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Assessing spatiotemporal changes in tiger habitat across different land management regimes

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Abstract. Human-induced habitat loss and degradation are increasing the extinction probability of many wildlife species worldwide, thus protecting habitat is crucial. The habitat of thousands of imperiled wildlife species occurs in a variety of land management regimes (e.g., protected areas, multiple-use areas), each exerting differing effects. We used the globally endangered tiger (*Panthera tigris*) to examine the relationships between habitat change and land management in Nepal's Chitwan district, a global biodiversity hotspot. We evaluated the effects of environmental and human factors on tiger habitat based on data acquired by motion-detecting cameras and space-borne imaging sensors. Spatiotemporal habitat dynamics in Chitwan National Park and a multiple-use area outside the park were then evaluated in three time periods (1989, 1999, and 2009). Our results indicate that tigers preferred areas with more grasslands and higher landscape connectivity. The area of highly suitable habitat decreased inside the park over the entire 20 year interval, while outside the park habitat suitability increased, especially from 1999 to 2009. The loss of highly suitable habitat inside the park may be associated with an increasing trend of unauthorized resource extraction by a rapidly growing human population, coupled with natural processes such as flooding and forest succession. In contrast, community-based management of natural resources and the prohibition of livestock grazing since the late 1990s likely improved tiger habitat suitability outside the park. Results of this study are useful for evaluating habitat change and guiding conservation actions across the tiger range, which spans 13 countries. Moreover, quantitatively assessing habitat change across different land management regimes in human-dominated areas provides insights for conserving habitat of other imperiled wildlife species around the world.

Key words: camera trap; community-based management; habitat change; N-mixture; *Panthera tigris*; protected areas; tiger.

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INTRODUCTION

Human demand for natural resources has transformed much of the earth's land surface (Sanderson et al. 2002), and between 10 and 20% of the world's remaining natural grasslands and forests are expected to be converted to agriculture, urban, and infrastructure by 2050 (MEA 2005). This conversion of natural ecosystems to areas used intensively by humans is considered the main cause of the current global decline in biodiversity and, by removing vast amounts of wildlife habitat, has put many wildlife species and communities at a greater risk of extinction (Liu et al. 2001, Sanderson et al. 2002, Viña et al. 2007).

Over 170,000 protected areas currently covering 12.7% of the world's land area have been set aside "to achieve the long term conservation of nature" and are considered a core part of the habitat conservation programs for many wildlife species (Bertzky et al. 2012). However, human activities within and adjacent to protected areas (e.g., development, collection of natural resources, livestock grazing, and poaching) are pervasive and threaten the conservation effectiveness of such areas (DeFries et al. 2005, Linkie et al. 2006, Western et al. 2009, Liu and Raven 2010). Furthermore, the current global protected area network covers small or no portions of the ranges of many imperiled wildlife species (Margules and Pressey 2000, Rodrigues et al. 2004). For example, 89% (3,467) of all imperiled wildlife species analyzed by Rodrigues et al. (2004) had either none or only part of their ranges covered by protected areas. Consequently, the habitat of many imperiled species is located on human-dominated multiple-use areas (Xu et al. 2006, Lepczyk et al. 2008), which typically allow for more extractive activities than in protected areas (García-Fernández et al. 2008). Thus, strategies that mitigate human impacts on wildlife habitat across different land management regimes, such as protected areas and multiple-use areas outside them, are important for realizing conservation goals (Bearer et al. 2008, Hull et al. 2011).

In this study, we examined the relationships between different land management regimes and habitat of the tiger (*Panthera tigris*), a globally endangered and widely valued species (Carter et al. 2012*a*). We chose tigers because their large space requirements necessitates landscape-scale approaches to habitat protection that encompass strictly protected and multiple-use areas, where nearly 80% of the tiger's remaining range occurs (Linkie et al. 2008, Forrest et al. 2011, Wikramanayake et al. 2011). Our two objectives were to: (1) evaluate changes in tiger habitat suitability from 1989 to 2009 on a section of Chitwan National Park and a nearby multiple-use area outside the park; and (2) assess the potential influence of resource management policies and practices inside and outside the park on observed changes in tiger habitat suitability.

Land management regimes in Chitwan, Nepal

Chitwan National Park (~100,000 ha) was established in 1973 to protect the biodiversity of the Himalayan lowlands, a globally important region for tigers (Sanderson et al. 2006). Since 1975, a contingent of the Nepal Army has been stationed inside the park with the task of patrolling the park to deter illegal activities such as wildlife hunting, logging, and collection of other natural resources (Martin 1992). These exclusion policies of the park created resentment among local people who felt that access to natural resources they relied on, such as fodder for livestock, thatch and timber for household construction, and fuelwood for cooking and heating, was denied without their consent (Nepal and Weber 1995*a*). To reduce park-people conflicts, a 'grass-cutting' program was initiated in 1976 to allow local residents to enter the park for several days (ranging from 20 days at the beginning of the program to 3 days in 2010) annually to legally collect thatch grass, reeds, rope bark, and rope grass (Stræde and Helles 2000). However, this concession only marginally offsets local demand for natural resources; thus, local residents also illegally collect various natural resources throughout the year (Nepal and Weber 1995*b*, Stræde and Treue 2006). Although illegal use of natural resources in the park does not automatically lead to wildlife habitat loss, the resource demands of the human population adjacent to the park, which has tripled from 1971 to 2011 (CBS 2012), may be degrading wildlife habitat inside the park, particularly tiger habitat.

To mitigate human pressure on Chitwan's natural resources, a buffer zone (75,000 ha)

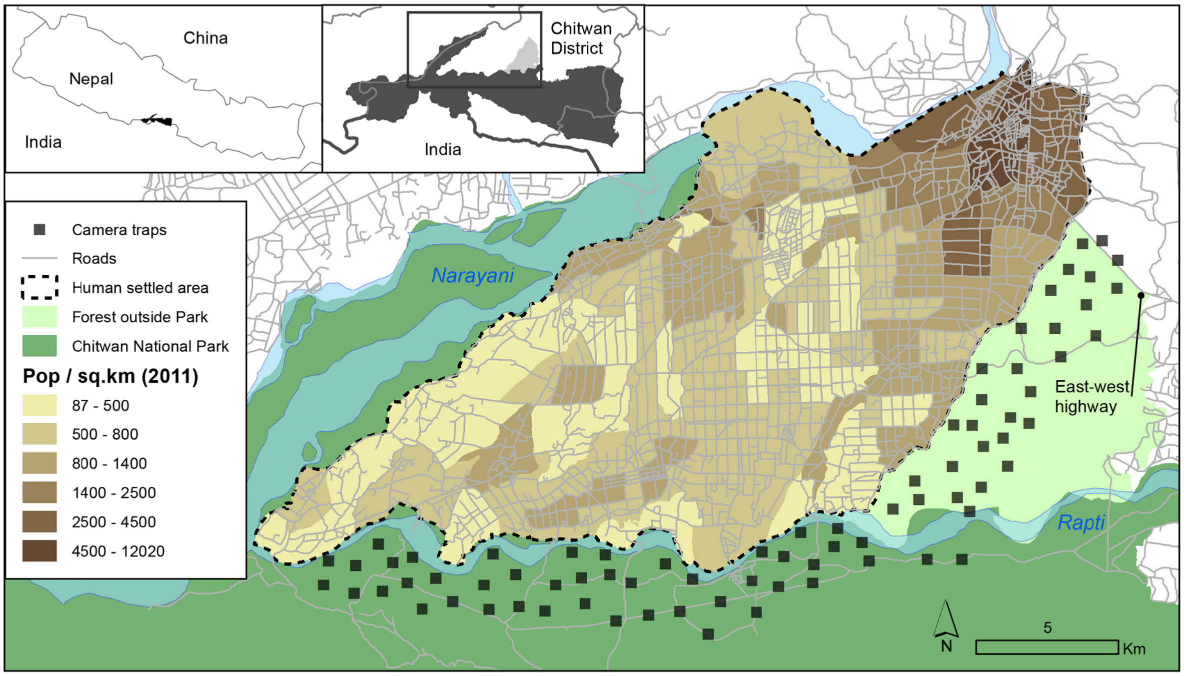

Fig. 1. Study site in Chitwan district, Nepal, where camera trap data on tigers were collected in 2010.

