w_{i,t} | p_{10}]^{1-z_{i,t}} \cdot [w_{i,t} | p_{11}]^{z_{i,t}} \cdot [z_{i,1} | \psi_1] \cdot [z_{i,t} | \phi_{t-1}]^{z_{i,t-1}} \cdot [z_{i,t} | \gamma_{t-1}]^{(1-z_{i,t-1})} \cdot [z_{i,t+1} | \phi_t]^{z_{i,t}} \cdot [z_{i,t+1} | \gamma_t]^{(1-z_{i,t})} \cdot [\boldsymbol{\beta}] [\boldsymbol{\phi}] [\boldsymbol{\gamma}] [r] [p_{11}] [p_{10}]$$

Full Conditional Distributions

$$[z_{i,t} | \cdot]$$

$z_{it} = 1$ for sites with both sources of data and $y_{it} > 0$. For all other sites

$$[z_{i,t} | \cdot] \propto [w_{i,t} | p_{11}]^{z_{i,t}} \cdot [w_{i,t} | p_{10}]^{1-z_{i,t}} \cdot ([y_{i,t} | r]^{z_{i,t}} \cdot 1_{y_{i,t}=0}^{1-z_{i,t}})^m \cdot [z_{i,t} | \phi_{t-1}]^{z_{i,t-1}} \cdot [z_{i,t} | \gamma_{t-1}]^{(1-z_{i,t-1})} \cdot [z_{i,1} | \psi_{i,1}] \cdot [z_{i,t+1} | \phi_t]^{z_{i,t}} \cdot [z_{i,t+1} | \gamma_t]^{(1-z_{i,t})}$$

We derive full conditional distributions for $z_{i,t}$ for cases where $t = 1$, $1 < t < T$ and $t = T$

$[z_{i,t} | \cdot]$ **when** $t = 1$

$$z_{i,1} \sim \text{Bern}(\tilde{\psi}_{i,1})$$

$$\tilde{\psi}_{i,1} = \frac{A}{A+B}$$

$$A = \binom{J_{i,1}}{w_{i,1}} p_{11}^{w_{i,1}} (1-p_{11})^{J_{i,1}-w_{i,1}} \cdot ((1-r)^{K_{i,1}})^m \cdot \psi_{i,1} \cdot \phi_1^{z_{i,2}} \cdot (1-\phi_1)^{1-z_{i,2}}$$

$$B = \binom{J_{i,1}}{w_{i,1}} p_{10}^{w_{i,1}} (1-p_{10})^{J_{i,1}-w_{i,1}} \cdot (1-\psi_{i,1}) \cdot \gamma_1^{z_{i,2}} \cdot (1-\gamma_1)^{1-z_{i,2}}$$

$[z_{i,t}|\cdot]$ when $1 < t < T$

$$z_{i,t} \sim \text{Bern}(\tilde{\psi}_{i,t})$$

$$\tilde{\psi}_{i,t} = \frac{A}{A+B}$$

$$A = \binom{J_{i,t}}{w_{i,t}} p_{11}^{w_{i,t}} (1-p_{11})^{J_{i,t}-w_{i,t}} ((1-r)^{K_{i,t}})^m \phi_t^{z_{i,t}+1} (1-\phi_t)^{(1-z_{i,t}+1)} \phi_{t-1}^{z_{i,t}-1} \gamma_{t-1}^{(1-z_{i,t}-1)}$$

$$B = \binom{J_{i,t}}{w_{i,t}} p_{10}^{w_{i,t}} (1-p_{10})^{J_{i,t}-w_{i,t}} \gamma_t^{z_{i,t}+1} (1-\gamma_t)^{1-z_{i,t}+1} (1-\phi_{t-1})^{z_{i,t}-1} (1-\gamma_{t-1})^{(1-z_{i,t}-1)}$$

