CARNIVORE ECOLOGY AND CONSERVATION: IMPLICATIONS FOR TIGER CONSERVATION AND MANAGEMENT IN NEPAL

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HEMANTA KAFLEY

Dr. Matthew E. Gompper, Dissertation Advisor

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The undersigned, appointed by the dean of the Graduate School, have examined the dissertation entitled

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Presented by Hemanta Kafley, a candidate for the degree of Doctor of Philosophy, and hereby certify that, in their opinion, it is worthy of acceptance.

Dr. Matthew E. Gompper

School of Natural Resources, University of Missouri

Dr. John R. Jones

School of Natural Resources, University of Missouri

Dr. Joshua J. Millspaugh

School of Natural Resources, University of Missouri

Dr. Hong He

School of Natural Resources, University of Missouri

Dr. Eric Dinerstein

Resolve Inc.

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DESCRIPTION OF CHAPTERS

The chapters of this dissertation were written as independent manuscripts, with the exception of Chapter I which I have included to tie together the overarching research questions literature review. Chapter II has been accepted to the journal *Wildlife Research* and is in press. Chapter III and Chapter IV were written as independent manuscripts with an intention to submit to two different peer-reviewed journals. Chapter V was published in 2014 in the journal *Wildlife Biology in Practice*. Hence, the references associated with each chapter are formatted somewhat differently, reflecting the requirements of the various publications. Because each chapter was written as an independent manuscript, some portions of their respective introductions, methods, figures, and references may overlap in content. The dissertation was also written using plural proper nouns to indicate co-authors.

CHAPTER I

INTRODUCTION

In human-dominated landscapes, habitat fragmentation and disturbance have confined many large carnivores to smaller protected areas (Linnell and Strand 2000, Dinerstein et al. 2006, Walston et al. 2010, Crooks et al. 2011, Wikramanayake et al. 2011, Gour and Reddy 2015, López-Bao et al. 2015). In smaller protected areas where carnivores are frequently exposed to anthropogenic pressures as a result of human-carnivore conflicts along protected area borders (Linnell and Strand 2000), the likelihood of extirpation of small populations is increased due to stochastic processes and strong edge effects (Woodroffe and Ginsberg 1998, Kowalczyk et al. 2015). Yet despite the issues inherent to relatively smaller protected areas, such areas remain critical for conserving global biodiversity (DeFries et al. 2007, Chapron et al. 2014). In Asia many smaller protected areas serve as source habitats for large carnivores such as tiger (*Panthera tigris*) and leopards (*P. pardus*). This dissertation includes four chapters based on research conducted on tigers and leopards in Chitwan National Park, a small but biodiversity-rich protected area that is an important source habitat for multiple large carnivore species in Nepal.

In the human-dominated Terai Arc Landscape of northern India and southern Nepal, tigers are primarily confined to relatively isolated protected areas such as Chitwan National Park, Bardia National Park, Parsa Wildlife Reserve and Shuklaphanta Wildlife Reserve in Nepal and Corbett National Park, Dudhwa National Park, and Katarniaghat Wildlife Sanctuary in India. These protected areas have high tiger densities and are important for the conservation of tigers in the region (Karanth and Nichols 1998, Karanth et al. 2004, Karanth et al. 2006, Jhala et al. 2008, Dhakal et al. 2014, Karki et al. 2015, Chanchani et al. 2016). The spatial occurrences of tigers within these relatively small (from the perspective of tigers) protected areas can be explained by fine-scale activity patterns (Carter et al. 2012, Sunarto et al. 2012, Steinmetz et al. 2013). An individual tiger uses only a fraction of its home range (Miquelle et al. 1999), and the unused portion of the home range may be used by other individuals, in turn facilitating higher population densities. In Chapter II of this dissertation, I report the fine-scale habitat association of tiger in Chitwan National Park.

The results in Chapter II unequivocally show that tiger occupancy at the fine spatial-scale depends on prey availability. Several other studies conducted at the landscape scale have also asserted that tiger habitat use or even abundance depends on prey. However, prey variable has been differently quantified and defined owing to the complexity of counting unmarked animals with certainty (Carbone et al. 2001, Royle 2004, Rowcliffe et al. 2008, Rovero and Marshall 2009, Carter et al. 2012). In chapter III of this dissertation I demonstrate the applicability of binomial mixture models to model animal abundance (Royle and Nichols 2003, Royle and Dorazio 2006, Denes et al. 2015, Chambert et al. 2016) from the camera trap data. The models show how the detectability-corrected prey abundance can be obtained from point count data obtained from camera trap surveys. To my knowledge, this approach has not been previously used for estimating prey abundance at fine spatial scales and has tremendous potential to contribute to wildlife monitoring projects.

The scientific literature is replete with theoretical and empirical studies of the ecological functions played by organisms at different trophic levels in structuring ecosystems (Hairston et al. 1960, Crooks and Soulé 1999, Terborgh et al. 1999, Ray et al. 2005, Ripple et al. 2014, Ford and Goheen 2015, Saint-Béat et al. 2015). Carnivores, at the top of the ecological pyramid, are usually considered as the top-down trophic regulators. Large terrestrial predators such as tigers are putatively important for their role as a "keystone species" (Wright et al. 1994, Ripple and Larsen 2000, Estes et al. 2011, Cho et al. 2013, Périquet et al. 2015), combining with energy input to modulate biomass of the lower trophic levels (Hairston et al. 1960, Oksanen et al. 1981). However, Levin (1970) notes that competitive exclusion between top predators, resulting either from resource competition or from competitive dynamics with respect to any limiting factors, including predation, also determine the community structure (Ripple et al. 2014, Wallach et al. 2015, Gompper et al. 2016). It is widely accepted that the traditional school of thought - increasing density of prey weakens competition among predators - does not necessarily hold true (Polis et al. 1989, Hunter and Caro 2008). In part this is because the intraguild dynamics among predators may mediate predator-prey dynamics (Jones and Barmuta 1998, Fedriani et al. 2000, Glen et al. 2005, Michel et al. 2016). Studies suggest that interspecific competition and overall community ecology can be a determining factor for guild populations (Hairston et al. 1960, Mac Nally 1983, Creel 2001, Chapron and López-Bao 2016).

In the chapter IV I examine the pattern of co-occurrence between tigers and leopards to test the hypotheses that the tiger (the top predator in the ecosystem) influences the habitat use of other carnivores and thereby may have a significant ecological role in determining mammalian community structure. Further, I address whether tiger-leopard interactions may be modulated by the abundance of prey and by disturbance factors such as livestock and human presence in the habitat. Our understanding of the important ecological role of top predators in different ecosystems has been formed from studies conducted in relatively simple aquatic and terrestrial ecosystems (Estes and Duggins 1995, Estes et al. 1998, Heithaus et al. 2008) (Connor and Simberloff 1979, Terborgh et al. 2001, Newsome and Ripple 2015, Schroeder et al. 2015), where a single top predator can be considered as a trophic regulator because it directly and indirectly drives the community structure at multiple other trophic levels. However, in an ecosystem where multiple predators exert influences on prey species, it is difficult to segregate the influence of particular predator species (Hairston et al. 1960). This is because regardless of the effect of any individual predator species, the collective impact of multiple predators has a dampening effect on trophic cascades (Finke and Denno 2004). Generally, the top predator is viewed as triggering trophic cascades which might blur the relative roles of other sympatric or mesopredators present in that ecosystem. Therefore, understanding the influence of the top predator on subordinate predators warrants consideration.

Competitive intra-guild dominance effects may magnify or ameliorate the top down effect from the predator guild (Hairston Jr and Hairston Sr 1997, Finke and Denno 2004, Hayward and Slotow 2009, Grassel et al. 2015, Wang et al. 2015, Björklund et al. 2016). A broad body of research has shown that competitive interactions among carnivore species can result in the exclusion of subordinate species from what is otherwise suitable habitat. Therefore, prior to an attempt to unweave the trophic cascade processes in a complex ecosystem, it is important to understand the competitive dynamics within the predator guild. Because few studies have investigated the ecological significance of competition among carnivores in complex tropical ecosystems (Gittleman and Gompper 2005), we do not fully understand how such interactions affect top-down processes, nor the potential effects of removing components of that guild.

Finally, chapter V of this dissertation explores the economic ability of a developing country to secure financial resources to sustain tiger conservation projects. Because conservation funding is always in short-supply, the problem is particularly acute in developing countries like Nepal. Despite the will of the government and support from international agencies, adequate funding is difficult to secure for conserving even iconic species like the tiger. In this context, Nepal is striving to identify and secure a sustainable financing mechanism to support tiger conservation programs. A tiger conservation program has been identified and designed for Nepal to meet its' global commitment of doubling the tiger numbers by 2022 (GTRP 2010, Wikramanayake et al. 2011). This chapter analyses the current funding of Nepal's tiger conservation program and the potential of Nepal to fund tiger conservation into the future. The successful conservation of ecosystems depends on a mix of environmental, social and economic factors. For nations that struggle financially to provide basic public services, the funding of ecosystem maintenance or conservation agendas often are not the highest priority for limited government dollars. This chapter identifies the alternative sources for developing and sustaining tiger conservation programs in Nepal.

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CHAPTER II

TIGERS (*PANTHERA TIGRIS*) RESPOND TO FINE SPATIAL-SCALE HABITAT FACTORS: OCCUPANCY-BASED HABITAT ASSOCIATION OF TIGERS IN CHITWAN NATIONAL PARK, NEPAL

Hemanta Kafley[A,B,F] , Matthew E. Gompper[A], Mandira Sharma[C], Babu R. Lamichane[D], Rupak Maharjan[E]

[A]Department of Fisheries and Wildlife Sciences, University of Missouri, Columbia, MO 65211, USA.

[B]Nepal Nature Foundation, Koteshwor, Kathmandu-34, Nepal.

[C]Department of Agriculture and Environmental Sciences, Lincoln University, Jefferson City, MO 65101, USA.

[D]National Trust for Nature Conservation, Biodiversity Conservation Center, Chitwan, Nepal.

[E]Department of National Parks and Wildlife Conservation, Chitwan National Park, Chitwan, Nepal

Abstract

Context. Source populations of many large carnivores such as tigers (*Panthera tigris*) are confined within relatively small wildlife refuges in human-dominated landscapes. Appropriate management of these populations may warrant understanding fine-scale use of habitat.

Aims. The aim of this study is to understand the fine spatial scale habitat associations of tigers in Chitwan National Park, Nepal.

Methods. We conducted camera-trap surveys across the park and applied an occupancy modeling approach to assess the probability of tiger detection and occurrence as a function of fine-scale habitat covariates.

Results. Tiger detection probability as a function of fine-scale habitat covariates was ≤ 0.20 compared to a constant detection model. Detectability patterns were best explained by models incorporating the effect of prey, slope and landcover type. Similarly, the best occupancy model incorporating the detection probability included prey, landcover type, water, and slope. Tiger occurrence patterns were positively associated with prey availability and certain landcover types such as grasslands. Contrary to expectation, occurrence probability decreased further from human settlements. However, as expected, the occurrence of tigers was higher in proximity to water sources.

Conclusions. Both tiger detection and occurrence are influenced by fine-scale habitat factors including prey availability. In small protected areas individuals may persist at high population densities by intensively focusing their activity on small portions of their home ranges.

***Implications*.** Our study provides insight into the fine spatial-scale occurrence probability of tigers, and thereby aids in developing appropriate habitat management strategies at the protected area level. Our approach is broadly applicable to the robust assessment of fine-scale wildlife-habitat associations of many wide-ranging species that are ecologically “confined” in smaller protected areas.

Additional keywords camera trapping, Chitwan National Park, fine-scale habitat association, occupancy modelling, *Panthera tigris*

Introduction

In human-dominated landscapes, habitat fragmentation and disturbance have confined many large carnivores to smaller protected areas (Linnell *et al.* 2000; Dinerstein 2006; Walston *et al.* 2010; Crooks *et al.* 2011; Wikramanayake *et al.* 2011). In smaller protected areas where carnivores are frequently exposed to anthropogenic pressures as a result of human-carnivore conflicts along protected area borders (Linnell *et al.* 2000), the likelihood of extirpation of small populations is increased due to stochastic processes and strong edge effects (Woodroffe and Ginsberg 1998). Yet despite the issues inherent to relatively smaller protected areas, such areas remain critical for conserving global biodiversity (DeFries et al. 2007). Unfortunately, these smaller protected areas are becoming increasingly isolated due to loss of surrounding natural habitats that normally act as buffers (DeFries *et al.* 2005). This is the case in South and Southeast Asia, where smaller protected areas represent a last resort for maintaining regional species richness and core habitat of critically endangered species (Seidensticker 2010; Walston *et al.* 2010).

For instance, in the human-dominated Terai Arc Landscape of northern India and southern Nepal, tigers (*Panthera tigris* Linnaeus, 1758) are primarily confined to relatively isolated protected areas such as Chitwan National Park, Bardia National Park, Parsa Wildlife Reserve and Shuklaphanta Wildlife Reserve in Nepal and Corbett National Park, Dudhwa National Park, and Katarniaghat Wildlife Sanctuary in India. These protected areas have high tiger densities and are important for the conservation of tigers in the region (Karanth and Nichols 1998; Karanth *et al.* 2004a; Karanth *et al.* 2006; Jhala *et al.* 2010; Karki *et al.* 2013). The spatial occurrences of tigers within these relatively small (from the perspective of tigers) protected areas can be explained by fine-scale activity patterns (Carter et al. 2012). An individual tiger uses only a fraction of its home range (Miquelle *et al.* 1999), and the unused portion of the home range may be used by other individuals, in turn facilitating higher population densities. Even in the Russian Far East, where home range size of tigers is large, they maintain exclusive territories allowing several animals to utilize the same areas containing a surplus of food resources (Hojnowski et al. 2012).

Although multiple landscape-scale habitat studies of tigers have been conducted (Karanth *et al.* 2011; Harihar and Pandav 2012; Barber-Meyer *et al.* 2013), few studies have addressed finer-scale habitat associations of the species (Linkie *et al.* 2006; Carter *et al.* 2012; Carter *et al.* 2013). At a landscape level, tiger occupancy decreases with prey depletion, human disturbance, and inferior habitat (Harihar and Pandav 2012; Barber-Meyer *et al.* 2013). However, habitat association of tigers in small protected areas is difficult to generalize. Attributing habitat occupancy in these areas to the factors observed as important at larger spatial scales may not provide the pragmatic information needed for making localized conservation planning decisions given the potential for prey biomass and human disturbance to vary dramatically across small landscapes. Furthermore, it is at this local-scale level that human-wildlife conflicts may arise, and thus understanding how large predators occupy protected habitats at finer scales may provide insights on how they use buffer zones, and where conflict with local people may occur (Carter *et al.* 2012).

Larger scale studies of tigers and other elusive carnivores are often based on presence / absence surveys (Linkie *et al.* 2010). This information is generally used to identify wildlife-habitat associations, assess population distribution or occupancy, and assess habitat suitability for the species. An inherent problem of this approach is that non-detections are treated as species absences. The potential bias due to false absences can be addressed by explicitly accounting for the imperfect detection of species (MacKenzie *et al.* 2002) or by adopting a sampling grid size much larger than the home range size of tigers (Linkie *et al.* 2010; Harihar and Pandav 2012; Barber-Meyer *et al.* 2013). Accounting for imperfect detection reduces the risk of underestimating tiger habitat use by treating 'non-detection' as an 'absence'. However, in the context of smaller tiger-bearing protected areas that are insular in nature and interspersed within a larger human-dominated landscape, mere information on occupancy might not be of great value for informing local-scale habitat management interventions. Investigating at such finer scales requires adopting a sampling regime that is smaller than an individual animal's home range size.

By assuming random movement of animals between the fine-scale sampling sites (Kendall 1999), the assumption of closure can be relaxed and 'occupied locations' can be interpreted as 'used locations' (MacKenzie *et al.* 2004). In this design, false absence can also be treated as a temporary absence of the species from a sampling unit that is smaller than the home range of the species (Linkie *et al.* 2006; MacKenzie *et al.* 2006). Using this approach, camera trapping data obtained by surveying a region in a grid that is smaller than the home range of the taxon of interest can be effectively employed to model the probability of occurrence or use as a function of site covariates (MacKenzie 2006) at a local scale.

In this study, we applied a single-species occupancy modeling approach (MacKenzie *et al.* 2006) to tiger occurrence data obtained with remote cameras to study patterns in the use of resource units within a single protected area that is, while seemingly large from a human perspective, perhaps small from the perspective of tigers (Manly *et al.* 2002). We model the probabilities of detection and occurrence of tigers from relatively fine-scale resource units to identify fine-scale habitat covariates impacting occurrence of tigers in the habitat. The probability of occurrence in this case would be analogous to the probability of use and the probabilities of detection and use may be functions of variables measured at the sampling units (MacKenzie 2006). Adopting the Design I framework (in the terminology of Manly et al. 2002) of the Resource Selection Probability Function (RSPF), we apply occupancy modeling techniques, model the probability of use of sites by tiger, and test the following hypotheses (Model structure is detailed in Table 1):

(i) As tigers are wide-ranging and perceived as habitat generalists (Miquelle *et al.* 1999; Sunquist *et al.* 1999), the occurrence of tigers is not influenced by landcover-related variables such as habitat types, slope, and availability of water measured at fine-scales.

(ii) As tiger density, occupancy and use of particular locations can be predicted by the availability of prey (Karanth *et al.* 2004b; Carter *et al.* 2012; Barber-Meyer *et al.* 2013), prey availability measured at fine-scale sampling sites may predict the intensity of habitat use at that scale.

(iii) Because proximity to settlements is considered as an index of disturbance, tigers will differentially use habitats further from human settlements.

(iv) Water availability is a critical limiting resource for tigers and their prey (Sunquist *et al.* 1999). Therefore, tiger prefer locations closer to major waterbodies.

Materials and Methods

Study area

Chitwan National Park harbors one of the most promising populations of tigers in the globally prioritized Terai Arc Landscape for tiger conservation, and is a priority protected area in Nepal. It lies in the south central lowlands in Nepal (27° 18’-27° 41’N latitude and 83° 41’-83° 49’E longitude) (Fig. 1) and is comprised of core park area (932 km^2) and the buffer zone (750 km^2) surrounding the park. The park lies between the two mid-mountain ranges: the siwalik (Churia) and the Mahabharat. The park is predominantly covered by forest [high density sal (*Shorea robusta* Gaertner f.) forest, low density sal forest, mixed forest, degraded forest and scrub vegetation, and riparian forest (Lehmkuhl 1994) covering ~ 70%]. Other land cover types include grassland (~8%), riverbank and exposed surfaces (~7%), and agriculture and settlement (15%) (Kafley *et al.2009*). The park provides refuge to over 70 mammal species including other carnivores [e.g. leopard (*Panthera pardus* Linnaeus, 1758), dhole (*Cuon alpinus* Pallas, 1811), jungle cat (*Felis chaus* Schreber, 1777), leopard cat (*Prionailurus bengalensis* Kerr, 1792) fishing cat (*Prionailurus viverrinus* Bennett, 1833) and jackal (*Canis aureus* Linnaeus, 1758)] and potential tiger prey species [e.g. gaur (*Bos gaurus* Smith, 1827), blue bull (*Boselaphus tragocamelus* Pallas, 1766), sambar deer (*Rusa unicolor* Kerr, 1792), barking deer (*Muntiacus muntjak* Zimmermann, 1780) , hog deer (*Heylaphus porcinus* Zimmermann, 1780), chital (*Axis axis* Erxleben, 1777), wild boar (*Sus scrofa*

Linnaeus, 1758), and four-horned antelope (*Tetracerus quadricornis* de Blainville, 1816)]. It offers one of the core habitats for a long-persisting tiger population (Smith *et al.* 1999) in Southeast Asia, boasts the largest population size (between 98-139 animals) and density (3.84/100 km^2; SD=0.34) in Nepal (Dhakal *et al.* 2014), and serves as a potential source population to maintain the tiger metapopulation in the Terai Arc Landscape in Nepal (Karki *et al.* 2013).

Field data collection

From 20 January to 22 March 2010, we used non-invasive camera traps to survey the occurrence of wildlife species across the Chitwan National Park in three blocks, including the entire core of the park as well as some areas of the buffer zone surrounding the park. To assess fine-scale habitat associations of tigers, we generated a 2km X 2km grid and overlaid it on the landscape using the fishnet tool in ArcGIS 9.3 (ESRI inc.) A total of 310 grids were surveyed with a pair of cameras in each grid. Placement of cameras (Moultrie, Alabama, USA) within each grid unit (Fig. 1) was based on the local expert opinion so as to maximize the chance of tiger 'capture'. Camera traps sites in adjacent grid units were at least ~ 1-3 km apart. Characteristics such as vegetation type, altitude, distance from settlements, and other potential covariates were not considered for camera placement. Hence, locations and site characteristics of camera sites are considered quasi-random and independent.

Each survey occasion included a 15-16 day trapping session. Disturbance during a survey, such as camera malfunction or theft resulted in missing data, and so these affected grids were excluded from subsequent analyses, resulting in suitable data from a total of 256 grids. Detections were defined as distinctive tiger photographs taken by either camera in the pair. For prey species (bison, blue bull, chital, sambar, hog deer, barking deer and wild boar), pictures taken at ≥ 30 minutes intervals are considered independent (Carter et al. 2012), unless independence could be inferred based on cues such as herd size and distinct characteristics of photographed animals. We assumed that any 4 km^2 grid in the park contains prey. Hence, sites that did not have any photographic capture of prey were assigned 2 photographic counts, thus avoiding the redundancy in data transformations that might arise from zero counts. Prey detection per grid cells was then standardized using z-transformation and used as a covariate and surrogate to the index of prey abundance.

GIS database and preparation

We used a gap-filled Level 1G (radiometrically and geometrically corrected and georeferenced) Landsat 7 Enhanced Thematic Mapper Plus (ETM+) satellite imagery (path 142/41) with a pixel resolution of 28.5m, acquired from global land cover facility (GLCF) (www.glcf.umd.edu/data/landsat). The imagery was from the same season (December, 2010) our camera trap survey was conducted. We used a supervised classification scheme (Lillesand *et al.* 2004) for classifying Landsat imagery into different land cover classes using Erdas Imagine software Version 8 (Erdas Inc.). The areas under different land cover types in each grid were calculated in GIS domain and z-transformed for standardization.

Elevation data for camera locations were collected during the field survey using Garmin Etrex handheld GPS units. Missing data on elevation were obtained by interpolating the values of available elevation points through kriging procedure (Stein 1999). We created a Digital Elevation Model (DEM) of the study area from the shuttle radar topography map (SRTM) obtained from the GLCF. Slopes of the survey grids were then derived from the DEM using spatial analyst tool in ArcGIS. Other derived variables obtained through GIS data management were distances from the nearest water sources and the nearest human settlements. However, we did not enter distance to water sources and distance to human settlement into our occupancy model as the park is bounded by major river systems and densely populated settlements are found immediately surrounding the park boundary. These variables were highly correlated with each other and also with elevation and slope. We also anticipated that these variables would not provide fine-scale variables characterizing the differences among the sample sites that we were interested in. However, we realize that these variables can potentially be important predictors. Therefore, we descriptively assessed the frequency of tiger detection in relation to these variables for providing a general picture of the tiger captures in the park. Furthermore, we also tested if the probability of occupancy of tigers obtained from the top model could independently be explained by these variables.

Data analysis

We constructed a detection history of tigers in each grid considering 24 hrs as a sampling occasion so that each grid had 16 sampling occasions. Detection of tigers in each sampling occasion was coded as ‘1’ and non-detection as ‘0’. We estimated detection probability and site occupancy following MacKenzie et al. (2002). The probability of detection p was estimated based on the two possible outcomes for each survey occasion: 1) the animal was detected, p; 2) the animal was not detected, $1-p$. Consequently, the probability of occupancy based on the detectability was translated as: 1) The site was occupied and the species was detected, $\Psi \times p$; 2) The species was present but not detected, $\Psi \times 1\text{-}p$; or 3) The species was not present and hence not detected, $1\text{-}\Psi$. We used single-species occupancy models (MacKenzie *et al.* 2006) to estimate the relative effect of prey, slope, and landcover type covariates at a fine scale on the probability of occurrence of tigers.

In our first analysis, we assumed that site occupancy was constant across the study sites. We modeled covariates on detection probability to identify the factors affecting probability of detection of tigers. Detectability was either modeled as a constant or varied with individual covariates. We also combined two or more covariates in possible combinations and modeled detection probability. Candidate models were then compared using Akaike's Information Criteria (AIC) (Burnham and Anderson 2002). We then modeled the occupancy incorporating the top-ranked model for probability of detection. Influence of different covariates on occupancy was again modeled either individually or additively combining covariates in different biological plausible combinations. The contribution of covariates to the models were assessed based on Akaike weight (Burnham and Anderson 2002). All analyses were performed with the program PRESENCE 3.1 (Hines 2006). Model fit was assessed for over dispersion in the global model using 1000 bootstrap (Burnham and Anderson 2002). The global models with c-hat > 4 were considered structurally inadequate (Burnham and Anderson 2002) and excluded from further analyses.

Results

A total of 4096 trap nights were conducted at 256 camera locations corresponding to each grid cell. During the camera trapping survey, we found direct evidence of occurrence of tiger (185 independent photographs) in 100 of the 256 sites surveyed, corresponding to a naïve probability of occupancy estimate of $\Psi = 0.3906$. Capture frequencies in different land cover types were fairly uniform when not adjusted to the proportion of available land cover types (Fig.2). Frequency of tiger capture in cameras gradually decreased with increasing altitude and slope. Tigers were captured as close as < 50 m and as far as ~ 11 km from the nearest settlements. The frequency of tiger capture was higher in grids closer to water sources and settlement areas (Fig.3). Tiger capture rate was not associated with the total number of sites surveyed for both distance from water sources (F=0.11, p=0.7473) and distance from settlements (F=2.88, p=0.1503).

The simplest model [$\Psi(.)p(.)$] with a constant probability of detection ($p = 0.09$, SE = 0.0085) across the study area estimated a constant probability of occupancy ($\Psi =$ 0.5028, SE = 0.0447) that was approximately 1.5 times greater than the naïve estimate, an estimate obtained by using the method of moments (MacKenzie et al. 2006). The top model that incorporated fine-scale habitat covariates to predict the influence of covariates on detectability while maintaining a constant occupancy probability indicated that the probability of detection was ≤ 0.20, almost 2 times higher than results predicted from the constant detection probability model. The effect of increased probability of detection in the top model also increased the probability of occupancy, $\Psi = 0.7322$, SE = 0.0707. Hence, the probability of detection of tigers is indeed a function of habitat covariates and our probability of occupancy was also dependent on the probability of detection.

Modeling probability of detection

Our top model for probability of detection [$\Psi(.)p(\text{covariates})$] indicated that land cover, prey and slope were the most influential habitat covariates (Table 2; summed model weights: prey = 98%; slope = 98%; landcover = 82%. The probability of detecting tigers increased in the grids with high prey encounter rate. Increasing slope had a negative influence on the probability of detection of tigers. Detectability was positively associated with increasing proportion of high density sal forest, mixed forest, riparian forests, grasslands and exposed surfaces. However, β coefficients of exposed surfaces, riparian forests and grasslands included zero within the 95% CI. Probability of detection was negatively influenced by low-density sal forest and degraded forest and scrub (Appendix A).

