

# Influence of prey depletion and human disturbance on tiger occupancy in Nepal

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## Introduction

Tigers (*Panthera tigris* Linnaeus, 1758) are globally endangered and continue to decline due to poaching, prey depletion and habitat loss (Dinerstein *et al.*, 2006). Although tiger research in Nepal dates back to over four decades (Smith *et al.*, 2010), previous tiger population assessments throughout the Terai Arc Landscape (TAL) were limited in terms of landscape and regional comparisons because they were conducted using varying methods (e.g. telemetry, camera-trapping, interviews with locals, etc.), during different periods (e.g. 1970s through 2000s) with varying duration (e.g. as brief as 3 months up to spanning a decade), sometimes in different places [e.g. individual protected areas (PAs)] and with varying

## Abstract

Tigers are globally endangered and continue to decline due to poaching, prey depletion and habitat loss. In Nepal, tiger populations are fragmented and found mainly in four protected areas (PAs). To establish the use of standard methods, to assess the importance of prey availability and human disturbance on tiger presence and to assess tiger occupancy both inside and outside PAs, we conducted a tiger occupancy survey throughout the Terai Arc Landscape of Nepal. Our model-average estimate of the probability of tiger site occupancy was 0.366 [standard error (SE) = 0.02, a 7% increase from the naive estimate] and the probability of detection estimate was 0.65 (SE = 0.08) per 1 km searched. Modeled tiger site occupancy ranged from 0.04 (SE = 0.05) in areas with a relatively lower prey base and higher human disturbance to 1 (SE = 0 and 0.14) in areas with a higher prey base and lower human disturbance. We estimated tigers occupied just 5049 (SE = 3) km<sup>2</sup> (36%) of 13 915 km<sup>2</sup> potential tiger habitat (forests and grasslands), and we detected sign in four of five key corridors linking PAs across Nepal and India, respectively indicating significant unoccupied areas likely suitable for tigers and substantial potential for tiger dispersal. To increase tiger populations and to promote long-term persistence in Nepal, otherwise suitable areas should be managed to increase prey and minimize human disturbance especially in critical corridors linking core tiger populations.

objectives (e.g. distribution, metapopulation structure, habitat quality and availability, social organization, dispersal, study design effects, etc.) (Sunkist, 1981; Smith, 1993; Smith, Ahearn & McDougal, 1998; Wegge, Pokharel & Jnawali, 2004; Gurung, Smith & Shrestha, 2006).

More recently, tiger distribution studies outside of Nepal have used a relatively new approach (occupancy surveys) to assess tiger presence at the landscape scale (Linkie *et al.*, 2006; Hines *et al.*, 2010; Karanth *et al.*, 2011; Wibisono *et al.*, 2011; Sunarto *et al.*, 2012). These studies differ from earlier research in Nepal, in part, by explicitly addressing the issue of detectability, accounting for search effort and analyzing additional covariates (e.g. relative prey abundance and human disturbance). The utilization of occupancy methods across various

tiger landscapes can also allow for more robust comparisons at regional scales (Wibisono *et al.*, 2011).

Occupancy methods are especially useful in sign-based surveys of tigers (elusive and occurring at relatively low densities) at the landscape scale (Linkie *et al.*, 2006; Hines *et al.*, 2010; Karanth *et al.*, 2011; Wibisono *et al.*, 2011; Sunarto *et al.*, 2012) because they explicitly address the issue of false absences (e.g. tiger tracks may be harder to detect in a leaf-littered forest than along a sandy riverbed, even if both areas are equally used; MacKenzie *et al.*, 2006; Nichols *et al.*, 2007). Occupancy analyses estimate two key parameters:  $\psi$ , the probability a site is occupied or used by a species; and  $p$ , the probability of detecting the species, given the species is present (MacKenzie *et al.*, 2006). Detection and non-detection data from repeat surveys within a season (e.g. repeat visits to the same site or multiple surveys on the same visit) are used to differentiate these two probabilities.

We conducted a rigorous, landscape-scale occupancy survey to provide benchmark data on tiger distribution during a succinct period and to assess the importance of various covariates on tiger presence throughout the TAL. The following points were specifically evaluated:

- (1) What is the spatial distribution of tigers throughout the TAL?
- (2) Do prey base and human disturbance influence this distribution?
- (3) Are tigers using the five key corridors connecting PA source populations?

## Materials and methods

### Study area

The 23 199 km<sup>2</sup> TAL (E80°04'–E85°30', N26°45'–N29°07') is a global priority landscape for tiger conservation (Wikramanayake *et al.*, 1998). The TAL stretches along the outer foothills of the Himalayas where the climate is subtropical monsoonal with three distinct seasons: cool-dry (November to February), hot-dry (March to June) and monsoon (July to October). The average temperature in the cool season drops to 10°C in January and rises to ~35°C in the hot-dry season (Pradhan, 2007).

