

ORIGINAL ARTICLE

Density and carrying capacity in the forgotten tigerland: Tigers in the understudied Nepalese Churia

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Abstract

While there are numerous wildlife ecology studies in lowland areas of Nepal, there are no in-depth studies of the hilly Churia habitat even though it comprises 7642 km² of potential wildlife habitat across the Terai Arc. We investigated tiger, leopard and prey densities across this understudied habitat. Our camera trapping survey covered 536 km² of Churia and surrounding areas within Chitwan National Park (CNP). We used 161 trapping locations and accumulated 2097 trap-nights in a 60-day survey period during the winter season of 2010–2011. In addition, we walked 136 km over 81 different line transects using distance sampling to estimate prey density. We photographed 31 individual tigers, 28 individual leopards and 25 other mammalian species. Spatial capture–recapture methods resulted in lower density estimates for tigers, ranging from 2.3 to 2.9 tigers per 100 km², than for leopards, which ranged from 3.3 to 5.1 leopards per 100 km². In addition, leopard densities were higher in the core of the Churia compared to surrounding areas. We estimated 62.7 prey animals per 100 km² with forest ungulate prey (sambar, chital, barking deer and wild pig), accounting for 47% of the total. Based on prey availability, Churia habitat within CNP could potentially support 5.86 tigers per 100 km² but our density estimates were lower, perhaps indicating that the tiger population is below carrying capacity. Our results demonstrate that Churia habitat should not be ignored in conservation initiatives, but rather management efforts should focus on reducing human disturbance to support higher predator numbers.

Key words: camera trapping, carrying capacity, churia habitat, *Panthera tigris tigris*, spatially explicit capture recapture

INTRODUCTION

The tiger [*Panthera tigris tigris* (Linnaeus, 1758)] is the top predator in the Indian subcontinent (Sunquist & Sunquist 2002) and plays an important role in shaping prey assemblages in the lower trophic levels (Karanth & Sunquist 1995). Despite their ecologically significant role in ecosystem health (Ritchie *et al.* 2012) and the history of concern for their survival, tiger populations are still being decimated (Seidensticker 2010) and

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their range has collapsed to less than 7% of their historic range (Sanderson *et al.* 2006; Walston *et al.* 2010). In addition to the tiger, the sympatric leopard [*Panthera pardus fusea* (Meyer, 1794)], has also experienced range reduction to only 65% of its historic range (Ripple *et al.* 2014). The primary drivers of declines for both carnivores include habitat loss and fragmentation, depletion of natural prey, and direct persecution by people (Karanth & Stith 1999; Balme *et al.* 2010; Walston *et al.* 2010). Conservation of these carnivores has been a global priority due to their vulnerability to extinction and their potential ability to structure ecosystems (Ripple *et al.* 2014), and because they also serve as umbrella species across a wide range of habitats (Wang & Macdonald 2009). In South Asia, tigers and leopards occupy a wide range of habitats, including alluvial floodplain grasslands (Smith 1993), seasonally dry sub-tropical, deciduous lowland forests (Seidensticker 1976; Odden *et al.* 2010), the porous bhabhars (Thapa *et al.* 2014), temperate areas up to alpine regions in the Himalayas for leopards (Wang & Macdonald 2009), and mangrove deltas for tigers in the Sunderbans (Seidensticker 1987; Loucks *et al.* 2010).

The Terai Arc Landscape (hereafter referred to as the Terai Arc) is a high priority landscape for tiger conservation containing 12 potential sub-populations con-

nected at varying degrees (Wikramanayake *et al.* 2004; Wikramanayake *et al.* 2010). The Churia, also called the Siwalikhs in India, is one of the youngest of 5 mountain ranges in Nepal (Hagen 1961) (Fig. 1) and occupies 13% of the total land surface (LRMP 1986) extending from the Brahmaputra River in the east in India to the Indus River in the west in Pakistan (Jhingran 1981). Forest density within the Churia is high (73% intact forest cover) (DFRS 2015) and conservation of the Churia is critical to maintain landscape connectivity across Nepal and India (Wikramanayake *et al.* 2004; Seidensticker *et al.* 2010; Jhala *et al.* 2011; Barber-Meyer *et al.* 2013). Unfortunately, the Churia of Nepal suffers from degradation and overexploitation via agricultural encroachment and poaching (Paudel *et al.* 2013; FRA/DFRS 2014).

The Churia range extends through a majority of tiger habitat across the Terai Arc, yet the classic studies on tiger ecology (ecological separation [Seidensticker 1976], dispersal and behavior [Smith 1985, 1993] and social organization [Sunquist 1981]) have focused instead on the lowland areas comprised of alluvial floodplain grasslands, riverine forests and climax *Shorea robusta* forests (Peet *et al.* 1999; Dinerstein 2003). Thus, Churia habitat remains a “forgotten tigerland” as its ecological role in tiger conservation has been overlooked because it is