Probability of occurrence

The global occupancy model with a constant p [Ψ(covariates)p(.)] was over dispersed (c-hat>4) and hence was not structurally adequate, indicating that probability of occupancy could not be estimated without accounting for detection probability. Incorporating the influence of the covariate-induced probability of detection, models clearly depicted that the probability of occupancy was a function of fine-scale habitat covariates. All covariates (land cover, water, slope and prey) included in the modeling were selected in the top model. The summed model weights for the covariates were: Prey = ~ 99%; Landcover = ~ 94%, Water = ~ 85% and Slope = ~ 82% (Table 3). Among the landcover covariates, probability of occurrence was positively associated with increasing proportion of the low-density sal forest and grasslands. Models predicted that increasing area of all other landcover types (high-density sal forest, mixed forest, riparian forest, degraded forest and scrub, and exposed surfaces) decreased the probability of occurrence. As expected, prey had a strong positive influence on the probability of occurrence of tigers (b= 4.8943 SE= 2.2146). Contrary to expectation, however, the occurrence probability of tigers was negatively associated with increased area of water sources (b= -2.5095, SE= 1.3167) (Appendix B). As predicted, the probability of occupancy of tigers decreased with increasing distances from water sources (F- 22.35, p<0.001). However, and also contrary to expectation, tiger occurrence probability increased near human settlements (F- 24.92, p<0.001) (Fig. 4). Grid specific probability of occurrence obtained from the top model was mapped to depict the variations across the study area (Fig. 5).

Discussion

Camera trapping for monitoring large carnivore populations in protected areas is a regular practice in Nepal and elsewhere (Jackson *et al.* 2006; Karanth and Nichols 1998; Tempa *et al.* 2013; Wang and Macdonald 2009). Few studies extend the scope of this monitoring beyond using the obtained information for simply documenting presence or, in the case of individually recognizable animals such as tigers, determining population size in the study areas (Carter *et al.* 2012; Carter *et al.* 2013). Through this study, we show that the camera trap data can also be effectively employed for answering novel questions on fine-scale habitat associations at the protected area level. Such an approach can also be used to help identify appropriate habitat management interventions for diverse wildlife species. For example, in the context of the Terai Arc Landscape where source populations of wild animals are confined within smaller protected areas in a human-dominated landscape, fostering preferred habitat types within the protected areas can potentially enhance opportunity to maintain viable populations (Kafley *et al.* 2009 ; Wikramanayake *et al.* 2011).

Identifying key habitat variables to which a species responds is important in ecological investigations (Verner *et al.* 1986; Scott *et al.* 2002). Occupancy-based sampling techniques using camera traps have been used in other tiger studies to estimate habitat suitability (Carter *et al.* 2013; Wong and Linkie 2013), density (Carter *et al.* 2012), probability of occurrence (Linkie *et al.* 2006), site occupancy and detection probability (O'Connell Jr *et al.* 2006) and habitat occupancy (Thorn *et al.* 2009; O'Connell *et al.* 2011). This study contributes to this literature by revealing the effect of habitat covariates measured at a fine spatial scale to the occurrence of tigers. Unlike a presence/absence approach to discerning wildlife-habitat associations, wherein uncertainty in classifying absence plagues the confidence of the results (Tyre *et al.* 2001; Hirzel *et al.* 2002; Gu and Swihart 2004; MacKenzie *et al.* 2006), this study effectively applies occupancy modeling techniques where the absence of an animal in any sampling site is defined as a temporary absence as determined by the detection history. Our results demonstrate that tigers respond to the fine-scale habitat covariates and the probability of occurrence of tigers was best explained by the function of habitat covariates. Identifying habitat covariates that determines probability of use of sites can inform management for laying out appropriate habitat management decisions. For example, degraded forest and scrub habitat is negatively associated with tiger occurrence in our study area (Appendix A2), and therefore may be considered for restoration or conversion to other cover types that facilitate tiger occurrence, such as grassland.

Tiger detectability and habitat use

Prey, slope and landcover had significant influence on detectability of tigers. The probability of detecting tigers was higher at sites with high prey encounter rates. There exists a functional relationship between abundances of large carnivores and their prey which can be observed across landscapes (Karanth *et al.* 2004b). Here we observe this pattern even within the fine-scale framework of a single protected area, as Chitwan tigers apparently selected sites with high prey abundance as characterized by high prey encounter rates derived from camera trap data. As with the cross-site analyses of Karanth et al (2004b), our results also are consistent with the hypothesis that tiger population declines are primarily a consequence of prey depletion (Karanth and Stith 1999). Higher prey abundance may result in additional activity of tigers within the particular area, resulting in overall higher detectability.

Increasing slope, low density sal forest, and degraded forest and scrub all had a negative influence on detection probability. These patterns may be a function of higher population densities (MacKenzie *et al.* 2005) at sites with relatively lower slopes in the park (DNPWC, unpublished data) and of the relatively dense understory in low density sal and degraded and scrub cover types, although the coefficients for degraded forest and scrub included zero within the 95% CI. Degraded forest and scrub are characterized by disturbed sparse forest including dense bushes that are typically less hospitable for wildlife species including tigers. All other landcover types were positively associated with the detectability of tigers. High density sal forest, mix forest and exposed surfaces (including open river banks) were significant whereas riparian forest (b=0.0568, SE= 0.0772) and grassland (b= 0.0104, SE= 0.1006) were not significant for predicting probability of detection (Appendix A1). Riparian forest and grasslands consist of relatively denser understory (Sunquist 1981) than other cover types that positively influenced tiger detectability. Low density sal forest and degraded forest and scrub with high understory in which tigers could conceal themselves might obstruct the field of view of cameras (Carter *et al.* 2013) compared to high density sal forest, which could have lowered the detection probability. Our probability of detection results support those of Carter et al. (2013), who found that detection of tigers in parts of the Chitwan National Park and the surrounding buffer zone is lower than in habitat types with dense understory. The results also conform to the common notion that detectability may be higher in areas with relatively open understory such as high density sal forest and exposed surfaces including river banks and open trails. Finally, our finding reinforces the practice of selecting camera sites in relatively open areas such as forest trails and river banks (Karanth and Nichols 1998; O'Brien *et al.* 2003) so as to maximize tiger capture probabilities.

As hypothesized, this study revealed that tigers use all habitat types available in the park and may be considered a habitat generalist. However, the use of landcover types is not consistent with availability when considered at a finer-scale grid size smaller than the home range of tigers. Rather, the occurrence probability of tigers increased with greater grassland habitat. Grasslands in Chitwan are amongst the most productive in the world (Dinerstein 2003) and contains important sources of water (Eisenberg and Seidensticker 1976). Water sources in grassland habitat may be more important as they embed within the preferred food sources of tiger’s prey species thereby attracting tigers to the grasslands. The habitats support tremendous biodiversity in the park including high densities of tiger prey, and virtually the entire population of the park’s rhinos *Rhinoceros unicornis* (Kafley *et al.* 2009; Kafley *et al.* 2015). Tigers may occur more often in these areas given the dense understory (Sunarto *et al.* 2012). Among other landcover types, high density sal forest that comprises over 50% of the park was negatively associated with the probability of tiger occurrence. Thus, although the high detectability of tiger in sal forest might give an impression of high probability of occurrence, the high detectability was likely due to the openness of the understory in sal forest rather than high occurrence per se.

Contrary to large spatial scale studies wherein forested areas are grossly identified as suitable areas, at a fine scale habitat use by tigers may suggest a different pattern. For instance, mixed forest and riparian forest that contain reasonably dense undercover were negatively associated with tiger occurrence. To confirm this inference we recommend future studies in different seasons, as our results are based on data collected during winter months when the deciduous mixed and riparian forest types might differently influence tiger and its prey. In particular, we recommend future studies of habitat associations in the wet season to contrast with the results that our study elucidated from dry season data.

Our analysis consistently showed that prey encounter rate was the most important covariate predicting the probability of occupancy of tigers. At a large spatial scale, Karanth et al. (2004b) demonstrated that large carnivore density can be effectively predicted from prey abundance. Thus, large spatial scale and fine spatial scale studies reveal similar effects of prey abundance on the probability of occurrence of tigers. Further studies might investigate whether higher probability of tiger occurrence as a result of high prey availability may limit active use of the sites by tigers, thereby allowing other tigers to venture into putatively occupied territories. This information might also explain the mechanism underpinning the occurrence of tigers in higher densities in the relatively smaller protected areas with high prey abundance (Carbone and Gittleman 2002; Karanth *et al.* 2004b).

This study also reveals that sites with higher slopes are less likely to be used than are sites in the flat floodplains. Slope can be considered as a measure of ruggedness since it represents the variance in altitude within a site. In Chitwan, higher slopes are characterized by higher elevations, rugged terrain, and potentially the unavailability of perennial water sources in dry season (Lehmkuhl 1994; Dinerstein 2003; Shrestha 2004; Seidensticker *et al.* 2010). Despite the availability of large prey species such as sambar and bison in these higher elevation areas, the apparent reduced accessibility due to terrain ruggedness might have resulted in lower tiger occurrence at higher slopes.

Probability of occurrence was higher in proximity to water sources. Water sources are important for tigers and their prey, and during hot periods tigers often rest by lying in the water (Schaller 2009). Tigers also occasionally lie in ambush at sites favored by their prey such as along waterbodies (Karanth and Sunquist 2000) and stalk their prey across open clearings near waterbodies (Thapar and Rathore 1989). Tigers selecting habitat in proximity to the perennial water sources may also be a function of breeding females attempting to minimize time away from their young (Seidensticker 2010).

Similar results were obtained with proximity to human settlements, which initially seems surprising; landcover types and other habitat features including the areas with high prey abundance that are selected most by tigers were in proximity to human settlements. Therefore, and consistent with recent findings by Carter et al. (2012), our results show that tiger occurrence is higher in proximity to the human settlements. The literature on wildlife-human interactions is replete with the assumption that distance to human settlements can be regarded as an index of human disturbance or a proxy of hunting pressure (Singh *et al.* 2010; Burton *et al.* 2012). While this assumption certainly holds in many instances (Zeng *et al.* 2005; Nellemann *et al.* 2007), it may not be always true, as from the perspective of the tigers in the Chitwan National Park, proximity to human settlements may not be considered as an index of human disturbance. Further, this represents a possible explanation for occasional tiger-human conflict along the village boundaries. Therefore, we recommend adopting caution while portraying distance to the human activity centers as a measure of human disturbance in wildlife occupancy studies. Although the underlying basis for increased tiger occurrence in proximity to human settlements is not clear, our study demonstrates that an increasing tiger density in the park might disproportionately increase tiger activity near human settlements and thereby escalate human-wildlife conflict. Hence, active habitat management to enhance the suitability of habitat towards the park core is recommended.

Conclusions and management implications

We demonstrate the applicability of occupancy modeling technique using camera trap data to understand the fine spatial-scale habitat associations of tigers. In the present context where occupancy modeling of wide-ranging species has been broadly adopted for larger landscape-scale investigations, this study indicates that studies conducted at fine spatial-scales, such as at the protected area level, can offer important insights on wildlife-habitat association that differ from those findings derived from larger-scale datasets. Such findings likely apply to diverse taxa. Nonetheless, and aside from the applicability of the technique adopted, our study revealed the responses of tigers to fine-scale habitat factors that can be pragmatically incorporated for monitoring, conservation and management strategies focused on how tigers use protected areas.

For example, our results can inform future tiger monitoring programs to fine tune the number and placement of cameras to enhance capture probability in the sites where probability of detection is low. Similarly, estimates of the probability of tiger occurrence as a function of the covariates used may serve as a baseline information to assess corresponding future changes in occurrence probability with changes that might occur in the covariates. In Chitwan, the vegetation assemblage is rapidly changing and a significant decrease in grassland habitat and biomass is apparent (Kafley *et al.* 2009; Lehmkuhl 1990; Peet *et al.* 1999). Declining grassland habitat unequivocally leads to the decline in prey species depending in that habitat. As tiger occurrence is positively associated with the proportion of available grassland, additional changes (as a result of management intervention) in grassland habitat may be tractably tied to predicted changes in the probability of tiger occurrence. Such approaches can inform management to identify areas that require intervention to increase habitat suitability for tigers and other species.

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Table 1. *A priori* hypotheses explaining tiger occurrence by habitat covariates measured at a fine scale in Chitwan National Park

Hypothesis	Model	Model structure	Decision criteria
No effects of habitat covariates on occurrence	$\psi(.)$	β_0	N/A
Prey positively affects to tiger occurrence	ψ(prey)	$\beta_0+\beta_1$ (prey)	$\beta_1 > 0$
Land cover types, prey, slope, and water all affect tiger occurrence	ψ(global)	$\beta_0+\beta_{1,\text{ landcover}}$ (landcover types)+ β_2 (prey) + β_3 (slope) + β_4 (water)	$\beta_{1,\text{ landcover types}} \neq 0$, $\beta_2 > 0$, $\beta_3 < 0$, $\beta_4 \neq 0$
Hypothesis based on outcome of probability of occurrence from the top model selected from the candidate models tested as above			
Distance from settlement positively influences occurrence	ψ(top model)	$\beta_0+\beta_1$ (Distance to settlement)	$\beta_1 > 0$, $p < 0.05$
Distance from major waterways negatively influences occurrence	ψ(top model)	$\beta_0+\beta_1$ (Distance to water sources)	$\beta_1 < 0$, $p < 0.05$

Table 2. Summary of the model selection procedure assessing the effect of fine-scale covariates on tiger detection probability (p), assuming ψ constant

Model	ΔAIC	AIC wt.	k	Deviance (-2LL)
p(landcover+prey+slope)	0	0.5882	11	1383.86
p(landcover+prey+slope+water)	1.77	0.2428	12	1383.63
p(prey+slope)	3.27	0.1147	4	1401.13
p(prey+slope+water)	4.77	0.0542	5	1400.63
p(slope)	18.01	0.0001	3	1417.87
p(landcover+slope)	19.99	0	10	1405.85
p(landcover+prey)	20.11	0	10	1405.97
p(landcover+water+prey)	21.92	0	11	1405.78
p(landcover+water+slope)	21.99	0	11	1405.85
p(prey)	30.91	0	3	1430.77
p(landcover)	40.55	0	9	1428.41
p(landcover+water)	42.08	0	10	1427.94
p(.)	47.85	0	2	1449.71
p(water)	49.1	0	3	1448.96

Table 3. Top models incorporating *p* for assessing the effect of fine-scale covariates on the probability of occupancy of tigers (*Ψ*)

Model	ΔAIC	AIC wt.	*K*	Deviance (-2LL)
ψ(landcover+water+prey+slope), p(landcover+prey+slope)	0	0.8142	21	1345.63
ψ(landcover+prey+water), p(landcover+prey+slope)	3.56	0.1373	20	1351.19
ψ(prey+water), p(landcover+prey+slope)	6.25	0.0358	13	1367.88
ψ(prey+slope), p(landcover+prey+slope)	10.37	0.0046	13	1372
ψ(landcover+prey), p(landcover+prey+slope)	10.56	0.0041	19	1360.19
ψ(prey), p(landcover+prey+slope)	11.04	0.0033	12	1374.67
ψ(slope), p(landcover+prey+slope)	13.95	0.0008	12	1377.58
ψ(landcover), p(landcover+prey+slope)	19.71	0	18	1371.34

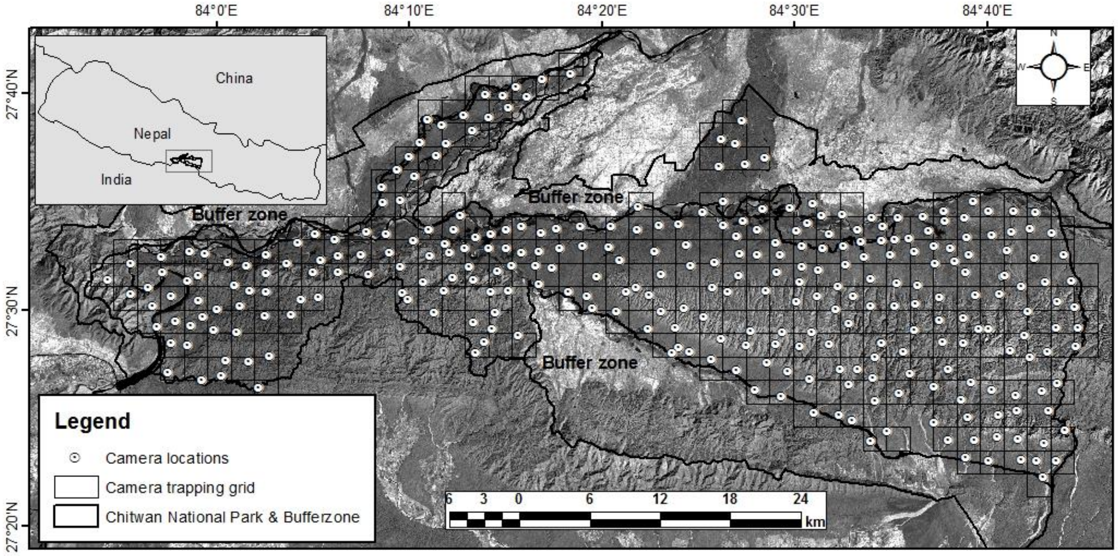
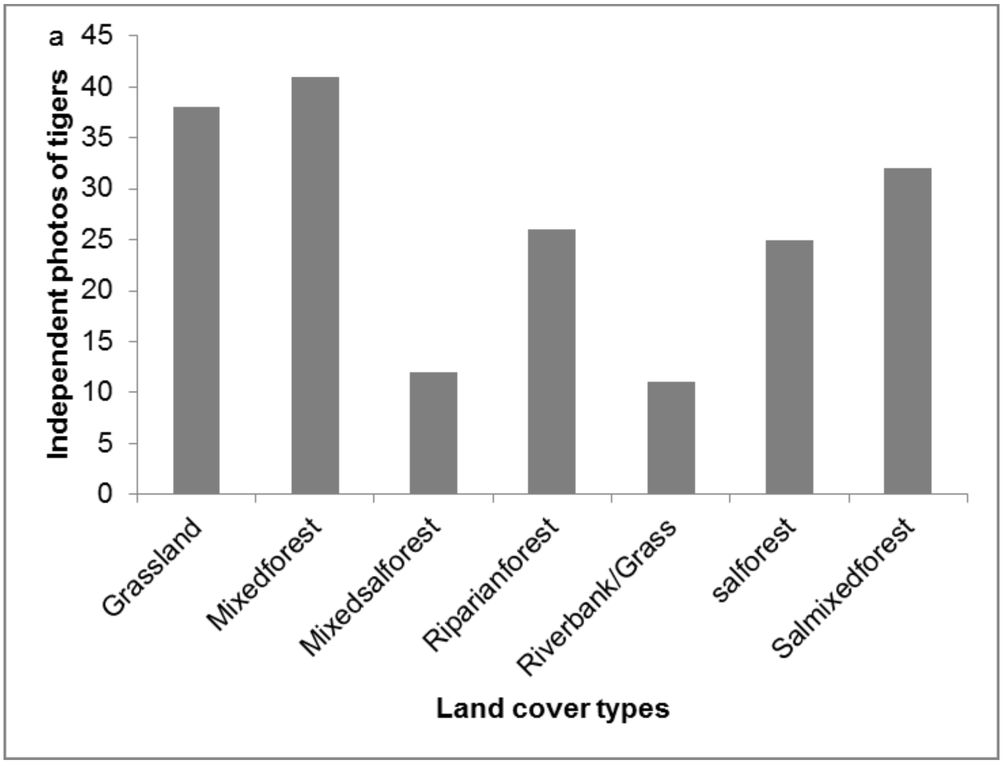
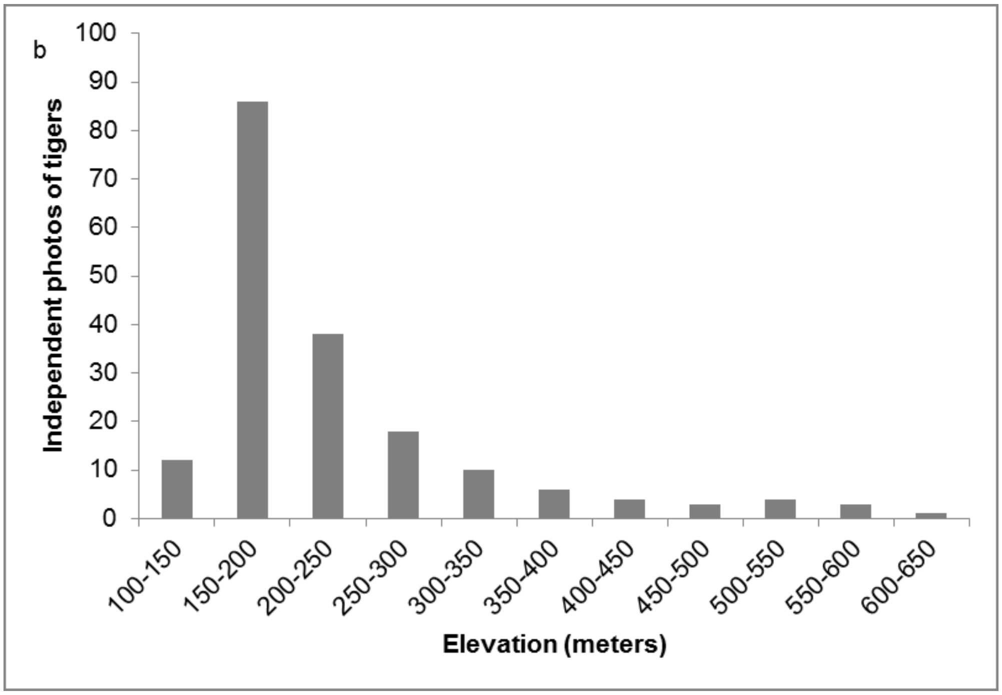


Figure 1. Chitwan National Park and Buffer Zone with sampling grid cells and camera locations overlaid on Landsat imagery. Inset: location of Chitwan National Park in Nepal


a
Independent photos of tigers
0
5
10
15
20
25
30
35
40
45
Grassland
Mixedforest
Mixedsalforest
Riparianforest
Riverbank/Grass
salforest
Salmixedforest
Land cover types


b
Independent photos of tigers
0
10
20
30
40
50
60
70
80
90
100
100-150
150-200
200-250
250-300
300-350
350-400
400-450
450-500
500-550
550-600
600-650
Elevation (meters)

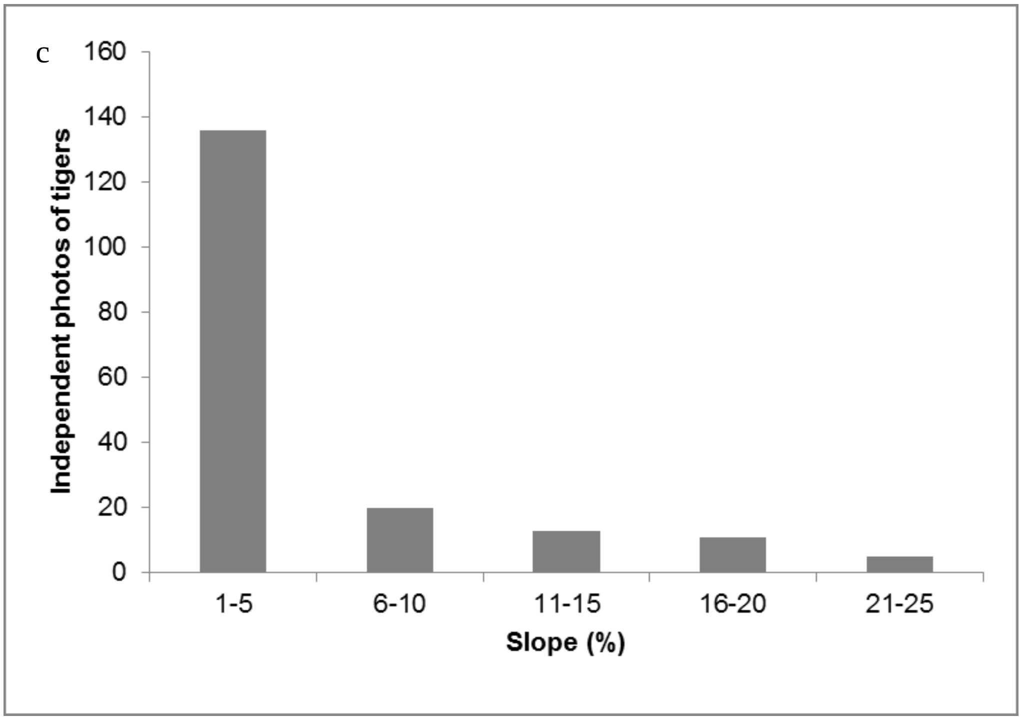
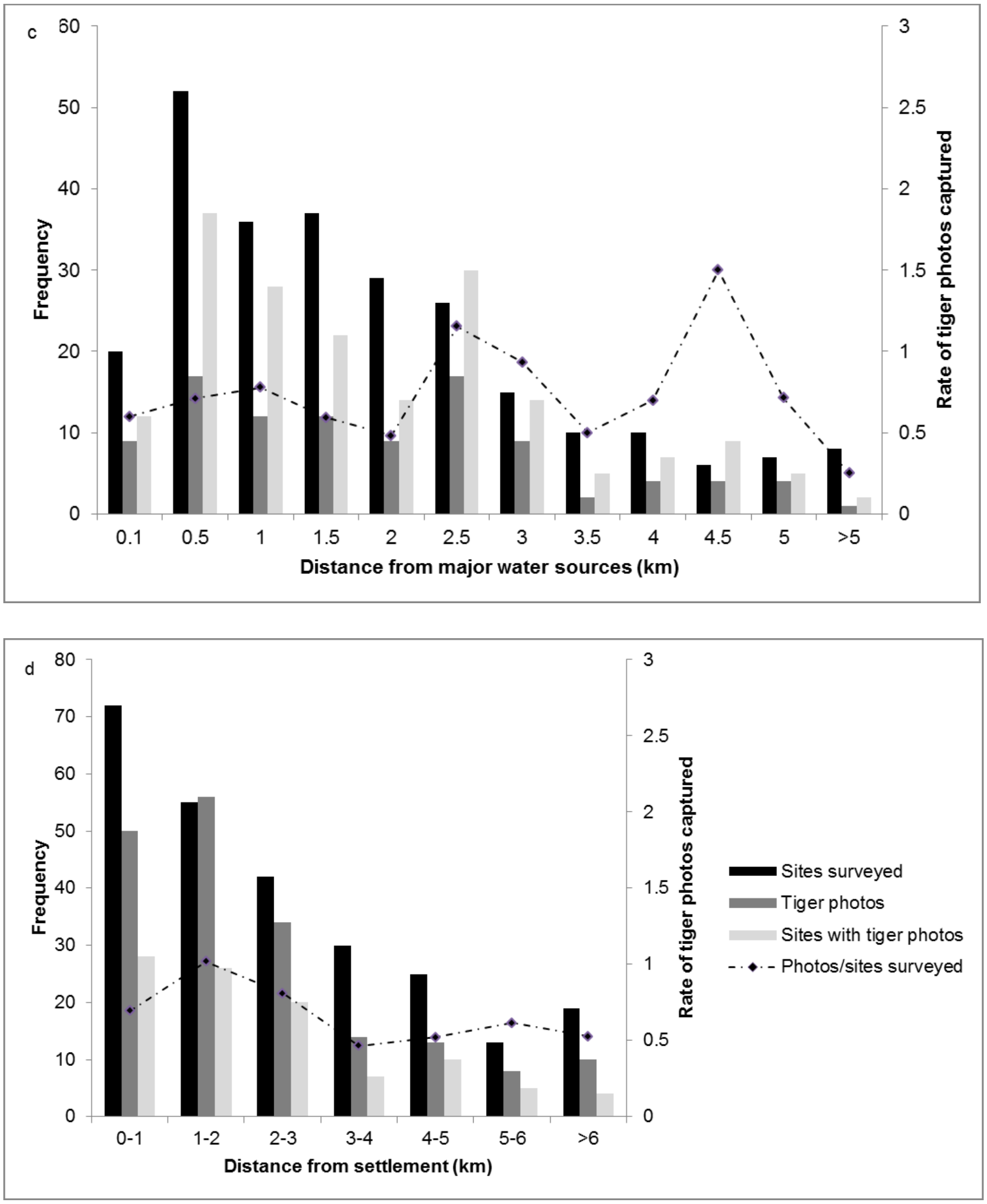


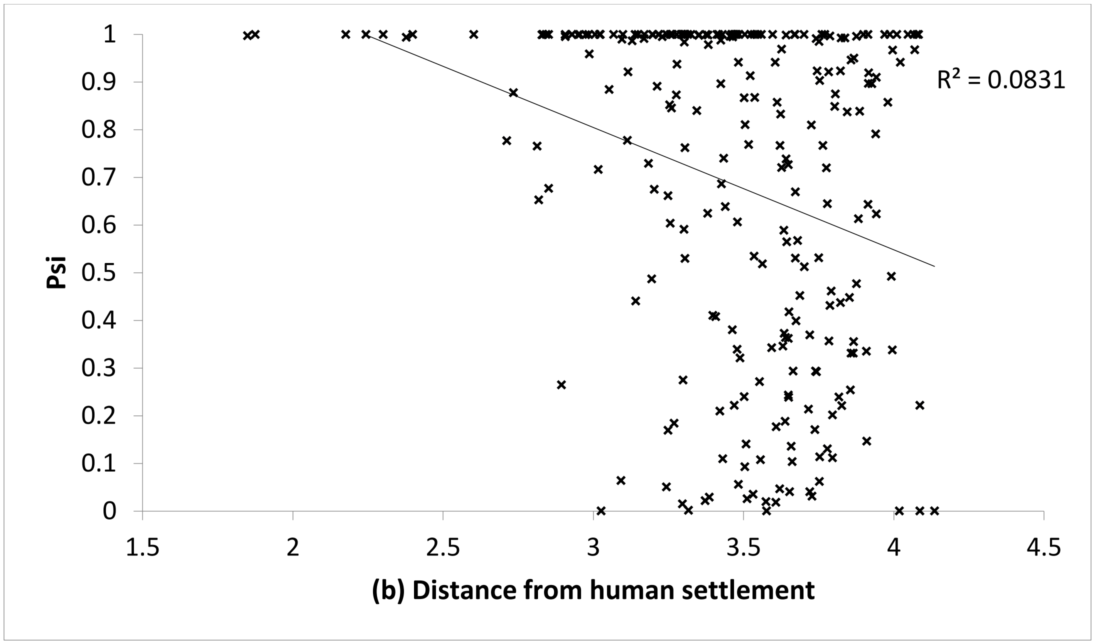
Figure 2. Frequency of tiger photo captures against (a) landcover types, (b) elevation, and (c) slope



Legend for Fig. 3.