The TAL forms part of the Terai Duar Savannah and Grasslands ecoregion with subtropical deciduous vegetation ranging from early successional floodplain communities to mature sal (*Shorea robusta*) forests. The alluvial grasslands and deciduous forests of TAL are prime tiger habitats (Wikramanayake *et al.*, 1998). Principal tiger prey includes chital deer (*Axis axis* Erxleben, 1777), wild boar (*Sus scrofa* Linnaeus, 1758), sambar deer (*Rusa unicolor* Kerr, 1792), swamp deer (*Rucervus duvaucelii* Cuvier, 1823), barking deer (*Muntiacus muntjak* Zimmermann, 1780), hog deer (*A. porcinus* Zimmermann, 1780), blue bull (*Boselaphus tragocamelus* Pallas, 1766) and gaur (*Bos frontalis* Lambert, 1804). Poaching of tigers and tiger prey is a significant threat to tiger persistence in the TAL (Mishra *et al.*, 2008).

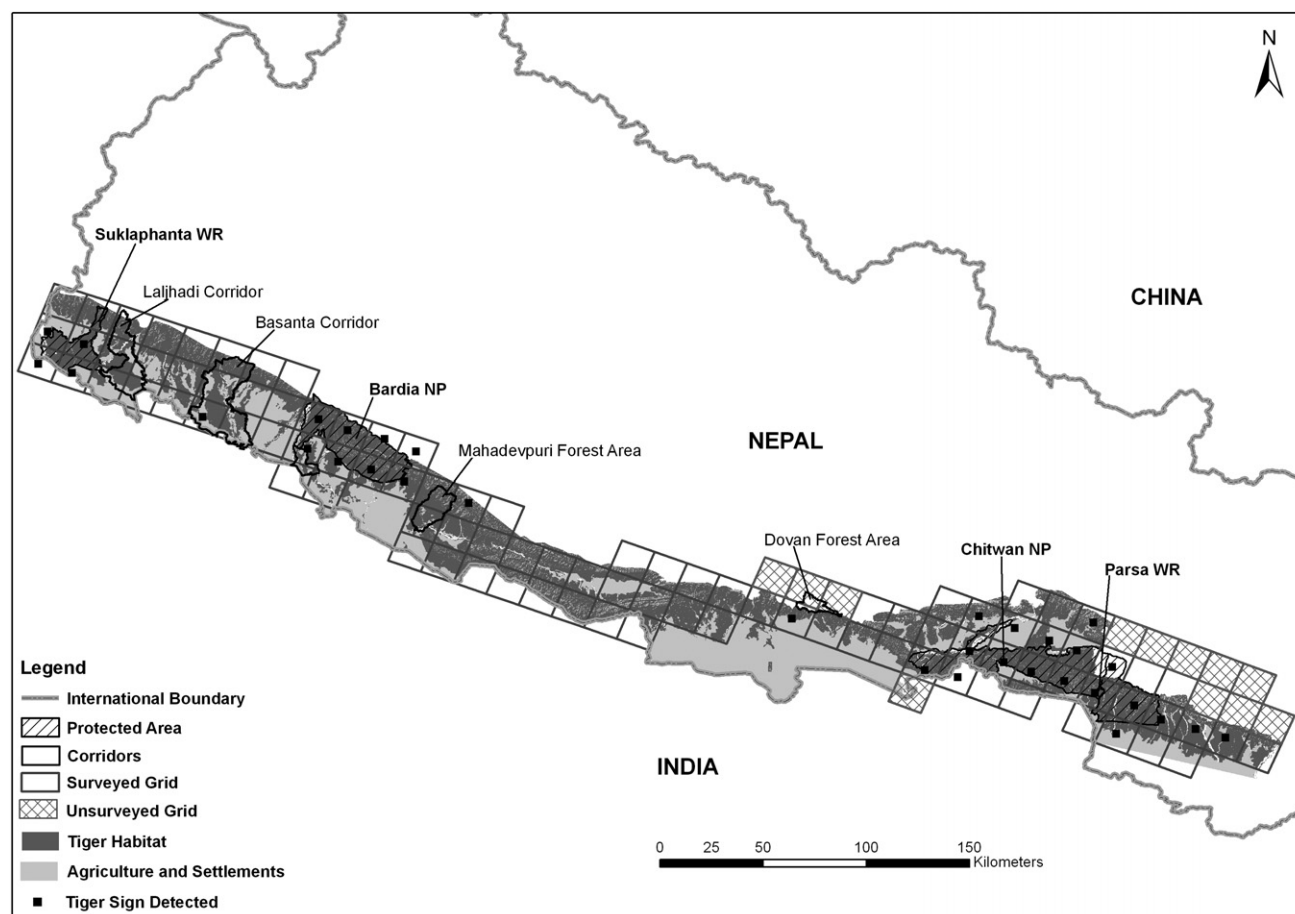
Tiger populations in Nepal are fragmented with core populations mainly located in four PAs; Parsa Wildlife Reserve,