surrounding the park was established in 1996 with the dual purpose of restoring ecosystem integrity and improving human livelihoods. For instance, livestock grazing was prohibited from the multiple-use areas outside the park as ecosystem degradation due to overgrazing had become a major concern (Sharma 1990, Gurung et al. 2009). To offset this imposition, 30–50% of the park's annual revenue must be invested into the surrounding buffer zone to support community development programs, including alternative income opportunities and infrastructure improvement (GoN 1993). In addition, forested areas in the buffer zone adjacent to human settlements, which previously were part of the State-controlled national forest system, were handed over to local user-group committees as community forests. Thus, user-group committees have had a considerable degree of management responsibility and control over resource use, for example, by dictating the amount and times of year when local people can collect fuelwood, timber, and fodder from the community forests (Nagendra et al. 2005). Previous research indicates that community-based resource management and restrictions on livestock grazing may be reversing deforestation and fragmentation outside the park (Gurung et al. 2008, Nagendra et al. 2008).

MATERIALS AND METHODS

Study site

Situated in south central Nepal, our study site (Fig. 1) was located in a river valley basin along the flood plains of the Rapti, Reu, and Narayani rivers with an elevational range of 150 m to 815 m. Climate in Chitwan is subtropical with a summer monsoon from mid-June to late-September, and a cool dry winter. Mean annual rainfall is 240 cm, 90% of which falls during the monsoon from June to September. Temperatures are highest (maximum 38°C) during the monsoon and drop to a minimum of 6°C in the post-monsoon period (October to January; Laurie 1982). The park and multiple-use area outside the park have retained the unique natural vegetation communities distinctive of the Himalayan lowlands, including *Sal* (*Shorea robusta*) forest, *khair* (*Acacia catechu*) and *sissoo* (*Dalbergia sissoo*) riverine forests, and grasslands dominated by species of the genera *Saccharum*, *Themeda*, and *Imperata* (Chaudhary 1998). As of 2011, human population in the areas adjacent to our study site (26,100 ha) was approximately 275,000 distributed in approximately 68,000 households (CBS 2012). The household number increased faster than population size during 1991 to 2011, similar to the global trend (Liu et al. 2003).

Tiger detection data

From January to April (i.e., the dry season before monsoon) in 2010, we assessed tiger occurrence using 19 pairs of digital Reconyx RM45 passive infrared motion detecting cameras (Reconyx Inc., WI, USA). Motion detecting cameras have been used to effectively measure wildlife activity in numerous sites (O'Connell et al. 2010). We established four adjoining sample blocks that covered naturally vegetated areas inside and outside the park. These sample blocks were roughly oriented parallel to the human settled area. Each block was then subdivided into a grid with nineteen 100 ha cells. To maximize the probability of detecting tigers across the spatial extent of our study site, a camera pair (hereafter a 'camera trap') was located at or close to the center of each grid cell along the nearest road, path, or animal trail. Thus, we set the camera traps at a total of 76 locations, 46 of which were inside the park and 30 outside. The grid size and sample block design were chosen to maximize the likelihood that all tigers in the area were detected, given female tiger home-range sizes in this region of approximately 1,500 ha (Sunquist 1981). Two cameras facing each other were used in each camera trap to simultaneously photograph both sides of an animal, thus increasing the probability of identifying individual tigers. We used a handheld Garmin eTrex (Garmin International Inc., KS, USA) global positioning system (GPS) receiver to record the location of each camera trap. The cameras were mounted on trees at approximately 1–1.5 m from the ground, angled downward and set to operate 24 h/day with no more than the minimum mechanical delay between sequential pictures.

We sampled the first block in the westernmost portion of the study site for 20 days and then moved eastward to sample the next blocks in succession, each for 20 days. We defined the camera trap as our sampling unit and one day (i.e., noon to noon the following day) as our sampling occasion. Therefore, cameras were set for a total of 1,510 trap-days, with 920 trap-days inside the park and 590 outside (one camera trap was damaged for 10 trap-days). We created a trap-by-occasion matrix, with rows i representing the camera trap sampling units and columns t representing the one-day sampling occasions. We identified individual tigers from the pictures using their unique stripe patterns (Karanth and Nichols 2002), and recorded the number of individual tigers for occasion t at trap i in the matrix.

Tiger habitat data

Environmental factors.—As longitudinal data on prey density across our study site did not exist, we chose to use land-cover composition and spatial configuration as factors in our models because previous studies show that those factors influence tiger dispersal, acquisition of prey, and tiger prey density (Seidensticker and McDougal 1993, Smith 1993, Shrestha 2004). In addition, these factors can be measured across space and through time using remotely sensed imagery, thus enabling assessment of habitat change.

We obtained a cloud-free, multi-spectral Landsat TM image (Path 142, row 41 WRS-2; resolution: 28.5 m × 28.5 m) for October 2009 to be consistent with the time period in which we collected tiger detection data (i.e., 2010). The image was obtained from the United States Geological Survey (USGS; http://glovis.usgs.gov) and was received geometrically corrected (i.e., level-1G product). Image processing was performed using ERDAS IMAGINE 9.3 (Leica Geosystems). We used an improved dark object subtraction method to radiometrically and atmospherically correct the image (Chavez 1996). An unsupervised classification algorithm using the ISODATA technique (Jensen 1996) was then applied to the image to produce 100 spectral classes. We used high-resolution Google Earth images (http://www.earth.google.com) and our knowledge of the area to merge the 100 spectral classes into six land-cover classes potentially related to tiger habitat: open water, grassland, *Sal* dominated forest, low density *Sal*, riverine forest, and barren (e.g., floodplain) (Shrestha 2004). Although the image was acquired in a different month (i.e., October) than when the tiger detection data was collected (i.e., January to April), the six land-cover classes derived from the

Table 1. Environmental and human factors potentially influencing tiger habitat selection in Chitwan, Nepal.

Covariate category/name	Description†
Environmental factors	
Area§	Total land-cover class area (ha)‡
Class mean patch size§	Area-weighted mean size of patches from each land-cover class
Number of patches¶	Total number of land-cover patches
Landscape mean patch size¶	Area-weighted mean size of all land-cover patches
Largest patch index¶	Approaches 0 when largest patch is increasingly small, and approaches 100 when entire area consists of a single patch
Correlation length¶	Equal to 0 when all patches consist of a single pixel, and increases as patch extent increases
Patch shape¶	Equal to 1 when all patches are square and increases with increasing patch shape irregularity
Patch contagion¶	Approaches 0 when patches are disaggregated and interspersed, and approaches 100 when patches are aggregated
Shannon's diversity index¶	Equal to 0 when there is only one patch in the landscape and increases as number of patch types increases
Human factors	
Road density	Sum (m) of road length
Distance to settlement	Distance (m) from camera trap location to nearest human settlement
Distance to forest road	Distance (m) from camera trap location to nearest forest road
Location	1 if inside park; 0 if outside the park

† All covariates are continuous and, except distance to settlement and road, were calculated within a circular area (radius of 400 m) around each camera trap location.