▬ Sites surveyed
▬ Tiger photos
▬ Sites with tiger photos
-·◆·- Photos/sites surveyed

Figure 3. Rate of tiger photo captures against (a) distance from major water sources and (b) distance from settlement



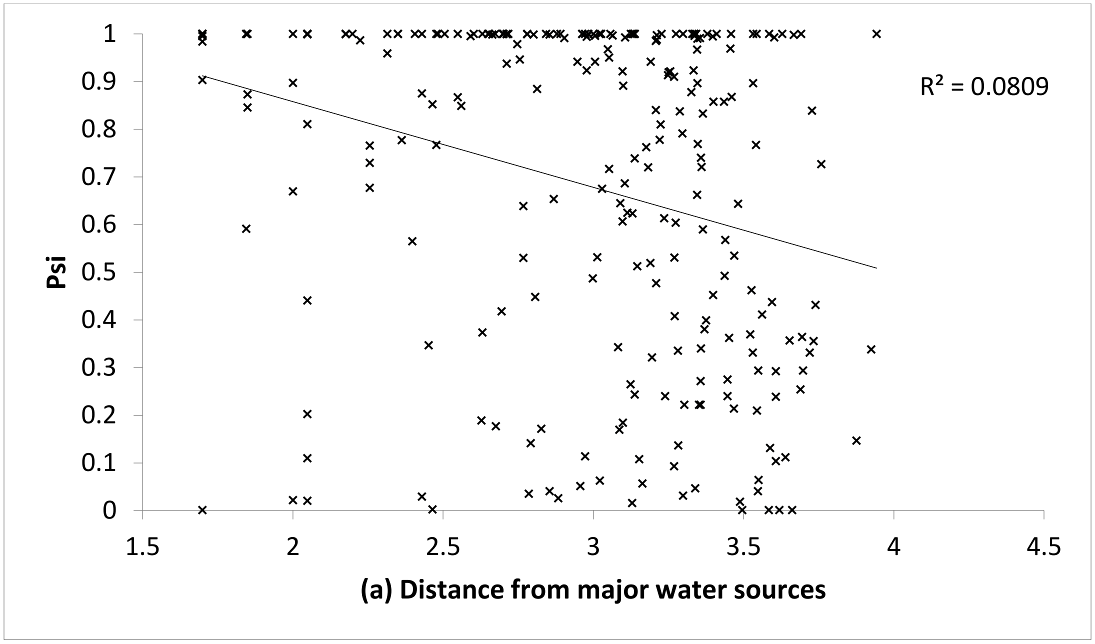


Figure 4. Association of tiger occurrence probability with (a) distance from major water sources (R^2 = 0.0809) and (b) distance from human settlements (R^2= 0.0831)

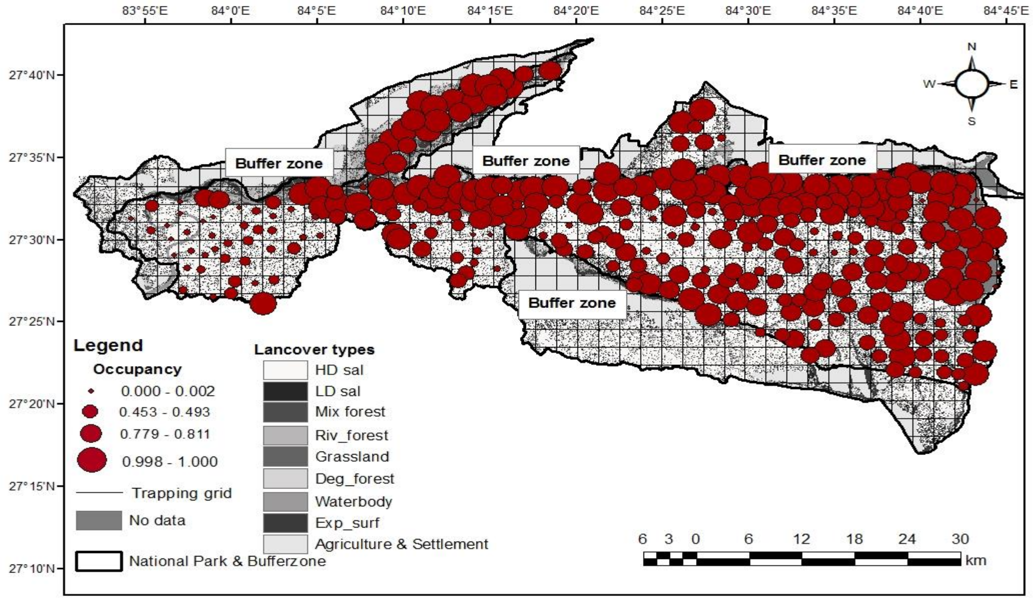


Figure 5. Probability of occurrence of tigers in Chitwan National Park and the surrounding buffer zone

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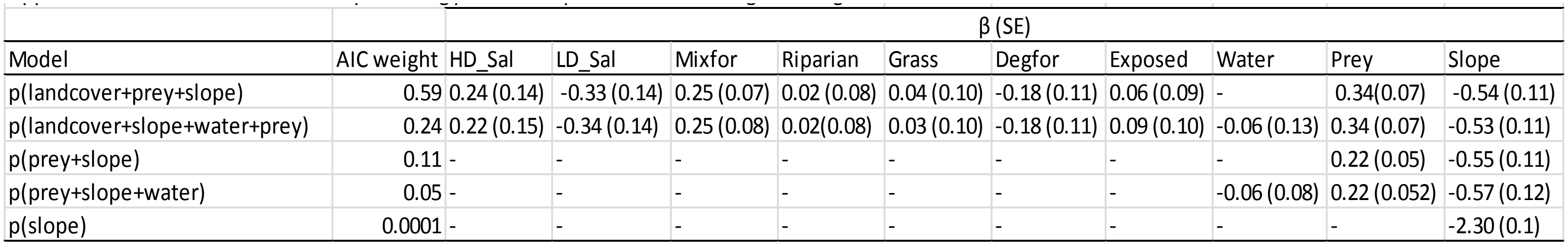
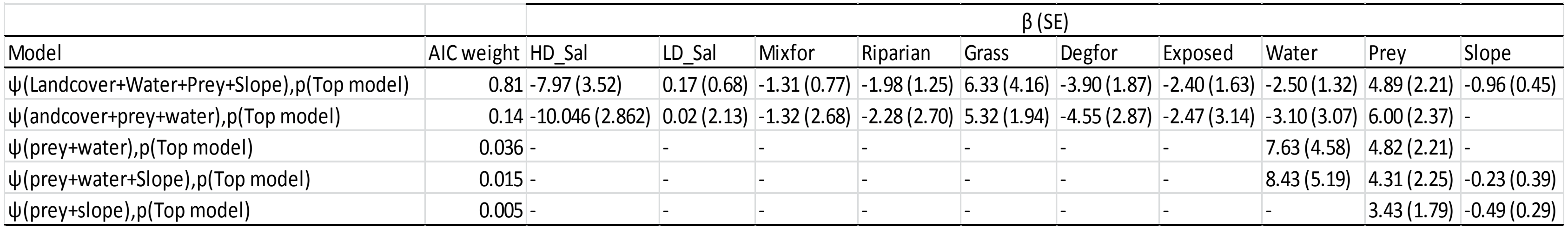
Appendix

A. Coefficient of covariates predicting *p* for the top 5 models receiving AIC weights



		β (SE)									
Model	AIC weight	HD_Sal	LD_Sal	Mixfor	Riparian	Grass	Degfor	Exposed	Water	Prey	Slope
p(landcover+prey+slope)	0.59	0.24 (0.14)	-0.33 (0.14)	0.25 (0.07)	0.02 (0.08)	0.04 (0.10)	-0.18 (0.11)	0.06 (0.09)	-	0.34(0.07)	-0.54 (0.11)
p(landcover+slope+water+prey)	0.24	0.22 (0.15)	-0.34 (0.14)	0.25 (0.08)	0.02(0.08)	0.03 (0.10)	-0.18 (0.11)	0.09 (0.10)	-0.06 (0.13)	0.34 (0.07)	-0.53 (0.11)
p(prey+slope)	0.11	-	-	-	-	-	-	-	-	0.22 (0.05)	-0.55 (0.11)
p(prey+slope+water)	0.05	-	-	-	-	-	-	-	-0.06 (0.08)	0.22 (0.052)	-0.57 (0.12)
p(slope)	0.0001	-	-	-	-	-	-	-	-	-	-2.30 (0.1)

B. Coefficient of covariates predicting ψ for the top 5 models receiving AIC weights



		β (SE)									
Model	AIC weight	HD_Sal	LD_Sal	Mixfor	Riparian	Grass	Degfor	Exposed	Water	Prey	Slope
ψ(Landcover+Water+Prey+Slope),p(Top model)	0.81	-7.97 (3.52)	0.17 (0.68)	-1.31 (0.77)	-1.98 (1.25)	6.33 (4.16)	-3.90 (1.87)	-2.40 (1.63)	-2.50 (1.32)	4.89 (2.21)	-0.96 (0.45)
ψ(andcover+prey+water),p(Top model)	0.14	-10.046 (2.862)	0.02 (2.13)	-1.32 (2.68)	-2.28 (2.70)	5.32 (1.94)	-4.55 (2.87)	-2.47 (3.14)	-3.10 (3.07)	6.00 (2.37)	-
ψ(prey+water),p(Top model)	0.036	-	-	-	-	-	-	-	7.63 (4.58)	4.82 (2.21)	-
ψ(prey+water+Slope),p(Top model)	0.015	-	-	-	-	-	-	-	8.43 (5.19)	4.31 (2.25)	-0.23 (0.39)
ψ(prey+slope),p(Top model)	0.005	-	-	-	-	-	-	-	-	3.43 (1.79)	-0.49 (0.29)

CHAPTER III

ESTIMATING PREY ABUNDANCE AND DISTRIBUTION FROM CAMERA TRAP DATA USING BINOMIAL MIXTURE MODELS

Hemanta Kafley[A,B,G] , Babu R. Lamichane[C], Rupak Maharjan[D], Bishnu Thapaliya[D], Nishan Bhattarai[E], Madhav Khadka[F], Matthew E. Gompper[A]

[A]School of Natural Resources, University of Missouri, Columbia, MO 65211, USA.

[B]Nepal Nature Foundation, Koteshwor, Kathmandu-34, Nepal.

[C]National Trust for Nature Conservation, Biodiversity Conservation Center, Chitwan, Nepal.

[D]Department of National Parks and Wildlife Conservation, Chitwan National Park, Chitwan, Nepal

[E]The Center for International Environment and Resource Policy, The Fletcher School, Tufts University, Medford, MA

[F]World Wildlife Fund Nepal Program, Kathmandu, Nepal

[G]Corresponding author: hemantakafley@gmail.com

Abstract

Abundance is a widely used metric in ecology. At a large spatial-scale absolute abundance may be estimated by capture-recapture, removal, or distance sampling methods. However, these techniques are less pragmatic for understanding abundance patterns at fine-scale levels. In most camera trapping studies, sampling the fine-scale abundance of prey species, which often serves as an important covariate for predicting predator ecology, is based on simple counts of animals captured in the camera traps. This method does not incorporate detectability of the species or take into account other ecological factors that might affect abundance. To overcome these limitations, we investigate the usage of binomial mixture models to estimate abundance of major prey species. We evaluate the mixture models using data from a camera trapping survey intended for a tiger *Panthera tigris* census in Chitwan National Park Nepal where the entire park was surveyed in 361 4-km^2 quadrats. We chose 4 prey species (chital (*Axis axi*s), sambar (*Rusa unicolor*), muntjac (*Muntiacus muntjac*) and wild boar (*Sus scrofa*)) that collectively account for >75% of prey biomass consumed by tigers. Abundance was modeled as a random effect with a Poisson or a negative binomial distribution, with the mean abundance affected by distance from water sources, elevation, and normalized difference vegetation index (NDVI). Probability of detection of prey species was kept constant across the quadrats but varied between species. For all species negative binomial models fitted data better than did Poisson models. For chital, sambar and muntjac top negative binomial covariate models were selected but the null model was the most parsimonious model for the wild boar. The most parsimonious chital model included effects of distance from water sources and elevation. the sambar model supported all three covariates- distance from water sources, elevation, and NDVI. Only distance from water sources was supported by the most parsimonious muntjac model. Abundance of chital was higher at lower elevation while sambar was more abundant at relatively higher elevations. Elevation did

not have a significant effect on abundance of muntjac and wildboar. NDVI had a positive effect on abundance of sambar. We conclude that binomial mixture models may be a robust approach for estimating abundance corrected for detectability or for estimating fine-scale local abundances from camera trapping survey data.

Introduction

Understanding of the spatial pattern of animal abundance and distribution is central to ecology (Krebs 2001) and is critical for the monitoring, conservation and management of many species (Yoccoz et al. 2001). However, animals are generally widespread or inconspicuous, and so abundance estimation has been a formidable challenge. Most field studies of abundance are based on count data obtained from examining sample units. The sample units may be of different form and sizes, such as avian point counts at different locations, along the specific transects, or aerial surveys (Robbins et al. 1986, Royle and Nichols 2003, Kéry 2008), removal sampling at point locations for estimating local abundance for fish population (Royle and Dorazio 2006), and for mammalian species, the counts obtained from camera traps surveys conducted in sample units of varying sizes and adopting different analytical techniques depending on species biology, objectives, and logistic constraints (Silver et al. 2004, Rovero and Marshall 2009, Carter et al. 2012).

Camera-trapping has long been used to assess mammal presence and is increasing used to assess mammal abundance. Capture-recapture models have been effectively used to estimate density of individually-identifiable species such as tigers (Karanth 1995, Karanth and Nichols 1998, Carter et al. 2012), jaguars (Silver et al. 2004) and ocelots (Trolle and Kéry 2003). Similarly, a few studies have used the photographic rate obtained from the camera trapping studies to estimate the densities of the individually-unidentifiable animals (Rowcliffe et al. 2008) such as ungulates (Rovero and Marshall 2009) and other cryptic mammals (Carbone et al. 2001). However, there are difficulties in using such approaches, especially when applied to species that are not individually recognizable from camera images. Hence, identifying other approaches that can be readily applied to estimate detectability corrected abundance of unmarked individuals from camera trap data will be useful. An approach that avoids the need for distance-based or observation-based field surveys will render monitoring efforts more efficient. Here we use binomial mixture models to estimate local abundance of the four main prey species of tigers (*Panthera tigris*) using the count data obtained from a camera trapping survey in Chitwan National Park, Nepal. Our approach avoids the challenges inherent in distance-based or observation-based analysis techniques.

Prey species that are not recognized individually cannot be counted with certainty. The probability of detection of the animals at every instance is < 1 and, hence, it is unlikely that all individuals are included in a survey. Thus, the abundance of these animals must be estimated. Many studies have used simple photographic counts as indices of relative prey abundance, assuming that the average detection probability for all prey species is constant. However, several studies have shown that this assumption does not hold (Link and Sauer 1998, Diefenbach et al. 2003, Selmi and Boulinier 2003, Kéry et al. 2005). Therefore, accounting for the difference in detection probability by using covariates or by directly estimating detectability, will result in a better estimate of true abundance (Kéry 2008).

In the Chitwan National Park, camera trapping surveys are conducted periodically (Dhakal et al. 2014) for monitoring large carnivore population densities, occupancy, and human-tiger interaction (Carter et al. 2012, Carter et al. 2013, Dhakal et al. 2014, Karki et al. 2015). In the process, large quantities of data (camera trap captures) on prey are generated that are potentially available for understanding prey abundance and distribution. Such data is potentially useful for understanding the biology of these prey species, as well as for improving our understanding of the distribution of predators. Recent studies in Chitwan have used these data to derive simple counts of prey captures in the camera traps as a surrogate of prey abundance

(Carter et al. 2012). However, this approach does not consider detectability of prey and hence may not depict correct patterns of prey abundance. Given that prey abundance and distribution in the Chitwan habitat, as in other habitats, can be a crucial factor determining abundance and occupancy of important predators such as tigers, a more refined mechanism for assessing prey abundance is needed.

In this paper, we demonstrate the use of camera trap data to estimate fine scale abundance of prey populations and characterize the effects of site-specific covariates on local abundance. In our case, typical covariates of interest such as elevation, distance from water sources and a Normalized Difference Vegetation Index NDVI (a surrogate to vegetation greenness that may be loosely defined as the landcover type with respect to the availability of vegetation cover) are those that describe habitat structure as relates to the abundance of the chosen prey species: chital (*Axis axi*s), sambar (*Rusa unicolor*), muntjac (*Muntiacus muntjac*) and wild boar (*Sus scrofa*). For temporally replicated data, obtained from the camera traps placed in spatially referenced quadrats, we use a binomial mixture model developed by Royale (2004) to estimate detectability-adjusted abundance. We do not anticipate potential covariate effects on detectability, given cameras are placed along open trails. However, we do anticipate effects of covariates on local abundance, knowledge of which can improve the precision of the abundance estimates (Kéry 2008). Our aims are (1) to test whether the binomial mixture model can be applied to estimate abundance of prey populations from the camera trapping data, (2) to draw attention to the opportunity to make use of the enormous database on prey generated during the camera trap studies, and (3) to test for the hypothesized effects of covariates on abundance estimates.

Methods

Study area and species

Chitwan National Park (27° 18’-27° 41’N latitude and 83° 41’-83° 49’E longitude) (Figure 1) harbors robust tiger and ungulate populations and is a priority protected area in Nepal. It is comprised of core park area (932 km^2) and a surrounding buffer zone (750 km^2). The park lies between the two mid-mountain ranges: the siwalik (Churia) and the Mahabharat. The park is predominantly (~ 70%) covered by forest [high density sal (*Shorea robusta* Gaertner f.) forest, low density sal forest, mixed forest, degraded forest and scrub vegetation, and riparian forest (Laurie 1978, Lehmkuhl 1994, Bhuju et al. 2007). Other land cover types include various types of grasslands (~8%), riverbank and exposed surfaces (~7%), and agriculture and settlement (15%) (Gurung 1983, Lehmkuhl 1990, 1994, Kafley et al. 2009) .

The high tiger density in Chitwan National Park (Dhungel and O'Gara 1991, Dhakal et al. 2014) has been attributed to the high prey density (Smith et al. 1999). We focused on four main prey species of tigers in Chitwan National Park: chital, sambar, muntjac and wild boar (Biswas and Sankar 2002, Thapa 2012, Dhakal et al. 2014, Thapa 2014). These species are commonly encountered in Chitwan (Seidensticker 1976, Dhungel and O'Gara 1991, Thapa 2012, Dhakal et al. 2014) and as such would provide enough detections to develop the model. Furthermore, these mammals are the principle tiger prey region-wide (Karanth and Sunquist 1995), constituting >75% of the tiger’s diet (Sunquist et al. 1999). Hence understanding their abundance and distribution would be insightful for tiger conservation and management beyond Chitwan National Park.

Field data collection and data management

We estimated relative abundance of select prey species using the data derived from a camera trap survey in the Chitwan Nation Park conducted between February to May in 2013 as part of the country's tiger monitoring protocol (Dhakal et al. 2014). We used camera traps to survey the occurrence of wildlife across the Chitwan National Park in three blocks, including the entire core of the park as well as some areas of the buffer zone surrounding the park. A total of 362 quadrats of size 2km X 2km distributed across the park were surveyed with a pair of cameras in each quadrat. Placement of cameras within each grid unit was based on the local expert opinion so as to maximize the chance of tiger capture. Camera traps sites in adjacent quadrats were at least ~ 1km and at most ~ 3 km apart (Figure 1). Aside from a focus on locations where tigers were expected to be captured, characteristics such as vegetation type, altitude, distance from settlements, and other variables were not considered for camera placement. Hence, locations and site characteristics of camera sites are considered quasi-random and independent. Elevation and geographic location for each camera site were collected using Garmin Etrex handheld GPS units (Garmin Inc.)

Each survey occasion included a 17-21 days trapping session. Disturbance during a survey, such as camera malfunction or theft resulted in missing data in one quadrat, and so the affected quadrat was excluded from the subsequent analyses, resulting in suitable data from a total of 361 locations. We used data obtained from only the first 17 days to avoid the variation in number of days sampled between locations. Thus we obtained 17 temporally replicated count data from 361 quadrats covering the entire park.

For each photograph of a prey species obtained from the geographically referenced camera locations we recorded species, date and time. Number of independent detections of animals/groups (later referred as animals) of any prey species represented counts of the animals detected. We summed the number of detections of animals for each species for each camera location. We define independent detection of animal as (i) consecutive photographs of identifiable different group based on cues such as group size and any other unique characteristics present in some animals in the group, (ii) consecutive pictures of individually-unrecognizable animals >30 minutes apart, and (iii) nonconsecutive pictures of animals. Counts of animals were thus derived from the independent detection of animals in the cameras.

Covariate selection

We hypothesized that spatial pattern of prey abundance would be influenced by proximity to water sources, elevation and normalized difference vegetation index (NDVI). Water availability is a critical limiting resource for most wildlife species in variety of ways (Adams and Thibault 2006, Smit et al. 2007) and prey species in Chitwan are not an exception (Sunquist et al. 1999). Thus we hypothesized that increasing distance from water sources will have inverse effect on abundance of all prey species.

In a topographically heterogeneous habitat in Chitwan, chital usually occupies low elevation areas in habitats such as lowland sal forests, riverine forests and floodplain grasslands (Mishra 1982). Hence, we expected that chital would have higher abundance at the lower elevation. Sambar deer are regarded as the only widespread forest deer (Menon and Daniel 2003). Consequently, it occupies mostly the highland forests and riverine forests in Chitwan (Mishra 1982) including short grass habitat at lowlands (Seidensticker 1976). Distance sampling conducted along the lowland habitat by Dhakal et al. (2014) shows highest density of chital in the park followed by sambar, although Thapa (2012) found that density of sambar to be higher than chital along the Churia range, the rugged and high elevation areas in Chitwan National Park.

Hence, we predict that the abundance of sambar would increase with increasing elevation. Muntjac and wild boar are ubiquitous in the Chitwan habitat and we were not able to predict the effect on abundance with respect to elevation in particular. Hence, we do not predict an effect of elevation on the abundance estimates for muntjac and wild boar.

NDVI has been used in wide range of applications from land cover classification to measuring primary productivity (DeFries and Townshend 1994, Gamon et al. 1995). In thus study, we use NDVI as a proxy for vegetation greenness (higher values correspond to more greenness) and assume that the forest-dwelling species are more abundant in location with higher NDVI compared to grassland species. This further leads us to the assumption that as the chital, that prefers grasslands and eciduous riverine forest over thick forests are more abundant on low NDVI areas. In contrast, sambar, that mostly prefer forested areas, is expected to have higher abundance in areas with higher NDVI. Similarly, as the muntjac and wild boar are ubiquitous in nature, with respect to the land cover types in the park, (Seidensticker 1976), we do not expect to find strong associations between their abundance and NDVI.

GIS database and preparation

We used a digital elevation model (DEM) (Figure 2A) of Chitwan National Park from the Shuttle Radar Topography Mission (SRTM) elevation data and verified elevations of camera trap locations measured in the field. We used Level 1G (radiometrically and geometrically corrected and georeferenced) Landsat 7 Enhanced Thematic Mapper Plus (ETM+) satellite imagery (path 142/41) with a pixel resolution of 28.5m, acquired from global land cover facility (GLCF) (www.glcf.umd.edu/data/landsat). The imagery was from the same season (December, 2010), but a different year then the camera trap survey. We used a supervised classification scheme (Lillesand et al. 2004) for classifying Landsat imagery to detect the water sources within the park using Erdas Imagine software Version 8 (Erdas Inc., Atlanta, GA). Waterbodies that were too small to be detected spectrally either due to size or being located under the dense tree canopy were included by performing visual on-screen digitization. We also used Google Earth images, historic archive of satellite images, and ground data to identify all existing water sources in the park as possible. We generated a raster grid surface yielding distance from water sources (Figure 2B) based on Euclidean distance algorithm in ArcGIS (ESRI Inc., Redlands, CA), then computed the distances from each camera locations to the nearest available water sources.

A composite NDVI map was derived based on 11 near cloud free Landsat images (Path 141 and 142 and Row 41: 6 Landsat 7 and 5 Landsat 5 Thematic Mapper images) acquired during December 2010- January 2011. A NDVI map from each Landsat scene was obtained from Landsat Ecosystem Disturbance Adaptive Processing System (LEDAPS) (Masek et al. 2006) method available through U.S. Geological Survey Earth Resources Observation and Science Center (www.espa.cr.usgs.gov). Cloud and cloud shadows were masked out using the F-mask tool (Zhu and Woodcock 2012, Zhu et al. 2015). The final NDVI composite map (Figure 2C) used average NDVI values from all cloud-free pixels.

Data Structure and model framework

We considered independent photographic capture of prey as a surrogate to point counts of the groups of the prey species. Thus, our data assumes that groups of prey species are counted at R sample sites, i=1,2,….,R with T temporal replication, j=1,2,….,T. Such counts can be viewed as realizations of a binomial random variable with site specific abundance index N_i and detection probability p. Observed counts (independent group counts manifested by independent photographs) $y_{i,j}$ for a number of sites i and temporal replicates j are then described by a binomial distribution with sample size N_i and detection probability p. Thus, our data resembles the data accrued from temporally replicated simple point counts such that the site-specific group counts ($y_{i,j}$) of prey species is an observed phenomena in sites *i* during temporally repeated surveys *j*. Observed $y_{i,j}$ likely arise from two processes: state process and observation process (Kery and Royle 2015). Simply, at any site, variation exists in observed $y_{i,j}$ owing to imperfect detection, and variability in abundance among sites is due to unobserved latent variable N_i in addition to the imperfect detectability.