Chitwan National Park, Bardia National Park (BNP) and Suklaphanta Wildlife Reserve (SWR) (Fig. 1) linked via corridors (determined by habitat, size, elevation and human disturbance; Wikramanayake *et al.*, 2004) across the TAL. Over the past decade, tiger presence has been confirmed from several corridors that connect PAs in Nepal and India (Wikramanayake *et al.*, 2010). Five critical corridors have been identified in the TAL: (1) the Khata Corridor connecting BNP Nepal and Katarniaghat Wildlife Sanctuary in India; (2) the Basanta Corridor connecting SWR and BNP in Nepal with Duduwa National Park in India; (3) the Laljhadi corridor connecting SWR in Nepal with Dudhuwa National Park in India; (4) the Mahadevpuri forest area joining BNP in Nepal with Sohalwa Wildlife Sanctuary in India; (5) the Dovan forest area joining the western and eastern portions of the TAL (Fig. 2). In addition to agricultural expansion and infrastructural development outside PAs owing to intense human pressure (248 people km<sup>-2</sup>), unsustainable extraction of forest resources and livestock grazing continue to intrude along PA boundaries (CBS, 2001).

### Occupancy survey

Our TAL-wide tiger occupancy survey included four PAs, buffer zones, corridors and adjoining potential tiger habitats (Fig. 1). The survey was completed during the cool-dry period from December 2008 to February 2009 to ensure seasonal consistency across sites. Our study used a modified cluster sampling design (Hines *et al.*, 2010) for logistical reasons and generally followed Tigers Forever (a joint project of the Wildlife Conservation Society and Panthera) protocols (Karanth *et al.*, 2008, 2011). We used sampling units (i.e. grid cells) of 225 km<sup>2</sup> because the largest home range of a male tiger is expected to be ~200 km<sup>2</sup> in South Asia (Karanth & Sunquist, 2000). We selected this grid cell size to allow for future potential linking of the occupancy parameter to a TAL-wide tiger abundance measure (Royle & Nichols, 2003; Hines *et al.*, 2010; Linkie *et al.*, 2010; Karanth *et al.*, 2011). We surveyed only grid cells that contained more than 10% (>22.5 km<sup>2</sup> patches) tiger habitat [grasslands and forests as determined by vegetative cover from geographic information system (GIS) data] and excluded habitat fragments <10 km<sup>2</sup> because we did not generally expect tigers to be resident in these smaller patches (Karanth *et al.*, 2008, 2011), although they may pass through them.

We mainly surveyed high probability locations for tiger sign detection (e.g. trails, ridgelines, roads, and river and stream beds) within each grid cell (Karanth *et al.*, 2008, 2011). A maximum of 40 km was surveyed per grid cell with each contiguous 1-km segment considered a 'spatial replicate' (Karanth *et al.*, 2008, 2011; Hines *et al.*, 2010). All grid cells were surveyed within 12–36 hrs (Karanth *et al.*, 2011) as our methods assumed spatial closure (i.e. occupancy on one spatial replicate assumes other spatial replicates are similarly 'occupied'; Hines *et al.*, 2010). To include an element of randomness in the spatial distribution of survey routes, prior to the survey we randomly selected one sub-cell (3.75 km × 3.75 km) per grid cell of those coded as tiger habitat that field



**Figure 1** The Terai Arc Landscape of Nepal with occupancy grid cells (coded for tiger sign detection) overlaid on tiger habitat (forest and grassland) and agriculture and settlement areas. WR, Wildlife Reserve; NP, National Park.

teams were required to enter as part of their surveys (Karanth *et al.*, 2011). The number of spatial replicates per grid cell (i.e. km walked) was proportionate to % tiger habitat (Karanth *et al.*, 2008, 2011).

Observers recorded each sighting of all study species (i.e. tigers and main prey). Throughout every 100-m segment of each 1-km replicate we also recorded each new instance of tiger tracks (e.g. as determined by direction of travel, size of tracks and number of tigers in the group such as cubs with mothers) and each instance of tiger scratch marks, scat and spray (Karanth *et al.*, 2008, 2011). For prey vocalizations, tracks and dung, we recorded only the first encounter of each type of evidence within each 100 m of each 1-km replicate (Karanth *et al.*, 2008, 2011). We recorded signs of human disturbance (e.g. livestock presence, poaching evidence, human-caused fire and other impacts on vegetation) in the same manner as prey (Karanth *et al.*, 2008, 2011).

