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Impacts of people and tigers on leopard spatiotemporal activity patterns in a global biodiversity hotspot

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ABSTRACT

Leopard population declines largely occur in areas where leopards and people frequently interact. Research on how leopards respond to human presence and competitors, like other predators, can provide important insights on leopard ecology and conservation in human-dominated regions; however, such research is lacking. Here we used data from field cameras in 2010 and 2011 to examine how human presence, prey, and tigers influence leopard spatiotemporal activity patterns in and around Nepal's Chitwan National Park, part of a global biodiversity hotspot. We found that leopards were adjusting their spatiotemporal activity patterns to both tigers and people, but by different mechanisms. Leopards spatially avoided tigers in 2010, but were generally active at the same times of day that tigers were. Despite pervasive human presence, people on foot and vehicles had no significant effect on leopard detection and space use, but leopard temporal activity was displaced from those periods of time with highest human activity. Temporal displacement from humans was especially pronounced outside the park, where there is a much greater prevalence of natural resource collection by local people. Continuing to evaluate the interconnections among leopards, tigers, prey, and people across different land management regimes is needed to develop robust landscape-scale conservation strategies.

1. Introduction

Leopards (*Panthera pardus*) are a top predator found throughout Africa, the Middle East, and Asia (Henschel et al., 2008). On one hand, they provide a number of key ecosystem functions, including the regulation of ungulate populations and suppression of mesopredators (Ripple et al., 2014). For example, trophic cascades in West Africa have occurred after declines in top predators, including the leopard, with unpredictable and often negative consequences on human communities (Ripple et al., 2014). On the other hand, although leopards are relatively widespread, the International Union for the Conservation of Nature indicates that leopards may soon qualify as "vulnerable" to extinction due to rapid declines in their numbers throughout much of their range (Henschel et al., 2008). Declines in leopard populations are largely the result of hunting for trade and human-induced habitat loss and fragmentation (Henschel et al., 2008). People also indiscriminately kill leopards in defense of humans and livestock (Ray et al., 2005).

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Given the frequency of interactions with people, it is important to ascertain how leopards respond to people and the mechanisms that govern those responses. However, there are few studies evaluating how humans impact fine-scale spatial (∼1 km) and temporal activities (diel time scale) of leopards (Kawanishi and Sunquist, 2004; Ngoprasert et al., 2007; Henschel et al., 2011). The nature of the relationships between people and leopards indicated by these studies, however, are equivocal. In central Gabon, for example, Henschel et al. (2011) found that leopard density decreased closer to human settlements. In Kaeng Krachan National Park, Thailand, Ngoprasert et al. (2007) found that leopards avoided human traffic inside the park in both space and time. In contrast, Kawanishi and Sunquist (2004) found no significant effect of human traffic on leopard spatiotemporal activity in Taman Negara National Park, Peninsular Malaysia.

Humans are not the only factor potentially affecting leopard behaviors and activities. Interspecific competition with other sympatric large carnivores may also impact leopard spatiotemporal activities (Seidensticker, 1976; Karanth and Sunquist, 2000; Hayward and Slotow, 2009; Wang and Macdonald, 2009; Odden et al., 2010; Vanak et al., 2013). For example, the tiger (*Panthera tigris*) is a key competitor across much of the leopard's range in Asia. Tigers are considered socially dominant to leopards (Seidensticker, 1976; Karanth and Sunquist, 2000; Odden et al., 2010). However, the impacts of tigers on leopard spatiotemporal activities differ across sites, with some studies indicating leopards avoid tigers in space and time (Seidensticker, 1976; Odden et al., 2010; Steinmetz et al., 2013), whereas other studies indicate high levels of spatiotemporal overlap (Karanth and Sunquist, 2000; Azlan and Sharma, 2006; Ramesh et al., 2012). Nevertheless, prey clearly plays a key role in mediating tiger–leopard interactions (Seidensticker, 1976; Karanth and Sunquist, 2000; Wang and Macdonald, 2009; Odden et al., 2010). Many regions support commingling populations of leopards, their competitors, and people. Research that quantitatively evaluates the impacts of both people and competitors on leopard spatiotemporal activity can provide important insights on leopard ecology and conservation in human-dominated regions, which prevail throughout the leopard range. However, there is a paucity of such research.