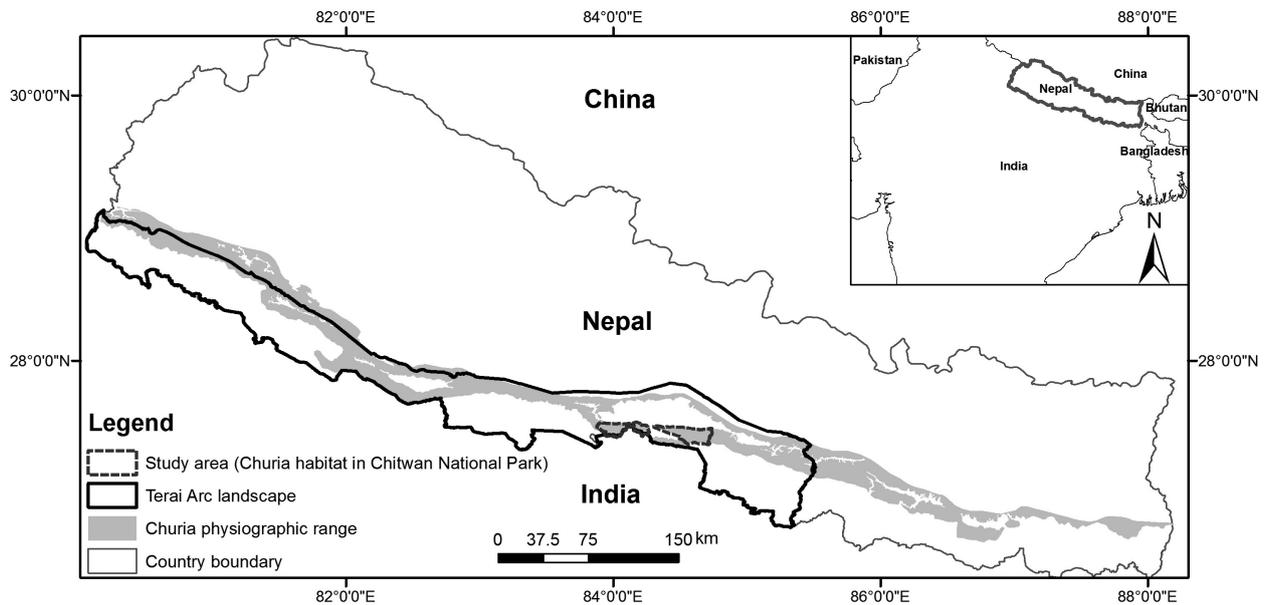


Figure 1 Churia physiographic range in Nepal covers 639 km² within Chitwan National Park and covers 7,642 km² across the Terai Arc Landscape.

generally seen as unsuitable or marginal habitat.

The first systematic tiger census carried out in Chitwan National Park (CNP) did not sample the Churia habitat (Karki *et al.* 2009). Following that, Karki *et al.* (2013), recorded a few individual tigers within the Churia in CNP during a camera survey. However, whether tigers frequented the extensive Churia hills was still unknown. A subsequent tiger census (Dhakal *et al.* 2014) sampled some Churia habitat but did not provide empirical evidence of the contribution of Churia habitat to tiger numbers in CNP. Thus, we provide the first systematic study of the Churia habitat examining tiger and leopard population ecology, and the prey base supporting these predators. Habitat and site-specific assessments are needed to make better informed conservation management decisions for these endangered species in Nepal.

The objectives of this study are to: (i) estimate densities of tigers and leopards in the Churia habitat using

spatially explicit capture–recapture methods; (ii) estimate potential prey density in the Churia habitat using a distance sampling approach; and (iii) predict tiger abundance within the Churia by extrapolating prey density to the entire area and relating prey biomass to predator energy needs. We address a gap in knowledge of tigers, their co-predators and prey in this important yet little known habitat. We expect our study will reveal that there are more tigers in CNP than previously thought, and, thus, will be positive news for tiger conservation across Nepal.

MATERIAL AND METHODS

Study area

This study was conducted within CNP in central Nepal (Fig. 2). The hilly Churia habitat covers 639 km² and is divided into 2 areas: one stretching between the low-

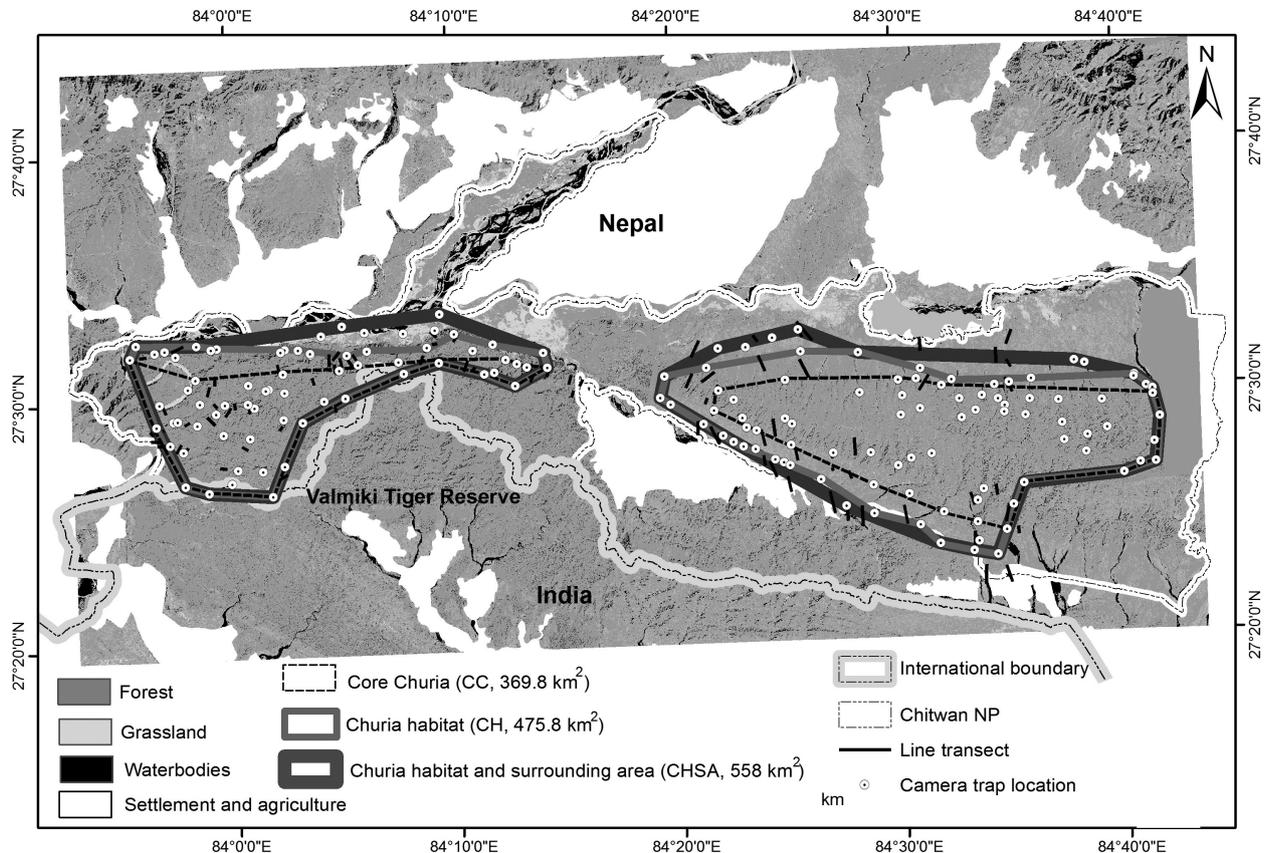


Figure 2 Study area showing camera trap and line transect spatial location in Chitwan National Park. Note that the hidden line is underneath the dark and grey lines in part of the figure.

land areas on the east (363 km²) and 2 between the lowland areas of Chitwan National Park and Valmiki Tiger Reserve on the west (276 km²). Churia habitat is adjacent to a southern valley with a human population density of 440 per km² (CBS 2011). The Churia habitat is the main corridor joining the Valmiki Tiger Reserve in India and the Parsa Wildlife Reserve in the east to form a Tiger Conservation Landscape (TCL) (Wikramanayake *et al.* 2004) known as Chitwan-Valmiki-Parsa Tiger Landscape (Chanchani *et al.* 2014b; Thapa *et al.* 2014).