In this context, a class of models developed by Royle (2004) allows for estimation of detection probability and abundance. Here, we assume that N_i is the local abundance (Royle and Dorazio 2006) of prey group for site *i*. Independent counts $\mathrm{y_{ij}}$ are then binomial random variables with index N_i and detection p, $y_{i,j} \sim$ Binomial (N_i, p). Considering the local abundance (N_i) parameters as the realizations of a random variable i.e. random effects, local abundance at site *i* can be given as $\mathrm{N_i} \sim \mathrm{g(N|\theta)}$, assuming g(N) be any plausible distribution of choice (Kéry et al. 2005). We considered Poisson and negative binomial mixture distributions for abundance (White and Bennetts 1996, Kery and Royle 2015) and the three hypothesized covariates for abundance while detectability was not assumed to vary in response to site-level covariates. We first fitted the Poisson distribution with mean λ, a natural choice for random spatial point pattern (Royle and Nichols 2003, Kéry et al. 2005). We then fit negative binomial distributions to identify the distribution that adequately fits the data (Bliss and Fisher 1953, White and Bennetts 1996) and compare the output of the different distributions considered.

In this case where three site covariates are available to explain the variation in expected abundance λ, site-specific λ is considered in the following form:

$$Log(\lambda_i) = \beta_0 + \sum_{i=1}^{3} x_i \beta_i$$

We assume no site-level covariates or observation covariates that might induce heterogeneity in detection probability among sites. Hence, our detection probability of an individual prey group will be in the form of

$$\text{Logit}(p) = \alpha_0$$

Given all groups in a sample unit have identical detection probabilities and detection is independent, probability of detecting any groups on the unit, say p_i can be given as

$$p_{i=1-(1-p)^{N_i}}$$

where p is the individual group level detection probability and in this case it is considered as constant across replicate samples of each local population N_i.

In total, 8 models were fit for each species and mixture type. We considered only additive models and no interaction terms were included. Within one mixture type, competing models were compared using AIC and ΔAIC from the most parsimonious model (Buckland et al. 1997, Burnham and Anderson 2002). To evaluate adequacy of the fitted models we generated 100 replicate data sets and assessed fit using parametric bootstrap procedure. Parameters for each replicate data set were computed and sum of squared errors of the replicated data sets and observed data set were compared to assess the model fit (Dixon 2002, Kéry et al. 2005, Manly 2006). Top models, with ΔAIC < 2 on the grounds of parsimony (Burnham and Anderson 2002), were discussed regarding the effect of the covariates to the abundance model for any particular species. We used AIC weight to discuss the covariates supported in the top parsimonious abundance models i.e. the models within 2 units of the most parsimonious model (MacKenzie 2006). However, the most parsimonious model was used to interpret the overall pattern of abundance as a function of included covariates. All analysis including parameter estimation and goodness-of-fit assessment was conducted in the package Unmarked (Fiske and Chandler 2011) in the R studio environment (RStudio 2015).

Results

Model selection and fitting

The covariate models were the most parsimonious abundance models for all species but wild boar. Both Poisson and negative binomial models included the same covariates or null model in the most parsimonious models for each species. Negative binomial distribution provided the most parsimonious models of abundance estimation for all species under investigation. Except for the Poisson abundance model for sambar, for all other species both Poisson and negative binomial abundance models included at least two top candidate models within 2 AIC units of the most parsimonious model. All species showed overdispersion of abundance relative to a Poisson distribution (Table 1).

Although the abundance estimates obtained from the Poisson mixture models had narrow confidence intervals compared to the negative binomial models (Table 2), in most cases the estimates were not realistic. For example, mean abundance for chital at a quadrat-level ($N_{quadrat}$=1.14) suggests that an average camera station captured one individual group of chital, a value that we believe exceeds the biological reality. Moreover, this estimate also does not conform to the mean observation per site (2.54 groups), or to the naïve occupancy (0.38) calculated based on the raw field observation data and at a low detection rate (0.12 SE=0.002) obtained from the most parsimonious Poisson model for chital. Similar results were obtained for the other three species (Table 2).

Parametric bootstrap analysis also showed that all the most parsimonious negative binomial models fit better than the corresponding Poisson models (Table 1). Null models with negative binomial distribution fit better than the most parsimonious Poisson model for all species except sambar. The null model under a negative binomial distribution was, in fact, the most parsimonious model for wild boar. Overall, negative binomial models fit better than Poisson models for all species. Therefore, we limit discussing Poisson abundance model just to compare the trends of abundance with respect to covariates with the trends observed in the most parsimonious negative binomial models, and discuss the most parsimonious negative binomial models for drawing inference on abundance and abundance distribution.

None of the species data provided sufficient information for AIC to clearly distinguish the most parsimonious negative binomial model (Table 2). For all species, at least two top models were within 2 AIC units of the most parsimonious model. Chital and sambar models included two top models each within 2 AIC units but muntjac and wild boar had four out of the eight fitted models. Similarly, for wild boar, the null model was most parsimonious and there were four models within the 2 AIC units of this top model. Top muntjac models also included the null model.

Covariate contribution to the abundance models

For chital, based on the AIC weight of the top models and associated covariates, distance from water and elevation had 100% support in the abundance models while NDVI had 27% support (Table 2). For sambar, the model support for the distance from water and elevation had

88% each and NDVI 55%. The support for the distance from water in the muntjack abundance model at 52% was lower than observed in the chital and sambar models. Similarly, the support for elevation and NDVI in the top muntjac abundance models were 12% and 11% respectively, lower than the support NDVI received in chital and sambar models. The muntjac null model had 23% support which is much higher than the elevation and NDVI covariates. For the wild boar, the most supported model (27%) was the null model. NDVI (22%) was the most supported covariate in wild boar abundance models and the support for distance from water and elevation was 12% each.

Effect of Covariates on the estimates of abundance

Coefficients of the covariates present in the top parsimonious Poisson and negative binomial models (models within 2 units of the AIC best fit model) are shown in Table 2, and the effects of covariates on estimates of abundance under the most parsimonious models are shown in figures 3-6. For all species except wild boar, abundance decreased with increasing distance from water in all the top parsimonious models both under both Poisson and negative binomial mixtures. One of the top Poisson wild boar abundance models showed a positive relationship with distance from water, but the most parsimonious model did not contain this effect and the coefficient was smaller than the standard error term.

Chital abundance had a negative relationship with elevation, while sambar abundance was positively associated with elevation in all top models. Muntjac and wild boar abundance also showed positive association with elevation in the top models, but the coefficients were either equal or less than the standard error term. Interestingly, the most parsimonious models for muntjac and wild boar do not include elevation.

One top Poisson model for chital indicated that abundance was positively associated with NDVI. However, the negative binomial model revealed a negative association between NDVI and chital abundance. The coefficients of NDVI associated with both of these models were less than the standard error term. Moreover, NDVI never appeared in the most parsimonious models for chital abundance. In contrast, both top models and the most parsimonious Poisson and negative binomial models for sambar showed increased abundance with increasing NDVI. All but one top models for wild boar abundance also showed positive association with NDVI. A negative binomial model for the wild boar showed a positive coefficient of NDVI that was less than the standard error term. Notably, for muntjac, the top models containing NDVI had a small coefficient and far less than the corresponding standard error to infer any relationship between muntjac abundance and NDVI.

Estimates of detectability and abundance

Detectability for all species was always higher in Poisson models compared to the negative binomial models (Table 2). The highest difference in detectability between Poisson and negative binomial models was seen in muntjac and wild boar followed by chital and sambar. Poisson models for muntjac and wildboar had ~8 times higher detectability than negative binomial models. Poisson model for chital had ~ 6 times and that of sambar had ~4 times higher detectability than the negative binomial models. In our most parsimonious models, estimates of group level detectability for chital (0.019, SE=0.003) and sambar (0.019, SE=0.002) were similar followed by muntjac (0.01, SE=0.002) and wild boar (0.009, SE=0.007).

Abundance estimates for quadrats ($N_{quadrat}$) and for all 361 quadrats combined (N_{total}) were higher in the negative binomial models than under the Poisson models (Table 1). $N_{quadrat}$ and N_{total} for the negative binomial covariate models were usually lower than null models except for muntjac covariate model that had slightly higher estimate for N_{total} and equal $N_{quadrat}$ estimates. In all cases, negative binomial models had very wide confidence intervals. Estimates under the negative binomial null models always had slightly wider confidence intervals than the corresponding covariate models. Covariate information thus improved the precision of estimates for the negative binomial models. In contrast, confidence intervals of the Poisson covariate models always had slightly wider confidence intervals than the corresponding null models, indicating that covariate information is decreasing the precision of the estimates.

Local abundance ($N_{quadrat}$) of the groups of chital was the highest (6.37, CI 3.57-15.59) followed by muntjac (5.79, CI 2.71-22.14), sambar (5.25, CI 2.66-15.51), and wild boar (2.91, CI 1.24-17.38). However, after correcting the estimates using the group size estimates of Dhakal et al. (2014), chital was the most abundant followed by sambar, muntjac, and wild boar. Total abundance (N_{total}) for chital groups was highest in the park followed by muntjak, sambar, and wildboar. Using group size estimates of Dhakal (2014) chital was still the most abundant species followed by sambar, wild boar and muntjac (Table 3).

Discussion

These results show the applicability of binomial mixture models (Royle 2004) for estimating population abundance of mammalian prey species from the type of count data commonly obtained from camera trap surveys. Although the philosophy of this approach to abundance estimation is not entirely new (Royle and Nichols 2003, Kéry et al. 2005, Royle and Dorazio 2006, Kéry 2008), its use in analyzing camera trap data reveals the potential to greatly expand how such datasets are valued and applied. A motivating interest for this study was whether prey data obtained from the camera trapping study focused on carnivores such as tigers can be modeled to obtain abundance estimates of prey. We also wanted to evaluate if the developed models conformed with hypothesized covariate-abundance relationships. As such, the results are encouraging, depicting expected covariate relationships and also identifiable parameters of the relationship.

Evaluation of mixture distribution and models

The performance of mixture models has been tested through various simulation-based and field-based studies (Royle 2004, Kéry et al. 2005, Royle and Dorazio 2006, Kéry 2008, Kery and Royle 2015). They are widely applied to model unbiased estimates of abundance of the closed populations following some defined distributions (Royle 2004). However, the estimates obtained may not be evaluated easily as the true biological populations in usually unknown. In this study, we did not have clear baseline data with which to to compare and validate our estimates. We base of our evaluation of mixture models on goodness-of-fit statistics, estimates of covariate coefficients, and magnitude of abundance estimates. Abundance estimates assuming negative binomial distribution for the abundance random effects were much higher than under Poisson distribution. Negative binomial mixtures, however, were superior for all four species based on AIC methods. Goodness-of-fit statistics obtained by bootstrap procedure also concurred with AIC based model selection procedure (Table 1). Thus, based on the results of both AIC model selection and bootstrap goodness-of-fit, we may estimate abundance under the models selected.

Modeling covariates

We used only three hypothesized covariates to potentially explain the variation in abundance of the select species across the study area. For each of the four species the effects of the covariates in the top models (both Poisson and negative binomial) were consistent with expectations. Although our representative samples did not essentially require covariate modeling

(Kéry et al. 2005), it did improve precision of the abundance estimates as depicted by the narrow confidence intervals compared to the null models (Table 1). Moreover, as our samples were not truely random, covariate modeling might be considered as an attempt to correct for sample selection bias (Kéry et al. 2005). Our results on wild boar abundance models, for which the null model was the most parsimonious with an adequate fit, demonstrates that specific covariates may be chosen just for one or a few species or even that the null model by itself may be sufficient for abundance estimation, depending on the objective of the analysis (Kéry et al. 2005).

Significant effects of distance from water on the abundance of the three cervids are unsurprising given the previously-observed affinity of cervids with water sources (Seidensticker 1976, Dinerstein 1980). Among the three cervids, distance from water sources had the highest effect on chital abundance (β= -0.85 SE= 0.18), followed by sambar (β= -0.23 SE= 0.09) and muntjac (β= -0.16 SE= 0.09) abundance. Schaller (2009) and Whitehead (1972) noted that water sources are not only an important factor determining chital distribution but their frequent visit to the water sources tend to localize the animals near these sources. Similarly, sambar association with pools (Whitehead 1972) might explain the strong negative associations of sambar abundance and the distance from water sources compared to that of muntjac. In contrast, the most parsimonious wild boar abundance model did not include distance from water (Thurfjell et al. 2009). One of the top models that did include water covariate but the parameter estimate was less than the standard error showing uncertain estimate (β= -0.05 SE= 0.09). Although wild boar also uses water sources for mud wallowing their congregation in proximity to the water sources is not documented.

Chital avoid high, rugged and steep terrain and do not tend ascend beyond 1000 meters (Schaller 2009), which is consistent with our findings where the most parsimonious model for chital abundance shows a strong negative relationship (β= -0.785 SE= 0.18) with elevation. For sambar, which may be found at altitudes of 3000-3600 meters (Whitehead 1972, Schaller 2009), our model depicts strong positive relationship between abundance and elevation (β= 0.435 SE= 0.09). In Chitwan, sambar density has been shown to be highest in the high elevation rugged terrain of churia (Thapa 2014). Counter intuitive relationship between elevation and abundances of wild boar and muntjac have been reported in a few empirical studies conducted in Chitwan (Thapa 2012, Dhakal et al. 2014, Thapa 2014). Therefore, based on our field observation and experiences we hypothesized that elevation may not affect the abundance of these species. As expected, our abundance models for these species did not show any predictable pattern of the effect of elevation on abundance.

Chital usually occupies riverine forests, moist or dry deciduous forests, as well as floodplain grassland, and do not penetrate deeply into evergreen forests (Schaller 2009). Therefore, we hypothesized that chital abundance would be higher at the areas with lower NDVI. However, NDVI did not improve predicted chital abundance. Two explanations may underpin this result. First, particularly in Chitwan, chital are seemingly ubiquitous (Seidensticker 1976) compared to other regions. Second, deciduous forests and grasslands may not provide adequate shade for chital (Geist 1998) during our survey season. This might have increased usage of forests with higher NDVI. Note that NDVI values were calculated based on December-January satellite images, near to our survey season when deciduous forests attain strikingly lower NDVI values relative to other seasons. Forests in general, and evergreen forests in particular, tend to have consistently higher NDVI values than grassland or deciduous riverine forests. Thus our survey season may underpin the lack of observed relationship between chital abundance and NDVI. Similarly, muntjac and wildboar are fairly well distributed among cover types, though they are considered primarily forest species. We anticipated that any effect of NDVI that might exist will not be discernible in the abundance model of these species. However, as expected we observed a positive effect of NDVI (β= 0.15 SE= 0.08) on the abundance of sambar, a predominantly a forest dwelling species (Whitehead 1972, Seidensticker 1976, Dhungel and O'Gara 1991, Schaller 2009).

Prey abundance

Our main objective was to evaluate if local abundance ($N_{quadrat}$) and total abundance (N_{total}) can be estimated reliably using binomial mixture model and we showed that the models resulted in seemingly valid estimates. However, lack previous data or methods to check such a fine-scale estimate of local abundances of all quadrats surveyed. Hence, we compare total animal abundance based on estimated total group abundance (N_{total}) with the most recent results derived from different years (Table 3).

Our calculation of total animal abundance based on the group sizes derived from several studies of the prey species show increased abundance of all the species at present relative to past estimates (Table 3). However, this result is merely because the recent studies reported larger group sizes of the species compared to the studies done in the past. Increases in group size may be a function of changes in resource availability (overall or seasonal) or to changes in predator pressures (Pulliam 1973, Underwood 1982). However, our abundance estimates may also reflect increased population sizes of these taxa. Thapa (2012) has also noted a remarkable increase in prey population at recent times compared to the studies conducted in the past.

In concurrence with other recent studies (Thapa 2012, Dhakal et al. 2014) our study revealed that chital is by far the the most abundant species at the quadrat level and across the park. Density estimates from these prior studies also indicate wild boar and sambar are almost equally abundant, favoring slightly towards wild boar. Our study also found that the difference in animal abundance between these species are similar, although we observed that the abundance of sambar was a little higher than the chital. This difference may be attributed to the behavioral ecology of these species and their relative elusiveness and we do not know clearly about these aspects of these species- for example the difference in their pattern of using forest trails that might impact capture rates in the camera trap survey (in our study) and the difference in elusiveness might impact the detection of animals differentially during distance sampling (in Thapa 2012 and Dhakal et al. 2014). The other reason for wild boar appearing more abundant than sambar in studies conducted by Thapa (2012) and Dhakal et al. (2014) may be attributed to their sampling areas. Both surveys were concentrated withing low land grassland and riverine forest, and while sambar uses these areas, they are also abundant in deep forest. For example, Thapa (2014) observed that churia forest has higher sambar density than that observed for all other prey species. Our data was collected from the uniformly distributed quadrats that were more representative of all cover types. Our results and all other previous studies showed that muntjac abundance was consistently lowest among all the prey species considered in this study.

In this paper, we use count data obtained from camera trap survey to derive detectability-corrected abundance estimates. Binomial mixture models selected by AIC had an adequate goodness-of-fit. The presence of the effects of covariates in the top models, and their directions, were as expected for each of the four species. The abundance estimates were comparable to the results from other rigorous observation-based or distance-based methods. Arguably, counts provide less information on abundance than the data based on individual identification or other comparable design such as distance sampling. However, these methods are labor intensive and restrictive to provide a net abundance estimate of the whole area sampled. Hence, we envision that, especially when the species are not individually-identifiable and we are also interested in identifying distribution of abundance at a fine-scale, mixture models based on counts derived from the camera traps are very competitive.

Conclusions

Binomial mixture models can be effectively applied to estimate abundance of prey species from camera trap data. The covariate relationships were as hypothesized, and the consequent abundance estimations were comparable with those gained from recent distance sampling surveys. To our knowledge, this is the first time mixtures models, have been applied to camera trap data. Adopting this method of abundance estimation will reduce the necessity of conducting observation-based or distance-based sampling surveys simultaneously with the camera trap survey. Furthermore, the yielding of quadrat level abundance estimates provides additional and crucial information that is rarely available.

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Table 1. Model selection (AIC), goodness-of-fit (GoF), and estimates of abundance (Ntotal and Nquadrat) under binomial mixture models for four prey species.

Species and models	Distribution	AIC	GoF		Abundance	
			SSE	p	N_{total}	$N_{quadrat}$
Chittal						
Covariate model	Poi	4306.7	1548	<0.001	431 (330-1025)	1.14 (0.84-2.23)
	NB	**4023.4**	**1641**	**0.327**	**2784 (1292-5630)**	**6.37 (3.57-15.59)**
Null Model	Poi	4552.3	1638	<0.001	370 (289-738)	0.90 (0.80-2.04)
	NB	4111.0	1681	0.327	2920 (1340-5911)	6.69 (3.71-16.37)
Sambar						
Covariate model	Poi	4536.1	1264	<0.001	517 (329-1018)	1.13 (0.91-2.84)
	NB	**4317.6**	**1299**	**0.109**	**2517 (960-5600)**	**5.25 (2.66-15.51)**
Null Model	Poi	4592.5	1296	<0.001	475 (319-879)	1.03 (0.88-2.43)
	NB	4341.9	1308	<0.001	2607 (983-5832)	5.44 (2.72-16.15)
Muntjac						
Covariate model	Poi	3496.9	769	<0.001	380 (240-893)	0.78 (0.66-2.47)
	NB	**3334.9**	**781**	**0.1**	**3163(981-7995)**	**5.79 (2.71-22.14)**
Null Model	Poi	3499.1	770	<0.001	378 (240-741)	0.76 (0.66-2.05)
	NB	3335.4	781	0.069	3150 (976-8008)	5.79 (2.70-22.18)
Wild boar						
Covariate model	Poi	-	-	-	-	-
	NB	-	-	-	-	-
Null Model	Poi	2298.9	358	0.039	242 (149-591)	0.46 (0.41-1.63)
	NB	**2264.8**	**359**	**0.337**	**2039 (447-6274)**	**2.91 (1.24-17.38)**

Table 2. Parameter estimates of the top models and a null model, animal/group level probability of detection (p), number of parameters (N), and model selection statistics (AIC, ΔAIC, AIC wt.) for the top parsimonious models within ΔAIC=2 or the next competing model if ΔAIC>2 under the Poisson and negative binomial mixture distributions of abundance. Most parsimonious model is in bold face. (w=distance from water sources, e=elevation, n=ndvi; estimates in parenthesis have either equal or larger SE than the estimates)

Species	Mixture	Lambda				p	N	AIC	ΔAIC	AIC wt.
	Models	const	w	e	n					
Chital Poisson	**lam(w+e)**	**-0.48**	**-1.21**	**-0.44**	*****	**0.12(0.006)**	**4**	**4306.72**	**0**	**0.71**
	lam(w+e+n)	-0.48	-1.21	-0.45	(0.02)	-	5	4308.50	1.78	0.29
	lam(.)	(0.02)	*	*	*	0.14(0.006)	2	4552.35	245.63	0
N Binomial	**lam(w+e)**	**1.39**	**-0.85**	**-0.78**	*****	**0.019(0.003)**	**5**	**4023.43**	**0**	**0.73**
	lam(w+e+n)	1.39	-0.85	-0.78	(-0.024)	-	6	4025.39	1.96	0.27
	lam(.)	2.09	*	*	*	0.019(0.003)	3	4111.02	87.59	0
Sambar Poisson	**lam(w+e+n)**	**0.27**	**-0.19**	**0.38**	**0.16**	**0.091(0.006)**	**5**	**4536.81**	**0**	**0.90**
	lam(.)	0.27	*	*	*	0.10(0.006)	2	4592.54	52.73	0
N Binomial	**lam(w+e+n)**	**1.83**	**-0.23**	**0.43**	**0.15**	**0.019(0.002)**	**6**	**4317.58**	**0**	**0.55**
	lam(w+e)	1.86	-0.23	0.47	*	-	5	4318.59	1.01	0.33
	lam(.)	1.98	*	*	*	0.018(0.002)	3	4341.89	24.31	0
Muntjac Poisson	**lam(w)**	**(0.04)**	**-0.13**	*****	*****	**0.083(0.006)**	**3**	**3496.93**	**0**	**0.38**
	lam(w+e)	(0.04)	-0.15	(0.03)	*	-	4	3498.72	1.79	0.16
	lam(w+n)	(0.04)	-0.13	*	(0.01)	-	4	3498.90	1.97	0.14
	lam(.)	(0.04)	*	*	*	0.084(0.006)	2	3499.06	2.13	0.12
N Binomial	**lam(w)**	**2.16**	**-0.16**	*****	*****	**0.01(0.001)**	**4**	**3334.96**	**0**	**0.29**
	lam(.)	2.17	*	*	*	0.01(0.002)	3	3335.44	0.48	0.23
	lam(w+e)	2.15	-0.17	(0.04)	*	-	5	3336.76	1.80	0.12
	lam(w+n)	2.15	-0.16	*	(0.03)	-	5	3336.84	1.88	0.11
Wild boar Poisson	**lam(.)**	**-0.40**	*****	*****	*****	**0.075(0.007)**	**2**	**2298.92**	**0**	**0.28**
	lam(n)	-0.41	*	*	0.13	0.075(0.007)	3	2299.85	0.93	0.18
	lam(w)	-0.40	(0.07)	*	*	-	3	2300.11	1.19	0.16
	lam(e)	-0.40	*	0.08	*	-	3	2300.35	1.43	0.14
N Binomial	**lam(.)**	**1.73**	*****	*****	*****	**0.009(0.007)**	**3**	**2264.85**	**0**	**0.27**
	lam(n)	1.70	*	*	(0.07)	-	4	2265.20	0.35	0.22
	lam(e)	1.70	*	(0.09)	*	0.009(0.007)	4	2266.44	1.59	0.12
	lam(w)	1.70	(0.05)	*	*	-	4	2266.49	1.64	0.12

Table 3. Animal abundance of prey species calculated based on group size suggested in Dhakal (2014). Group abundance estimated under the most parsimonious abundance models were simply multiplied with the group sizes.