‡ Land-cover classes included open water, grassland, *Sal* dominated forest, low density *Sal*, riverine forest, and barren.

§ Class metric.

¶ Landscape metric.

image are spectrally distinct from one another making their separation robust to seasonality. To eliminate outlier pixels (i.e., misclassified pixels), we applied a 3 × 3 majority filter to the land-cover map (Gurney and Townshend 1983). We assessed the accuracy of the land-cover classification map using 300 randomly selected pixels (i.e., 50 pixels per land-cover class), whose land-cover class was determined in contemporary high spatial resolution images, accessed in Google Earth (Biradar et al. 2009).

To determine habitat selection by tigers at fine spatial scales (i.e., smaller than the average tiger home-range size), we used a circular area with a radius of 400 m (i.e., ca. 50 ha) around each camera trap location. We chose this scale for two reasons. First, radio-telemetry data of tigers in Chitwan collected over many years indicate that they actively search for prey within a radius of approximately 400 m (Ahearn et al. 2001). Second, 50 ha is roughly the same size as home ranges for several tiger prey species (e.g., barking deer [*Muntiacus muntjak*], hog deer [*Axis porcinus*], and spotted deer [*Axis axis*]) in Nepal (Moe and Wegge 1994, Odden and Wegge 2007). In each 50 ha circular area surrounding each camera trap we summarized the land-cover composition (i.e., areas of each class) in the 2009 map. In addition, we used FRAGSTATS 3.3 (McGarigal et al. 2002) to calculate nine class-level and landscape-level metrics (Table 1) from the 2009 land-cover map to characterize the spatial configuration of the different land-cover classes. These metrics were calculated using a neighborhood of eight pixels surrounding each focal pixel. The environmental factors included in the model cover a wide array of land-cover information including patch area, edge, shape, and interspersion (Riitters et al. 1995). These factors are often associated with the spatial distribution and habitat selection of herbivores (Kie et al. 2002) and carnivores (Michalski and Peres 2005).

Human factors.—Proximity to human settlements or human-made landscape features (e.g., roads) may also influence habitat selection by tigers (Kerley et al. 2002, Johnson et al. 2006). Park and buffer zone boundary data were obtained from the world database on protected areas (www.protectedplanet.net). We calculated the distance from each camera trap to the border of the human settled area as delineated by the boundary of the park/buffer zone. Road vector data were obtained from a 1996 survey performed by the Nepal Survey Department (www.dos.gov.np). This road vector coverage was updated to include roads constructed after 1996 by digitizing roads visible in high resolution imagery accessed through Google Earth. All roads within the study site were minor unpaved roads, except for two unpaved roads (one inside and one outside the park) that were used comparatively more often by local people to travel across the forest. Using the updated road vector layer, we calculated the distance from each camera trap to the nearest road. We also calculated the road density within the 50 ha circular area surrounding each camera trap location. Lastly, we created a dummy variable that indicated whether the camera trap was inside or outside the park (Table 1).

Modeling tiger habitat selection

We used N-mixture models (Royle 2004) to estimate the relative effect of environmental (derived from the 2009 image) and human factors (Table 1) on the spatial variability of tiger abundance from the 2010 camera trap data. Using model results we predicted location-specific tiger "abundance." The abundance index indicated whether a location is more or less likely to be visited by tigers (Linkie et al. 2010). Thus, the abundance index was used as a surrogate of tiger habitat suitability based on the assumption that habitat conditions in a location are directly related to the number of times it is visited by the target species (Boyce and McDonald 1999).

We let n_{it} denote the number of individual tigers detected at trap i (=1, 2, ..., R) and occasion t (=1, 2, ..., T). We assumed that the tiger population being sampled was demographically closed so that the number of detected individuals may be viewed as independent and identically distributed binomial random variables:

$$n_{it} \sim \text{Binomial }(N_i, p)$$

where N_i is tiger abundance at trap i and p is the detection probability. The N_i were regarded as random effects with a Poisson distribution with mean λ. We chose a Poisson variant of the N-mixture model because it has been shown to generate more ecologically realistic parameter estimates than the negative binomial and zero inflated negative binomial variants (Joseph et al. 2009). Mean trap abundance, λ_i, was allowed to vary in response to all environmental and human factor covariates by adopting a log-linear model:

$$\log(\lambda_i) = \beta_0 + \sum_{k=1}^{K} x_{ik}\beta_k \qquad (1)$$

where x_{ik}; $k = 1, 2, \ldots, K$ are the K measurable covariates and β is a K-dimensional vector of covariate parameters for trap i. Detection probability, p, can vary with time in addition to trap-specific covariates (i.e., environmental and human factors) (MacKenzie et al. 2002). To create a time-specific covariate, we calculated the Julian date (Hein et al. 2009) for each day that the traps were operational. Detection probability was allowed to vary in response to time and trap-specific covariates using a logistic regression model:

$$\text{logit}(p_i) = \alpha_0 + \sum_{k=1}^{K} x_{ik}\alpha_k \qquad (2)$$

where p_i is the probability that a tiger will be detected at trap i and α is a K-dimensional vector of covariate parameters. The integrated likelihood from all R traps was established as:

$$L(p, \lambda|\{n_{it}\}) = \prod_{i=1}^{R}\left\{\sum_{N_i=\max_t n_{it}}^{\infty}\left(\prod_{t=1}^{T}\text{Bin}(n_{it}; N_i, p)\right)f(N_i; \lambda)\right\}.$$

Conventional maximum likelihood was used to estimate parameters from this integrated likelihood.

Models were ranked according to their second-order Akaike's information criterion (AIC$_\text{c}$), with higher-ranked models having lower AIC$_\text{c}$ values (Burnham and Anderson 1998). Because several models with different combinations of covariates performed comparatively well (i.e., $\Delta\text{AIC}_\text{c} < 4$), we averaged model results (i.e., covariate coefficients) from the top-ranked models using multi-model inference (Anderson 2007). Model-averaged coefficient estimates were considered significant if their unconditional 95% CIs did not include zero.

We used parametric bootstrapping to evaluate the goodness-of-fit of the top-ranked models. We simulated 100 data sets from each of the top-ranked models and fit the models to the data using the Freeman-Tukey fit statistic. We then compared the value of the Freeman-Tukey fit statistic of the observed data set to the fit statistics of the simulated data sets. A model was considered to adequately fit the observed data if the observed fit statistic value did not exceed the 0.05 percentile of the distribution of the fit statistics calculated from the simulated data sets (Sillett et al. 2012). Model specification, parameter estimation, averaging, and goodness-of-fit were performed using the 'unmarked' and 'AICcmodavg' packages in the R software (Fiske and Chandler 2011).

Mapping tiger habitat suitability

We processed Landsat TM and ETM+ images from November 1989 and December 1999 using the same procedures we used to process the 2009 image. Accuracy of the land-cover maps obtained for 1989 and 1999 was not evaluated due to unavailability of reference data covering these time periods. Nevertheless, accuracy of these maps was expected to be similar to that of the 2009 land-cover map, since map production followed the same procedures (including image pre-processing to account for atmospheric effects).