Churia habitat is rugged, ranging from 150 to 714 m in elevation. The ecosystem is dynamic, the substrate is fragile, the top soil is thin, and landslides are common as the monsoon season (June–September) progresses. Habitat is composed of mixed deciduous forest with Sal forest (*Shorea robusta*) interspersed with other tree species like *Terminalia alata*, *Syzygium cumini* and *Lagerstroemia parviflora*. Tigers, leopards and dholes [*Cuon alpinus* (Pallas, 1811)] are the top carnivores found in the Churia. Potential prey include gaur [*Bos gaurus gaurus* (Lydekker, 1907)], sambar [*Rusa unicolor* (Kerr, 1792)], chital [*Axis axis* (Erxleben, 1777)], barking deer [*Muntiacus muntjak* (Zimmermann, 1780)], wild boar [*Sus scrofa* Linnaeus, 1758] and primates.

Camera trap survey

We conducted our camera trap survey in the winter season from December 2010 to March 2011. Based on a preliminary assessment of potential sites, we divided the study area into 4 blocks each measuring on average 132 km² (SE 23.70). Each block was further divided into 2 × 2 km grid cells and we deployed camera stations within each cell. Due to the ruggedness of the study area, the team (20 field assistants) spent an average of 544 h per block searching for carnivore signs (e.g. scrapes, scat, scent marks, claw marks/rakes and pug-marks) to select appropriate camera sites within our predetermined grid cells. We set pairs of cameras at 148 locations based primarily on accessibility, with an average of 40 (SE: 3.0) camera stations per block. At each station, we used combinations of camera trap models (e.g. Moultrie D50, Moultrie D55 and Bushnell). We selected an additional 13 locations in the lowland areas surrounding the Churia habitat. The inter-trap distance between 2 consecutive stations ranged from a minimum of 0.6 km to a maximum of 3.52 km, with an average distance of 1.56 km (SE 0.09). To maximize capture probabilities, we positioned camera traps along river banks (dry and wet, $n = 119$), animal and human trails ($n = 29$), and fire-lines ($n = 10$), where the presence of car-

nivore signs was high and because predators are known to follow these routes (Karanth & Nichols 2002; Karki *et al.* 2013). Due to a limited number of cameras, we followed the 4th design protocol of Karanth and Nichols (2002) and rotated camera traps from block to block sequentially to cover the area of interest. We followed standard protocols for deploying camera traps (Karanth & Nichols 2002; Karki *et al.* 2013).

Churia habitat is contiguous to lowland forest, which is thought to hold the highest density of tigers (3.84 per 100 km²; Chanchani *et al.* 2014) in CNP. Thus, there is a potential edge effect with movement of wide-ranging tigers likely to occur across the transition zone from the high density lowlands into the Churia. To discount the potential edge effect (i.e. distance to lowland) on detection, abundance and density, we divided the study areas into 3 spatial scales (Fig. 2). In total, we sampled 576 km² of Churia habitat and surrounding area (denoted CHSA), with 161 locations including those 13 stations in the lowland area. We then subsampled 475 km² of only the Churia habitat (denoted CH), with 148 locations without the 13 stations in the lowland, and, finally, we further subsampled 369 km² of the core Churia (denoted CC) with 94 locations. We used a discrete distance of 2 km into the Churia from the lowland edge to define the core and all carnivores captured within CC as “core animals,” similar to Gerber *et al.* (2012). This geographical division allows comparing population density across spatial scales.

Prey survey

We used a distance sampling approach based on line transect surveys to estimate prey density based on visual detection of animals (Buckland *et al.* 1993, 2001; Lancia *et al.* 1994). The team spent a total of 8160 h in the field prior to the survey to assess field topography. Because water sources tend to dictate the distribution of the ungulates (Mondal *et al.* 2013), we spatially located 81 line transects at variable distances from water sources (seasonal and perennial) and each transect was surveyed twice. We randomly placed the start of the first location and traversed 136 km of line transects in a north–south direction with average transect length of 1.41 km (range 0.19 to 4.08 km). Two observers walked and counted animals on either side of the transect between 0700–0900 and 1700–1900 hours (Karanth & Nichols 2002). We conducted surveys in the dry seasons of 2011 (eastern section) and 2012 (western section) when visibility is higher due to shedding of leaves and natural vegetation clearing by early forest fires (Di-

nerstein 2003). Upon detection, we recorded vegetation type, weather conditions, time, date, species, number of animals, radial sighting distance (measured with the digital rangefinder), sighting angle between animal clusters and the transect, and animal behavior upon, and following, detection.

Species identification and capture events

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

Individual identification and capture history

Individual tigers and leopards were identified based on their unique natural stripe and rosette patterns, respectively, on their flanks, limbs, foreheads, fore-quarters and tails (Miththapala *et al.* 1989; Karanth 1995). Three field assistants independently identified individual tigers and leopards. When there was disagreement on the identification of an individual camera-trapped tiger, it was excluded from the analysis. We developed 3 datasets of capture histories at 3 spatial scales (CHSA, CH and CC). Although cameras were operational for 15 days, all 161 locations had functional cameras for 12 continuous days with no missing data. Therefore, we used 12 sampling occasions as encounter occasions for developing capture histories.

Predator density and abundance estimation

We used recently developed spatially explicit capture–recapture (SECR/SCR) techniques that apply spatial information directly in the density estimation process (Efford 2004; Borchers & Efford 2008; Royle *et al.* 2009a,b). We compared maximum likelihood-SECR (denoted ML-SECR) and Bayesian SCR (denoted B-SCR) approaches in estimating density. Using the program DENSITY, we applied the estimated log-likelihood and root pooled spatial variance (RPSV) (Efford *et al.* 2004; Tredick & Vaughan 2009) to determine the appropriate buffer size surrounding the trapping grid. Then we modeled the detection process either as half-normal, hazard rate or negative exponential. Using the best detection function, we then allowed g_0 (the capture probability at the center of an individual's home range) and

sigma, σ (a function of the scale of animal movement), to vary using 2-class finite mixture (h2) and/or a behavioral response (b). Thus, a half-normal detection function model with constant g_0 and 2-class finite mixture of sigma would be represented as HN $g_0(\cdot)$ sig(h2). We ranked all models using sample size-adjusted Akaike's information criterion (AICc) and used model averaging to determine density estimates at all spatial scales (CHSA, CH and CC).