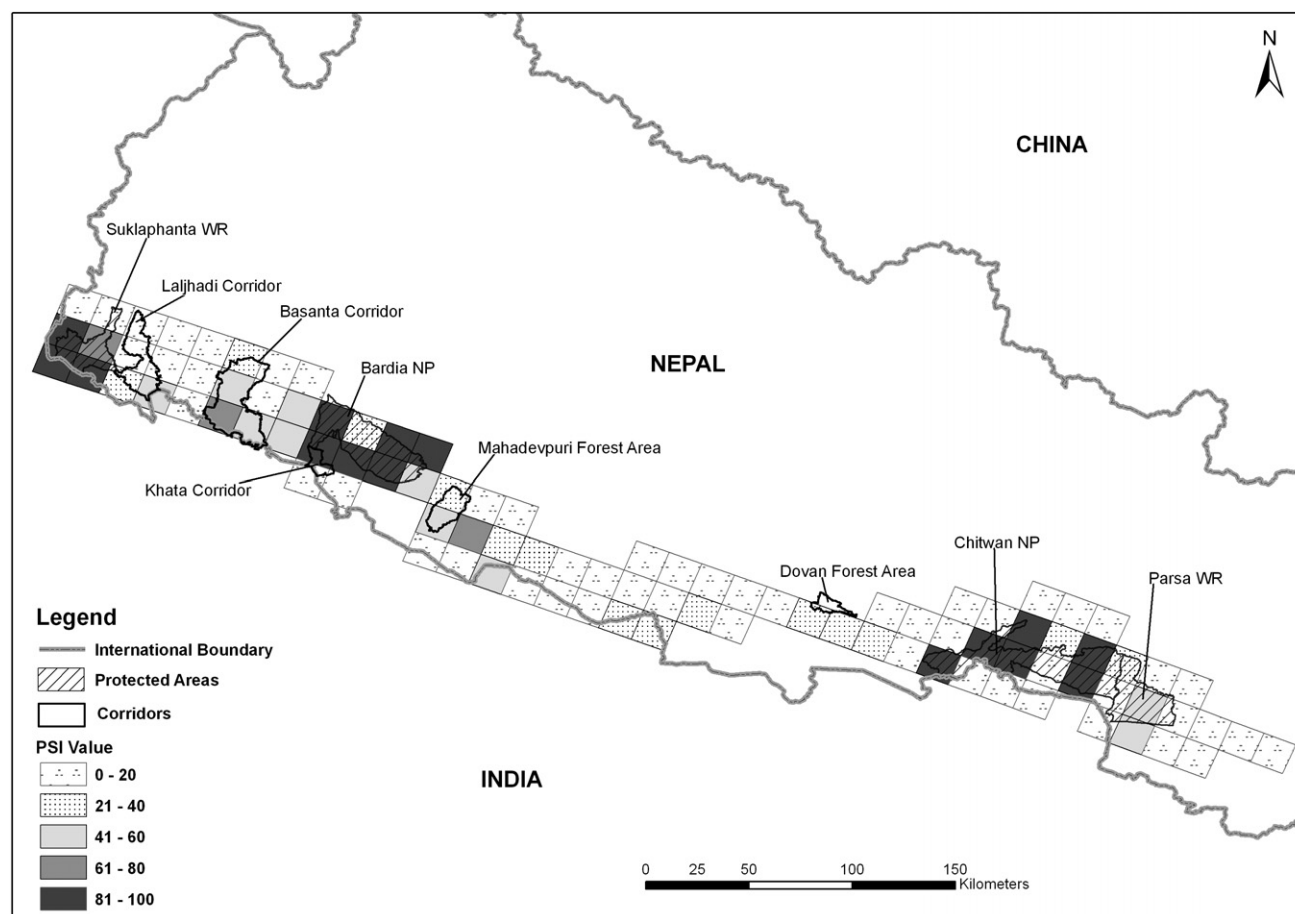
Unfortunately, observers with intermediate experience mainly surveyed outside of PAs. Because of this, and because only one survey inside a PA did not result in tiger sign detection, we did not have enough variability in our data to assess

the influence of PA status on occupancy or detection. For future surveys, we recommend that observers of varying experience be evenly distributed across management schemes.

We surveyed 2016.5 km across 96 grid cells out of the 108 covering the TAL (Fig. 1). Twelve grid cells were not surveyed because of logistic difficulties (mainly steep mountain areas) and therefore, inferences are limited to the surveyed cells. We were not aware of any tiger evidence from these unsurveyed areas, and there were not large blocks of forest to support resident tigers, although a tiger may occasionally pass through. We commenced contiguous survey walks 1–2 km from settlements in 76 (79%) grid cells and from campsites in the remaining 20 (21%) grid cells. We detected 790 tiger signs (561 sets of tracks, 121 scratch marks, 96 scats, 9 sprays, 2 sites where tigers killed prey and 1 direct sighting).

### Occupancy analysis

We used Program PRESENCE v. 3 (Hines, 2006) to model tiger occupancy and used Akaike Information Criteria (AIC) to compare and select models (Burnham & Anderson, 2002).



**Figure 2** Survey grid cells across the Terai Arc Landscape, Nepal, showing the probabilities of tiger occupancy ( $\psi$ ) [values are model-averaged estimates from model 5,  $\psi(P + H), \theta_0, \theta_1, p(O)$ ; model accounting for spatial correlation with the probability of occupancy influenced by the prey and human disturbance indices and detection probability influenced by observer experience and model 13, identical to model 5 but lacking the human disturbance index]. WR, Wildlife Reserve; NP, National Park.