$[z_{i,t}|\cdot]$ when $t = T$

$$z_{i,T} \sim \text{Bern}(\tilde{\psi}_{i,T})$$

$$\tilde{\psi}_{i,T} = \frac{A}{A+B}$$

$$A = \binom{J_{i,T}}{w_{i,T}} p_{11}^{w_{i,T}} (1-p_{11})^{J_{i,T}-w_{i,T}} ((1-r)^{K_{i,T}})^m \phi_{T-1}^{z_{i,T}-1} \gamma_{T-1}^{(1-z_{i,T}-1)}$$

$$B = \binom{J_{i,T}}{w_{i,T}} p_{10}^{w_{i,T}} (1-p_{10})^{J_{i,T}-w_{i,T}} (1-\phi_{T-1})^{z_{i,T}-1} (1-\gamma_{T-1})^{(1-z_{i,T}-1)}$$

$[\beta|\cdot]$

$$[\beta|\cdot] \propto \prod_{t=1}^S \prod_{i=1} [z_{i,1}|\psi_{i,1}][\beta]$$

$[\phi_t|\cdot]$

Since ϕ_t describes a survival probability, this is relevant only to those sites where $z_{t-1} = 1$. Therefore, conditioning on sites that are occupied at time t-1 we get

$$\begin{aligned}
[\phi_t|\cdot] &\propto \prod_{z_{i,t-1}=1} [z_{i,t}|\phi_t][\phi_t] \\
[\phi_t|\cdot] &\propto \prod_{z_{i,t-1}=1} \phi_t^{z_{i,t}} (1-\phi_t)^{1-z_{i,t}} \cdot \phi_t^{\alpha_\phi-1} \cdot (1-\phi_t)^{\beta_\phi-1} \\
[\phi_t|\cdot] &\propto \phi_t^{\sum_{z_{i,t-1}=1} (z_{i,t}) + \alpha_\phi - 1} \cdot (1-\phi_t)^{\sum_{z_{i,t-1}=1} (1-z_{i,t}) + \beta_\phi - 1} \\
\phi_t &\sim \text{Beta}\left(\sum_{z_{i,t-1}=1} (z_{i,t}) + \alpha_\phi, \sum_{z_{i,t-1}=1} (1-z_{i,t}) + \beta_\phi\right)
\end{aligned}$$

$[\gamma_t|\cdot]$

Since γ_t describes a colonization probability, this is relevant only to those sites where $z_{t-1} = 0$. Therefore, conditioning on sites that are unoccupied at time t-1 we get

$$\begin{aligned}
[\gamma_t|\cdot] &\propto \prod_{z_{i,t-1}=0} [z_{i,t}|\gamma_t][\gamma_t] \\
[\gamma_t|\cdot] &\propto \prod_{z_{i,t-1}=0} \gamma_t^{z_{i,t}} (1-\gamma_t)^{1-z_{i,t}} \cdot \gamma_t^{\alpha_\gamma-1} \cdot (1-\gamma_t)^{\beta_\gamma-1} \\
[\gamma_t|\cdot] &\propto \gamma_t^{\sum_{z_{i,t-1}=0} (z_{i,t}) + \alpha_\gamma - 1} \cdot (1-\gamma_t)^{\sum_{z_{i,t-1}=0} (1-z_{i,t}) + \beta_\gamma - 1} \\
\gamma_t &\sim \text{Beta}\left(\sum_{z_{i,t-1}=0} (z_{i,t}) + \alpha_\gamma, \sum_{z_{i,t-1}=0} (1-z_{i,t}) + \beta_\gamma\right)
\end{aligned}$$

$[p_{11}|\cdot]$

Since p_{11} describes the detection probability of the uncertain method it applies only to sites where $z_{i,t-1} = 1$