To help fill these information gaps, we examined how human presence, tigers, and prey influence leopard spatial and temporal activity patterns in and around Nepal's Chitwan National Park, part of a global biodiversity hotspot (Myers et al., 2000). The park (932 km^2), established in 1973, supports both leopards and tigers as well as various prey species, including spotted deer (*Axis axis*), barking deer (*Muntiacus muntjak*), hog deer (*Axis porcinus*), gaur (*Bos gaurus*) wild boar (*Sus scrofa*), and sambar (*Rusa unicolor*) (Bhattarai and Kindlmann, 2012; Carter et al., 2012; Thapa et al., 2014). A buffer zone (750 km^2) surrounding the park was established in 1996. The buffer zone includes several forest tracts, but also includes human settlements with a growing human population estimated at over 300 000 in 2010 (UNEP/WCMC, 2011). Regular human presence in the forests inside the park and outside the park in the buffer zone consists mostly of people on foot, including local residents harvesting natural resources from the forest, tourists walking through the forest, and Nepal Army personnel who regularly patrol the park for illegal activities. In addition, vehicles carrying Army personnel and tourists are common on the forest roads.

We explore two hypotheses in this paper: (1) leopards adjust their spatiotemporal activity patterns to avoid people and tigers; and (2) leopard spatiotemporal patterns overlap those of major prey species. To test these hypotheses, we use recently-developed occupancy models that account for spatial autocorrelation, as well as spatially-explicit leopard density models and temporal activity and overlap analyses. The methodological tools and techniques used in this paper could be useful for assessing interspecific and anthropogenic impacts on various wildlife species in many regions around the world.

2. Materials and methods

2.1. Study site

Chitwan National Park (Fig. 1) (27°30′N–27°43′N, 84°9′E–84°29′E) is situated in south central Nepal. The park is located in a river valley basin along the flood plains of the Rapti, Reu, and Narayani Rivers with an elevation range of 150–815 m. Climate in Chitwan is subtropical with a summer monsoon season from mid-June to late-September, and a cool dry winter. The park and remaining forests in the buffer zone outside the park have retained the 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; Carter et al., 2013).