We predicted our occupancy data would follow a single season custom spatial correlation model (Hines *et al.*, 2010). There are two probabilities associated with this correlation: (1)  $\theta_0$ , the probability that tiger sign is present on a segment given that the grid cell is occupied and tiger sign *was not* present on the previous segment and (2)  $\theta_1$ , the probability that tiger sign is present on the segment given that the grid cell is occupied and tiger sign *was* present on the previous segment. We expected  $\theta_1$  to be greater than  $\theta_0$  because tigers tend to follow trails. Because data collection commenced 1–2 km from settlements and campsites, the initial  $\theta_0$  is essentially a different parameter compared with the other  $\theta_0$ 's because there are no preceding segments that have been surveyed, hence it is unknown as to whether tiger sign was on or off the previous trail segment. Therefore, we expected the initial  $\theta_0$  to be somewhere between the  $\theta_0$  and  $\theta_1$  values for the subsequent segments. To evaluate these predictions we tested three base models (models 1–3, Table 1).

Next using the base model with the lowest AIC and the saturated model of probability of occupancy,  $\psi$  (i.e. prey index

and human disturbance index were included), we assessed the influence of three covariates (observer experience, prey index and human disturbance index) on  $p$ , the estimated probability of detecting tiger sign on a replicate given presence on a replicate (Hines *et al.*, 2010). All combinations of covariates were tested (models 5–11, Table 2). The probability of detection model with the lowest AIC was then used as the model from which we assessed the influence of two covariates (prey index and human disturbance index) on the probability of occupancy,  $\psi$  (models 5 and 12–14, Table 3) (Karanth *et al.*, 2011).

We assessed team observer experience (O) at the grid cell level as either extensive or intermediate based on the team's previous field experience. Although intensive training was conducted prior to the survey, we were interested in whether variation in previous experience might influence a team's ability to detect tiger sign, thereby, influencing the detection probability ( $p$ ).

We also assessed the influence of two site-specific covariates (i.e. prey index and human disturbance index) on  $p$  and  $\psi$ . To calculate the prey index we considered only ungulate prey such



**Table 1** Model selection results using Akaike Information Criteria (AIC)<sup>a</sup>

Model	Model No.	$\Delta$ AIC	W	Model likelihood	k
$\Psi(\cdot), \theta_0, \theta_1, p(\cdot)^b$	3	0	0.9989	1.0000	4
$\Psi(\cdot), \theta_0, \theta_1, p(\cdot)$ (all $\theta_0$ 's =)	2	13.67	0.0011	0.0011	4
$\Psi(\cdot), p(\cdot)$	1	133.60	0	0.0000	2

<sup>a</sup>Given are the Model No. (model number), relative difference in AIC values compared with the top ranked model ( $\Delta$ AIC), AIC model weight (W) and number of parameters in the model (k).

<sup>b</sup>The model is defined as  $\Psi(\cdot), \theta_0, \theta_1, p(\cdot)$  where the probability of occupancy ( $\Psi$ ) is constant and the probability of detection ( $p$ ) is influenced by spatial correlation (with the initial  $\theta_0$  not equal to other  $\theta_0$ 's).

**Table 2** Model selection results for the probability of detection ( $p$ ) using Akaike Information Criteria (AIC)<sup>a</sup>

Model	Model No.	$\Delta$ AIC	W	Model likelihood	k
$\Psi(P + H), \theta_0, \theta_1, p(O)$	5 <sup>b</sup>	0	0.5099	1.0000	7
$\Psi(P + H), \theta_0, \theta_1, p(O + H)$	9	1.70	0.2180	0.4274	8
$\Psi(P + H), \theta_0, \theta_1, p(O + P)$	8	1.98	0.1895	0.3716	8
$\Psi(P + H), \theta_0, \theta_1, p(O + P + H)^c$	11	3.70	0.0802	0.1572	9
$\Psi(P + H), \theta_0, \theta_1, p(H)$	7	12.59	0.0009	0.0018	7
$\Psi(P + H), \theta_0, \theta_1, p(\cdot)$	4	12.82	0.0008	0.0016	6
$\Psi(P + H), \theta_0, \theta_1, p(P + H)$	10	14.58	0.0003	0.0007	8
$\Psi(P + H), \theta_0, \theta_1, p(P)$	6	14.78	0.0003	0.0006	7

<sup>a</sup>Given are the Model No. (model number), relative difference in AIC values compared with the top ranked model ( $\Delta$ AIC), AIC model weight (W) and number of parameters in the model (k).

<sup>b</sup>This is the same 'model 5' in Table 3 and 4.