The three time periods comprised intervals of time roughly prior to (i.e., 1989–1999), and after (i.e., 1999–2009) the implementation of buffer zone policies in the multiple-use area outside the park. Restrictions on livestock grazing outside the park did not take effect until community forest user groups were organized. This happened about a couple of years after the buffer zone was established in 1996 (N. M. B. Pradhan, *personal communication*).

For 1989, 1999, and 2009 we combined covariate GIS layers and the model-averaged parameter estimates to assign a tiger "abundance" value to pixels on a grid with a spatial resolution equal to that of the Landsat imagery (i.e., 28.5 m × 28.5 m). First, covariate GIS layers for each time period were produced using ArcGIS 10 and FRAGSTATS, wherein a circular window with a 400 m radius was passed over each pixel in the grid and metrics at the class or landscape level were calculated at the focal pixel. Then, using the covariate GIS layers and parameter estimates as input, we took the exponent of the right-hand side of Eq. 1 to estimate per-pixel tiger abundances (i.e., per-pixel estimates of λ) for all three time periods.

To avoid over-extrapolation, the maps of tiger habitat suitability obtained were restricted to the areas accessible to tigers detected by the cameras. Habitat suitability outside the park was mapped in the naturally vegetated area south of the 'East-West' highway, which delineates the northern boundary of the buffer zone (Fig. 1). Within-park habitat suitability was mapped in an area delineated by the Churia hills to the west, the park border to the north, and one-half the mean maximum distance traveled (MMDM/2) by the tigers in the southern and eastern boundaries of the park. MMDM/2 was determined as the distance between the two farthest capture locations for all individual tigers, and is often used to delineate the effective sample area for population density estimates (Karanth and Nichols 1998). Maps of habitat change from 1989 to 1999 and 1999 to 2009 were created by calculating the per-pixel difference in tiger habitat suitability between the respective time periods. Changes in the area of different habitat suitability categories were assessed for each land management regime across time. Mean change and 95% confidence intervals in habitat suitability were calculated at 100 m intervals away from the human settled area up to 3,000 m. We chose 3,000 m because local people do not usually travel farther to collect natural resources.

RESULTS

Tiger detections

We obtained a total of 131 adult tiger detections, with 92 and 39 detections inside and outside the park, respectively. We identified 17 individual adult tigers across all camera traps. Twelve adults were detected inside the park and 6 were detected outside the park, with one tiger being photographed in both areas. Across our study site, 75% (57/76) of all camera traps were triggered by tigers. A larger percentage of cameras outside the park (83%) were triggered by tigers than inside the park (70%). The number of tiger detections at each camera trap ranged from 0 to 9 inside the park ($\bar{x} = 2$), and 0–4 outside the park ($\bar{x} = 1.3$). MMDM/2 was 2,371 m.

Changes in land cover

Overall accuracy of the 2009 land-cover map was 85.3% suggesting that the classification procedure adequately represented the land-cover classes in the study area (Congalton 1991). Land-

Table 2. Land-cover areas (ha) for each time period.

Land cover	1989	1999	2009
Entire study site			
Water	800	691	797
Grassland	4852	4952	4722
Sal forest†	11602	11089	10281
Riverine forest	1308	1561	2421
Barren	355	625	698
Inside park			
Water	640	593	637
Grassland	3447	3461	3124
Sal forest†	7333	7129	6423
Riverine forest	1209	1169	1995
Barren	184	462	635
Outside park			
Water	160	99	160
Grassland	1396	1482	1588
Sal forest†	4269	3961	3858
Riverine forest	99	393	426
Barren	170	162	64

† Comprises *Sal* dominated and low-density *Sal* forest.

cover classifications for all three time periods revealed that from 1989 to 2009 grassland area decreased (−323 ha) inside the park and increased (192 ha) outside the park (Table 2). In contrast, barren land-cover, which mostly consisted of sandy floodplain, increased (451 ha) inside the park and decreased (−106 ha) outside the park. *Sal* forest decreased both inside (−910 ha) and outside the park (−411 ha) while riverine forest increased both inside (786 ha) and outside (327 ha) the park over the 20 year period (Table 2).

Predictors of detection probability and tiger habitat

We ran approximately 200 models with different combinations of variables. Model $\mathrm{AIC_c}$ values ranged from 892.35 to 873.05. The bootstrap *P* values for the top-ranked models (Table 3) based on the Freeman-Tukey fit statistic were 0.45, 0.46, 0.51, and 0.47, suggesting the models fit the data adequately. Model-averaging indicated that tiger abundance was positively associated with correlation length (β = 0.32, 95% CI: 0.06–0.57) and grassland area (β = 0.23, 95% CI: 0.04–0.42), suggesting that tigers selected areas consisting of more connected land-cover patches and with more grassland. Detection probability was negatively associated with riverine forest area (β = −0.37, 95% CI: −0.69 to −0.06) and Julian date (β = −0.44, 95% CI: −0.75 to −0.12), suggesting that tigers were less likely to be detected in areas with more riverine forest and later in the sampling period. With the covariates set to zero (i.e., mean), detection probability was 0.02 (SE = 0.008) across all traps in the study site.

Tiger habitat suitability and its changes

Tiger habitat suitability, as measured using a per-pixel abundance index, ranged from 1.64 to 11.07 ($\bar{x}$ = 4.38), 1.53 to 11.08 ($\bar{x}$ = 4.38), and 0.63 to 11.73 ($\bar{x}$ = 4.36) for 1989, 1999, and 2009, respectively. The habitat suitability index (HSI) in all three time periods was the most heterogeneous along the Rapti River and in areas adjacent to human settlements, whereas relatively homogenous and moderate habitat suitability tended to occur within the core of the inside study site (Fig. 2). The mean tiger HSI was higher inside (1989: 4.54, 1999: 4.54, 2009: 4.46) than outside the park (1989: 4.09, 1999: 4.1, 2009: 4.23) at all three time periods, although the difference in mean HSI inside and outside the park diminished through time (i.e., 10.98%, 10.55%, and 5.35% in 1989, 1999, and 2009, respectively).

The relatively small changes in mean HSI values through time conceal rather large changes in different HSI categories. Across the entire study site, approximately 110 ha overall became more suitable habitat (i.e., HSI categories 5–6, 6–7) from 1989 to 1999 (Table 4, Fig. 3A). However,

Table 3. Summary of tiger habitat models.

Model	*K*	$\mathrm{AIC_c}$	$\Delta\mathrm{AIC_c}$	w_i	LL
λ(correlation length + grassland area)*p*(riverine area + Julian date)	6	873.05	...	0.48	−429.92
λ(correlation length + grassland area)*p*(riverine area + Julian date + road density)	7	874.29	1.24	0.26	−429.32
λ(correlation length + grassland area)*p*(riverine area + Julian date + location)	7	875.16	2.1	0.17	−429.76
λ(correlation length + grassland area)*p*(riverine area + location)	6	876.49	3.44	0.09	−431.64

Notes: Covariate coefficient estimates were averaged from these four top-ranked models. λ is the index of abundance, *p* is the detection probability, $\Delta\mathrm{AIC_c}$ is the difference in $\mathrm{AIC_c}$ values between each model and the model with the lowest $\mathrm{AIC_c}$ value, w_i is the $\mathrm{AIC_c}$ model weight, and LL is the logarithm of the likelihood. *K* = Number of model parameters including intercepts and covariates, location = location of the camera trap (i.e., inside or outside Chitwan National Park). The empty cell indicates that the model in that row had the lowest $\mathrm{AIC_c}$ value.