2.2. Data collection and analyses

From January to May in 2010 and 2011 (i.e., the dry season before the monsoon), we used digital Reconyx RM45 passive infrared motion detecting cameras (Reconyx Inc., WI, USA) to determine the frequency of leopards, tigers, prey, and humans present at different locations within the study site. Motion-detecting cameras have been used in many other studies of leopards and tigers (Karanth and Nichols, 1998; Ngoprasert et al., 2007; Lynam et al., 2009; Carter et al., 2012; Athreya et al., 2013). In both years, we sampled the exact same locations inside and outside the Chitwan National Park in four successive blocks, each sampled for approximately 20 days at approximately 20 locations. The four adjoining sample blocks (with an aggregate area of approximately 100 km^2) encompassed naturally vegetated areas inside the park and in a forest tract in the buffer zone that surrounds the park. The sample blocks were oriented roughly parallel to the human settled area outside the park. Each block was initially subdivided into a grid with approximately twenty 100-ha cells. A camera pair (hereafter a 'camera trap') was located at or close to the center of each grid cell along the nearest forest road, path or animal trail with
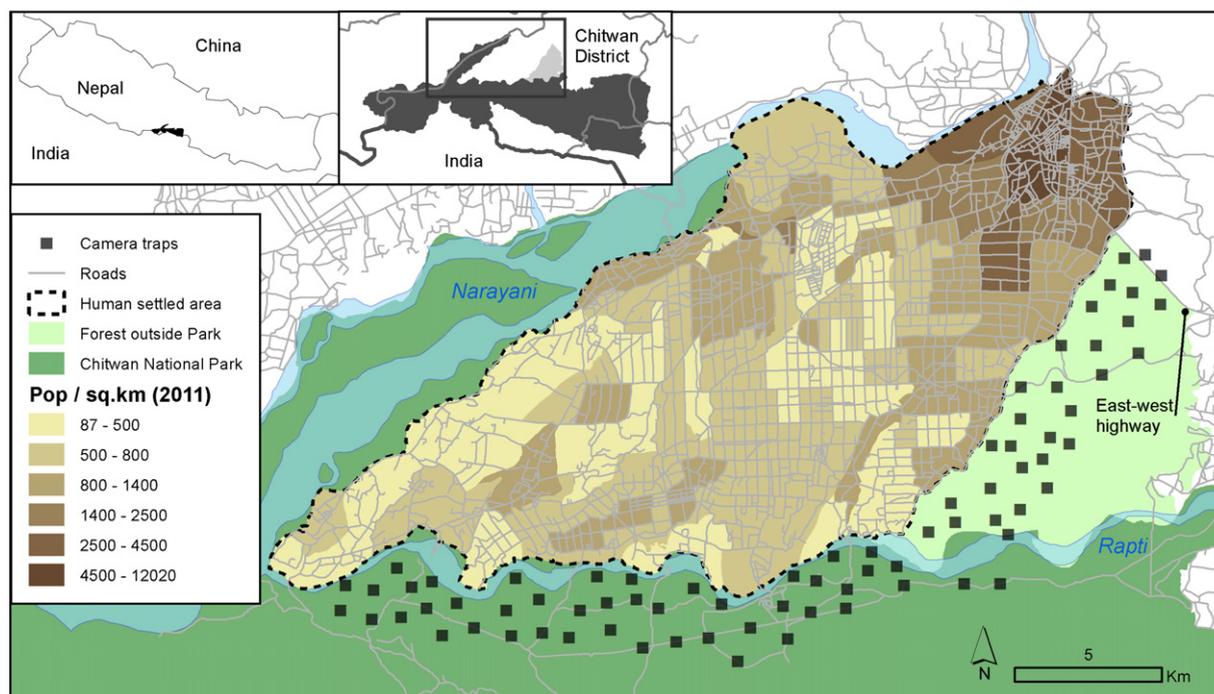
Fig. 1. Study site in Chitwan, Nepal. Camera traps were placed inside Chitwan National Park and a multiple-use forest corridor outside of the park in 2010 and 2011.

approximately 1 km between each camera trap (Fig. 1). The cameras in the camera trap were oriented towards each other in order to capture both flanks of any individual that passed through the site, and use the images for later identification. The geographical location of each camera trap was recorded using a GPS receiver.

The sampling occasion was 1 day (24 h period from 1200 to 1200 h). We sampled each location for 20 days to optimize the opportunity of detecting an animal if it is present while also minimizing the probability of population closure violations as much as possible (Karanth et al., 2004; Wegge et al., 2009; Athreya et al., 2013). Furthermore, sampling for at least 20 days has been shown to provide stable occupancy and detection probabilities, and maximize their precision (Hamel et al., 2013). In 2011, we also sampled one additional location in each block; thus, we placed camera traps in a total of 76 locations in 2010 and 79 locations in 2011 (one trap was stolen in 2011). Camera traps operated 24 h each day and with only minimum mechanical delay between each "capture". For each picture, we recorded entity (i.e., leopard, tiger, prey species, human, or vehicle), location (based on trap identification), date, temperature, and time. We summed the number of detections for each entity for each camera trap. We calculated detection frequency (number of detections per 100 trap-days) of each species, people on foot, and vehicles at each camera trap according to the methods of Johnson et al. (2006). Leopard individuals were identified on the basis of their specific spot pattern. Because leopard cubs (individuals approximately <1 year old) usually remain with their mothers and have high levels of mortality they were also removed from the data analysis to minimize violations of population closure and biasing density estimates (Athreya et al., 2013). The Mann–Whitney *u* statistic was used to test for significant differences in detection frequencies of each entity inside and outside the park within and between years.