<sup>c</sup>The global model is defined as  $\Psi(P + H), \theta_0, \theta_1, p(O + P + H)$  where the probability of occupancy ( $\Psi$ ) is influenced by the prey index (P) and the human disturbance index (H) and the probability of detection ( $p$ ) is influenced by spatial correlation (with the initial  $\theta_0$  not equal to other  $\theta_0$ 's), observer experience (O), the prey index (P) and the human disturbance index (H).

**Table 3** Model selection results for the probability of occupancy ( $\Psi$ ) using Akaike Information Criteria (AIC)<sup>a</sup>

Model	Model No.	$\Delta$ AIC	W	Model likelihood	k
$\Psi(P + H), \theta_0, \theta_1, p(O)^b$	5 <sup>c</sup>	0	0.6649	1	7
$\Psi(P), \theta_0, \theta_1, p(O)$	13 <sup>d</sup>	1.37	0.3351	0.5041	6
$\Psi(H), \theta_0, \theta_1, p(O)$	14	39.08	0	0	6
$\Psi, \theta_0, \theta_1, p(O)$	12	41.33	0	0	5

<sup>a</sup>Given are the Model No. (model number), relative difference in AIC values compared with the top ranked model ( $\Delta$ AIC), AIC model weight (W) and number of parameters in the model (k).

<sup>b</sup>The model is defined as  $\Psi(P + H), \theta_0, \theta_1, p(O)$  where the probability of occupancy ( $\Psi$ ) is influenced by the prey index (P) and the human disturbance index (H) and the probability of detection ( $p$ ) is influenced by spatial correlation (with the initial  $\theta_0$  not equal to other  $\theta_0$ 's) and observer experience (O).

<sup>c</sup>This is the same 'model 5' in Table 2 and 4.

<sup>d</sup>This is the same 'model 13' in Table 4.

as deer, bovids (gaur and blue bull) and wild boar because tiger density has been correlated with ungulate prey density (Karanth *et al.*, 2004). Because in some cases observers were unable to reliably distinguish between chital, hog deer and muntjac sign, we did not remove muntjac from the prey variable to assess whether large prey were more important (Karanth *et al.*, 2011) but rather retained all deer in the prey index (P). We calculated the index in each grid cell as:  $P = (D$

$+ B + W)/S$ , where D is the sum of unique deer species detections across all 100 m segments in a particular grid cell, B = bovid and W = wild boar, respectively, and S is the total km surveyed in that grid cell.

In addition to the impact that humans have on tiger occupancy through prey depletion (which would be captured primarily in the prey index covariate), we were interested in four other major types of human disturbance (H) and included these in our analysis; livestock presence (L), evidence of poaching (E), human-caused fire (F) and other impacts on vegetation (V) such as encroachment, logging, tree felling, grass cutting, etc. We first scaled each type of disturbance to values ranging from 0–1. We then weighted the scaled disturbance values based on their expected relative contributions to tiger occupancy (weights detailed in equation below). Because we were unable to find published quantitative effects of human disturbance on tiger occupancy, we used expert opinion (biologists, wildlife field technicians and park personnel) to derive the weights (M. B. Pandey, Chief Warden, and J. B. Karki, Department of National Parks and Wildlife Conservation; B. Tamang and H. B. Tamang, National Trust for Nature Conservation; K. Thapa, P. Khanal and G. J. Thapa, World Wildlife Fund Nepal; personal communication). For example, evidence of poaching (E) was given the highest weight among the disturbances, 0.35, because this was believed to have a stronger influence in deterring tigers compared with livestock presence (L), fire (F) and other impacts on vegetation (V). We calculated the human impacts index (H) in

each grid cell as:  $H = (L \cdot 0.2) + (V \cdot 0.25) + (E \cdot 0.35) + (F \cdot 0.2)$ . We did not assess the sensitivity of the human disturbance index component weights on model performance.

Prior to including the prey and human disturbance indices as covariates in our models, we assessed their correlation in PAST version 2.07 (Hammer, Harper & Ryan, 2001). We scaled continuous covariates in PRESENCE prior to occupancy analysis. Following Karanth *et al.*, 2011, we did not assess the detectability of the prey or human disturbance signs because we were reasonably confident that these signs would be detected at this scale and as these variables were covariates, we were not explicitly interested in absolute measures of these indices.

We calculated the fraction of available tiger habitat occupied by tigers as the sum of the grid cell-specific model-averaged site occupancy estimates multiplied by the corresponding grid cell-specific area of tiger habitat (grasslands and forests as determined by vegetative cover from GIS data following area stipulations outlined above), divided by total available tiger habitat (Karanth *et al.*, 2011). Because our interest was in the overall proportion of cells that were occupied at the time of the surveying, and because all cells within the area of interest were surveyed (i.e. we were not generalizing results to the 12 cells that were unsurveyed because of logistic difficulties), conditional occupancy probabilities were used. These probabilities are conditional upon the actual observations at a particular cell (MacKenzie *et al.*, 2006). For example, while the overall occupancy probability may be estimated as 0.6 (as an example), if tiger sign was detected at least once during the survey, we know that at that time the cell was definitely occupied so the conditional probability is 1.0. We calculated the standard error (SE) for tiger habitat occupied based on conditional occupancy probabilities ( $\psi^c$ ) which was approximated by  $\sqrt{\left[ \sum_{i=1}^s \hat{\psi}_i^c (1 - \hat{\psi}_i^c) \right] / (s - s_D)}$  where  $s$  is number of cells surveyed and  $s_D$  is number of cells where tiger sign was detected.