We also used a Bayesian SCR approach (Royle *et al.* 2009a) and the program SPACECAP (Gopalaswamy *et al.* 2012) ver. 1.1.0 (Gopalaswamy *et al.* 2014), implemented in R package version 3.10, to estimate felid densities. We used a habitat extent of 15 km around the minimum convex polygon (MCP) delineated by the outermost boundary of the camera trap locations of the CHSA to represent the state space, S , of locations of probable tiger and leopard home range centers, and generated a grid of hypothetical home range centers with equally spaced points each 1 km² apart. The habitat extent (15 km) roughly represents Chitwan Valley and the Valmiki Tiger Reserve, which are historically known to have tiger and leopard habitat (Dinerstein 2003; Seldensticker *et al.* 2010). After removing the 2086 km² area of settlements (villages and agriculture areas), the area of carnivore habitat over which these activity centers were uniformly distributed was 3255 km². We used 3 standard input data files (animal capture locations and dates, trap deployment dates and locations, and hypothetical activity centers). We used the half-normal detection function and included a behavioral response in the detection process. We performed 400 000 iterations, of which the initial 50 000 were discarded as the burn-in; the thinning rate was set at 1. Augmentation values were set at 300 individuals (over 5 times the expected number of approximately 50 animals) for CHSA, 180 individuals in CH, and 180 individuals for CC for both tigers and leopards. We used the Geweke diagnostic statistics (Geweke 1992) and the $|Z| < 1.6$ score to determine model convergence (Gopalaswamy *et al.* 2012).

We followed Srivathsa *et al.* (2015) for calculating the effective sampled area across each spatial scale (CHSA, CH and CC). We used the estimated sigma (σ) value derived from converged B-SCR models for each scale and added the buffer as sigma (σ) \times sqrt (5.99) to the camera trap array for estimating effective sampled areas. We also calculated tiger and leopard abundance by multiplying the estimated density from SCR models by the respective effective sampled areas (Royle *et al.* 2013).

Distance sampling

We used the program DISTANCE (Thomas *et al.* 2010) to estimate the density of each potential prey species in Churia habitat. We used exploratory data analysis to check for potential violations of the assumptions such as heaping and evasive movements, data truncation to remove outliers, and readjusted bin sizes of detection functions to improve the model fit. We used the conventional distance sampling (CDS) analysis engine for modelling detection functions and generating final density estimates. We determined the best models based on lowest AIC value and goodness of fit (GoF-p) tests. For competing models (e.g. models with $< 2 \Delta AIC$), we calculated the model weight (w) and used model averaging techniques incorporating the most parsimonious models to derive the final estimates (Burnham & Anderson 2002). Due to low detection and sample sizes, we did not use any covariates to evaluate influence on prey density. Due to differing detection functions for each species, we summed the species-specific density estimates to determine overall ungulate density (Karanth & Nichols 1998) rather than pooling all detections and estimating a single overall prey density. We calculated overall biomass of prey found in CH using average body size taken from the literature (Karanth & Sunquist 1995; Harihar *et al.* 2011).

Predicting tiger density

Churia habitat within CNP spans 639 km² and we predicted the tiger density that could be supported based on the ungulate density and biomass (Karanth *et al.* 2004; O'Kelly *et al.* 2012; Harihar *et al.* 2014). Predicting tiger densities based on preferred prey (sambar and wild pig) potentially yields results describing the carrying capacity of tigers (Hayward *et al.* 2012; Harihar *et al.* 2014). However, no information on preferred prey from Churia habitat is available. While sambar and wild pig are preferred prey, chital and barking deer are preyed upon in accordance with their availability (Hayward *et al.* 2012). Therefore, we combined these 4 prey species' density estimates in predicting potential tiger densities. We used the scaling relationships developed by Karanth *et al.* (2004) specific to tigers, which also incorporate the cropping rate by tigers to be 10% from all the available prey (Karanth & Sunquist 1992) and an average kill rate of 50 ungulates per tiger per year (Karanth & Stith 1999; Miller *et al.* 2013).

RESULTS

Species identified in Churia habitat

We amassed 35 130 photographs in 2097 trap nights after removing 123 trap nights of camera malfunctions. A total of 15.64% of the animal photos were from 25 mammalian species, including 12 species of carnivores (Table 1). We gathered a total of 477 photographs of carnivores, including top predators: tigers ($n = 85$), leopards ($n = 67$) and dholes ($n = 22$). We recorded one event each of a leopard and a tiger with cubs, indicating that breeding females are using Churia habitat.

We identified 8 species of ungulates in the Churia based on camera trap photographs (Table 1), direct observations and indirect signs (pellets and tracks). The principle wild prey species of tigers, leopards and dholes are: large size animals (>50 kg) – gaur and sambar; medium size animals (20–50 kg) – chital, muntjac and wild pig. Nilgai (*Boselaphus tragocamelus* (Pallas, 1766)), >50 kg). Himalayan serow (*Capricornis thar* (Hodgson, 1831)), 20–50 kg) and four-horned antelope (*Tetracerus quadricornis* (de Blainville, 1816)), 20–50 kg) were also recorded but were rarely detected. In addition to ungulates, we also recorded small-bodied primates (<20 kg) – tarai gray langur [*Semnopithecus hector* (Pocock, 1928)] and rhesus monkey [*Macaca mulatta* (Zimmermann, 1780)]. Among the large and medium sized animals, sambar and barking deer had the highest trapping rate, with 13.26 and 5.48 photos per 100 TN, respectively (Table 1). Among the primates, tarai gray langurs had the highest trapping rate (4.29 photos per 100 TN).

Predator individual identification

Two independent observers agreed on 100 and 96% of the individual identifications of tigers ($n = 57$) and leopards ($n = 43$), respectively. We identified 31 (14 M: 15 F: 2 U) individual adult tigers and 28 (13 M: 6 F: 9 U) individual adult leopards in the Churia and surrounding area (CHSA). In just the Churia habitat (CH), we identified 26 (11 M: 13 F: 2 U) individual tigers and (11 M: 6 F: 7 U) individual leopards, while in the core Churia (CC) we found 6 (5 M: 1 F) individual tigers and 13 individual leopards (5 M: 5 F: 3 U).