$$\begin{aligned}
[p_{11}|\cdot] &\propto \left(\prod_{t=1}^T \prod_{z_{i,t}=1} [w_{i,t}|p_{11}]\right)^{z_{i,t}} [p_{11}] \\
[p_{11}|\cdot] &\propto \left(\prod_{t=1}^T \prod_{z_{i,t}=1} \binom{J_{i,t}}{w_{i,t}} (p_{11})^{w_{i,t}} (1-p_{11})^{J_{i,t}-w_{i,t}}\right)^{z_{i,t}} \frac{\Gamma(\alpha_{p_{11}} + \beta_{p_{11}})}{\Gamma(\alpha_{p_{11}})\Gamma(\beta_{p_{11}})} (p_{11})^{\alpha_{p_{11}}-1} (1-p_{11})^{\beta_{p_{11}}-1} \\
[p_{11}|\cdot] &\propto p_{11}^{\sum_{z_{i,t}=1} (w_{i,t})} (1-p_{11})^{\sum_{z_{i,t}=1} (J_{i,t}-w_{i,t})} (p_{11})^{\alpha_{p_{11}}-1} (1-p_{11})^{\beta_{p_{11}}-1} \\
p_{11} &\sim \text{Beta}\left(\sum_{z_{i,t}=1} (w_{i,t}) + \alpha_{p_{11}}, \sum_{z_{i,t}=1} (J_{i,t}-w_{i,t}) + \beta_{p_{11}}\right)
\end{aligned}$$

$[p_{10}|\cdot]$

Since p_{10} is the false-positive probability for the uncertain method this is applicable only to sites where $z_{i,t-1} = 0$

$$\begin{aligned}
[p_{10}|\cdot] &\propto \left(\prod_{t=1}^T \prod_{z_{i,t}=0} [w_{i,t}|p_{10}] \right)^{1-z_{i,t}} [p_{10}] \\
[p_{10}|\cdot] &\propto \left(\prod_{t=1}^T \prod_{z_{i,t}=0} \binom{J_{i,t}}{w_{i,t}} \right) (p_{10})^{w_{i,t}} (1-p_{10})^{J_{i,t}-w_{i,t}})^{1-z_{i,t}} \frac{\Gamma(\alpha_{p_{10}} + \beta_{p_{10}})}{\Gamma(\alpha_{p_{10}})\Gamma(\beta_{p_{10}})} (p_{10})^{\alpha_{p_{10}}-1} (1-p_{10})^{\beta_{p_{10}}-1} \\
[p_{10}|\cdot] &\propto p_{10}^{\sum \sum_{z_{i,t}=0} (w_{i,t})} (1-p_{10})^{\sum \sum_{z_{i,t}=0} (J_{i,t}-w_{i,t})} (p_{10})^{\alpha_{p_{10}}-1} (1-p_{10})^{\beta_{p_{10}}-1} \\
p_{10} &\sim \text{Beta}(\sum \sum_{z_{i,t}=0} (w_{i,t}) + \alpha_{p_{10}}, \sum \sum_{z_{i,t}=0} (J_{i,t}-w_{i,t}) + \beta_{p_{10}})
\end{aligned}$$

$[r|\cdot]$

Since r is the detection probability for the certain method this is applicable only to sites where $z_{i,t-1} = 1$

$$\begin{aligned}
[r|\cdot] &\propto \left(\prod_{t=1}^T \prod_{z_{i,t}=1} [y_{i,t}|r] \right)^{z_{i,t}} [r] \\
[r|\cdot] &\propto \left(\prod_{t=1}^T \prod_{z_{i,t}=1} \binom{K_{i,t}}{y_{i,t}} \right) r^{y_{i,t}} (1-r)^{K_{i,t}-y_{i,t}})^{z_{i,t}} \frac{\Gamma(\alpha_r + \beta_r)}{\Gamma(\alpha_r)\Gamma(\beta_r)} r^{\alpha_r-1} (1-r)^{\beta_r-1} \\
[r|\cdot] &\propto r^{\sum \sum_{z_{i,t}=1} (y_{i,t})} (1-r)^{\sum \sum_{z_{i,t}=1} (K_{i,t}-y_{i,t})} r^{\alpha_r-1} (1-r)^{\beta_r-1} \\
r &\sim \text{Beta}(\sum \sum_{z_{i,t}=1} (y_{i,t}) + \alpha_r, \sum \sum_{z_{i,t}=1} (K_{i,t}-y_{i,t}) + \beta_r)
\end{aligned}$$