2.3. Occupancy models

We evaluated the space use of leopards across the study site for 2010 and 2011 using occupancy models. Animals may be present at a location but not detected by a camera (i.e., imperfect detection) due to a number of reasons, including the orientation of the animal relative to the camera or obstruction by vegetation. The effects of imperfect detection on estimates of space use and other measures, like density, can be significant (MacKenzie et al., 2002). Occupancy models are ideal for camera trap data, because they formally account for imperfect detection and allow both the probability of an animal occurring and being detected at a location to vary in response to covariates. Given our fine spatial scale camera trapping grid (i.e., multiple camera trap locations within leopard home range), true absences (no detection because camera trap not within leopard home range) and pseudo-absences (no detection though camera trap is within leopard home range) cannot be differentiated. Thus, for our study, 'occupancy' is better interpreted as 'usage' (MacKenzie and Royle, 2005; Linkie et al., 2006). We assume animals move randomly between the fine-scale sampling sites, which relaxes the assumption of population closure typically required for occupancy models.

To ensure covariate data in the occupancy models were comparable between the two years, we omitted data from sample locations that were sampled in one year but not the other. Data from 75 camera trap locations were thus included in the

models. We included the following covariates in our model of leopard space use: detection frequencies of each of the six major prey species (i.e., wild boar, spotted deer, barking deer, hog deer, gaur, or sambar) and a combined count of the major prey species, tigers, people on foot, and vehicles. We included the following detection covariates: a dummy variable indicating whether the trap was inside ("1") or outside ("0") the park, distance of the trap to the nearest forest road, and distance to human settlement as delineated by the boundary of the park/buffer zone forest. Park and buffer zone boundary data were obtained from the World Database on Protected Areas (www.protectedplanet.net). 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.

The usual approach to estimating occupancy does not account for spatial autocorrelation (Johnson et al., 2013). Spatial autocorrelation may be present in the occupancy process because adjacent sample locations will likely exhibit occupancy rates more similar than those farther apart. In addition, spatial autocorrelation among predictor variables can produce strong cross-correlation between the predictor and a latent spatial effect. Not addressing spatial autocorrelation may lead to biases and overestimated precision in occupancy model results (Johnson et al., 2013). Thus, we used a recently-developed restricted spatial regression (RSR) occupancy model that explicitly incorporates spatial structure (Johnson et al., 2013). The RSR model uses a probit link function instead of logit link, which is typically used in occupancy models, because the probit function confers increased computational efficiency. To formally account for spatial autocorrelation, the RSR model includes a spatial random effect, η (Johnson et al., 2013). This spatial process assumes that the probabilities of occurrence and/or covariate values between sample locations are unrelated (i.e., do not have any influence on one another) beyond a certain distance threshold. We set the distance threshold for detecting spatial structure in neighboring sample locations at 3 km based on observed locations of leopards and the spatial distribution of camera traps. Bayesian inference was used to estimate parameters. We specified flat prior distributions for both the detection and occupancy processes, and a Gamma (0.5, 0.0005) distribution for the spatial process (Johnson et al., 2013). After a burn of 10 000 iterations, parameter posterior distributions were computed from 40 000 iterations and used to find parameter mean, SD, and 90% Bayesian credible interval (BCI) values. Occupancy models were performed using the package "stocc" in program R (R Development Core Team, 2009).

2.4. Density models

In addition to space use, we estimated leopard density across the study site for 2010 and 2011. To estimate density we used spatially-explicit capture–recapture (SECR) models, which account for imperfect detection. The SECR models combine leopard capture histories and the spatial coordinates of the captures to estimate density (Royle et al., 2009a). SECR models were used because they calculate density without relying on an arbitrary buffer zone (e.g., minimum convex polygon), which has been shown to inflate density estimates by between 20% and 200% (Obbard et al., 2010). The SECR model we used also relaxes the assumption of geographic closure, but instead accounts for animal movement and detection probability based on activity centers (Gardner et al., 2009). The SECR models were specified with a Bernoulli encounter process, in which a leopard could only be detected once in each trap per sampling occasion. A half-normal detection function was then applied to relate the Bernoulli encounter process to spatial movements of leopards. Since a Bayesian modeling framework had been used, all-zero encounter histories (5× the number of identified leopards) were used to augment each model. After a burn of 1000 iterations, parameter posterior distributions were computed from 49 000 iterations and used to find parameter mean, SD, and 95% BCI values (Royle et al., 2009b). Density models were performed in SPACECAP, which has been used previously to estimate leopard density (Singh et al., 2010; Athreya et al., 2013).