Predator density and abundance estimation

The hazard rate (HZ), negative exponential (NE) and half-normal (HN) detection functions, and variation in σ and g_0 explained by behavior and/or heterogeneity, provided the best fit for the CHSA, CH and CC datasets, respectively (Table 2). Density estimates per 100 km² \pm

Table 1 Trapping success (activity index: number of independent photo-captures per 100 trap nights) of mammalian species identified in the Churia camera trap survey along with their conservation status in Nepal (NPWCA 1973) and in region based on IUCN Red list (IUCN 2013)

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

NPWCA, National Parks and Wildlife Conservation Act.

SE for tigers were similar via DENSITY and SPACECAP, respectively, at 2.28 ± 0.74 and 2.86 ± 0.51 in CHSA; 2.26 ± 0.72 and 2.21 ± 0.42 in the CH; and 1.54 ± 1.00 and 2.08 ± 1.13 in the CC. Leopard densities were more variable between techniques, especially for the CHSA and CC, and possibly increased in the core Churia. Leopard densities from DENSITY and SPACECAP, respectively, were 3.32 ± 2.29 and 5.11 ± 0.14 in the CHSA; 3.78 ± 2.61 and 4.00 ± 1.00 in the CH; and

9.75 ± 13.72 and 4.46 ± 0.11 in the CC (Tables 2 and 3, Fig. 3).

Using the B-SCR (SPACECAP) density estimates multiplied by the effective sample areas, we estimated tiger and leopard abundances ($\bar{N} \pm \text{SEM}$) to be 55 ± 9.88 and 85 ± 2.37 in CHSA, 43 ± 8.19 and 67 ± 16.80 in CH, and 20 ± 10.86 and 67 ± 16.01 in CC (Table 4), respectively.

Table 2 Model selection results for density estimates (\hat{D} , number/100 km²) using photographic capture–recapture data for tiger and leopard populations in DENSITY (ML-SECR) across 3 spatial scales: Churia habitat and surrounding areas (CHSA), Churia habitat (CH) and core Churia (CC) in Chitwan National Park

Scale	Buffer size (m)	Predator	Model selection	K	AICc	ΔAICc	w	Density (SEM)
CHSA	12000	Tiger	HZ g0[b]s[.]	4	798.25	0	0.46	2.31 (0.67)
			HZ g0[b]s[b]	5	799.71	1.46	0.22	2.58 (0.82)
		Leopard	NE g0[.]s[b]	3	476.28	0	0.35	2.31 (0.08)
			NE g0[b]s[.]	3	476.69	0.41	0.29	2.85 (0.08)
CH	15000	Tiger	NE g0[b]s[.]	4	724.78	0	0.30	1.80 (0.45)
			NE g0[.]s[h2]	5	725.16	0.38	0.25	3.08 (0.94)
			NE g0[b]s[b]	5	725.57	0.79	0.20	2.21 (0.64)
			NE g0[.]s[.]	3	725.72	0.94	0.19	2.10 (0.52)
		Leopard	NE g0[.]s[b]	3	435.89	0	0.27	2.48 (0.09)
			NE g0[b]s[.]	3	436.19	0.30	0.24	2.94 (0.08)
			NE g0[.]s[.]	2	436.41	0.52	0.21	4.20 (1.25)
			NE g0[h2]s[.]	4	436.49	0.6	0.20	7.33 (3.70)
CC	5000	Tiger	HN g0[.]s[b]	3	148.46	0	0.50	1.55 (1.00)
			HN g0[b]s[.]	3	148.48	0.02	0.49	1.60 (1.00)
		Leopard	HN g0[.]s[b]	3	180.47	0	0.43	8.95 (1.36)
			HN g0[b]s[.]	3	180.48	0.01	0.43	9.88 (1.37)

AICc, Akaike’s information criterion corrected for small sample size; ΔAICc, delta; AICc; b, variation due to behavioral response; g_{0s}, capture probability at home range center; h2, 2-class finite mixture probability for heterogeneity; HN, half-normal detection function; HZ, hazard rate detection function; K, number of parameters; NE, negative exponential detection function; s, spatial scale parameter of capture function; w, Akaike model weight. [.] represents the null model or constant. Only competing models (ΔAICc < 2) are shown.

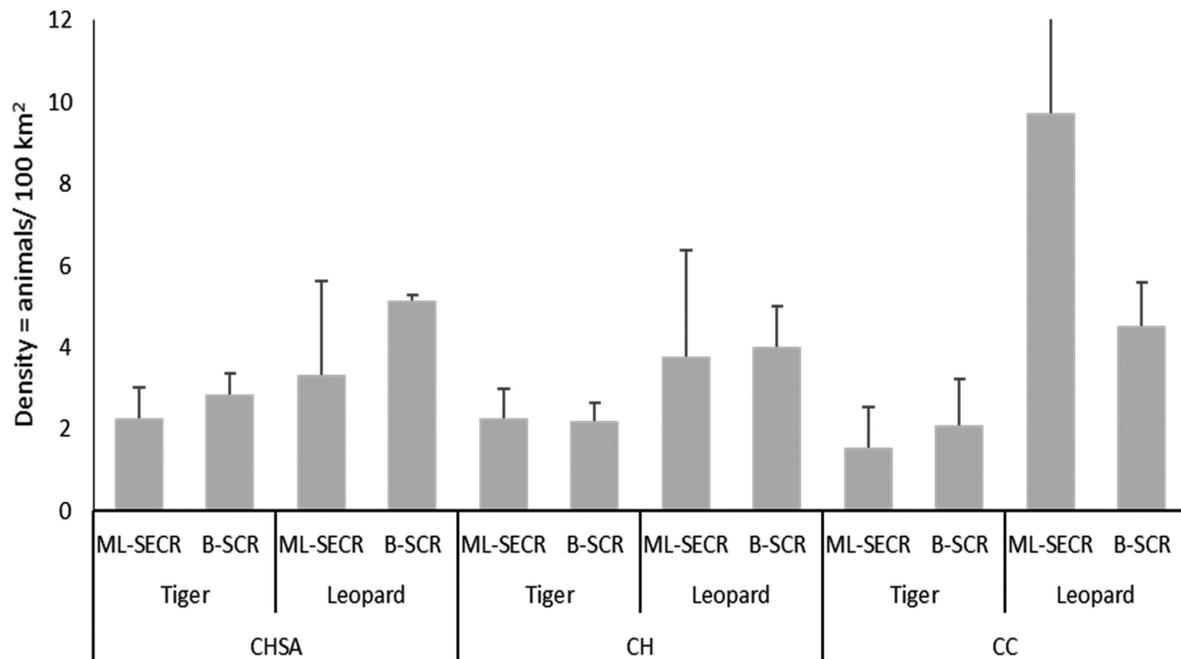


Figure 3 Density estimates per 100 km² of tigers and leopards across the three spatial scales in Churia habitat. SECR models using maximum likelihood (ML-SECR) and Bayesian (B-SECR) approaches were implemented in Churia habitat and surrounding area (CHSA), Churia habitat (CH), and core Churia (CC), which starts 2 km in from the churia/lowland border.