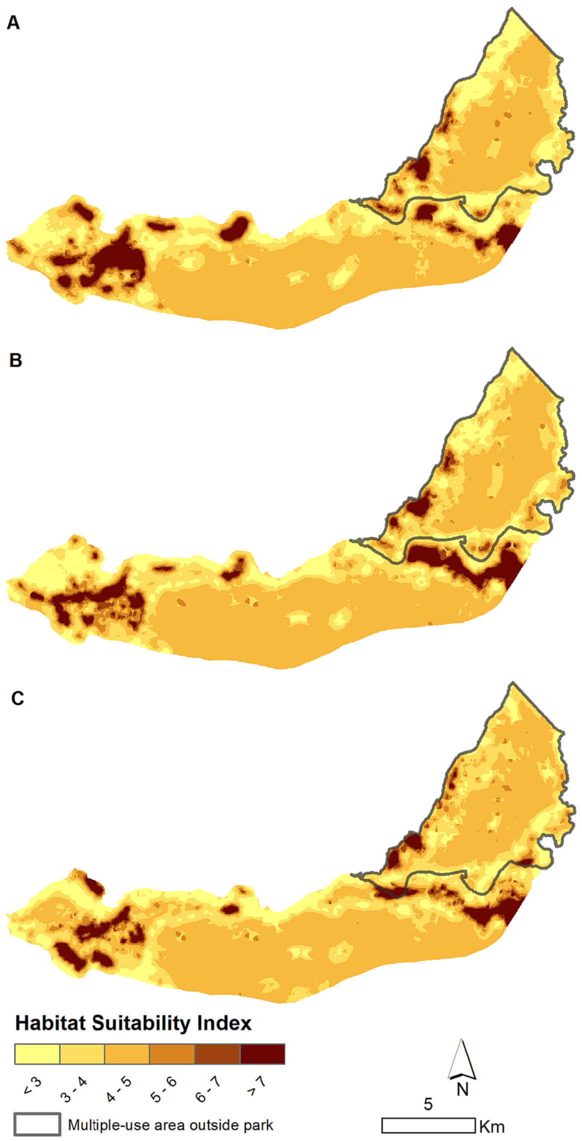

Fig. 2. Map of estimated tiger habitat suitability inside and outside Chitwan National Park in three time periods: (A) 1989, (B) 1999, and (C) 2009.

Table 4. Areas (ha) of different tiger habitat suitability index (HSI) categories for each time period.

HSI category	1989	1999	2009
Entire study site			
< 3	2798	2817	2530
3–4	4189	4081	4459
4–5	9616	9590	9847
5–6	825	897	786
6–7	489	532	453
> 7	1001	998	834
Inside park			
< 3	1622	1897	1773
3–4	2737	2343	2740
4–5	6560	6573	6705
5–6	601	672	560
6–7	382	430	348
> 7	911	893	676
Outside park			
< 3	1176	920	758
3–4	1452	1738	1719
4–5	3057	3016	3143
5–6	224	225	225
6–7	107	102	104
> 7	90	105	157

from 1999 to 2009, approximately 350 ha of habitat in the three highest HSI categories (12 to 17% of each category) downgraded to lower HSI categories (i.e., 3–4 and 4–5). Inside the park, approximately 100 ha became more suitable habitat (i.e., HSI categories 5–6, 6–7) from 1989 to 1999, although the lowest HSI category increased by 275 ha (17%, Table 4, Fig. 3B). Moreover, from 1999 to 2009, approximately 410 ha of habitat in the three highest HSI categories (17 to 24% of each category) downgraded to lower categories (i.e., 3–4, 4–5), resulting in a net decline in habitat suitability inside the park over that time. In contrast, outside the park, over 400 ha in the lowest HSI category upgraded to more suitable habitat over the 20 year interval (Table 4, Fig. 3C). The highest HSI category increased by 52 ha (50%) from 1999 to 2009, contributing to a net increase in the HSI outside the park over that time.

Per-pixel change in tiger habitat suitability from 1989 to 1999 and 1999 to 2009 ranged from −7.56 to 7.37 and −7.59 to 8.34, respectively. Negative values are associated with habitat becoming ‘less suitable’ over time, while positive values are associated with habitat becoming ‘more suitable’ over time (Fig. 4). Habitat suitability inside the park changed the most along the Rapti River and in the large grassland/riverine complexes to the west and east. Habitat suitability outside the park changed the most along the border with the human settled area (Fig. 4).

From 1989 to 1999, the mean change in the tiger habitat suitability across the entire study site was negative at distances of 100 to 1,800 m away from the human settled area, with the low point (−0.7 in HSI) occurring at about 600 m from the human settled area (Fig. 5A). From 1999 to