Species	**Group abundance**		**Group size**	**Animal abundance**	
	N(total)	**N(quadrat)**		**Total**	**Quadrat**
Chital	2784	6.37	13.65	38001.6	86.9505
Sambar	2517	5.25	1.86	4681.62	9.765
Muntjac	3163	5.79	1.29	4080.27	7.4691
Wild boar	2039	2.91	2.18	4445.02	6.3438

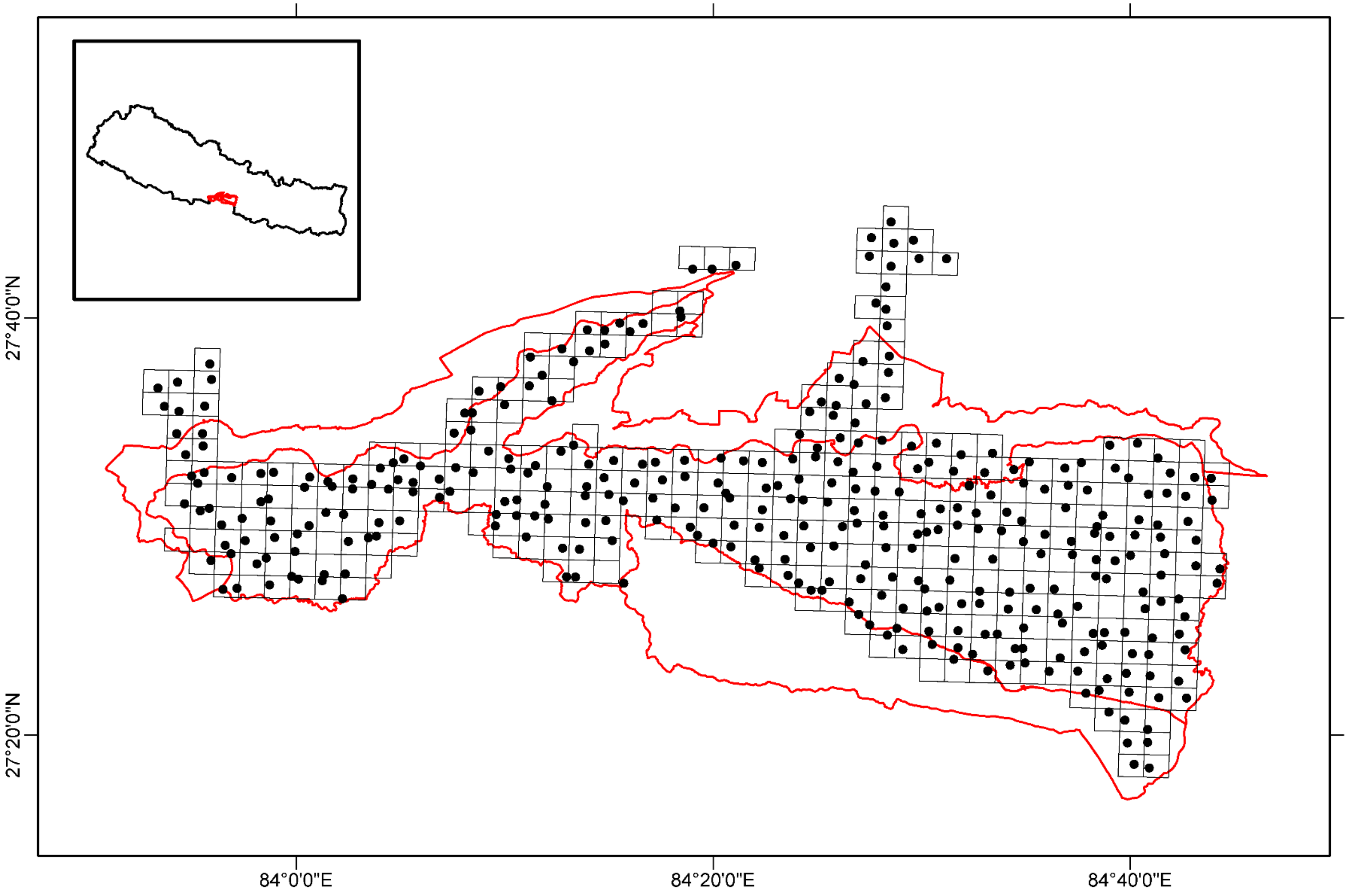

Figure 1. Camera trap stations in 2 km x 2 km quadrat across Chitwan National Park and surrounding locations (In set: location of Chitwan National Park in Nepal)

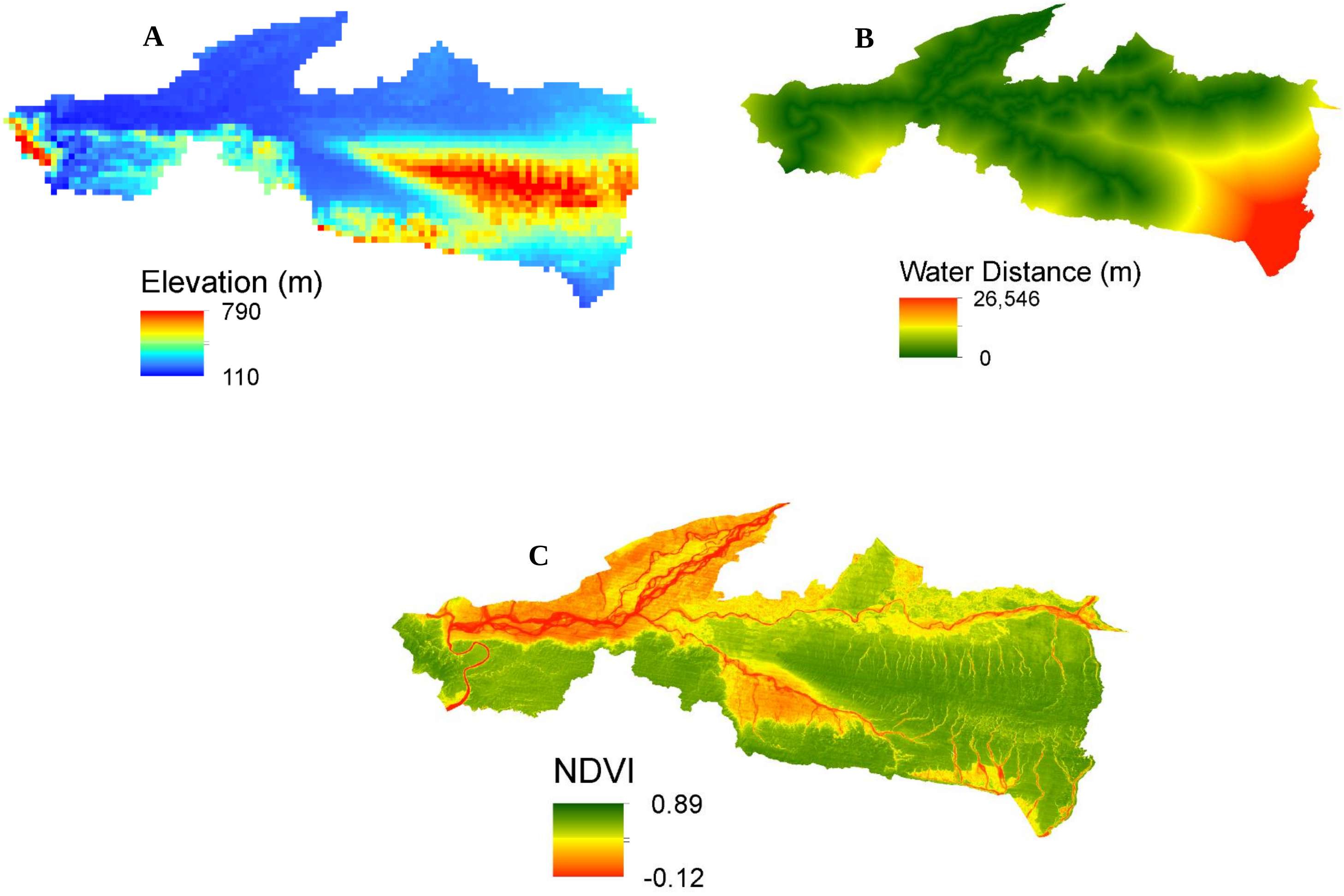

Figure 2. Digital elevation model (A), distance from the major water sources (B), and composite NDVI map of Chitwan National Park

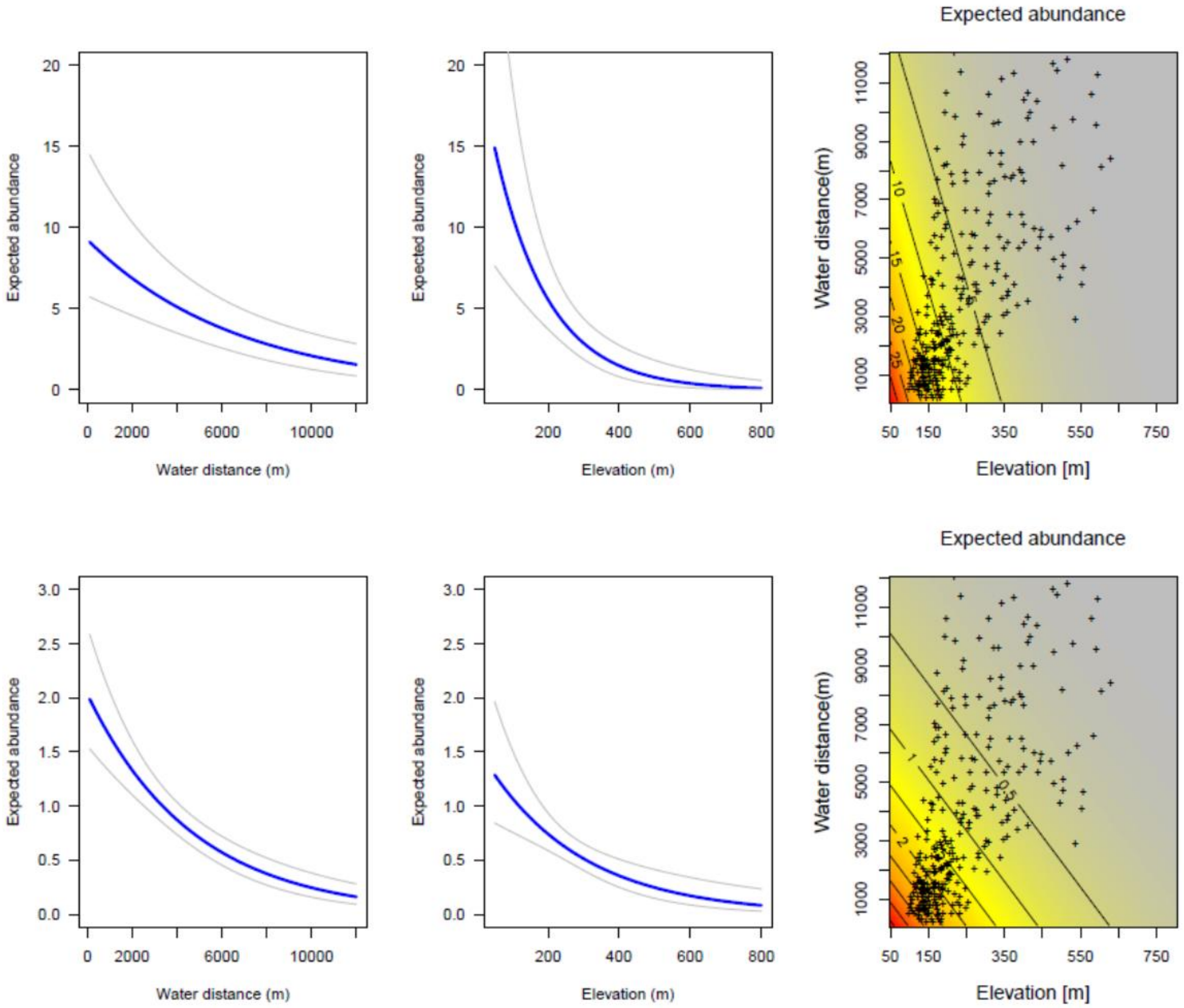

Figure 3. Effect of water distance and elevation on abundance estimates for chital based on the most parsimonious negative binomial model (upper row) and Poisson mixture model (lower row).

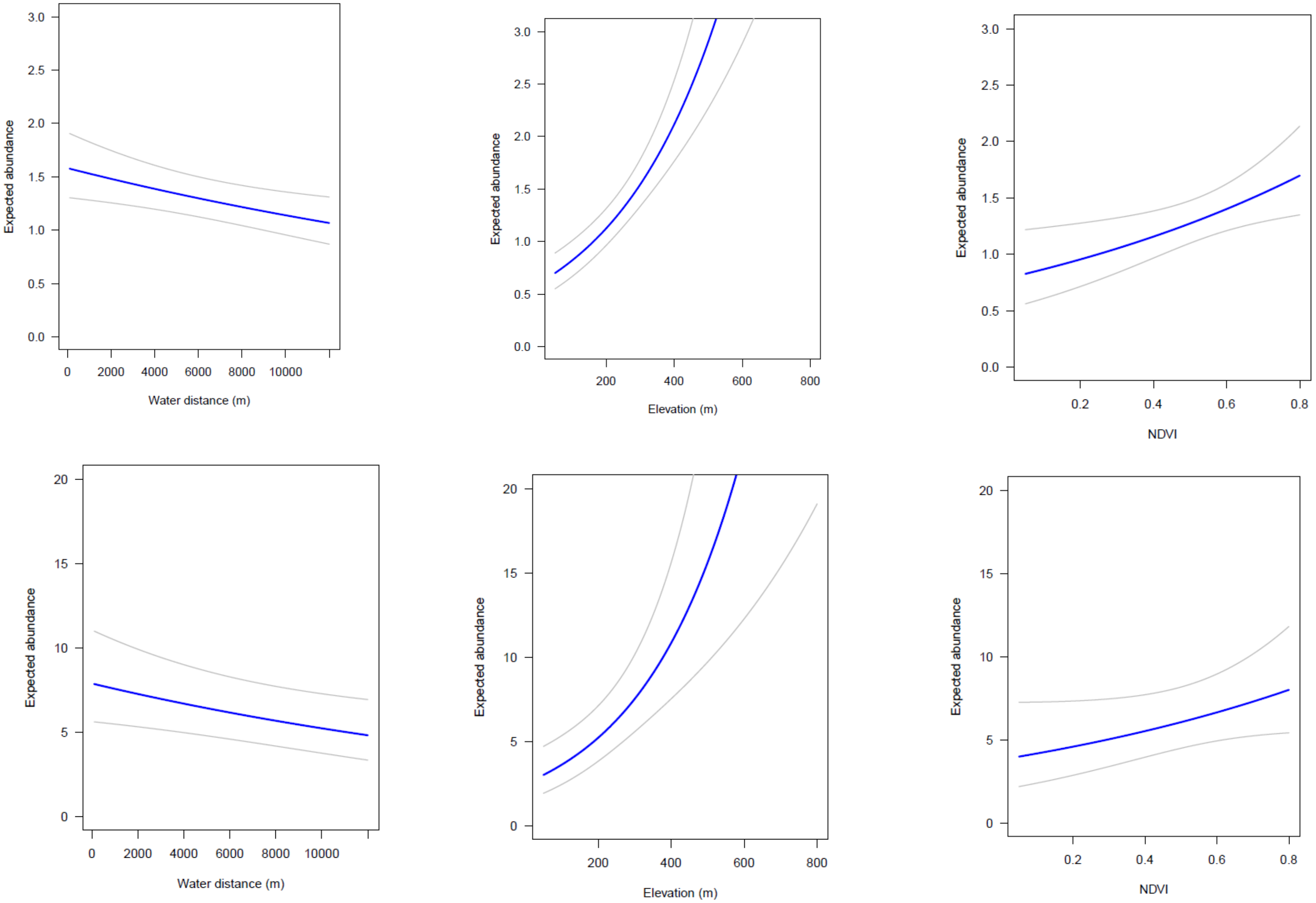

Figure 4. Effect of covariates on abundance estimates for sambar based on the most parsimonious negative binomial model (upper row) and Poisson mixture model (lower row).

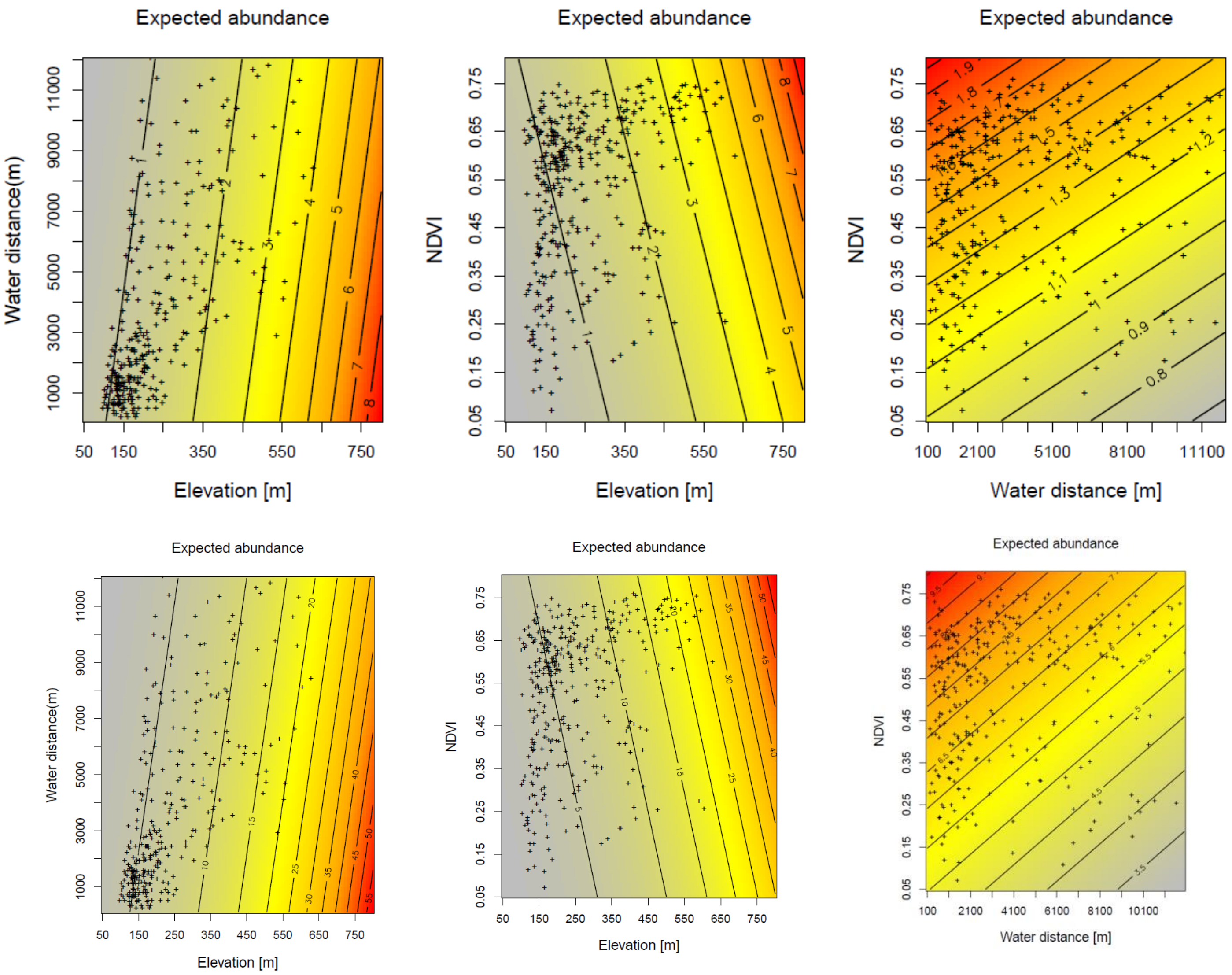

Figure 5. Effect of paired-covariates on abundance estimates for sambar based on the most parsimonious negative binomial model (upper row) and Poisson mixture model (lower row).

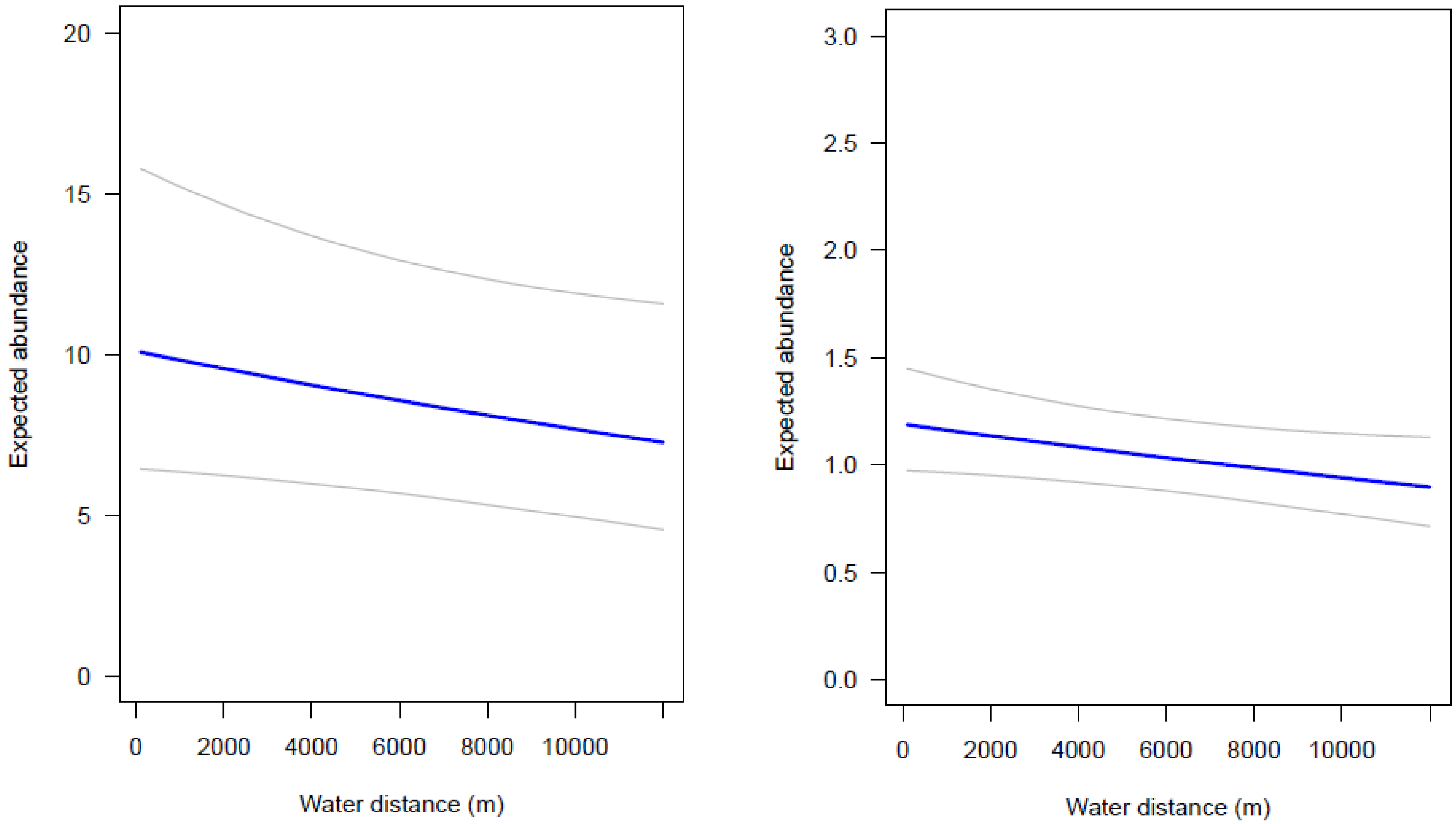

Figure 6. Effect of water distance on abundance estimates for muntjac based on the most parsimonious negative binomial model (left) and Poisson mixture model (right).

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CHAPTER IV

HOW DO TIGERS AND LEOPARDS CO-OCCUR? INTRAGUILD INTERACTIONS IN RESPONSE TO HUMAN AND LIVESTOCK DISTURBANCE IN CHITWAN NATIONAL PARK

Hemanta Kafley[A,B,G] , Babu R. Lamichane[C], Rupak Maharjan[D], Madhav Khadka[E], Nishan Bhattarai[F], Matthew E. Gompper[A]

[A]School of Natural Resources, University of Missouri, Columbia, MO 65211, USA.

[B]Nepal Nature Foundation, Koteshwor, Kathmandu-34, Nepal.

[C]National Trust for Nature Conservation, Biodiversity Conservation Center, Chitwan, Nepal.

[D]Department of National Parks and Wildlife Conservation, Kathmandu, Nepal

[E]World Wildlife Fund Nepal Program, Kathmandu, Nepal

[F]The Center for International Environment and Resource Policy, The Fletcher School, Tufts University, Medford, MA

[G]Corresponding author: hemantakafley@gmail.com

Abstract

Intraguild interactions among large predators can have important implications for carnivore demography, and for the community ecology of both predators and prey. Prey availability may be a major factor determining the nature of these interactions. In a human-dominated landscape where anthropogenic disturbance is common, difference in the response of predators to various forms of disturbance might alter the usual interaction patterns. How tigers (*Panthera tigris*) and leopards (*Panthera pardus*) respond to prey and disturbance, and the influence of these factors on interactions between these top predators can provide important insights on their ecology and conservation. We conducted camera trap surveys in 361 locations in and around Chitwan National Park, Nepal, in 2013 to examine how prey abundance, and disturbance factors such as human presence and livestock use of the habitat, might influence habitat use by tigers and leopards independently and when co-occurring. Single-species single-season models and two-species single-season models were developed to examine hypotheses on unconditional detection and occupancy and species interaction respectively. We found that the use of the habitat by livestock negatively influenced tiger detection but positively increased leopard detection. Pervasive human use of the park had negative impacts on tiger occupancy while the abundance of chital and sambar had a positive influence. Despite significant prey overlap between tigers and leopards, none of the native prey species predicted leopard habitat occupancy. However, habitats used extensively by livestock were also used by leopards. Further, we found strong evidence that leopard occupancy was conditional on tiger presence. Higher tiger occupancy in prey rich areas and low leopard occupancy in the sites where tigers are present suggests interference or exploitative competition between the species. These findings, and a species interaction factor between tigers and leopards of < 1 clearly indicate that leopards avoid tigers, but their adaptation to human disturbance and livestock enable them to persist in fringe habitats despite negative

interactions with tigers. These results show how two large and competing predators co-occur in an ecological system that is under heavy disturbance pressure.

Introduction

The functional role a species plays in a community depends on interspecific interaction strengths, which for members of the same guild may be particularly strong (Harley 2003, Soulé et al. 2003, Pilfold et al. 2014, Ripple et al. 2014). Competition between a dominant predator and a subordinate predator may result in a range of possible equilibria, including stable coexistence to spatio-temporal segregation (Holt and Polis 1997, Berger et al. 2008, Schuette et al. 2013, Robinson et al. 2014, Palomares et al. 2016). The ecological mechanisms underpinning these interactions are exploitative and interference competition, which at an extreme may take the form of intraguild predation (Fuller and Keith 1981, Polis et al. 1989, Creel et al. 2001, Arim and Marquet 2004, de Oliveira and Pereira 2014). When this intraguild competition involves the largest predators, “top down” effects can influence the make-up of carnivore communities as well as the broader community and ecosystem structure and function (Gompper 2002, Ritchie et al. 2012, Ripple et al. 2014, Sergio et al. 2014, Gompper et al. 2016). Moreover, exploitative and interference competition among coexisting predators has resulted in the evolution of strategies for avoidance or co-occurrence and may influence the populations’ abilities to persist in the face of anthropogenic and natural disturbances (Fuller and Keith 1981, Creel et al. 2001, Vanak and Gompper 2010, Ritchie et al. 2012, Ripple et al. 2014, Carter et al. 2015).

Conceptually, it is well established that interspecific competition among predatory carnivores is usually asymmetric (Lawton and Hassell 1981, Persson 1985). Interference competition can affect the subordinate competitor through exploitative and interference competition, including agonistic interactions that result in such as behaviors such as intraguild predation (Palomares and Caro 1999), kelptoparasitism (Gorman et al. 1998, Carbone et al.

2005) and predator avoidance through spatial and or temporal habitat segregation (Mills and Gorman 1997, Linnell and Strand 2000).

Tigers (*Panthera tigris*) are the largest terrestrial predators in tropical Asia. Interference competition and hence increased aggression, putatively due to food overlap (Karanth and Sunquist 2000, Wegge et al. 2009), towards leopards (*P. pardus*) has been reported (Seidensticker 1976, Odden et al. 2005). This competition may underpin population densities of the subordinate species. For example, in Bardia National Park, Nepal, an increase in tiger density, attributed to significant increases in the density of ungulates did not contribute to leopard population growth rates (Linnell and Strand 2000, Wegge et al. 2009). Yet the two species do co-occur in many regions. This co-occurrence may be mediated influenced by landscape variability and by the spatial scale of examination (Palomares et al. 2016). For instance, wolves (*Canis lupus*) exterminated coyotes (*C. latrans*) from the Isle Royale, USA while their co-occurrence in mainland areas may be facilitated by habitat associations and avoidance behaviors (Thurber et al. 1992).

Predators are known to have differential abilities in making use of the human-modified habitats (Gompper and Vanak 2008, Ripple et al. 2014, Gompper et al. 2015). Indeed, coexistence of large carnivores in such habitats may be facilitated by factors such as human disturbance, prey abundance, habitat heterogeneity, and by adjusting spatio-temporal activity among several others (Seidensticker 1976, Seidensticker et al. 1990, Karanth and Sunquist 1995, Odden et al. 2010, Bhattarai and Kindlmann 2012, Carter et al. 2015). Tigers are a top predator found throughout 13 countries in Asia (Sunquist et al. 1999, Schaller 2009, Wikramanayake et al. 2011) and leopard, though a subordinate predator to tiger, is also a top predator throughout Africa, the Middle East, and Asia (Seidensticker et al. 1991, Uphyrkina et al. 2001, Henschel et al. 2010). In Chitwan National Park, Nepal, tigers, leopards and their prey exist in a landscape that is often used by humans and their livestock. There is paucity of information on how disturbance factors may govern responses of interacting carnivores at a fine-scale investigation. Given the high frequency of interactions with human and livestock in the park, we hypothesize that these disturbance factors, in addition to prey abundance and distribution patterns, might affect tiger-leopard coexistence. To address this topic, we applied detectability-corrected two-species occupancy models (MacKenzie 2006) to infer co-occurrence patterns of tigers and leopards with respect to prey abundance and disturbance factors.

Despite significant overlap in diet, leopards coexist with tigers in the Terai Arc (Seidensticker 1976, Seidensticker et al. 1990, Odden et al. 2010, Thapa 2012), but how they do so is unclear. Here we build habitat models for tigers and leopards that incorporate abundances of prey, livestock, and local people and test the effect of also incorporating this information in co-occurrence models. Thus, this study aims to enhance our understanding of coexistence of carnivores and its implication for predator conservation by assessing how prey, livestock and human use influence use of habitat at a fine-scale by two top predators and whether these factors explain patterns of coexistence. We examine four hypotheses: (1) leopard detection and habitat use is independent of the use of habitat by local people; (2) livestock presence in the habitat may enhance use of the habitat by leopards; (3) tiger habitat use is negatively influenced by both livestock and human use but positively influenced by the prey abundance; (4) leopards avoid habitat occupied by tigers.

Methods

Study area

Chitwan National Park (27° 18’-27° 41’N latitude and 83° 41’-83° 49’E longitude) (Figure 1) harbors robust predator and prey populations and is a priority protected area in Nepal. It is comprised of core park area (932 km^2) and a surrounding buffer zone (750 km^2). The core park is relatively less disturbed, with an exception of many forest trails used by local people and tourists. In contrast, the peripheral areas along the edges of the park and buffer zone are subject to disturbance from livestock grazing and from local people who harvest forest products and travel through the park. The buffer zone suffers additional disturbance as this area is primarily a multiple use zone, although wildlife conservation in these areas is also a priority and hence mechanisms to minimize the disturbance are in place. The park is predominantly (~ 70%) covered by forest [high density sal (*Shorea robusta* Gaertner f.) forest, low density sal forest, mixed forest, degraded forest and scrub vegetation, and riparian forest (Laurie 1978, Lehmkuhl 1994, Bhuju et al. 2007). Other land cover types include various types of grasslands (~8%), riverbank and exposed surfaces (~7%), and agriculture and settlement (15%) (Gurung 1983, Lehmkuhl 1990, 1994, Kafley et al. 2009).