Table 3 The posterior summaries of model parameters from Bayesian spatially explicit capture–recapture (B-SCR) for tigers' and leopards' density estimates (\hat{D} , number/100 km²) across Churia habitat and surrounding areas (CHSA), Churia habitat (CH) and core Churia (CC) in Chitwan National Park, Nepal implemented in SPACECAP (Gopalaswamy *et al.* 2012) along with Geweke diagnostic statistic

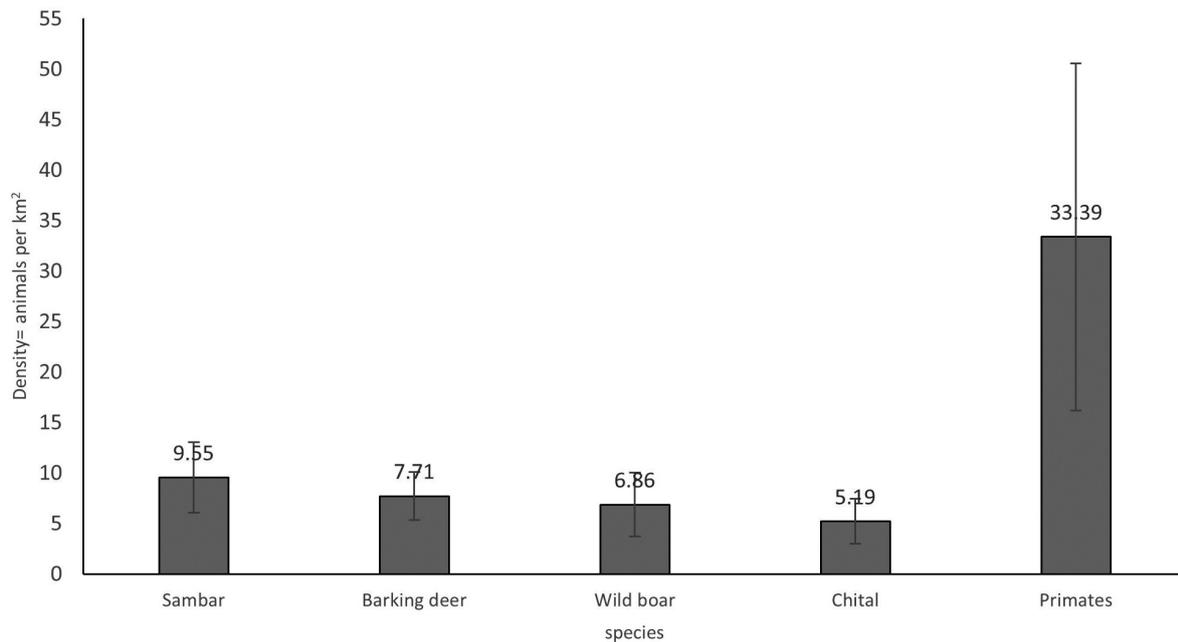
Scale	Predator	Parameter	Posterior mean	Posterior SD	95% lower HPD level	95% lower HPD level	Geweke's statistics z score
CHSA	Tiger	Sigma	3534.77	373.53	2816.33	4267.13	-0.65
		lam0	0.02	0.00	0.01	0.03	1.01
		Psi	0.33	0.07	0.21	0.46	0.27
		Nsuper	93.05	16.66	62.00	125.00	0.22
		Density	2.86	0.51	1.94	3.87	
		<i>p</i>	0.02	0.00	0.01	0.03	
	Leopard	Sigma	3080	627	2060	4340	-0.73
		lam0	0.01	0.00	0.00	0.02	0.50
		Psi	0.29	0.85	-1.35	1.94	-0.34
		Beta	0.51	0.14	0.26	0.80	-0.22
		Nsuper	166.00	45.90	84.00	259.00	-0.20
		Density	5.11	0.14	2.67	8.05	
		<i>p1</i>	0.01	0.00	0.00	0.02	
		<i>p2</i>	0.01	0.01	0.00	0.03	
CH	Tiger	Sigma	3757.74	414.41	2972.09	4581.41	-1.51
		lam0	0.03	0.01	0.02	0.04	0.99
		Beta	-0.33	0.56	-1.43	0.73	-0.58
		Psi	0.35	0.07	0.21	0.50	0.53
		Nsuper	72.06	13.69	46.00	98.00	0.57
		Density	2.21	0.42	1.41	3.01	
		<i>p1</i>	0.03	0.01	0.02	0.04	
	Leopard	<i>p2</i>	0.02	0.01	0.00	0.04	
		Sigma	3106.18	613.24	2107.57	4287.85	-0.23
		lam0	0.01	0.00	0.00	0.02	-0.94
		Psi	0.63	0.15	0.36	0.95	1.40
		Nsuper	128.26	30.93	72.00	190.00	1.41
		Density	4.00	1.00	2.00	6.00	
		<i>p</i>	0.01	0.00	0.00	0.02	
CC	Tiger	Sigma	1537.74	785.03	558.52	3137.74	-1.02
		lam0	0.05	0.03	0.01	0.12	0.22
		Psi	0.36	0.20	0.05	0.78	-0.20
		Nsuper	67.54	36.69	10.00	143.00	-0.19
		Density	2.08	1.13	0.31	4.39	
		<i>p</i>	0.05	0.03	0.01	0.11	
		Leopard	Sigma	2810.00	2160.00	569.00	7860.00
	lam0		0.02	0.02	0.00	0.05	-0.97
	Psi		0.00	0.00	0.00	0.00	-1.27
	Nsuper		0.76	0.18	0.41	1.00	-1.25
	Density		147.00	34.70	80.00	194.00	
	<i>p</i>		4.52	1.07	2.46	5.96	