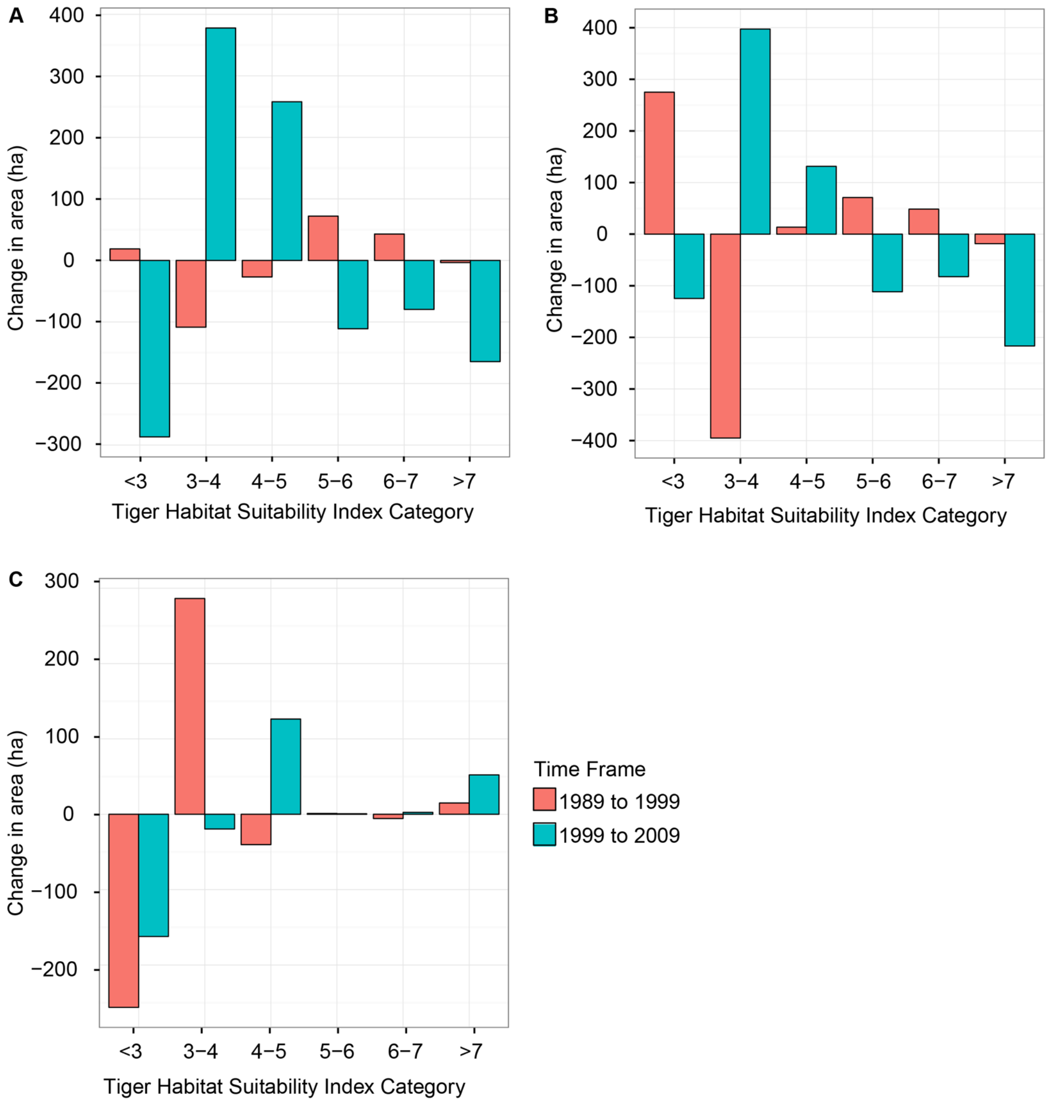

Fig. 3. Change in area (ha) of different tiger habitat suitability index categories from 1989 to 1999 and 1999 to 2009 for (A) entire study site, (B) inside the park, and (C) outside the park.

2009, the mean change in the HSI was positive (ranging from 0.1 to 0.4) at distances of 100 to 1,700 m, with the changes significantly different from those that occurred from 1989 to 1999 within the same distance interval. Beyond 1,700 m the mean change was negative, reaching a low point (−0.41) at approximately 2,500 m. In general, a similar pattern to the entire study site was evident inside the park over the 20 year period, although the magnitudes of the negative changes were greater (Fig. 5B). Mean change in the habitat suitability outside the park from 1989 to 1999 was initially negative at 100 m and then became positive from 200 m to a distance of 1,000 m. The positive changes that occurred from 200 m to 1,000 m outside the park were significantly different from the negative changes that occurred within the same distance interval inside the park during the same time period (Fig. 5B, C). Beyond 1,000 m, mean changes outside the park from 1989 to 1999 were negative. From 1999 to 2009, mean change outside the park peaked around 300 m (0.62) and remained positive until approximately 1,800 m, with most of the changes within

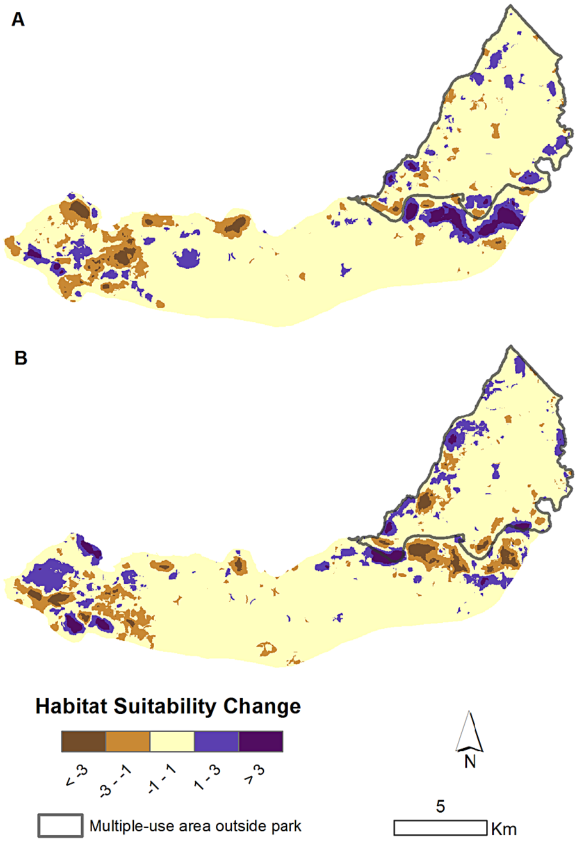

Fig. 4. Map of change in estimated tiger habitat suitability inside and outside Chitwan National Park from (A) 1989 to 1999 and (B) 1999 to 2009.

1,800 m significantly more positive than those that occurred from 1989 to 1999 (Fig. 5C).

DISCUSSION

Factors affecting tiger habitat and detection

Alluvial grasslands support high densities of tiger prey and contain important sources of water (Eisenberg and Seidensticker 1976, Sunquist 1981). Thus, tigers may select areas with more grassland to look for prey and obtain water. Unlike land-cover types with relatively low understory density, grasslands may also provide adequate cover for tigers' hunting activities (Sunarto et al. 2012). Correlation length can be considered a measure of connectivity since it represents the average distance a tiger can move within a land-cover patch before encountering a patch boundary. Contiguous land-cover patches may facilitate movement and dispersal across the landscape (Short Bull et al. 2011). Our results regarding tiger preference for contiguous land-cover patches at a fine spatial scale, support those of Sunarto et al. (2012), which found that tigers in Sumatra prefer large contiguous forest tracts with dense understory.

Since the understory of riverine forest is typically more dense than *Sal* forest (Sunquist 1981, Lehmkuhl 1994), understory vegetation may be more likely to obstruct the field of view of cameras in riverine forest than in *Sal* forest, which could have lowered detection probability. In addition, as animal/walking trails in riverine forests are perhaps smaller and less defined than other forest types, tigers may traverse riverine forests along multiple, unpredictable routes and consequently be detected less often by our cameras. There are two possible reasons why detection probability decreased over time. By monitoring breeding tigers from 1973 and 1989, Smith and McDougal (1991) showed that the distribution of births throughout a year was not significantly different from a uniform distribution, although a peak in births did occur between May and July. Prior to this peak, females may be less active, which could lower detection probability as compared to time periods earlier in the year. Another possible explanation is that tigers are generally less active and mobile in March and April when temperatures increase (Seidensticker 1976). By formally accounting for variation in detection probability as a function of riverine forest and time, the N-mixture model used in this study provides more reliable estimates of tiger habitat suitability across the entire study site (Royle 2004).

Habitat change across different land management regimes

Protected areas in many temperate and tropical regions have experienced declines in wildlife habitat as a result of human impacts (Liu et al. 2001, DeFries et al. 2005, Linderman et al. 2005). While the overall estimated suitability of tiger habitat in Chitwan National Park was high over the 20 year study period (Table 4), persistent and increasing human pressures may have degraded habitat suitability through time. We found that habitat inside the park became less suitable for tigers from 1989 to 1999 in the areas closest to human settlements. Likewise, Nagendra et al.