2.5. Temporal activity and overlap analyses

Two steps were followed to assess inter-specific temporal interactions (Ridout and Linkie, 2009; Linkie and Ridout, 2011). First, a non-parametric kernel density function was employed to estimate daily activity patterns of leopards, tigers, prey, people on foot, and vehicles. Kernel bandwidths were selected based on procedures developed in Taylor (2008). Second, co-efficients of overlapping, Δ, ranging from 0 (no overlap) to 1 (complete overlap) were used to measure the extent of overlap between two kernel density estimates (i.e., daily activity patterns). Overlap was defined as the area under the curve formed by taking the minimum of the two kernel density estimates at each point in time. Specifically, we used the overlap procedure labeled as $\hat{\Delta}_1$ in Ridout and Linkie (2009). We used 10 000 bootstrap samples to measure $\hat{\Delta}$ 95% confidence intervals (CI) (Linkie and Ridout, 2011). The calculated $\hat{\Delta}$ was compared between leopard and tiger, leopard and prey species, as well as leopard and human presence with respect to inside or outside the park for each year. Temporal overlap analyses were performed in program R (R Development Core Team, 2009) using the 'overlap' package.

3. Results

We had 107 independent detections of leopards over the entire 2-year study period (Table 1). Leopards triggered nearly 40% of the camera trap locations in 2010, and just over 30% in 2011. Thirteen individual leopards were detected in 2010 and 17 were detected in 2011 (Table 1). However, there was high turnover in leopard individuals detected across our study site

Table 1

Summary of 2010 and 2011 camera trap sampling efforts and leopard data.

	2010		2011	
	Inside park	Outside park	Inside park	Outside park
Number of days camera traps were operational	68	44	72	51
Total trap-days	920	590[a]	1091	735
Number of trap locations	46	30	48	31
Number of leopards detections	24	26	20	27
Number of individual leopards detected[b]	7	6	9	8
Number of trap-days/leopard detection	38	23	54	27

[a] Total trap-days outside park was 590 instead of 600 because one camera trap was damaged for 10 trap-days.
[b] No individual leopards were detected both inside and outside the park in 2010 or 2011.
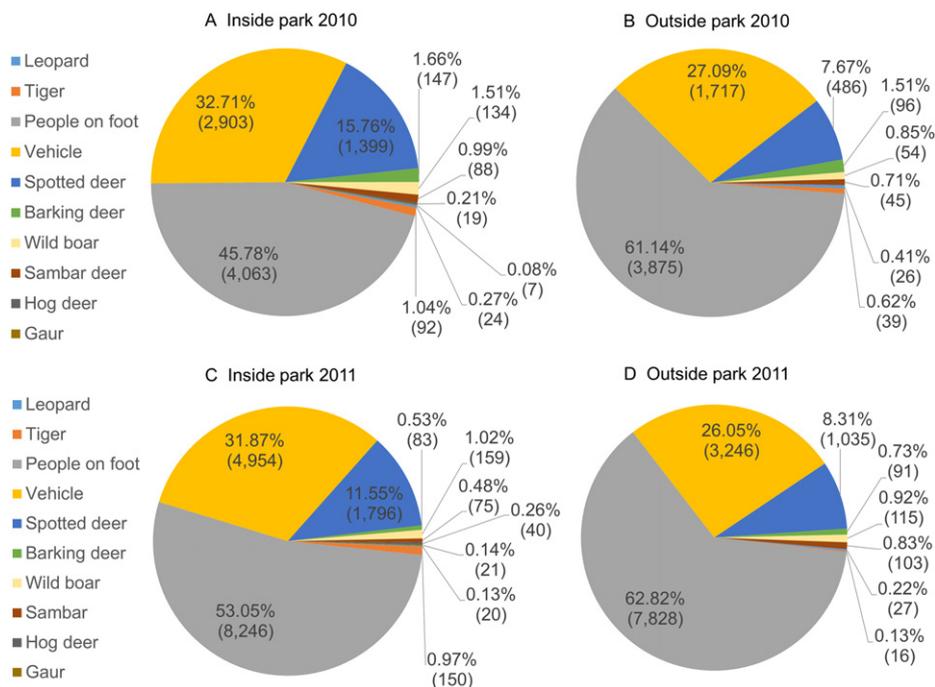