Sigma ($\hat{\theta}$) is scale parameter related to animal movement, lam0 is the intercept of expected encounter frequency, Psi is the ratio of the number of animals present within the state space, S, to the maximum allowable number. Nsuper is the number of activity centers in S. *p* is the detection probability. Density is Nsuper divided by S representing number of animals per 100km². A |z score| < 1.6 shows convergence of the estimated parameter

Table 4 Capture and recapture of tiger and leopard population across the Churia habitat and surrounding areas (CHSA), Churia habitat (CH) and core Churia (CC) in Chitwan National Park, Nepal

Spatial scale	MCP	Predator	M_{t+1}	Recaptured Individuals	$\hat{\sigma}$ (m)	ETA (km ²)	Abundance (SEM)	Density (SEM)
CHSA	558	Tiger	31	16	3535	1936.82	55 (9.88)	2.86 (0.51)
		Leopard	28	9	3080	1670.28	85 (2.37)	5.11 (0.14)
CH	475.83	Tiger	26	15	3758	1950.23	43 (8.19)	2.21 (0.42)
		Leopard	24	9	3106	1679.63	67 (16.80)	4.00 (1.00)
CC	369.79	Tiger	6	1	1538	961.11	20 (10.86)	2.08 (1.13)
		Leopard	13	2	2810	1497.09	67 (16.01)	4.52 (1.07)

Density estimates (\hat{D} , number of tigers/100 km²) based on B-SCR with the estimated population size (\hat{N}) from B-SCR (Srivathsa *et al.* 2015). MCP, minimum convex polygon surrounding camera traps; M_{t+1} , number of individual captures; sigma ($\hat{\sigma}$) scale parameter related to animal home range size; ETA, effective trapping area (sigma \times sqrt (5.99))

**Figure 4** Individual density estimates (\hat{D} , no per km²) along 95% CI (Confidence Intervals) modeled in Program DISTANCE for major prey species of the Churia habitat (CH).

Prey density

In 136 km of transect surveys we recorded 117 sightings of 4 species of ungulates (sambar, chital, muntjac and wild pig) and 46 sightings of 2 species of primates (tarai gray langur and rhesus monkey). We had only 2 detections of gaur ($n = 2$) and, thus, gaur were discarded

from further analysis. Among the principle prey, sambar had the highest densities ($\hat{N} \pm SE$) at 9.55 ± 1.76 animals/km², while chital density was lowest at 5.19 ± 1.11 animals/km² (Fig. 4). Summing the top 4 species-specific densities (sambar, chital, wild pig and muntjac) into 1 estimate resulted in overall prey density of 29.31 animals/km² in the Churia habitat. Overall density of all

wild prey, including the primates, was 62.70 animals/km² with contributions from the top 4 wild ungulates of 47%. The overall estimated biomass of all wild ungulates (sambar, chital, wild pig and muntjac) was 2450 kg/km².

Potential tiger densities

Based on the Karanth *et al.* (2004) equation, our estimated density of potential prey (29.31 individuals/km²) would be capable of supporting 5.86 tigers/100 km² within the 639 km² of Churia habitat (CH), which translates into a total of 37 individual tigers.

DISCUSSION

This is the first detailed study to investigate densities of sympatric tigers, their common sympatric predators, leopards, and their prey in the Churia habitat (Dinerstein 2003; Seidensticker *et al.* 2010). The results serve as baseline information for Churia habitat within the protected areas system. We (i) identified 12 species of carnivores, with tigers, leopards and wild dogs being the top carnivores, including evidence of breeding for tigers and leopards; (ii) found higher numbers of leopards than tigers; (iii) found evidence that leopard density may be higher in the Churia core while tiger density remained similar across spatial scales; (iv) recorded 8 species of potential prey with body size greater than 15 kg, including new records for Himalayan serow, four-horned antelope and nilgai; (v) determined total prey density to be 62.70 animals/km², 47% (29.31 animals/km²) of which consist of 4 species of wild ungulates known as dominant prey in the lowland areas; and (vi) found tiger densities to be lower than that predicted based on available ungulate biomass.

While the Government of Nepal conducted 2 surveys in CNP (Karki *et al.* 2012; Dhakal *et al.* 2014;) neither study offered information on the specific contribution of the Churia habitat to overall tiger abundance in the park. Based on our density estimates we predict the Churia of CNP to contain from 9.8 to 26.6 tigers. Considering that the previously estimated tiger population size for CNP is approximately 121 tigers (Dhakal *et al.* 2014), our estimates could add additional tigers and, thus, represent an increase of 8–22% above the previous estimate. However, we do not know how many tigers exclusively inhabit the Churia. Of the 31 total individual tigers identified in this study, 21 were captured exclusively in Churia habitat (representing a possible 17% increase from the previous abundance estimate), while 6 were exclusively

captured in the Churia core habitat (CC). The remaining tigers ($n = 4$) were found in both the Churia and lowland habitats. In addition, we characterized 11 individuals as transients (i.e. captured only once), a much higher percentage than the 18% transients found by Karanth *et al.* (2006) in India. The high degree of transient tigers in our study could be due to tigers dispersing from lowland areas in search of suitable home range in the Churia. More research is needed, perhaps with GPS collared tigers, to assess the extent to which tigers live exclusively in Churia habitat. Presence of a female tiger with cubs suggests, at the very least, that some tigresses in the CH are using this habitat while rearing cubs. Although approximately 50% of tigers photographed in the CH were female, only one female occurred exclusively in the CC, suggesting that females may not rely exclusively on Churia habitat for their needs.

Interestingly, the population size of leopards within the Churia is similar to the total population size estimated for the entire Chitwan National Park (Thapa 2012), suggesting a substantially underestimated leopard population size in previous studies in CNP. We found 13 individual leopards exclusively captured in core Churia (CC) compared to 24 leopards in Churia habitat (CH). These findings contradict the conventional idea of the Churia as unsuitable or marginal habitat (Smith *et al.* 1999) for tigers and leopards. Leopard numbers have been shown to be lower where tiger densities are higher (Harihar *et al.* 2011); perhaps the lower densities of tigers allow higher densities of leopards in the Churia.