We did not extend our occupancy modeling to an abundance-index (Royle & Nichols, 2003). As illustrated by Royle & Nichols (2003), abundance-induced heterogeneity can lead to different conclusions (Linkie *et al.*, 2010; Karanth *et al.*, 2011) if tiger abundance is influencing the local occupancy parameters and replicate-level detection probabilities. Our use of modeling methods detailed by Hines *et al.* (2010) did not address this potential issue, but allowed us to follow established analysis methods for studies such as ours that generally follow the Tigers Forever protocols (Karanth *et al.*, 2008, 2011). We also note that for the spatial dependence models we tested (Hines *et al.*, 2010), there is currently no goodness-of-fit test available in PRESENCE.

## Results

### Occupancy survey

Our naive occupancy estimate was 0.344 (33/96). Of the grid cells surveyed, 18 (19%) were categorized as within PAs, and

tiger sign was detected in 17 (94%) of them. Only the grid cell in and around the Mahadevpuri sector (surveyed for just 5 km based on tiger habitat) did not result in tiger sign detection (Fig. 2). Seventy-eight (81%) grid cells were categorized as outside of PAs and tiger sign was detected in 16 of these (21%).

### Occupancy analysis

Because the prey and human disturbance indices were not correlated ( $r = -0.03$ ,  $P = 0.73$ ) both covariates were included in model testing. All models receiving AIC weight included the prey index and observer expertise covariate (Table 3). As predicted and similar to what Karanth *et al.*, 2011 found, model-averaged estimates showed the probability of tiger sign presence on the first replicate (initial  $\theta_0 = 0.47$ ,  $SE = 0.01$ ) was higher than the probability of tiger sign presence on a replicate given absence on the previous replicate (subsequent  $\theta_0 = 0.12$ ,  $SE = 0.03$ ) and the probability of tiger sign presence on a replicate, given presence on the previous replicate ( $\theta_1$ ) was 0.86 ( $SE = 0.07$ ).

The model-averaged probability of site occupancy ( $\psi$ ) estimate was 0.366 ( $SE = 0.02$ , a 7% increase from the naive estimate) and the probability of detection ( $p$ ) estimate was 0.65 ( $SE = 0.08$ ) per 1 km searched. Grid cell-specific tiger site occupancy estimates ranged from 0.04 ( $SE = 0.05$ ) in areas with higher human disturbance and a relatively lower prey base to 1 ( $SE = 0.00$  and 0.14) in areas with lower human disturbance and a relatively higher prey base (Fig. 2). Across sites,  $p$  was 0.73 ( $SE = 0.04$ ) for observers with extensive experience and 0.22 ( $SE = 0.03$ ) for those with intermediate experience. While tiger sign was detected in all but one of the five major corridors (Dovan forest area, Figs 1 and 2), we estimated tigers occupied only 5049 ( $SE = 3$ ) km<sup>2</sup> (36%) of 13 915 km<sup>2</sup> potential tiger habitat.

Also similar to the findings of Karanth *et al.*, 2011, our  $\beta$  estimate coefficients for covariates influencing tiger occupancy indicate that the prey index had a significant positive influence whereas the human disturbance index had a negative though weaker influence (Table 4).

## Discussion

### Prey depletion and tiger occupancy

Our model-averaged tiger occupancy estimate (0.37) was lower than that found for tigers in a south-western India study (0.67) conducted at the scale of 188 km<sup>2</sup> grid cells, whereas our replicate-level probability of detection (0.65) was much higher (0.17, Karanth *et al.*, 2011). Tiger sign across the TAL was detected at a much higher rate within PAs than in areas categorized as outside of PAs (94 vs. 21%). We predicted this based, in part, on differing levels of prey and human disturbance (although differing management is also likely important, we did not have enough variation in our data to explore this). As demonstrated by the  $\beta$  coefficient estimates from our top models and similar to the findings of Karanth *et al.*, 2011, the prey index was highly influential in predicting tiger occupancy. Our results are consistent with the hypothesis that prey

**Table 4** Model-specific  $\beta$  coefficient estimates [standard errors (SE)] for covariates influencing tiger occupancy ( $\psi$ ) in the Terai Arc Landscape, Nepal. Only models receiving Akaike Information Criteria weight are reported

Model	Model No.	$\beta_0$ (SE)	$\beta_P$ (SE)	$\beta_H$ (SE)
$\psi(P + H), \theta_0, \theta_1, p(O)^a$	5 <sup>b</sup>	-1.576 (0.635)	3.885 (1.123)	-0.278 (0.166)
$\psi(P), \theta_0, \theta_1, p(O)$	13 <sup>c</sup>	-2.329 (0.497)	3.526 (0.988)	–

<sup>a</sup>The model is defined as  $\psi(P + H), \theta_0, \theta_1, p(O)$  where the probability of occupancy ( $\psi$ ) is influenced by the prey index (P) and the human disturbance index (H) and the probability of detection ( $p$ ) is influenced by spatial correlation (with the initial  $\theta_0$  not equal to other  $\theta_i$ 's) and observer experience (O).