Chitwan National Park supports a high tiger density (Dhungel and O'Gara 1991, Dhakal et al. 2014a, Karki et al. 2015) which has been attributed to a high prey density (Smith et al. 1999). It is the core habitats for a long-persisting tiger population (Smith et al. 1999) in Southeast Asia, boasts the largest population size (98-139 animals) and density (3.84/100 km^2) in Nepal (Dhakal et al. 2014), and serves as a potential source population to maintain the tiger metapopulation in Terai Arc Landscape (Smith et al. 1999, Karki et al. 2013). Chitwan National Park also supports a robust leopard population (Seidensticker et al. 1990, Thapa 2012) and diverse and high-density populations of prey species [sambar deer (*Rusa unicolor* Kerr, 1792), barking deer (*Muntiacus muntjak* Zimmermann, 1780), chital (*Axis axis* Erxleben, 1777), wild boar (*Sus scrofa* Linnaeus, 1758)].

Data collection and preparation

Between February and May in 2013 we used camera traps to survey the occurrence of large predators, prey, and humans across the Chitwan National Park in three blocks, including the entire core of the park as well as some areas of the buffer zone surrounding the park. Motion-detecting camera trapping surveys have been widely used in Chitwan and many other study sites for studying diverse taxa including tigers and leopards (Karanth and Nichols 1998, Carbone et al. 2001, Carter et al. 2012, Thapa 2012, Carter et al. 2013, Thapa 2014). A total of 362 quadrats of size 2km X 2km distributed across the park were surveyed with a pair of cameras (hereafter a 'camera trap') in each quadrat. Camera trap locations within each grid unit was determined based on the local expert opinion so as to maximize the chance of tiger capture. As such, they were located along the forest road, foot path, stream bed, ridge lines, or animal trail. Camera traps in adjacent quadrats were at least ~ 1km and at most ~ 3 km apart (Figure 1). Aside from a focus on locations where tigers were expected to be captured, habitat and site characteristics such as vegetation type, altitude, distance from settlements, and other variables were not considered for camera placement. Hence, locations and site characteristics of camera sites are considered quasi-random and independent. Geographic location for each camera trap was collected using Garmin Etrex handheld GPS units (Garmin Inc.)

The survey included a 17-21 trapping occasions, where an occasion was 1 day (24-hrs duration). Camera malfunction or theft resulted in missing data in one quadrat, and so the affected quadrat was excluded from the subsequent analyses, resulting in suitable data from a total of 361 locations. We used data obtained from only the first 17 days to avoid the variation in number of days sampled between locations. Given our fine spatial scale quadrat size with respect to the home ranges of tigers and leopards, we assume random movement of animals between the quadrats. Hence individual animals do not have to be continually present at a site for the site to be classified as occupied. This phenomenon relaxes the assumption of population closure for occupancy models such that our occupancy is better interpreted as ‘use’ (MacKenzie and Royle 2005, MacKenzie 2006, Robinson et al. 2014, Carter et al. 2015).

For each photograph of a tiger, leopard, and prey species obtained from the geographically referenced camera traps we recorded species, date and time. Number of independent detections of prey species (individuals or groups) represented counts of the species detected. We summed the number of detections of the species for each camera location. For each species we define independent detection as (i) consecutive photographs of identifiable individual/group based on cues such as group size and any other unique characteristics present in some animals in the group (ii) consecutive pictures of individually-unrecognizable animals >30 minutes apart, and (iii) nonconsecutive pictures of animals. Counts of prey species were thus derived from the independent detection of animals in the cameras. As people can be easily recognized in the photographs, we summed all independent photographs of individual/group of people that were captured in the camera traps at each location. Photographs of tigers and leopards were used to create detection history for the species over the entire survey period. Thus we had detection and non-detection history for both species for the 17 survey occasions, where ‘1’ represented detection of the animals in each 24-hr day/night survey occasion and ‘0’ represented non-detection.

Covariate Analyses

We assessed the influence of livestock, local people, and prey on tiger and leopard detection probability and occupancy. Because local people and livestock pose significant disturbance to wild animals (Ngoprasert et al. 2007, Harihar et al. 2009, Karanth et al. 2011, Barber-Meyer et al. 2013), wariness in animals could negatively influence the detection and occupancy of either carnivore. In contrast, prey availability is a major factor determining density and occupancy of predators and hence increases occupancy (Karanth et al. 2004, Barber-Meyer et al. 2013).

Detections of local people and livestock at each camera trap were summed from the 17 survey occasions and standardized to develop 'human' and 'livestock' covariates. We used two covariates: abundance of sambar and chital separately representing prey abundance. The abundance of the prey species was estimated using binomial mixture models (Chapter III). We did not use abundance of wild boar as a separate covariate, despite it being an important prey for both tiger and leopard, because wild boar abundance was best predicted by a null model that yielded equal abundance values across the camera trap sites. Muntjac, a next important prey, was also not included in the models because muntjac and chital abundance was strongly correlated (Kendall's $\tau = 0.74$, $p<0.001$).

Human and livestock covariates were used as a proxy for disturbance, but we predicted that the effect of these covariates would differ in predicting detection and occupancy of tigers and leopard. For example, while tigers may avoid humans and livestock thereby decreasing their detectability and occupancy, leopard detectability might be negatively affected due to wariness but their occupancy may not. Similarly, in a prey rich habitat like Chitwan, tiger detection and occupancy may be negatively influenced by the presence of livestock but as a result of interference competition with tigers, leopards may occupy fringe habitats used by livestock. Hence, we anticipated a positive relationship of leopard detection and occupancy with livestock abundance.

Because there is a significant overlap in prey species between tigers and leopards (Karanth and Sunquist 1995, Ramakrishnan et al. 1999, Thapa 2012, Thapa 2014), we foresee a positive relationship between prey abundance and occupancy of either carnivore. However, the relationship of prey abundance and leopard occupancy may not be as significant as that of prey and tiger, as tigers may select prey-rich areas pushing leopards towards the peripheral prey-poor areas (Seidensticker et al. 1990, Karanth and Sunquist 1995, Johnsingh and Negi 2003, Odden et al. 2010).

Modeling approach

We used a single-species occupancy modeling approach as described by (MacKenzie et al. 2002, MacKenzie et al. 2006) using program PRESENCE v. 11.0 (MacKenzie et al. 2006) to evaluate the space use of tigers and leopards across the study site. We used a two-step process for model selection. First, we identified the best detection models for each species holding occupancy constant ($\Psi(.)$). All possible combinations of covariates were used to fit 4 detection models (Table 1) each for tiger and leopard. Using the best detection covariate (only 'livestock' appeared as the best detection covariate for both tigers and leopards) from the best detection models, we then developed a set of 16 models each (Appendix A) for identifying best occupancy covariates for both species (Table 2). Using the best detection and occupancy covariates from these analyses, we then developed a set of 86 models (Appendix B) using single-season two-species models adopting conditional two-species model parameterization (Richmond et al. 2010) in PRESENCE v. 11.0. The description of the parameters used in the conditional two-species occupancy model was adopted from Richmond (2010) and is presented in Table 3.

We fit additive models that included combinations of all four covariates representing prey and disturbance for conditional occupancy while only livestock was included as the covariate affecting detectability. We model-averaged the top 5 models (Table 4), which had a cumulative AIC weight of 100 percent, to obtain estimates of conditional occupancy and detection probability. The above models were developed for testing the effect of (1) tiger presence and detection on leopard presence and detection, (2) tiger presence on leopard occupancy, and (3) the effect of livestock, prey and people on occupancy of both species. First, we predicted that detectability of tigers would be higher than the detectability of leopards in co-occupied sites whether tiger was detected ($r^{A}>r^{BA}$) or not detected ($r^{A}>r^{Ba}$). Next, we predicted that occupancy of leopards would be lower if the sites are also occupied by tigers due to exploitation or interference completion ($\Psi^{BA}< \Psi^{Ba}$). Third, we predicted that detectability of leopards will be same in the co-occupied sites regardless of tiger detection or non-detection ($r^{BA}=r^{Ba}$) in the sites. Finally, we predicted that tigers and leopards are less likely to co-occur, manifesting spatial avoidance, than would be expected by chance. The species interaction factor (SIF) between tigers and leopards, representing a likelihood ratio of co-occurrence (MacKenzie 2006, Richmond et al. 2010) was calculated as

$$SIF = \frac{\Psi^{\mathrm{A}}\Psi^{\mathrm{BA}}}{\Psi^{\mathrm{A}}(\Psi^{\mathrm{B}}\Psi^{\mathrm{BA}} + (1-\Psi^{\mathrm{A}})\Psi^{\mathrm{Ba}}}$$

Using conditional parameterization (Richmond et al. 2010), an SIF value of one is obtained if two species occur independently, <1indicates that the subordinate species B is less likely to co-occur with the dominant species A, and an SIF value > 1 indicates that co-occurrence of the two species is more likely than expected by chance.

Results

Presence of human, livestock, prey and the predators

We found evidence of human presence in 36 percent of the quadrats surveyed (130 out of total 361) at varying intensity of human photographs recorded per quadrat (Figure 2). A total of 815 independent photographs of human were recorded during the survey with a maximum of 25 photographs (mean = 2.25 and sd = 4.71) per quadrat (Figure 3). Similarly, 20 percent of the quadrats had 340 independent photographs of livestock (Figure 2). Maximum number of photographs taken was 22 (mean = 0.94, sd= 2.62) per quadrat (Figure 3). Tiger photos were recorded in 37 percent of the sites surveyed, with a maximum of 9 independent photographs (mean = 0.71 and sd = 1.3) captured per site (Figure 3). Similarly, leopard photos were recorded in 30 percent of the sites surveyed, with a maximum of 5 independent photos (mean = 0.53 and sd = 0.96) per site (Figure 3). Photographs of both tigers and leopards were taken in 45 camera traps (ca. 12 percent of the total camera traps deployed) (Figure 4). The results of the binomial mixture models (see chapter III) show that mean chital abundance was 105.43 animals (sd = 88.13, range = 318.99) per quadrat. The mean abundance of sambar was 12.97 animals (sd = 7.05, range = 42.38) per quadrat. The standardized abundance distribution of both prey species is shown in Figure 2.

Effect of covariates on predator detectability and occupancy

Livestock was the only covariate affecting detection rates for both tigers and leopards (Table 1). For tigers, the top models with livestock had a cumulative Akaike weight of > 0.99 and the most supported model alone had the weight of 0.72. Livestock was negatively associated with detectability of tigers (β = -0.512, SE = 0.154). For leopards, the top models with livestock had a cumulative Akaike weight of 0.90 and the most supported model alone had a weight of 0.66. Livestock had a positive influence on detectability of leopards (β = 0.189, SE = 0.068).

Single-season single-species occupancy models supported our prediction that tiger occupancy was best predicted by prey abundance. Chital and sambar abundance were the best supported covariates (cumulative Akaike weights: 0.95 and 0.84 respectively) followed by human and livestock (cumulative Akaike weights: 0.5 and 0.28 respectively). However, livestock was not supported by the most parsimonious model (Table 2). As expected chital (β = 1.31, SE = 0.33) and sambar (β = 0.43, SE = 0.20) abundances had positive influences on tiger occupancy while livestock had a negative influence (β = -0.32, SE = 0.16). The model-averaged occupancy of tigers was 0.5368 (±0.2227). Surprisingly, none of the covariates except livestock were supported in the most parsimonious leopard occupancy model. The model support for livestock (AIC weight = 0.69), was followed by chital (0.37), and human and sambar (0.21 each). None of the other covariates except livestock were supported in the model within 2 AIC units of the most parsimonious model. As expected, livestock had a positive impact on leopard occupancy (β = 0.65, SE = 0.34). The model-averaged occupancy of leopards was 0.4295 (±0.0919).

Tiger-leopard co-occurrence

We used the best supported corresponding covariates from the detectability and occupancy models for the conditioning two-species occupancy models. Our co-occurrence models included only livestock for detection and all four covariates for occupancy. The most parsimonious model predicting occupancy included chital, sambar and livestock. In the top 5 models that received any AIC weight, chital was the most supported covariate (cumulative AIC weight = 1.0) followed by sambar (0.99), livestock (0.93), and human (0.48). The probability of detection of a leopard was 0.06 ±0.01.

We hypothesized that the probability of detecting a leopard would decrease at the sites occupied by tigers. This prediction was not supported as the leopard detectability was similar regardless of the detection or non-detection of tiger ($p^{B}=r^{BA}=r^{Ba} \sim 0.06$). Indeed, the model-averaged detection probability of tiger was higher in co-occupied sites than at sites where leopard was not present i.e $r^{A}>p^{A}$.

We hypothesized that the probability of leopard occupancy would decrease at sites co-occupied by tigers as a results of competition. Model-averaged occupancy of leopards when tigers were not present was higher (0.968±0.052) than when tigers were present (0.348±0.179, such that as expected, $\Psi^{Ba} > \Psi^{BA}$. We used model-averaged occupancy estimates to calculate the SIF between tigers and leopards. The independent SIF of all sites was < 1 indicating that leopards avoided tigers even at a fine-spatial scale. However, 25 percent sites that had SIF > 0.9 depicting only slight avoidance. However, in the majority of the fine-scale sites the species depicted strong avoidance with SIF < 0.9 (Figure 4). The model-averaged SIF across all sites was 0.662±0.074), indicating avoidance between the two species.

Discussion

The presence of carnivore species has long been viewed as a function of three factors: prey availability, habitat suitability, and intraguild interference competition (Linnell and Strand 2000, Creel 2001, Creel et al. 2001, Fuller and Sievert 2001, Vanak and Gompper 2010, Gompper et al. 2016). While the regular observation of striking patterns of interference competition has received extensive attention from predator ecologists (Creel and Creel 1996, Linnell and Strand 2000, Périquet et al. 2015) such that it is something of the norm to assume that interference competition is a fundamental driver of the distribution and abundance of a predator species (Creel and Creel 1996, Berger and Gese 2007, Vanak and Gompper 2010, Newsome and Ripple 2015), recent studies have suggested that it is the nuanced interactions of interference competition with resource availability and habitat suitability that more fully defines the occurrence of any one species of carnivore (Gompper et al. 2016, Kajtoch et al. 2016). Our results reveal how anthropogenic disturbance can interact with natural regulatory factors such as the abundance of prey and intraguild competitive dynamics to mediate the co-occurrence of large predators. Our best-supported models indicated that intraguild interactions between tigers and leopards are modulated by prey abundance and apparent differences in responses of the carnivores to human disturbance.

Oriol-Cotterill et al. (2015) argues that large carnivores may be subject to landscapes of fear from human interference similar to that described for the responses of prey species to risk of predation. Chitwan National Park receives extensive use by human and their livestock (Figures 3 and 4). When viewed in the context of our single species models, tiger occupancy was strongly and positively influenced by prey abundance while negatively associated with human use. This pattern has been previously documented for tigers inhabiting diverse landscapes across their range (Karanth and Sunquist 1995, Kerley et al. 2002, Harihar and Pandav 2012, Barber-Meyer et al. 2013), including in the Terai Arc. For instance, Carter et al (2012) found that tigers were adjusting their activity in space and time in response to type and magnitude of human response in the park. Similarly, Chanchani et al. (2016) found that tiger habitat use at a fine spatial-scale was high in areas associated with abundant preys and declined as human and livestock use increased.

Such patterns are not unique to tigers. For instance, Smith et al. (2015) reports that human-induced fear resulted in increased kill rates by puma as a result of a decline in kill site fidelity and consumption time in response to increased anthropogenic activities. Thus, various types and intensities of human use of the habitat impart significant threat to the habitat use by the large carnivores (Ripple et al. 2014).

For leopards, one might expect a similar patterns of anthropogenic disturbance avoidance, compounded by the need to also avoid tigers. However, our results revealed that leopard occupancy was higher in sites that were extensively used by livestock, with prey abundance and human use having relatively little strength in predicting patterns of leopard occupancy. In Chitwan National Park the fringe habitats used by livestock are not devoid of wild prey. Although in low density, wild prey, combined with high livestock and domestic dog densities in these habitats apparently provide sufficient food for leopards (Thapa 2012). Other studies also suggest a tolerance of leopards to human and livestock and their potential to occupy sites that are seemingly resource-poor (Seidensticker 1976, Seidensticker et al. 1990, Odden et al. 2010, Wasim et al. 2014) relying on domestic ungulates as their major prey (Athreya et al. 2016). As seen for other taxa, disturbed habitats may be important for the persistence of the subordinate leopards when the prey-rich habitat is dominated by larger, apex tiger (Linnell and Strand 2000, Steinmetz et al. 2013). Indeed, in regions where tigers are present leopards might survive best in areas with low wild prey abundance and relatively higher human use because these areas act as refugia.

The odds of a leopard being present versus absent at a site given an absence of tigers ((Probability leopard present/probability leopard absent) | tiger absent)) was 30.15:1, and the odds of leopards being present versus absent given the presence of tigers ((Probability leopard present/probability leopard absent) | tiger present)) was 10:1. Thus these odds ratios indicate that leopards were approximately three times more likely to be present when tigers were absent. We attribute these patterns to the similar dietary and habitat needs of the two species. In other words, habitat that is good for tigers is also good for leopards. However, the odds of a leopard occupying a site increased in the absence of tigers, indicating that the presence of tigers reduces the occurrence of leopards at these sites. Leopards were much more likely to occupy sites with high livestock density that were avoided by tigers. Thus, the avoidance of livestock-rich areas and the areas with high human traffic by tigers (Harihar and Pandav 2012, Barber-Meyer et al. 2013) were important predictors of the variance in habitat occupancy by leopards and were driver of the fine-spatial scale habitat segregation between tigers and leopards. We suggest that leopards essentially use the habitats that cannot be utilized by tigers resulting in competitive exclusion at the fine scale. Use of these fringe habitats by leopards may be facilitated by the presence of non-native prey. Thapa (2012) reported that in Chitwan habitats that were “prey-poor”, the decline in consumption of chital (from >50% to 14%) was offset by predation on livestock and dogs.

The low power of wild prey (e.g. chital and sambar) abundance in predicting leopard habitat use, was contradictory to our expectation. It may be that the flexibility of leopard feeding strategies combined with the availability of diverse prey species in and around Chitwan might have dampened the effect of fine-scale heterogeneity of prey species abundance (Mizutani and Jewell 1998, Carter et al. 2015). As such, avoiding prey rich areas (Mueller et al. 2016) may reduce the intraguild predation cost of co-occurring with tigers, as expected under the competition risk hypothesis (Palomares et al. 2016). In the prey rich habitats such as Chitwan, where an apex predator is present at high density, dietary and fine-scale habitat flexibility allows leopards to avoid tigers at a fine spatial-scale while co-occurring in the landscape.

Consequently, conditional two-species occupancy models revealed that while the abundance of chital and sambar positively influenced tiger occupancy, livestock abundance influenced occupancy negatively. Human abundance that negatively impacted tiger occupancy in single-species model was unrelated to tiger space use when tiger occupancy was conditional on leopard presence. This finding suggests that livestock abundance in the park also plays a crucial role in determining co-occurrence of tigers and leopards. We suggest that the habitat segregation of tigers and leopards may be a result of intraguild competition (both interference and exploitative competitions) and that the competition is modulated by disturbance factors such as livestock and humans in addition to the availability of prey.

Our results clearly indicate that leopards avoid tigers even at a fine-spatial scale, but we note that ca. 25 percent of the sites that has SIF > 0.9 may have been experiencing at least some degree of species overlap. The nature of the interactions between these predators in the areas with relatively higher SIF is uncertain. As the population of tiger is recently increasing in Chitwan National Park (Dhakal et al. 2014, Karki et al. 2015), collecting species interaction data from these co-occupyed sites will enable stronger inferences about the dynamics of competition between tigers and leopards, and in particular, the relative importance of exploitative and interference competition. In western Nepal, the declaration of Bardia National Park, resulted in an increase in the tiger and chital populations, but no increase in the leopard population (Wegge et al. 2009). Such patterns might be expected if tigers directly or indirectly reduce the suitability of a site for leopards. Detail investigation of Chitwan sites with differing tiger densities, and differing human impacts, would be valuable for understanding how leopards will respond to the loss or restoration of an apex predator.

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Table 1. Model selection results for 4 single-species single-season occupancy models identifying detection covariates for tiger and leopard. All models assumed that tiger and leopard detection and occupancy are independent between the two species. K is the number of parameters, ΔAIC is the difference in AIC values with respect to the most parsimonious model, AIC wt indicates the relative support for each model included. -2LL is the deviance, -2 log likelihood of each model.

Tiger				
Model	**ΔAIC**	**AIC wt**	**K**	**(-2LL)**
Ψ(.),p(Livestock)	0	0.7257	3	1940.76
Ψ(.),p(Livestock+Human)	1.96	0.2724	4	1940.72
Ψ(.),p(.)	12.82	0.0012	2	1955.58
Ψ(.),p(Human)	13.76	0.0007	3	1954.52
Leopard				
Ψ(.),p(Livestock)	0	0.6663	3	1639.09
Ψ(.),p(Livestock+Human)	1.97	0.2488	4	1639.06
Ψ(.),p(.)	4.85	0.059	2	1645.94
Ψ(.),p(Human)	6.49	0.026	3	1645.58

Table 2. Model selection results for 4 single-species single-season occupancy models identifying occupancy covariates for tiger and leopard. All models assumed that tiger and leopard detection and occupancy are independent between the two species. (Models with no AIC wt have been omitted).

Tiger				
Model	**ΔAIC**	**AIC wt**	**K**	**(-2LL)**
Ψ(Chital+Sambar+Human),p(Livestock)	0	0.3029	6	1906.02
Ψ(Chital+Sambar),p(Livestock)	0.04	0.2969	5	1908.06
Ψ(Chital+Sambar+Livestock+Human),p(Livestock)	1.46	0.146	7	1905.48
Ψ(Chital+Sambar+Livestock),p(Livestock)	1.9	0.1172	6	1907.92
Ψ(Chital),p(Livestock)	3.66	0.0486	4	1913.68
Ψ(Chital+Human),p(Livestock)	3.67	0.0484	5	1911.69
Ψ(Chital+Livestock+Human),p(Livestock)	5.3	0.0214	6	1911.32
Ψ(Chital+Livestock),p(Livestock)	5.58	0.0186	5	1913.6
Leopard				
Ψ(Livestock),p(Livestock)	0	0.2219	4	1635.31
Ψ(Chital+Livestock),p(Livestock)	0.37	0.1845	5	1633.68
Ψ(.),p(Livestock)	1.78	0.0911	3	1639.09
Ψ(Livestock+Human),p(Livestock)	2	0.0816	5	1635.31
Ψ(s+Livestock),p(Livestock)	2.21	0.0735	5	1635.52
Ψ(Chital+Livestock+Human),p(Livestock)	2.33	0.0692	6	1633.64
Ψ(Sambar +Chital+Livestock),p(Livestock)	2.36	0.0682	6	1633.67
Ψ(Sambar),p(Livestock)	3.25	0.0437	4	1638.56
Ψ(Human),p(Livestock)	3.5	0.0386	4	1638.81
Ψ(Chital),p(Livestock)	3.58	0.0371	4	1638.89
Ψ(Sambar +Chital+Livestock+Human),p(Livestock)	4.32	0.0256	7	1633.63
Ψ(Sambar +Human),p(Livestock)	5	0.0182	5	1638.31
Ψ(Sambar +Chital),p(Livestock)	5.24	0.0162	5	1638.55
Ψ(Chital+Human),p(Livestock)	5.29	0.0158	5	1638.6
Ψ(.),p(.)	6.63	0.0081	2	1645.94
Ψ(Sambar +Chital+Human),p(Livestock)	6.98	0.0068	6	1638.29

Table 3. Parameters used in the single-season conditional two-species occupancy model. Table adapted from Richmond et al. (2010).

Parameter	Description
Ψ^{A}	Probability of occupancy of species A
Ψ^{BA}	Probability of occupancy of species B, given species A is present
Ψ^{Ba}	Probability of occupancy of species B, given species A is absent
p^{A}	Probability of detection of species A, given species B is absent
p^{B}	Probability of detection of species B, given species A is absent
r^{A}	Probability of detection of species A, given species B is present
r^{BA}	Probability of detection of species B, given both species are present and species A is detected
r^{Ba}	Probability of detection of species B, given both species are present but species A is not detected

Table 4. Model selection results for top 5 conditional two-species single-season occupancy models identifying species interactions. (See Appendix A for the details of the entire model set).

Model	ΔAIC	AIC wt	K	(-2LL)
Ψ^{A},Ψ^{BA},Ψ^{Ba}(Chital+Sambar+Livestock); p^{A},p^{B},r^{A},r^{BA},r^{Ba}(Livestock)	0.00	0.5094	12	3560.56
Ψ^{A},Ψ^{BA},Ψ^{Ba}(Chital+Sambar+Human+Livestock); p^{A},p^{B},r^{A},r^{BA},r^{Ba}(Livestock)	0.38	0.4213	13	3558.94
Ψ^{A},Ψ^{BA},Ψ^{Ba}(Chital+Sambar+Human); p^{A},p^{B},r^{A},r^{BA},r^{Ba}(Livestock)	4.16	0.0636	12	3564.72
Ψ^{A},Ψ^{BA},Ψ^{Ba}(Chital+Sambar); p^{A},p^{B},r^{A},r^{BA},r^{Ba}(Livestock)	9.35	0.0048	11	3571.91
ΨA,ΨBA,ΨBa(Chital); pA,pB,rA,rBA,rBa(Livestock)	12.69	0.0009	10	3577.25

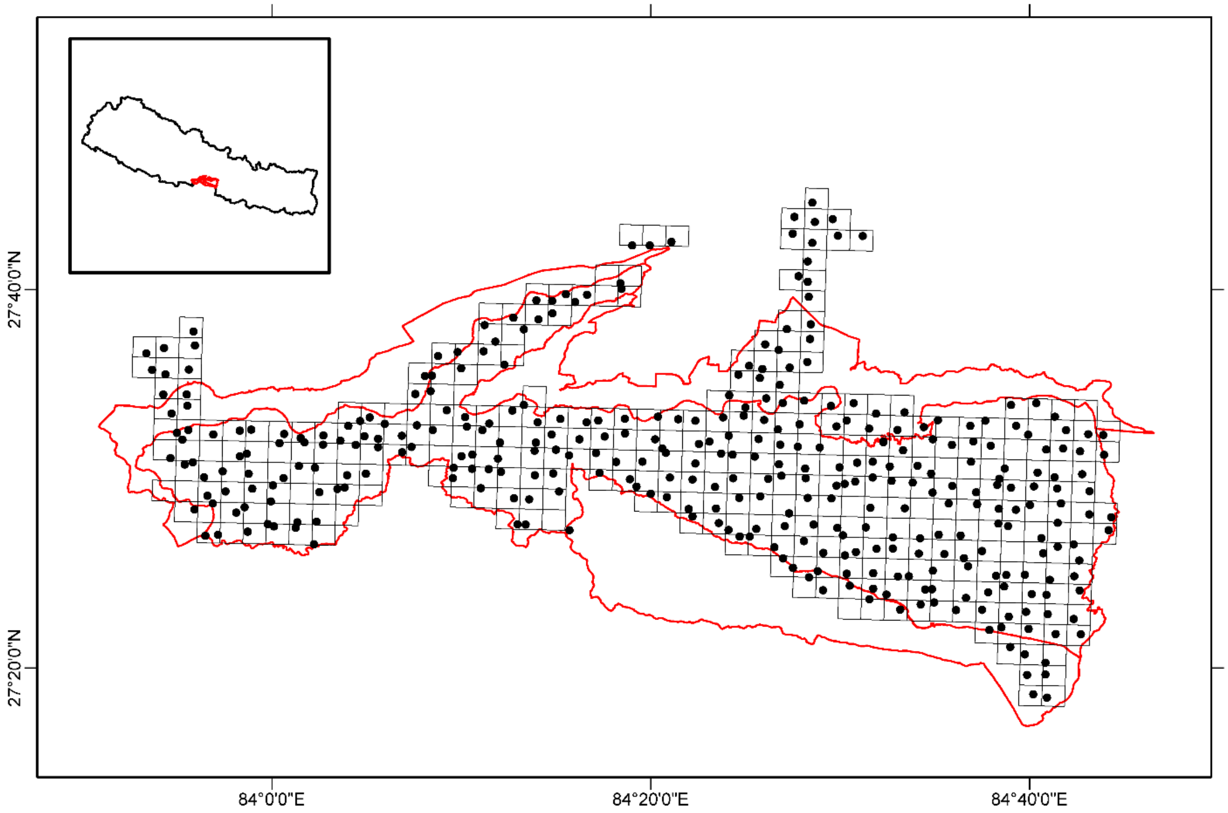

Figure 1. Location of Chitwan National Park in Nepal, distributed quadrats and camera locations.