Fig. 2. Percentages of leopards, tigers, people on foot, vehicles, and six major prey species detected inside and outside Chitwan National Park, Nepal, in 2010 (A, B) and 2011 (C, D). Number of detections is indicated in parentheses.

between the two years. Three of the leopards inside the park were detected both in 2010 and 2011, while only one of the leopards outside the park was detected in both years.

Tigers were detected more frequently than leopards, except outside the park in 2011 (Fig. 2, Table 2). For comparing against leopards, seventeen individual tigers were detected in 2010 and 21 were detected in 2011 based on an earlier study using the same dataset (Carter et al., 2012).

High numbers of prey were recorded across the study site during the 2-year period (Fig. 2, Table 2). The mean prey detection frequency across the study site was 56–79 times greater than mean leopard detection frequency during the 2-year period. A vast majority (75%–80%) of the prey detected were spotted deer. In both years, mean prey detection frequency inside the park did not significantly differ from outside the park (Table 2).

Human presence was also pervasive across our study site, with people and vehicles triggering 85% of the camera traps and accounting for 85% of all detections (Fig. 2). In both years, mean detection frequency of people on foot inside the park did not significantly differ from outside the park. However, mean detection frequency of people on foot across the study site increased by 55% from 2010 to 2011, with people on foot inside the park significantly increasing over the 2-year period (Table 2). Across the study site people on foot were 3–4.4 times more common than prey during the 2-year period.

Neither individual prey species covariates nor the combined prey species covariate had any significant effects on leopard space use. For simplicity, we present occupancy model results using the combined count of the major prey species (Tables 3, 4). Model results indicate that the probability of detecting leopards was higher outside the park than inside the park and was inversely related to distance from forest roads in both years (Tables 3, 4). In 2010, leopard space use was significantly negatively related to tigers, although this relationship did not persist in 2011. With all covariates set to their mean, leopard

Table 2

Detection frequencies (mean ± SE) of leopards, tigers, people on foot, vehicles, and prey species in portions inside and outside Chitwan National Park in 2010 and 2011.

Category	2010		2011	
	Inside park	Outside park	Inside park	Outside park
Leopard	2.61 ± 0.71	4.33 ± 1.01	1.70 ± 0.45	3.65 ± 0.98
Tiger	10 ± 1.8	6.7 ± 1[*]	**13.9 ± 2.5**	**2.3 ± 0.6**[*]
People on foot	456.8 ± 89.2[*]	716.7 ± 152.3	745.4 ± 136.9[*]	1041.3 ± 207.2
Vehicles	339.7 ± 88.2	286.8 ± 193.9	**455.4 ± 124.7**	**378 ± 252.67**
Major prey animals	213.48 ± 37.82	142.50 ± 26.35	197.51 ± 27.83	187.31 ± 30.02
Spotted deer	163.6 ± 36.7	103.5 ± 25.4	164.6 ± 27.7	145.2 ± 27
Barking deer	**18 ± 5.4**	**20.2 ± 4.4**	**7.4 ± 1.3**	**12.4 ± 1.9**
Wild boar	17.7 ± 3.1	10.2 ± 2.2	14.9 ± 3.1	15.7 ± 3.4
Sambar	11.8 ± 4.1	8.7 ± 2.4	6.8 ± 2.2	13.9 ± 2.5
Hog deer	2.3 ± 0.9	−±	3.7 ± 1.2	−±
Gaur	0.8 ± 0.5	−±	2.1 ± 1.7	−±

Values in bold indicate within-year samples that were significantly different from one another (Mann–Whitney u test, $P < 0.05$). Hog deer and gaur were not detected outside the park in both years.