While tiger density in the CH is half that in the lowland areas of CNP (Karki *et al.* 2013) and Bardia National Park (Dhakal *et al.* 2014), it is still comparable to multiple sites in India, such as Pakke Tiger Reserve (Chauhan *et al.* 2006), Chilla Range (Harihar *et al.* 2011) and Tadoba and Bhadra Tiger Reserve (Karanth *et al.* 2004), and higher in density than in Bhutan (Wang & Macdonald 2009), Myanmar (Lynam *et al.* 2009) and Malaysia (Kawanishi & Sunquist 2004). Leopard density in the Churia is very similar to the high density areas in the bhabhars of Parsa Wildlife Reserve in Nepal (Thapa *et al.* 2014), the mountains of Kuiburi National Park in Thailand (Steinmetz *et al.* 2013), Manas Tiger Reserve in India (Borah *et al.* 2013), and the Irrigated Valley in Akole Tahsil, Maharashtra, India (Athreya *et al.* 2013). This highlights the suitability of the Churia habitat for leopards.

Both spatial CMR approaches gave similar results for tigers but leopard densities were more variable. Recent research shows that trap deployment and small trapping

polygon could affect the estimates from SECR/SCR models (Tobler & Powell 2013). However, trapping grids in our study were large, ranging from 370 km² for CC to 557 km² for CHSA, and multiple camera traps were deployed within each animal's home range. Nevertheless, we would suggest further work to confirm the stability of our estimates for leopards given the relatively high estimate yet poor precision for the core Churia.

In the absence of anthropogenic factors, carnivore densities are known to be directly correlated with prey densities (Carbone & Gittleman 2002; Karanth *et al.* 2004). Sambar and wild boar are preferred prey of tigers (Hayward *et al.* 2012) and we found both in relatively high densities in the Churia. Sambar are forest ungulates showing preference for deciduous forest with high understory cover (Schaller 1967; Dinerstein 1980), conditions prevalent in the Churia across the Terai Arc (Johnsingh *et al.* 2004). The wild boar has a highly variable diet, contributing to its generalist species status and wide distribution (Ballari & Barrios-García 2014), and wild boar are widely distributed across the Churia (Thapa & Kelly 2016). Availability of sambar and medium-sized prey like wild boar could explain the tiger's density recorded in the Churia habitat.

Leopards, in contrast, preferentially prey on species within a weight range of 10 to 40 kg (Hayward *et al.* 2006). Abundant medium-sized ungulate prey (size: 35–50 kg, density: 13.3 animals per km²) in addition to primates (33.39 animals per km², predominately grey langur) could explain the high leopard density in the Churia habitat. Barking deer were the most abundant medium-sized ungulate, likely due to their preference for closed forest habitat and high undergrowth found in the Churia (Dinerstein 1980; Teng *et al.* 2004; Wegge *et al.* 2009), and are likely an important prey for leopards. In addition, leopards have been shown to use habitat not used by tigers, purportedly to avoid competition with them (Seidensticker 1976; Odden *et al.* 2010). We found some evidence of potentially higher leopard density inside the core of the Churia compared to tigers, which had similar density at all spatial scales. Leopard predominance in the core of the Churia could be related to avoiding the highly dense tiger population in the lowlands (Seidensticker 1976; Karki *et al.* 2013), the high availability of medium-sized prey, and leopards' ability to hunt primates that live in more forested environments (Wada 2005).

The tiger population in the Churia habitat within CNP may be lower than carrying capacity based on prey biomass. Our highest density estimate was 4.17 tigers per

100 km², whereas projected tiger density extrapolated from prey biomass was 5.86 tigers per 100 km². Tigers and leopards are sympatric carnivores in Churia habitat competing for shared prey species at relatively low density. Thus, prey biomass alone may not be the only predictor of tiger carrying capacity considering that there is dietary overlap between tigers and leopards, and that sharing prey with leopards may lower the carrying capacity of tiger in Churia habitat. However, leopards tend to be more flexible in their diet than tigers and can, perhaps, better tolerate deteriorating habitat conditions (Johnsingh 1983) and shift toward smaller prey (like barking deer) to survive (Ramakrishnan *et al.* 1999). Prey selection among the competing carnivores should be further explored (Karanth & Sunquist 1995) in the Churia.

Direct persecution through poaching may cause tigers to be below carrying capacity and 10 years of political insurgency (1996–2006) in Nepal has had a direct effect on biodiversity as noted by an increasing trend in unrecorded wildlife-related crime during this period (Karki *et al.* 2013). In addition, direct persecution of prey by people in Churia habitat occurs in the form of illegal hunting, which is prevalent across the transboundary with India, and illegal harvesting of non-timber forest products is high. Decreasing illegal activities could enrich prey populations, further increasing tiger carrying capacity (O'Kelly *et al.* 2012; Harihar *et al.* 2014) across the Churia in CNP. Anti-poaching strategies for protected areas like SMART (Spatial Monitoring and Reporting Tool) (Thapa *et al.* 2013) should be implemented in Chitwan to allow landscape scale planning across all habitat zones and management sectors.

If similar prey densities prevail across the Churia habitat outside CNP, then the 1200 km² of Churia habitat in the Chitwan Valley alone could support up to approximately 70 tigers following the Karanth *et al.* (2004) models used in this study. Furthermore, the total area of Churia habitat within Terai Arc is 7642 km², representing the potential for holding substantially more tigers. Enhancement of prey populations and the establishment of successful community forest programs (Agrawal & Ostrom 2001; Seidensticker *et al.* 2010) outside the core areas could be a win-win situation for tigers and be beneficial to sympatric leopards as well. CNP is contiguous with Valmiki Tiger Reserve sharing a majority of the Churia habitat. Transboundary efforts to reduce human-related disturbances in Churia, and Churia-specific monitoring of the tiger and leopard populations could aid in better understanding the conservation status

of these predator populations in Valmiki Tiger Reserve (Jhala *et al.* 2011).

This study is the first to focus on a habitat thought to be unsuitable or of poor quality for tigers. Our results highlight the fact that the Churia habitat should no longer remain a “forgotten tigerland.” Simply by inclusion of this habitat as suitable, albeit at lower density, we have shown that more tigers occur in CNP than previously thought (Smith *et al.* 1999), and previous estimates of total tiger numbers for Nepal are likely underestimates. Given the large amount of this habitat type available in the Terai Arc, our study highlights the important contribution of Churia in fostering tiger conservation across this region (Seidensticker *et al.* 2010; Wikramanayake *et al.* 2010). Conservation initiatives should include the Churia as suitable habitat, expand research efforts there, and focus on reducing human disturbance and protecting prey populations to support higher numbers of threatened and endangered carnivores.

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