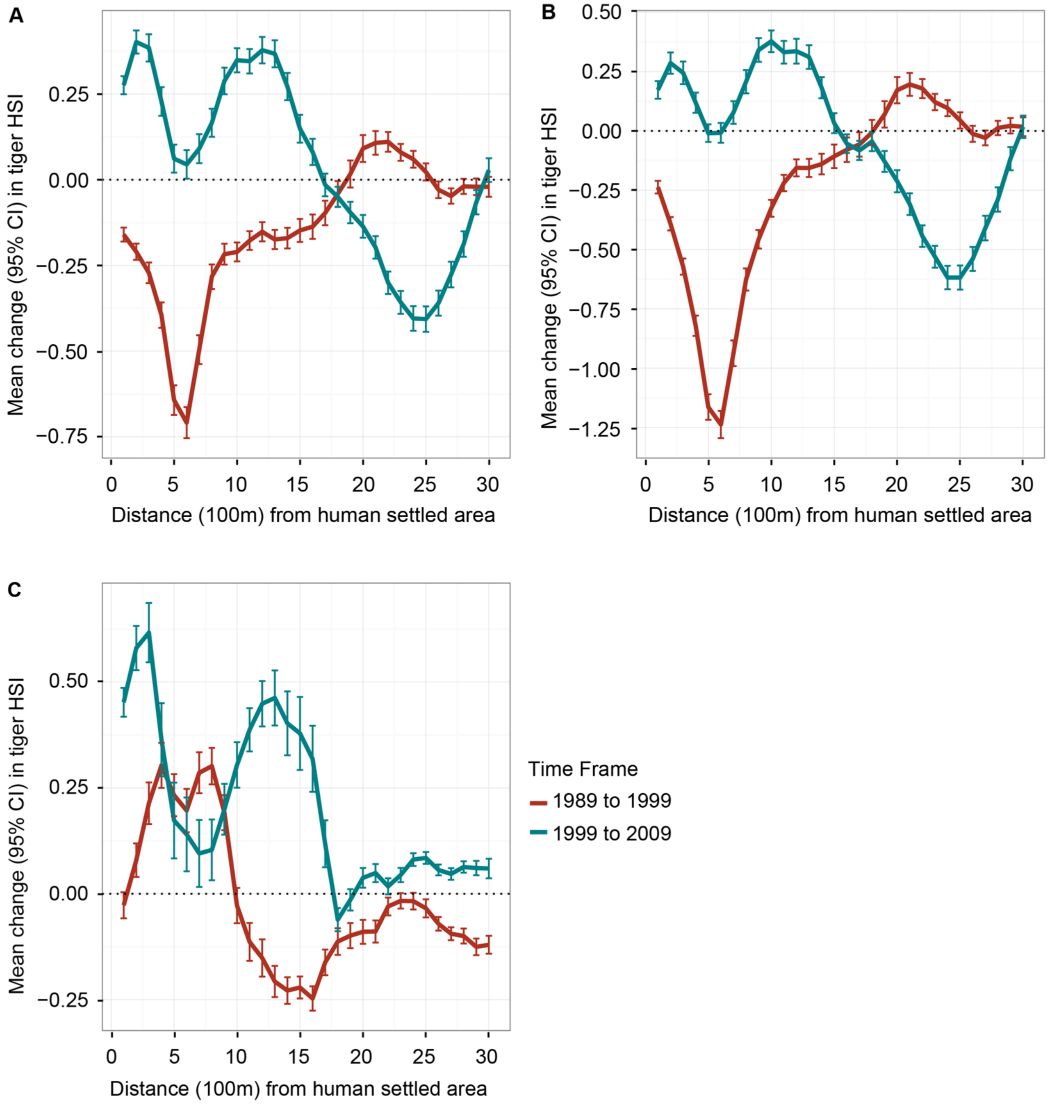

Fig. 5. Mean change (95% CI) in estimated tiger habitat suitability index (HSI) from 1989 to 1999 and 1999 to 2009 by distance from human settled area for (A) entire study site, (B) inside the park, and (C) outside the park.

(2008) indicated that forest degradation from 1989 to 2000 was more extensive along the park periphery than in the multiple-use areas outside the park. Nagendra et al. attribute this comparatively higher forest degradation inside the park to high natural resource demands by local people. A household living near Chitwan National Park, on average, collects approximately 2,200 kg of fuelwood and fodder annually from within the park (Stræde and Treue 2006). We found that habitat suitability inside the park increased somewhat in the areas closest to human settlements from 1999 to 2009, however, habitat suitability decreased in areas deeper inside the park. Although it is possible that this shift resulted from natural forest dynamics, these changes may indicate that human resource collection activities occurred deeper inside the park during that time frame. A similar pattern was shown inside China's Wolong Nature Reserve, where local people traveled farther from their homes to collect fuelwood after the fuelwood supply was depleted in the areas nearest to them (He et al. 2009).

Stræde and Treue (2006) indicated that households living near Chitwan National Park on average collect 6%, 5%, and 17.8% of their annual timber, fuelwood, and fodder needs, respectively, from inside the park. The majority of timber and fuelwood collected from inside the park was *Sal* (Stræde et al. 2002), which is considered the most valuable (thus most exploited) tree species in the region (Nagendra 2003). Removal of forest understory and woody biomass from the park may have reduced hiding cover for tigers (Sunarto et al. 2012) and induced land cover fragmentation (Gasparri and Grau 2009). In addition, Stræde and Helles (2000) noted that demand for park resources, especially grasses, by local people has been steadily increasing. Therefore, the decline in grassland area inside the park, and consequential loss of highly suitable tiger habitat, may be partially attributed to substantial anthropogenic pressure (Peet et al. 1999, Stræde and Helles 2000).

Other disturbances such as flooding and fire also likely affected tiger habitat suitability. The heterogeneity in habitat suitability along the northern boundary of the park is likely due, in part, to the movement of the Rapti River, which constantly erodes, deposits alluvium, and changes course across the floodplain (Peet et al. 1999). When the river changes course some areas become inundated while other areas where the river once was are rapidly colonized by *S. spontaneum* grasses (Peet et al. 1999). In addition, fire, naturally or human caused, delays the succession from grasslands to riverine forest. However, fire cannot prevent succession entirely because of variations in fire intensity and occurrence (Lehmkuhl 1994). Thus, decreasing grasslands and *Sal* forest and the corresponding increase in riverine areas observed inside the park over the 20 year period may be due to a combination of human and natural disturbances. Despite the degradation of highly suitable areas inside the park, especially from 1999 to 2009, tiger numbers inside the park appear to be stable (Carter et al. 2012*b*). This is perhaps because the change in habitat suitability to date is not large or extensive enough to induce a substantial change in tiger numbers. Alternatively, a time-lag may exist between changes in habitat suitability and tiger numbers.

As the area outside the park was considered heavily degraded prior to its establishment as the buffer zone (Sharma 1990), resource collectors likely had to travel relatively far into the multiple-use area to find adequate supplies of high-quality resources. Extracting natural resources from deeper inside the multiple-use area may have induced the average decrease in estimated tiger habitat suitability from 1989 to 1999 within 1.5 km from human settlements. The prohibition of livestock grazing and institutionalization of community-based resource management outside the park shortly after the buffer zone was established in 1996 substantially altered resource consumption patterns. For example, the removal of domestic livestock likely enabled the area outside the park to support a greater density of wild prey animals (Gurung et al. 2008) and provide better hiding cover for tigers. The control of overharvesting of shared natural resources in community forests in the buffer zone may also have improved tiger habitat outside the park. This is supported by improvements in estimated habitat suitability occurring mostly in areas adjacent to human settlements that are designated as community forests. In addition, as resource extraction policies and practices influence the spatial distribution of human activities, these, in turn, affect the spatial configuration of the land cover. As such, before the buffer zone was established, uncontrolled open-access resource extraction likely fragmented the land cover. In contrast, the coordinated management of forest tracts by user-group committees after the buffer zone was established may have helped reverse this fragmentation (Nagendra et al. 2008), and thus improved tiger habitat suitability.