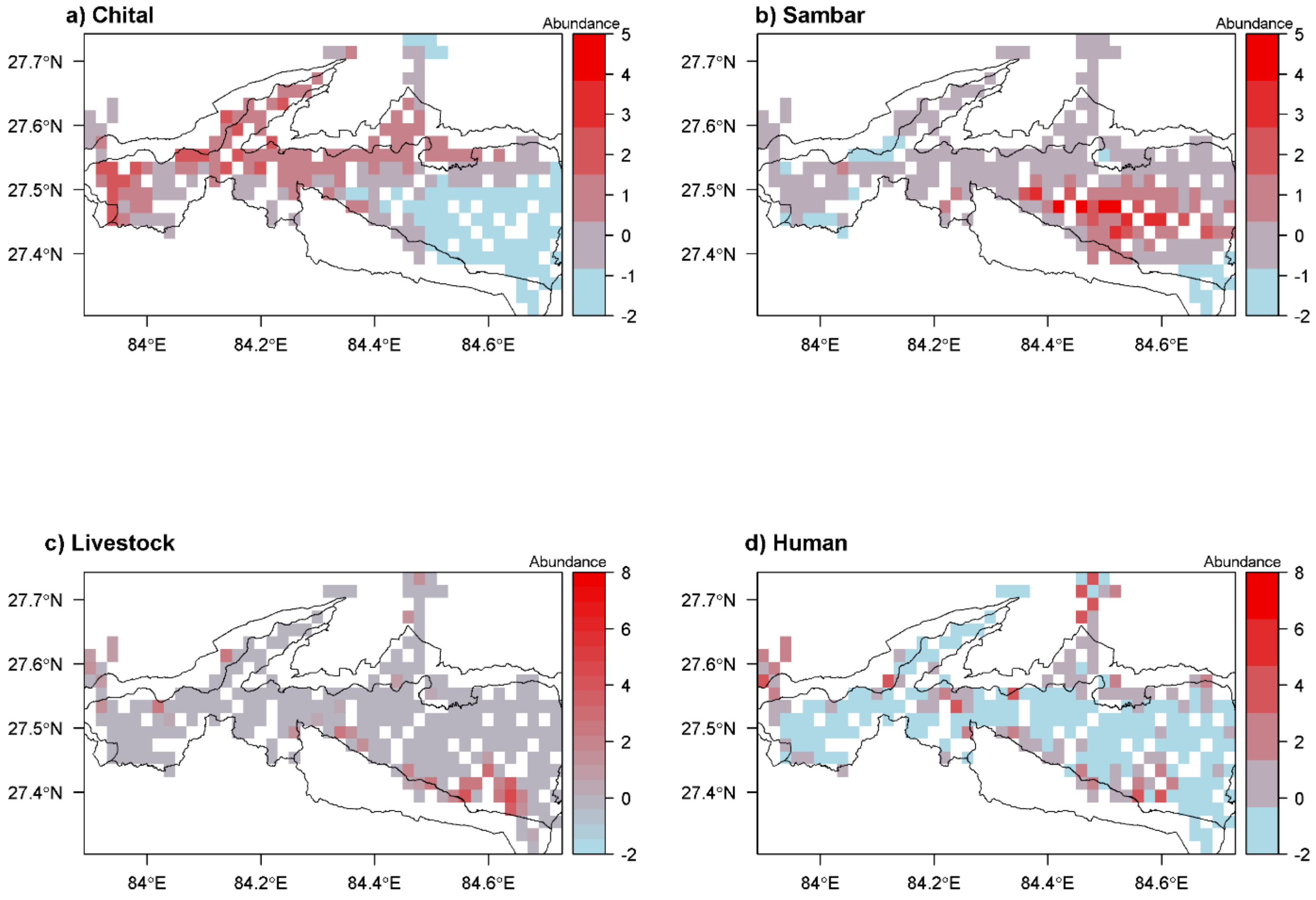

Figure 2. Estimated abundance of chital and sambar (detectability corrected) and of livestock and human abundance based on number of independent detections in each camera trap location.

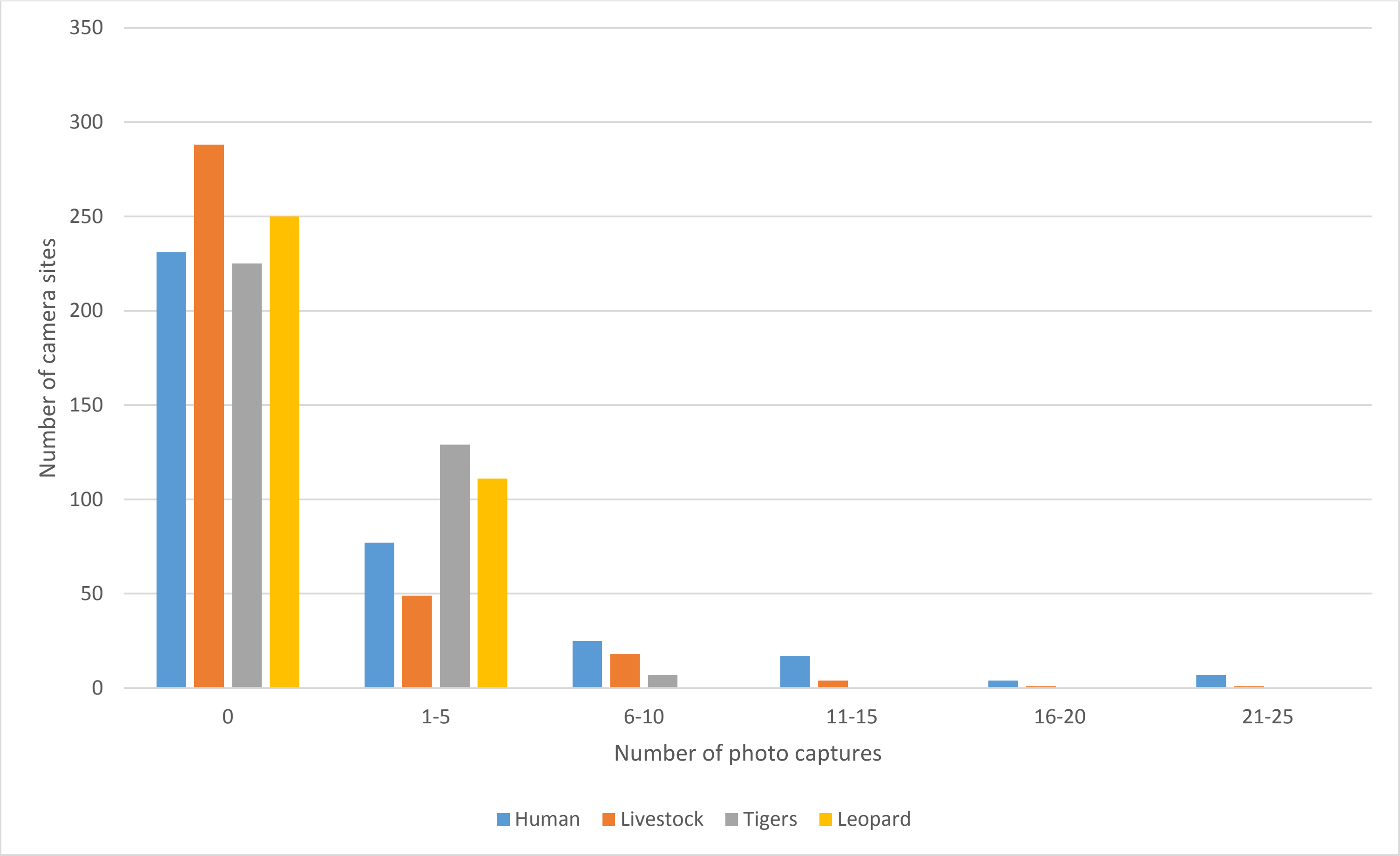

Figure 3. Number of photographs of human, livestock, tigers, and leopards captured in different number of camera sites.

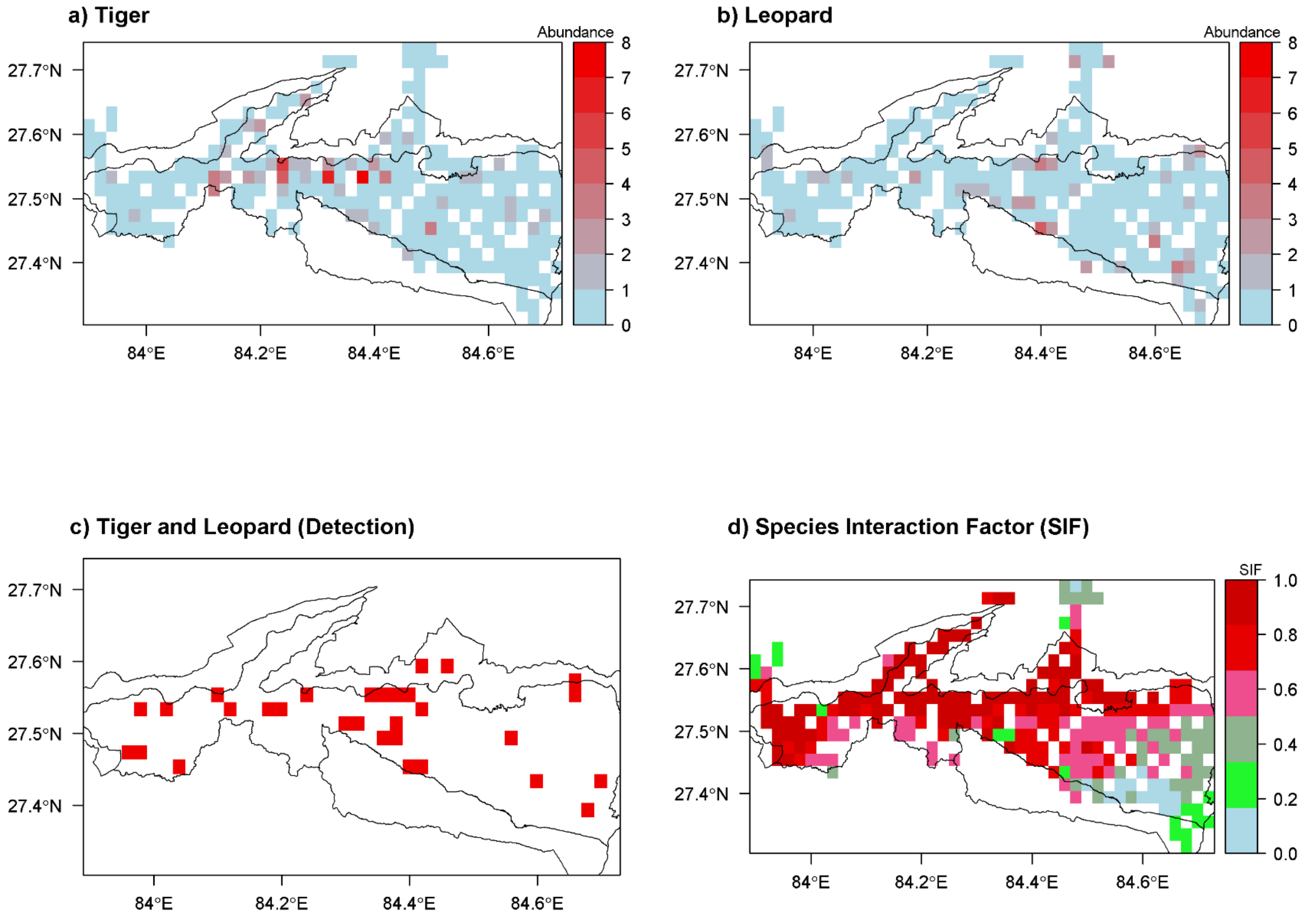

Figure 4. Detection and non-detection of tiger (a) and leopard (b). The number of independent photographs captured at the detected sites are labelled as abundance. Solid red blocks (c) shows the sites where both tigers and leopards were detected and species interaction factor (SIF) distribution (d) across the study area.

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Appendix A Occupancy models of tiger and leopard evaluating the effect of covariates on occupancy probability.

Tiger				
Model	**ΔAIC**	**AIC wt**	**K**	**(-2LL)**
Ψ(Chital+Sambar+Human), p(Livestock)	0	0.3029	6	1906.02
Ψ(Chital+Sambar), p(Livestock)	0.04	0.2969	5	1908.06
Ψ(Chital+Sambar+Livestock+Human), p(Livestock)	1.46	0.146	7	1905.48
Ψ(Chital+Sambar+Livestock), p(Livestock)	1.9	0.1172	6	1907.92
Ψ(Chital), p(Livestock)	3.66	0.0486	4	1913.68
Ψ(Chital+Human), p(Livestock)	3.67	0.0484	5	1911.69
Ψ(Chital+Livestock+Human), p(Livestock)	5.3	0.0214	6	1911.32
Ψ(Chital+Livestock), p(Livestock)	5.58	0.0186	5	1913.6
Ψ(.), p(Livestock)	28.74	0	3	1940.76
Ψ(Sambar), p(Livestock)	29.70	0	4	1939.72
Ψ(Livestock), p(Livestock)	30.55	0	4	1940.57
Ψ(Human), p(Livestock)	30.61	0	4	1940.63
Ψ(Sambar+Livestock), p(Livestock)	31.45	0	5	1939.47
Ψ(Sambar+Human), p(Livestock)	31.50	0	5	1939.52
Ψ(Livestock+Human), p(Livestock)	32.38	0	5	1940.4
Ψ(.), p(.)	41.56	0	2	1955.58
Leopard				
Ψ(Livestock), p(Livestock)	0	0.2219	4	1635.31
Ψ(Chital+Livestock), p(Livestock)	0.37	0.1845	5	1633.68
Ψ(.), p(Livestock)	1.78	0.0911	3	1639.09
Ψ(Livestock+Human), p(Livestock)	2	0.0816	5	1635.31
Ψ(s+Livestock), p(Livestock)	2.21	0.0735	5	1635.52
Ψ(Chital+Livestock+Human), p(Livestock)	2.33	0.0692	6	1633.64

Ψ(Sambar +Chital+Livestock), p(Livestock)	2.36	0.0682	6	1633.67
Ψ(Sambar), p(Livestock)	3.25	0.0437	4	1638.56
Ψ(Human), p(Livestock)	3.5	0.0386	4	1638.81
Ψ(Chital), p(Livestock)	3.58	0.0371	4	1638.89
Ψ(Sambar +Chital+Livestock+Human), p(Livestock)	4.32	0.0256	7	1633.63
Ψ(Sambar +Human), p(Livestock)	5	0.0182	5	1638.31
Ψ(Sambar +Chital), p(Livestock)	5.24	0.0162	5	1638.55
Ψ(Chital+Human), p(Livestock)	5.29	0.0158	5	1638.6
Ψ(.), p(.)	6.63	0.0081	2	1645.94
Ψ(Sambar +Chital+Human), p(Livestock)	6.98	0.0068	6	1638.29

Appendix B Two-species Single-season occupancy models examining the co-occurrence of tigers and leopards in response to the covariates (c- chital, s- sambar, li- livestock, hu- human).

Model	**ΔAIC**	**AIC wt**	**K**	**(-2LL)**
psiA,psiBA,psiBa-(c+s+li),pA,pB,rA,rBA,rBa- (li)	0.00	0.5094	12	3560.56
psiA,psiBA,psiBa-(c+s+hu+li), pA,pB,rA,rBA,rBa- (li)	0.38	0.4213	13	3558.94
psiA,psiBA,psiBa-(c+s+hu),pA,pB,rA,rBA,rBa- (li)	4.16	0.0636	12	3564.72
psiA,psiBA,psiBa-(c+s),pA,pB,rA,rBA,rBa- (li)	9.35	0.0048	11	3571.91
psiA,psiBA,psiBa- (c),pA,pB,rA,rBA,rBa- (li)	12.69	0.0009	10	3577.25
psiA,psiBA,psiBa- (li),pA,pB,rA,rBA,rBa- (li)	23.90	0.0000	10	3588.46
psiA,psiBA,psiBa-(s+li),pA,pB,rA,rBA,rBa- (li)	24.60	0.0000	11	3587.16
psiA,psiBA,psiBa-(li+hu),pA,pB,rA,rBA,rBa- (li)	25.78	0.0000	11	3588.34
psiA,psiBA,psiBa-(s+li_hu),pA,pB,rA,rBA,rBa- (li)	26.44	0.0000	12	3587
psiA,psiBA,psiBa,pA,pB,rA,rBA,rBa	27.86	0.0000	8	3596.42
psiA,psiBA,psiBa- (s),pA,pB,rA,rBA,rBa- (li)	30.34	0.0000	10	3594.9
psiA,psiBA,psiBa- (hu),pA,pB,rA,rBA,rBa- (li)	37.87	0.0000	10	3602.43
psiA,psiBA,psiBa-(s+hu),pA,pB,rA,rBA,rBa- (li)	38.58	0.0000	11	3601.14
psiA,psiBA,psiBa- (c+s+hu) ,pA,pB,rA,rBa- (li)	61.91	0.0000	11	3624.47
psiA,psiBA,psiBa- (c+s),pA,pB,rA,rBa - (li)	62.40	0.0000	10	3626.96
psiA,psiBA,psiBa- (c) ,pA,pB,rA,rBa - (li)	62.56	0.0000	9	3629.12

psiA,psiBA,psiBa- (c+s+li+hu) ,pA,pB,rA,rBa- (li)	63.91	0.0000	12	3624.47
psiA,psiBA,psiBa- (c+s+li),pA,pB,rA, rBa- (li)	64.11	0.0000	11	3626.67
psiA,psiBA,psiBa- (s) ,pA,pB,rA,rBa- (li)	79.10	0.0000	9	3645.66
psiA,psiBA,psiBa- (li) ,pA,pB,rA,,rBa- (li)	79.59	0.0000	9	3646.15
psiA,psiBA,psiBa- (hu) ,pA,pB,rA,,rBa- (li)	79.94	0.0000	9	3646.5
psiA,psiBA,psiBa- (s+li) ,pA,pB,rA,,rBa- (li)	80.19	0.0000	10	3644.75
psiA,psiBA,psiBa- (s+hu) ,pA,pB,rA,,rBa- (li)	80.60	0.0000	10	3645.16
psiA,psiBA,psiBa- (li+hu),pA,pB,rA,,rBa- (li)	81.40	0.0000	10	3645.96
psiA,psiBA,psiBa- (s+li+hu) ,pA,pB,rA,,rBa- (li)	81.96	0.0000	11	3644.52
psiA,psiBA,psiBa- (c+s+hu) ,pA,pB,rA,rBA- (li)	517.74	0.0000	11	4080.3
psiA,psiBA,psiBa-(c+s),pA,pB,rA,rBA- (li)	518.81	0.0000	10	4083.37
psiA,psiBA,psiBa- (c) ,pA,pB,rA,rBA- (li)	519.56	0.0000	9	4086.12
psiA,psiBA,psiBa- (c+s+li+hu) ,pA,pB,rA,rBA- (li)	519.74	0.0000	12	4080.3
psiA,psiBA,psiBa- (c+s+li) ,pA,pB,rA,rBA- (li)	520.47	0.0000	11	4083.03
psiA,psiBA,psiBa- (li) ,pA,pB,rA,rBA- (li)	539.65	0.0000	9	4106.21
psiA,psiBA,psiBa- (s+li) ,pA,pB,rA,rBA- (li)	540.28	0.0000	10	4104.84
psiA,psiBA,psiBa- (hu) ,pA,pB,rA,rBA- (li)	540.64	0.0000	9	4107.2
psiA,psiBA,psiBa- (li+hu) ,pA,pB,rA,rBA- (li)	541.00	0.0000	10	4105.56
psiA,psiBA,psiBa- (s) ,pA,pB,rA,rBA- (li)	541.27	0.0000	9	4107.83
psiA,psiBA,psiBa (s+hu) ,pA,pB,rA,rBA- (li)	541.39	0.0000	10	4105.95

psiA,psiBA,psiBa- (s+li+hu) ,pA,pB,rA,rBA- (li)	541.55	0.0000	11	4104.11
psiA,psiBA,psiBa- (c+s+hu) ,pA,pB,rA- (li)	554.93	0.0000	10	4119.49
psiA,psiBA,psiBa- (c+s) ,pA,pB,rA- (li)	556.14	0.0000	9	4122.7
psiA,psiBA,psiBa- (c+s+li+hu),pA,pB,rA- (li)	556.93	0.0000	11	4119.49
psiA,psiBA,psiBa- (c) ,pA,pB,rA,rA- (li)	556.94	0.0000	8	4125.5
psiA,psiBA,psiBa- (c+s+li),pA,pB,rA- (li)	557.72	0.0000	10	4122.28
psiA,psiBA,psiBa- (li) ,pA,pB,rA- (li)	576.92	0.0000	8	4145.48
psiA,psiBA,psiBa- (s+li) ,pA,pB,rA- (li)	577.55	0.0000	9	4144.11
psiA,psiBA,psiBa- (hu) ,pA,pB,rA- (li)	578.04	0.0000	8	4146.6
psiA,psiBA,psiBa- (li+hu) ,pA,pB,rA- (li)	578.24	0.0000	9	4144.8
psiA,psiBA,psiBa- (s),pA,pB,rA- (li)	578.78	0.0000	8	4147.34
psiA,psiBA,psiBa- (s+li+hu) ,pA,pB,rA- (li)	578.79	0.0000	10	4143.35
psiA,psiBA,psiBa- (s+hu),pA,pB,rA- (li)	578.79	0.0000	9	4145.35
psiA,psiBA,psiBa (c+s+hu) ,pA,pB,,rBa - (li)	623.52	0.0000	10	4188.08
psiA,psiBA,psiBa- (c+s+li+hu) ,pA,pB,,rBa- (li)	625.14	0.0000	11	4187.7
psiA,psiBA,psiBa- (c+s) ,pA,pB,,rBa- (li)	626.27	0.0000	9	4192.83
psiA,psiBA,psiBa- (c+s+li),pA,pB,,rBa - (li)	626.78	0.0000	10	4191.34
psiA,psiBA,psiBa- (c),pA,pB,,rBa- (li)	627.33	0.0000	8	4195.89
psiA,psiBA,psiBa- (li) ,pA,pB,,rBa- (li)	645.54	0.0000	8	4214.1
psiA,psiBA,psiBa- (s+li) ,pA,pB,,rBa- (li)	646.05	0.0000	9	4212.61
psiA,psiBA,psiBa-(li+hu) ,pA,pB,,rBa- (li)	646.34	0.0000	9	4212.9
psiA,psiBA,psiBa- (s+li+hu) ,pA,pB,,rBa- (li)	646.78	0.0000	10	4211.34
psiA,psiBA,psiBa- (hu) ,pA,pB,,rBa- (li)	648.19	0.0000	8	4216.75

psiA,psiBA,psiBa- (s+hu) ,pA,pB,,rBa- (li)	648.92	0.0000	9	4215.48
psiA,psiBA,psiBa- (s) ,pA,pB,,rBa- (li)	649.98	0.0000	8	4218.54
psiA,psiBA,psiBa- (c+s+hu),pA,pB- (li)	1107.90	0.0000	9	4674.46
psiA,psiBA,psiBa- (c+s+li+hu),pA,pB- (li)	1109.79	0.0000	10	4674.35
psiA,psiBA,psiBa- (c+s),pA,pB- (li)	1109.80	0.0000	8	4678.36
psiA,psiBA,psiBa - (c),pA,pB- (li)	1110.84	0.0000	7	4681.4
psiA,psiBA,psiBa- (c+s+li),pA,pB- (li)	1110.92	0.0000	9	4677.48
psiA,psiBA,psiBa- (li) ,pA,pB- (li)	1130.15	0.0000	7	4700.71
psiA,psiBA,psiBa - (s+li) ,pA,pB- (li)	1130.79	0.0000	8	4699.35
psiA,psiBA,psiBa- (li+hu) ,pA,pB- (li)	1131.27	0.0000	8	4699.83
psiA,psiBA,psiBa- (s+li+hu) ,pA,pB- (li)	1131.82	0.0000	9	4698.38
psiA,psiBA,psiBa- (hu) ,pA,pB- (li)	1131.90	0.0000	7	4702.46
psiA,psiBA,psiBa- (s+hu) ,pA,pB- (li)	1132.70	0.0000	8	4701.26
psiA,psiBA,psiBa- (s) ,pA,pB- (li)	1133.22	0.0000	7	4703.78

CHAPTER V

ALTERNATIVE FINANCING SCHEMES FOR TIGER CONSERVATION IN NEPAL

Hemanta Kafley[1, 2, *], Matthew E. Gompper[1], Felix Spinelli[3], Krishna L. Poudel[4], Bishnu P. Thapaliya[5]

[1]Department of Fisheries and Wildlife Sciences, University of Missouri, Columbia, MO 65211, USA.

[*]Email: hkc5b@mail.missouri.edu

[2]Nepal Nature Foundation, Koteshwor, Kathmandu-34, Nepal

[3]221 W, Grant St., Bozeman, MT 59715, USA

[4]Department of Agricultural Economics, University of Missouri, Columbia, MO 65211, USA

[5]Chitwan National Park, Kasara, Chitwan, Nepal

Abstract

Many scientists and conservation workers agree that global tiger numbers in key areas could double by 2022 if efforts are taken immediately. Countries facing declining tiger numbers and having the ability to meet this goal have produced national tiger recovery plans that outline necessary program activities and their associated costs. To assess the financial feasibility of the tiger conservation program in Nepal and to recommend viable alternatives to secure funds to cover long-term tiger conservation costs, we conducted financial analyses of tiger conservation programs in Nepal. Our results show that the present funding level fails to cover the long-term costs of taking the recommended steps for tiger conservation. Thus there is a need to identify and secure alternative funding sources to supply approximately a 100% increase in revenues currently generated from tiger-bearing protected areas assuming a continuance of the current level of funding by the government. This finding is troublesome given the magnitude of the financial burden associated with necessary steps to increase the tiger population, plus the fact that no policy instrument exists that can target the revenue generated by the protected areas specifically for tiger conservation. To achieve financial sustainability of the tiger conservation program, alternative financial mechanisms warrant serious consideration. One alternative institutional mechanism could be a tiger conservation trust fund that would be entrusted to secure a wide range of financing from domestic and international sources to ensure financial sustainability of the Nepal's tiger conservation program.

Key words: *Conservation finance, Conservation economics, Panthera tigris, Conservation trust fund*

Introduction

The successful conservation of ecosystems depends on a mix of environmental, social and economic factors. For nations that struggle financially to provide basic public services, the funding of ecosystem maintenance or conservation agendas often are not the highest priority for limited government dollars. In many of these situations, the opportunity costs of maintaining wilderness is perceived as higher than the benefits to the local community or the government – especially in a short-term context [1]. Because short-term solutions yield poor long-term outcomes, global communities recognize that funding remedies are needed to address this short-term investment decision so that conservation of the world's remaining natural systems can be achieved.