<sup>b</sup>This is the same 'model 5' in Table 2 and 3.

<sup>c</sup>This is the same 'model 13' in Table 3.

depletion is an important factor in the current decline of wild tiger populations and a significant constraint on their recovery (Karanth & Stith, 1999). While Karanth *et al.*, 2011 found tigers occupy an estimated 66% of available tiger habitat, we estimated tigers occupied just 36% indicating significant unoccupied areas potentially suitable for tigers. Therefore to increase tiger occupancy, otherwise suitable areas with depleted prey bases should be managed with an important focus on increasing the primary prey base for tigers.

### Human disturbance and tiger occupancy

Similar to Karanth *et al.*, 2011, our  $\beta$  coefficient estimates from the top model (Table 4) indicate human disturbances negatively influenced tiger occupancy in ways beyond prey depletion. Because the human disturbance covariate incorporated livestock presence, the impact of humans on vegetation, fires and evidence of poaching, mitigating these factors should be considered to increase tiger occupancy.

### Observer experience and detection

While observer experience appeared to be an important variable in predicting detection probability, observers with intermediate experience mainly surveyed outside PAs (areas with lower tiger abundance) so detectability as it relates to tiger abundance may be an issue (Royle & Nichols, 2003; Karanth *et al.*, 2011). It may also be that substrates differ outside of PAs (i.e. tracks are not as readily imprinted) or tigers may behave differently outside of PAs and do not use the traditionally preferred habitats as readily (e.g. perhaps even in areas of equal tiger occupancy tracks may not be as likely in riverbed areas outside of PAs due to high human use). Unfortunately, we could not test the influence of PA status on  $p$  because all but one grid cell designated 'majority inside PA' resulted in tiger sign detection.

### Corridors and tiger persistence

The TAL was conceptualized as a landscape where the PAs are linked via corridors to promote dispersal of wide-ranging species from protected source populations, especially tigers (Wikramanayake *et al.*, 1998, 2004). Tiger sign was detected in all of the 5 major corridors except the Dovan forest area (Figs 1 and 2) indicating good potential for tiger dispersal and genetic exchange (Wikramanayake *et al.*, 2004, 2011). We

recommend additional research on the Dovan forest area with an aim to improving that corridor's functionality. Of course, while highly productive PAs (i.e. high tiger reproduction and survival) are critical if corridors are to serve a significant conservation purpose in allowing routine tiger dispersal, corridors may also be important by facilitating tiger relocation following natural or human disasters that render previously suitable habitat inhabitable.

### Management recommendations and future research

Our results demonstrate it is essential to support abundant prey while minimizing human disturbance such as ongoing tiger poaching for the effective recovery of tiger populations in Nepal. Recent management actions implemented within PAs to achieve these goals include increased patrol frequency, development of new guard posts, reinstatement of guard posts abandoned during recent civil strife and grassland management comprising rotational grazing and controlled burning. Within corridors waterholes have been developed and grasslands managed to increase prey and community-based anti-poaching units are being mobilized to reduce illegal activities (e.g. poaching, human-caused forest fires, etc.).

Because healthy protected source populations are key to tiger persistence (Karanth *et al.*, 2011), we propose that source populations be rigorously monitored for vital-rate estimation (e.g. annual camera trapping within PAs). Furthermore, because tiger occupancy is very high within PAs and lower outside (Fig. 2), we recommend corridors be monitored seasonally to determine patterns of tiger use and to detect additional human encroachment which can happen very quickly. We also recommend monthly briefs on the poaching of and retaliatory killing of tigers and spatial and temporal patrolling efforts and yearly reporting on human–tiger and livestock–tiger conflicts through the TAL.

To build upon the foundation of benchmark data we present, we recommend a TAL-wide tiger occupancy survey every 4 years. Beyond presence, future surveys may indicate changes in tiger reproduction (as indexed by cub tracks), the prey base, poaching intensity and other human impacts. Future research may also include multistate site occupancy models to assess tiger breeding (Stith & Kumar, 2002) and links between occupancy metrics and abundance estimates generated from camera trapping (Royle & Nichols, 2003;

Nichols *et al.*, 2007; Karanth *et al.*, 2011). The strategic and comprehensive monitoring we propose here will allow managers to make informed decisions regarding tiger conservation in Nepal during these critical times for tigers Asia-wide.

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