The improvement of estimated tiger habitat suitability outside the park is independently supported by an increasing frequency of tiger sightings over the last decade (DNPWC 2007). While searching for tiger tracks and kills from 1999 to 2003, Gurung et al. (2006) did not find any evidence of breeding females (i.e., adult female tracks with cub tracks) in the multiple-use area outside the park. From our 2010 camera trap data, we identified a female tiger living completely outside the park and accompanied by three of her cubs, suggesting that the habitat outside the park has improved over the last decade. Currently, tiger densities inside and outside the park in our study site seem to be comparable (Carter et al. 2012*b*). Attacks on people outside the park have also increased since the late 1990s (Gurung et al. 2008), thus efforts to mitigate human-tiger conflicts (Carter et al. 2013) are vital to fostering coexistence in Chitwan. The main purpose of community forests is to sustainably provide natural resources to local communities; however, their formation does not automatically lead to the protection and/or improvement of tiger habitat. Moreover, the demands, practices, and compositions of the community forest user groups are constantly changing, and consequently, tiger habitat may degrade in the future in areas where it is currently improving. Therefore, coupled with efforts to mitigate human-tiger conflicts, we suggest that tiger habitat suitability be monitored regularly inside and outside the park (using procedures similar to those reported here) to ensure that the land continues to support tigers.

Land management policies and practices inside and outside the park and their impacts on tiger habitat are not mutually exclusive. These two land management regimes adjoin each other in space, with the effects of one likely having direct and/or indirect effects on the other. For instance, while local people legally extract natural resources from the buffer zone outside the park, it appears that the products obtained do not fully substitute those collected inside the park (Stræde and Treue 2006). Therefore, given projected human population growth and current per-capita resource demands in Chitwan (Stræde and Treue 2006, CBS 2012), protecting tiger habitat will become increasingly difficult over time. As such, policies that reduce human reliance on local natural resources (e.g., encouraging the use of non-wood fuel sources and improved livestock breeds) and actively managing tiger habitat are urgently needed (Hjortsø et al. 2006, Gurung et al. 2009, Thornton 2010). Furthermore, participatory-based management of ecosystems in and around the park, wherein local people are partners in designing, implementing, and enforcing resource management actions, may also foster sustainable conservation of tiger habitat over the long-term (Agrawal and Ostrom 2001). Such institutional arrangements, for instance, may enable the creation and maintenance of grasslands and early successional vegetation types in Chitwan through coordinated management efforts, including tree thinning and grassland cutting and burning (Brown 2003, Smit 2004).

Methodological considerations

In this study we assumed that tigers within the Chitwan ecosystem remained closed to demographic change for 89 days, which may be appropriate in this context as tigers are long-lived and Chitwan has relatively long seasons (O'Brien and Kinnaird 2011). We also assumed that the determinants of tiger habitat suitability remained unchanged from 1989 to 2009, which may be appropriate as tiger-habitat relationships characterize fundamental interactions between tigers and their environment (Morrison et al. 2006). However, tigers may have adjusted their space use over the 20 year period as a result of changes in the composition and distribution of prey, the density of tigers, and/or human disturbances. For example, although tigers may be habituated to the road network that currently occurs in the study site, the construction of roads in the past may have strongly disturbed tiger space use and consequently decreased habitat suitability of areas surrounding the roads for extended periods of time.

Our results on habitat suitability only refer to the dry season (i.e., January to April). Yet, tigers may select areas differently at different times of the year. For example, the use of grasslands by tigers may decrease in the wet season because the grasslands are periodically inundated, which forces prey animals to move to drier ground in upland forests (Sunquist 1981). Nevertheless, our findings are likely valid across seasons because the factors influencing habitat suitability identified in this study are similar to those from several other studies that spanned different seasons (Seidensticker 1976, Sunquist 1981, Smith et al. 1998). Collecting longitudinal (i.e., annual) tiger occurrence data across different seasons in conjunction with data on environmental and human factors in future studies will eliminate confounding issues of temporal variation in tiger habitat selection. Integrating such information with detailed data on individual-level tiger behaviors (e.g., from GPS collars) would explicitly link individual and population-level processes, and potentially allow for the design of adaptive models of habitat suitability that better capture temporal dynamics in habitat selection (Persson and De Roos 2003).

Although wildlife abundance is generally correlated with habitat suitability (Boyce and McDonald 1999), in some cases it is possible to find low or no relation between wildlife abundance and habitat selection (Liu et al. 2011). For instance, occurrences in suitable habitat may be low due to hunting or disease or to lack of colonization due to dispersal barriers. Conversely, animal occurrences in low quality habitat may be high, because less competitive juveniles are relegated to those areas (Van Horne 1983), or animals use those areas as travel corridors. However, circumstances such as these seem to be uncommon in our study site as tiger poaching in Chitwan has been relatively low since the end of the civil war in Nepal in 2006. Furthermore, tigers seem to have colonized the entire study site before the study was performed, and with the exception of the Rapti River, no obvious barriers to tiger movement (e.g., expanses of cultivated or urban developed land) are conspicuous.

Explicitly linking habitat conditions to tiger survival and reproduction would potentially enable evaluating changes in tiger population size in areas under different management regimes. However, with the data collected in this study we were unable to quantitatively relate changes in tiger habitat suitability to tiger population dynamics and persistence. As a result, it is still unclear how the changes observed affect tiger population viability in the area.

CONCLUSIONS

Our first study objective (i.e., evaluate changes in tiger habitat suitability from 1989 to 2009) was addressed through the integration of data obtained from camera traps and remotely-sensed imagery. Our results indicated that the estimated habitat suitability was higher inside the park than outside; however, over the 20-year study period a gradual decline in habitat suitability was observed inside the park while a gradual improvement was observed outside the park. Our second study objective (i.e., assess the potential influence of resource management policies and practices on observed changes in tiger habitat suitability) was addressed using a thorough literature review combined with personal knowledge of the study site. This analysis suggested that the top-down, exclusion policies of the National Park have not adequately stopped the natural resource collection activities of a growing human population from impacting tiger habitat inside the park. In contrast, habitat improvement outside the park occurred after policies that involved local people in the management of local natural resources (e.g., preventing livestock grazing) were implemented.

Degradation of highly suitable habitat inside the park is concerning and warrants assiduous monitoring to ascertain whether or not this trend is continuing, and if so, actions to reverse the trend should be pursued (e.g., actively managing grasslands, creating and maintaining communal grasslands outside park, encouraging the use of non-wood fuels). Expanding the involvement of local people in the management of local natural resources may help improve tiger habitat suitability in Chitwan and in important multiple-use areas that link tiger source populations in protected areas (Wikramanayake et al. 2004). However, the costs to local people (e.g., tiger attacks on people and livestock) must be carefully addressed for the long-term conservation of tigers and their habitat.

In addition to Chitwan, our study methods and analyses can be applied to protected areas distributed throughout the tiger's range to determine if habitat suitability has decreased, remained stable, or increased therein. Furthermore, by extending the evaluation of habitat change beyond protected areas to multiple-use areas, both of which are integral components of landscape-scale conservation initiatives, researchers can also assess how effective are a plethora of management practices and policies (e.g., integrated conservation and development projects, community-based natural resource management, etc.) at maintaining or expanding tiger habitat throughout their range. Effective tiger habitat conservation strategies will also promote the conservation of thousands of other imperiled animal and plant species that use the same ecosystems as tigers, such as the Indian elephant (*Elephas maximus indicus*), the Indian rhino (*Rhinoceros unicornis*), the sloth bear (*Ursus ursinus*), the dhole (*Cuon alpinus*), and the gaur (*Bos gaurus*) (Joshi et al. 1995, Karanth and Sunquist 1995, Wikramanayake et al. 1998, Nyhus and Tilson 2004). Information on how (e.g., dynamics in key habitat determinants) and where (e.g., specific locations and regions) habitat is changing will ultimately help guide conservation actions in human-dominated regions, which prevail throughout the ranges of many if not all of these and other imperiled species.

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