In this context, Nepal is striving to identify and secure a sustainable financing mechanism to support tiger conservation programs. A tiger conservation program has been identified and designed for Nepal to meet its' global commitment of doubling the tiger numbers by 2022 [2, 3]. This paper analyses the current funding of Nepal's tiger conservation program and the potential of Nepal to fund tiger conservation into the future. Current and future gross costs of tiger conservation in Nepal are estimated in this analysis, something that is rarely conducted for any species and has never been conducted for tigers. Because this analysis finds a serious short-fall in current funding with funding levels needed to achieve tiger conservation goals, alternative potential funding sources are presented and discussed in the context of ensuring the sustainability of tiger conservation programs in Nepal into the future.

Tigers are globally revered and tiger conservation is probably the highest funded conservation program in Nepal. As tigers are recognized as the umbrella species in the regional ecosystem, conservation efforts targeted for tigers have cascading positive impacts on the conservation of biodiversity system-wide [2, 4, 5]. Therefore, a higher conservation cost for tigers is more easily justified when taking into account its positive, synergistic impact on other species and ecosystem services [5]. However, the ability of a developing country such as Nepal to meet the required costs for conservation and sustain efforts to meet the goal of doubling Nepal's tiger population poses a major obstacle for Nepal and the global conservation community.

Funding for conservation, especially when dealing with a goal of improving overall habitat and biodiversity, is always limited [6, 7]. One concrete example of the umbrella species effect brought about by improved tiger habitat is the enhancement of other native wildlife species, such as elephant, rhino, and deer. Although not quantified in this analysis, such general and widespread benefits are apparent in Nepal and should be convincing even with a limited focus on tiger conservation. At a minimum, the estimation of associated expected costs of tiger conservation can provide crucial information if efforts are implemented successfully to halt extinctions of other species [8]. However for most of the terrestrial sites of global conservation significance, the costs of reducing extinction risk by effective and sustained best management practices are largely unknown [8]. Through a National Tiger Recovery Plan (NTRP) Nepal has stated its commitment to develop a comprehensive financial plan that will ensure that full costs of the tiger program are met and maintained in perpetuity [3, 9]. In Nepal, the government has estimated the annual cost for tiger conservation programs as currently roughly $6.5 million (GTRP 2010-22). This estimate is purely a financial calculation and cannot be considered as a total economic cost. Although this amount represents only 0.125 percent of total government spending, any additional money to increase tiger conservation efforts would need all stakeholders including the Nepalese government authority to fully understand all the benefits and costs of action or inaction. This holds true whether benefits are measured in monetary values or in physical values (e.g. species or ecosystem attributes wherein carnivores provide a useful purpose of keeping populations of other species in check). In addition, results of economic analyses may not always be the driving force determining the goals of biodiversity conservation investment [10] especially in the case of carnivore conservation where the direct costs at a local level may lead to a short-term solution that does not consider long-term ramifications – a classic case of a "market failure" in the natural resource literature [11]. Large carnivores such as tigers are valued at global or national scale but the costs are usually born at the local level, creating "market failure" that escalates human-carnivore conflict [12] and might be an underlying cause of carnivore declines [11].

Financial analysis establishes the magnitude of costs of capital investments and weighs these against financial benefits of a program. In the context of tiger conservation programs in Nepal, investment costs include financial resources required to maintain and protect the tiger-bearing protected areas (hereafter 'TBPAs') and the broader Terai Arc Landscape (hereafter 'TAL') encompassing approximately 12.3 million acres in Nepal and neighboring India, and conducting other specific tasks pertaining to tiger conservation (see the GTRP 2013-14 implementation plan for a breakdown of program costs) beyond the immediate habitats occupied by tigers [13].

The benefit stream referred to in this case is not the typical set of benefits in most environmental economic studies. It does not include economic values generated by overall ecosystem services and tourist spending generated from tiger conservation, but rather simply refers to the existence of a positive gap between expected program funding and program costs. In a sense, this analysis can be thought of as a budget analysis, weighing the possible annual funding with program costs. Program funding includes income from donations obtained from national and international funding agencies for tiger conservation activities, regular cash flow set-aside by the government, and other finances committed by international development organizations such as the World Bank and the United Nations Development Program. The financial analysis also integrates other possible future financing sources as benefits, modified to account for the terms and conditions of financing. Wildlife premiums, either linked to, or independent of, carbon and non-carbon payments for ecosystem services (PES) [4], could also potentially be included in the benefit stream.

Methods

We used a capital budgeting [14] approach for our analyses and estimated Net Present Value (NPV) and Benefit Cost (B/C) ratio [15]. NPV and B/C ratio are widely used for assessing sustainability of conservation projects [16]. NPV is defined as the present value (PV) of the net income stream accruing to the tiger program [17]. NPV calculation requires a discount rate, the rate reflecting the public’s preference for money to be received in the future. The market cost of borrowing money from banks and other financial institutions is the general interest rate charged to entities and is widely interpreted as the public's discount rate for various financial analysis purposes [16, 18, 19]. If the tiger conservation program cannot generate an income stream sufficient to pay back the loan plus the interest, then the program lacks financial sustainability. The B/C ratio is the ratio of the PV of the benefit stream and the PV of the cost stream. Thus, in this paper the B/C ratio can be interpreted as the difference in the stream of expected available funding compared to the stream of expected costs. A ratio greater than 1, at the current discount rate, indicates that the funding levels exceeds the costs (i.e., the program is financially sustainable). If the ratio falls below 1, the costs outweigh the funding level and the financial sustainability of the program cannot be assured [17].

Costs and funding levels for tiger conservation program were estimated based on information from government authorities and other stakeholders, such as international or non-governmental organizations (I/NGOs). We consider two types of costs: basic cost and optimal cost [20] of tiger conservation programs based on the data available and the existing practice of cost estimation [9]. These costs are determined based on two assumptions: 1) Basic cost for tiger conservation is the cost required to maintain TBPAs in Nepal (costs of programs implemented by the government in the TBPAs and the costs of government endorsed conservation projects conducted by partner organizations in or outside the protected areas); 2) Optimal cost is defined as the cost that the government deems necessary to improve tiger conservation outcomes reflected in the proposed required costs associated with the Global Tiger Recovery Program 2010-2022. Because the economic costs of tiger conservation are beyond the scope of this study, any opportunity costs of tiger conservation, or the positive/negative externalities of conservation programs, are not considered. Hence, direct expected financial funding needed for the tiger conservation program is considered as cost. Similarly direct financial inflows in the TBPAs including government funding and TBPAs' income constitute the revenues for further analytic purpose.

The NPV criterion of the Capital Budgeting Approach [17, 21], which uses the discounting formulas for a non-uniform or uniform series of payments to value the projected cash flows for each investment alternative at one point in time, was used to conduct sensitivity analysis of sustainability under different revenue and cost alternatives. The formulae used to obtain the discount factor, NPV and the B/C ratio are:

Discount factor, $df = \frac{1}{(1+r)^t}$ 1

Present value of cashflow, $PV = FV \times \frac{1}{(1+r)^t}$ 2

Net Present Value, $NPV = \sum_{t=1}^{n} \frac{C_t}{(1+r)^t} - C_0$ 3

Where

t = the time of the cash flow

n = the total time of the project

r = the discount rate

C_t = the net cash flow (the amount of cash) at time t.

C_0 = the capital outlay at the beginning of the investment time ($t = 0$)

The decision making framework of these financial indicators [21] was adopted to identify the sustainability of the tiger conservation program (Table 1). Sensitivity analyses were conducted based on the same criteria given above by creating alterative scenarios based on different levels of support from existing funding sources and assumed expected higher incoming cash flows from higher revenues generated by TBPAs. Potential finances from any sources that could not be quantified in terms of amount of support are discussed qualitatively and not included in the analyses.

Results and Discussion

Tiger conservation costs and funding

The average annual basic cost of tiger conservation in Nepal from 2014 through 2023 was estimated to be US $5.2 million. The average annual funding level secured from internal government sources for covering these costs was approximately US$3.2 million. Thus there was an annual short-fall of US $2.0 million for meeting the basic cost during the 10-year period from 2014 to 2023 (Table 2). This gap increases when one considers the additional funding needed to finance the ‘optimal’ level of effort to meet the goal of a doubling tiger population.

The optimal cost of tiger conservation in Nepal, as proposed by the government to achieve the targets mentioned in NTRP, would add approximately US$1.5 million [9] to the basic 2014-2023 cost level, increasing average annual total costs to US$6.7 million (See appendix for the cost and revenue composition). Compared to the static secured funding level of US$3.2 million, the annual deficit for sustaining the program would increase to US$3.6 million or US$36.0 million over the 10-year period from 2014 to 2023. Hence, the results show that funding must increase by 65% over current levels to meet basic costs and more than double over current funding to match the proposed optimum funding. Thus, our analysis shows that the government funding cannot meet the growing conservation costs, even if income generated by TBPAs is included (Fig. 1). A 20% increase in TBPA income in addition to the government budget would meet the total cost of the basic and optimum conservation efforts by the year 2023. In the best-case scenario, if TBPA income is doubled and combined with the government funding, the total funding would meet the optimum cost of tiger conservation in the year 2016 and beyond.

In a recent study [22] conducted in the areas within the TAL of Nepal, the proposed cost for managing that landscape for achieving the integrated biodiversity conservation with a special focus on tiger conservation is estimated as >US$20 million per year. Against these annual costs, the study identified only US$4 million per year in secured committed funding and US$2 million per year coming from prospective investors in TAL [22]. Using this scenario, the cumulative total of this annual US$14 million funding short-fall produced a 10-year gap of US$140 million over the 2014 – 2023 projection period. These estimates, reflecting both the basic and optimal cost scenarios, reinforce our findings that Nepal’s tiger conservation program is not financially sustainable given current costs and committed funding.

Sensitivity analyses and I/NGO support

Financial analyses found that Nepal’s tiger conservation program is not financially sustainable through current government funding alone for both the basic cost scenario and optimal cost scenario (both producing negative NPVs and B/C ratios of < 1). The addition of increased income from TBPAs in the benefit stream did not change these results. To meet the optimum cost of tiger conservation, TBPAs would need to double their gross revenues. Only at this income scenario, would the NPV be positive and the B/C ratio approach 1 (Fig. 2). However, anticipating a sudden increase in park revenue of this magnitude is not presently realistic.

One means to remedy this situation is to identify alternative revenue streams. Given that funds pledged to Nepalese conservation programs by international non-governmental organizations (I/NGOs), and in particular, by World Wildlife Fund Nepal (WWF Nepal), has a long history, including these contributions as a sustainable source of revenue deserves attention. Sensitivity analysis including the revenue through WWF Nepal, but excluding revenue from TBPAs, produced a negative NPV and a B/C ratio of less than one. However, revenues from WWF Nepal supplementing constant revenues for TBPAs (adjusting for inflation) produced a positive NPV and a B/C ratio greater than one. Thus, the funding secured through I/NGOs such as the WWF Nepal program is vital for the sustainability of Nepal's tiger conservation program.

Despite the positive result that we identified by increasing TBPA income and by including revenues from I/NGOs, several concerns exist. First, support from I/NGOs may not be forthcoming in any given year. Second, and perhaps more importantly, present Nepal policy does not allow the revenue generated by TBPAs to be directly applied to offset the costs of tiger conservation programs. For example, 30-50% of current total revenues are channeled to buffer zone communities that reside outside the TBPAs (National Parks and Wildlife Conservation Act 1973 Fourth Amendment) and the remaining funds are retained by the central government.

Carbon Payment (REDD+), Wildlife Premiums, and Dept-for-Nature Swaps

The Reduced Emissions from Deforestation and Forest Degradation (REDD) program, and the REDD+ program (which extended the scope of REDD and includes the role of conservation, sustainable forest management, enhancement of forest carbon stock and climate related aspects) are United Nations-based efforts to create financial value for the carbon stored in forests. The program offers incentives to developing countries for reducing emissions from forestlands and adopting low-carbon paths to sustainable development. This international financing mechanism of carbon payments can be leveraged to make payments for forest biodiversity as well [23, 24]. The carbon market potentially provides great opportunity to secure forest resources in developing countries by offering financial incentives to protect forests. In Nepal, this would also protect tigers and generate fiscal resources. The mechanism for REDD implementation in Nepal is still in a preliminary stage. There is no set mechanism nationally and internationally for the appropriate payment system [25]. However, projects examining how forest carbon credits and payments for other ecosystem services (biodiversity, water/food provisioning, soil conservation, etc.) can be pursued are underway [26, 27]. In the current context, carbon payments can be considered as potential financial sources in the long-term, but cannot be viewed as a source of sustainable finances for on-going tiger conservation programs in Nepal. Moreover, no data exists on carbon stock availability in the tiger inhabited landscape or on the price of per unit area carbon sequestrated. Hence, projecting the value of carbon that could be sequestered in Nepal’s forests within the range of tiger conservation landscape is analytically unfeasible and unrealistic. We suggest the need to design a pilot project to explore the potential finances that could be generated through carbon payments for supporting tiger conservation program. If appropriately designed and successfully implemented, carbon payment through REDD+ could be a reliable and sustainable source of funding for tiger conservation.

Dinerstein et. al. (2010) suggest that a World Bank-catalyzed wildlife carbon fund that creates a premium carbon-related market for wildlife conservation would be a complementary mechanism to REDD+ [28]. This mechanism would ensure co-benefits for wildlife through the carbon payments. The benefit of this approach for the priority conservation programs such as the tiger conservation program is that the funds will be available from the outset and focused, creating incentives to develop projects targeting wildlife. We recommend the REDD implementing agencies and conservation institutions collaboratively work to identify mechanisms that incorporate wildlife conservation as one of the major targets within REDD+ projects. Indeed, conservation finance in Nepal needs to go beyond traditional government or donor funding by exploring innovative market-based approaches [4, 28-30] such as debt-for-nature swaps, environmental funds, payment for ecosystem services (PES) and any other performance-based payment strategies.

Debt-for-nature swaps are financial transactions that involve renegotiation of the terms of a developing country's debt between an outside agency (I/NGOs or credibly established trust funds) or creditor (typically a developed country) and debtor country. Under this mechanism, the public debt of the developing country is purchased at a discount by a third-party and retired in exchange for government commitments to fund conservation programs by the developing country [31]. Debt-for-nature-swaps have been a major source of funding for securing start-up capital for conservation trust funds in many countries in Latin America and a few countries in Asia and Africa [29, 31]. A study in Nepal [32] emphasized that Nepal has high potential for these swaps because Nepal has a high level of foreign debt, the country's financial inability to otherwise allocate adequate resources to meet the increasing cost of maintenance of the natural habitats, and the country's demonstrated commitment towards the environment conservation. However, a more recent feasibility assessment would be needed to establish Nepal's current position to undertake this venture and to project potential success. If applicable, this mechanism could potentially secure the capital for establishing a conservation trust fund, perhaps one exclusively targeted for tiger conservation, in Nepal.

Increased domestic finances

The TBPAs and community forests in the Nepalese TAL have high potential to generate revenues through tourism. In recent years, the number of tourists visiting protected areas in Nepal has grown (Department of National Parks and Wildlife Conservation, unpublished data), and this tourism is a potential source of employment and foreign currency, thereby creating a mechanism to achieve sustainable economic development [33]. Tourists visiting Chitwan National Park were willing to pay almost three times more than the current park entrance fee for their visit to the park [34]. Periodic adjustment of entrance fees could ensure increased income to the community without the risk of cutting tourist numbers. The increased income that goes to the buffer zone community might not directly contribute for offsetting the costs for tiger conservation but it can tremendously help in lowering the cost of conservation. If the buffer zone, or community forests, can support their costs of conservation through increased income, the overall gap in tiger financing could be substantially reduced.

Securing cash flow from environmentally responsible citizens and corporate businesses in the country can further reduce this funding gap. Locally, Nepal should aim at raising funds from within the country by creating awareness of local entities to accept the responsibility for maintaining the natural system they operate in. Finding a mechanism to generate a sustainable source of funding via local citizenry, regardless of its size, through any form of contributions or charges, would contribute to a narrower funding gap. These contributions and charges could be obtained from any direct or indirect beneficiaries such as Nepali tourists visiting wilderness areas, local or large-scale businesses, and pledges from individuals and organizations. This, as yet untapped, internal financing source could potentially emerge as a sustainable source of finance for Nepal's tiger conservation program.

Tiger Conservation Trust Fund

In many developing countries, environmental trust funds have played a pivotal role in ensuring the long-term financial sustainability of conservation programs [29]. We envision a Tiger Conservation Trust Fund (TCTF) in Nepal that would not only be a financial mechanism, but also an institutional arrangement to convene different actors in tiger conservation for enabling collaborative program planning and implementation. Such a framework could even cross international borders, as India has also pledged to double their tiger population. A well-funded, focused trust fund could avoid duplication of programs, provide a long-term perspective, and help channel funds more appropriately to priority projects. Conservation trust funds are usually registered as autonomous legal entities, although they can be established under a variety of different legal regimes depending on a country's legal provision. Although the legality of the establishment of a

Nepali conservation trust fund is beyond the scope of this paper, we recommend identifying an appropriate model that encourages active participation of civil society and non-governmental bodies. Considering the importance placed on tigers by the government, we propose a mixed board including members from relevant government authorities and local stakeholders, as well as natural resource specialists. This would facilitate coordination among stakeholders and avoid the hindrances that might be posed in the absence of government representation. External audits, on a regular basis, would assure accountability of how funds are secured and dispersed. The major capital investments for the trust fund would come from bilateral (bilateral grants and debt-for nature-swaps) and multilateral (e.g. UNDP-Global Environment Facility) donors, international foundations and I/NGOs. Hence, the trust fund would need to be established so that it retains the mandate to negotiate with these funding sources and receive the funds. We also emphasize the potential role of the trust fund in seeking domestic funding sources. Though there are numerous I/NGOs that strive to provide funding for conservation in Nepal, few organizations that we are aware of have been able to secure funds from individual or corporate donors within the country. A TCTF could emerge as the credible institutional mechanism that can tap funding from these sources.

Concluding Comments

Conservation funding is always in short-supply. The problem is particularly acute in developing countries like Nepal. Despite the will of the government and support from international agencies, adequate funding is difficult to secure for conserving even iconic species like the tiger. Past aid, in combination with government support, has allowed Nepal to make significant progress towards fulfilling its commitment to the global tiger conservation agenda, and there is an active tiger recovery plan in place that objectively aims at contributing to the global goal of doubling the tiger population by 2022 by doubling Nepal's own tiger population. However, most of the funds allocated by the government towards tiger conservation are spent in salaries and wages of staff, expenditure on capital assets and other operating costs. Relatively few funds are left for program expenses and especially for targeted activities such as anti-poaching activities, trade-control and habitat maintenance and management. Therefore, the proposed recommendation to create the TCTF that could aggregate funding from various sources, such as from international and indirect investment made by the income generated by the local communities, deserves serious consideration.

In the context of overall biodiversity conservation as well as for tiger conservation, international funds have played an important role in enabling conservation initiatives. Funds from the WWF have been dedicated to maintaining wilderness characteristics of the TAL, thereby conserving the biodiversity of the system while improving the livelihood of local community. Similarly, the National Trust for Nature Conservation, a prominent Nepalese NGO secures funding from various international funding agencies to conduct conservation programs through the Biodiversity Conservation Center and the Bardia Conservation Program (in the TAL). One of the caveats about internationally secured funding through aid and donations as well as NGO-derived funds, however, is that such funds cannot be guaranteed for long-term project operation and maintenance. The establishment of the TCTF would provide such certainty by creating a national financing mechanism for financing long-term tiger conservation programs.

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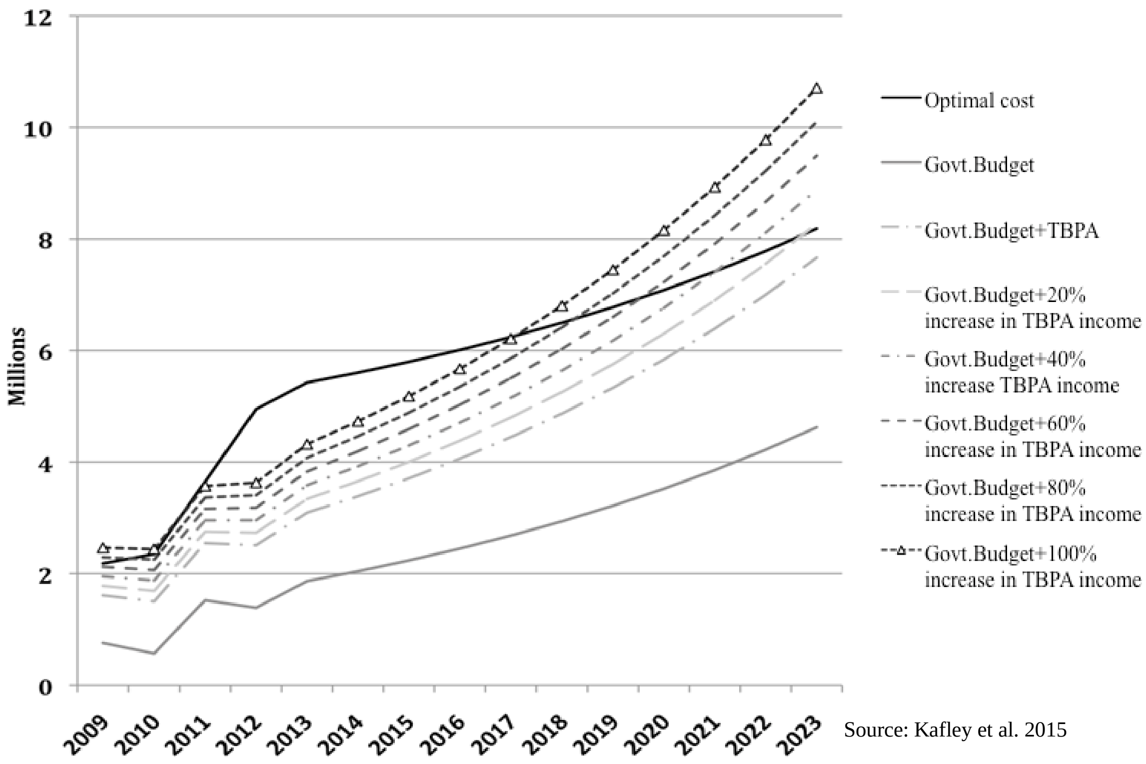
Table 1. Decision making framework.

	Decision Criteria		
Financial tool	Sustainable	Indifference	Unsustainable
B/C ratio	If, >1	Equal to 1	< 1
NPV	> 0	Equal to 0	< 0

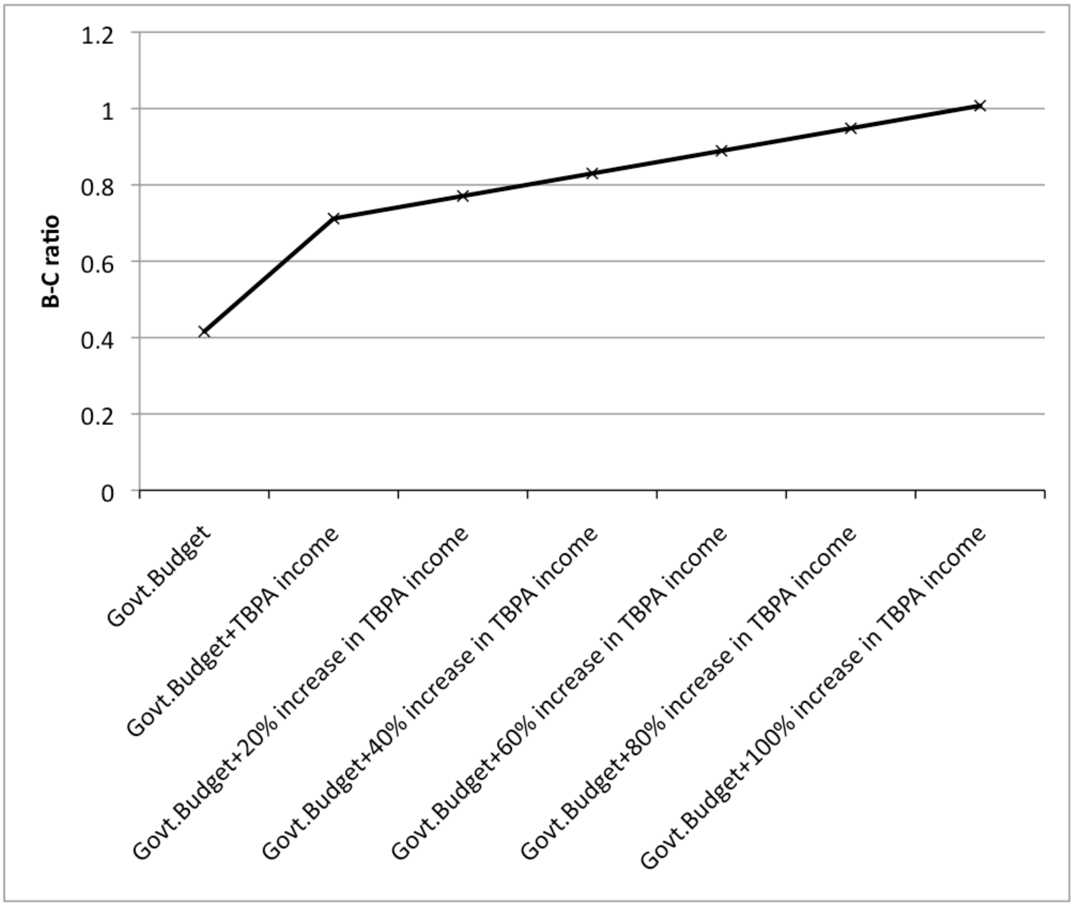
Table 2. Average annual costs (in US$) of tiger conservation program. Past (2009-2013) costs are based on known expenditures. Future costs (2014-2023) are cost projections from past expenditures and additional cost estimations. Basic cost is based on government budget that reflects costs for maintaining TBPAs plus regular program budget of currently operating INGOs that implement tiger conservation programs based on government approved programs and activities inside or outside of TBPAs. Government budget represents past annual fiscal support for TBPAs and the projected support by the government of Nepal. Optimum cost represents the costs estimated by the government for implementing tiger conservation program (NTRP, 2010) across the tiger range in Nepal. (See Appendices A.1 and A.2 for cost composition)

Years	Optimum cost	Basic cost	Government budget
2009 - 2013	3710980	2843813	1220512
2014 - 2023	6738893	5244803	3178893



Source: Kafley et al. 2015

Figure 1 Optimal cost of tiger conservation and income generated under different scenarios that include the government budget, the government budget plus the income of tiger bearing protected area (TBPAs), and the government budget plus TBPA income that is allowed to increase by 20-100%.



Source: Kafley et al. 2015

Figure 2. Benefit-cost ratio of the Nepalese tiger conservation program under scenarios that include solely government funding, government funding plus the funds generated by tiger-bearing protected areas (TBPAs), and government funding plus increased income from TBPAs.

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VITA

Hemanta Kafley was born in Biratnagar, Nepal where he completed his high school studies in 1995. He obtained an Associate degree in Forestry in 1998 and a Bachelor degree in Forestry in 2005 both from the Tribhuvan University, Institute of Forestry, Pokhara Campus, Pokhara, Nepal. He began his professional career in wildlife conservation in January 2000 as a Park Ranger in the Department of National Parks and Wildlife Conservation of the Government of Nepal. He served in the field of wildlife conservation and research for over a decade. He obtained a Post Graduate Diploma degree in Remote Sensing & Geographic Information System with a specialization in Forestry and Ecology application from the Center for Space Science and Technology Education in Asia and the Pacific (CSSTEAP, an institution affiliated to the United Nations), Dehradun, India in 2007. He also obtained a next Post Graduate Diploma degree in International Wildlife Conservation Practice from the Wildlife Conservation Research Unit (WildCRU), University of Oxford, UK in 2009 and began his PhD research at the University of Missouri in January 2010.