[*] Between-year samples within the same row were significantly different (Mann–Whitney u test, $P < 0.05$).

Table 3

Summary of occupancy (space use) model results for leopards across study site inside and outside Chitwan National Park, Nepal, in 2010.

Model component	Covariate	Mean	SD	90% BCI
Detection	(Intercept)	−1.679	0.123	(−1.881, −1.478)
	Dist. Settlement	−0.014	0.066	(−0.115, 0.102)
	Dist. Road	−0.213	0.094	(−0.366, −0.058)
	Park	−0.290	0.161	(−0.551, −0.028)
Space use	(Intercept)	3.537	1.688	(0.833, 6.222)
	People on foot	1.027	1.328	(−1.019, 3.268)
	Vehicle	0.584	1.377	(−1.528, 2.752)
	Major prey	1.403	1.406	(−0.875, 3.56)
	Tiger	−2.758	1.667	(−5.174, −0.039)

Dist., distance. Park, dummy variable indicating if camera trap were inside park. Covariates are considered to have significant effect on leopard space use if their 90% Bayesian credible intervals (BCI) do not cross zero.

Table 4

Summary of occupancy (space use) model results for leopards across study site inside and outside Chitwan National Park, Nepal, in 2011.

Model component	Covariate	Mean	SD	90% BCI
Detection	(Intercept)	−1.653	0.130	(−1.865, −1.442)
	Dist. Settlement	−0.065	0.084	(−0.204, 0.071)
	Dist. Road	−0.406	0.125	(−0.606, −0.198)
	Park	−0.652	0.188	(−0.974, −0.363)
Space use	(Intercept)	2.639	1.423	(0.543, 4.768)
	People on foot	1.231	1.121	(−0.317, 2.927)
	Vehicle	2.554	2.231	(−0.861, 6.08)
	Major prey	1.172	1.214	(−0.406, 3.146)
	Tiger	0.420	1.068	(−0.996, 1.964)

Dist., distance. Park, dummy variable indicating if camera trap were inside park. Covariates are considered to have significant effect on leopard space use if their 90% Bayesian credible intervals (BCI) do not cross zero.

detection probability across the study site was 0.03 in 2010 and 0.02 in 2011. Leopards were estimated to occur across 81% of the sample locations in 2010 and 77% of the sample locations in 2011.

Figs. 3 and 4 illustrate that the estimated space-use probabilities from the occupancy models generally fit well with leopard observations across space. The standard errors of the space-use probabilities (Figs. 3(C), 4(C)) are relatively well distributed across space, with no obvious visual pattern. The posterior mean of the spatial variance parameter, σ, was sufficiently different from zero in 2010 and 2011 (90% BCI = 0.003–0.08), indicating that spatial autocorrelation was significantly contributing to overall variability of the space-use process across the study site in both years. The posterior mean of the η process (Figs. 3(D), 4(D)) indicates those sampling locations where the covariates underpredict (blue) and overpredict (red) space use. For example, in 2011, ψ values in the western portion of the study site would be higher based on the fixed-effects portion of the model. The spatially correlated random effects (η process) in this region indicates the ψ values that needed to be adjusted downward by negative (red) values because they were too high for the observed occupancy.

Leopard density was relatively high across the study site in both years. Leopard density across the study site was 5.67/100 km^2 (95% BCI = 3.19–8.33) in 2010 and 9.11/100 km^2 (95% BCI = 4.79–13.3) in 2011. Although leopard density was approximately 60% greater in 2011 than in 2010, the difference was not significant due to large Bayesian credible intervals.
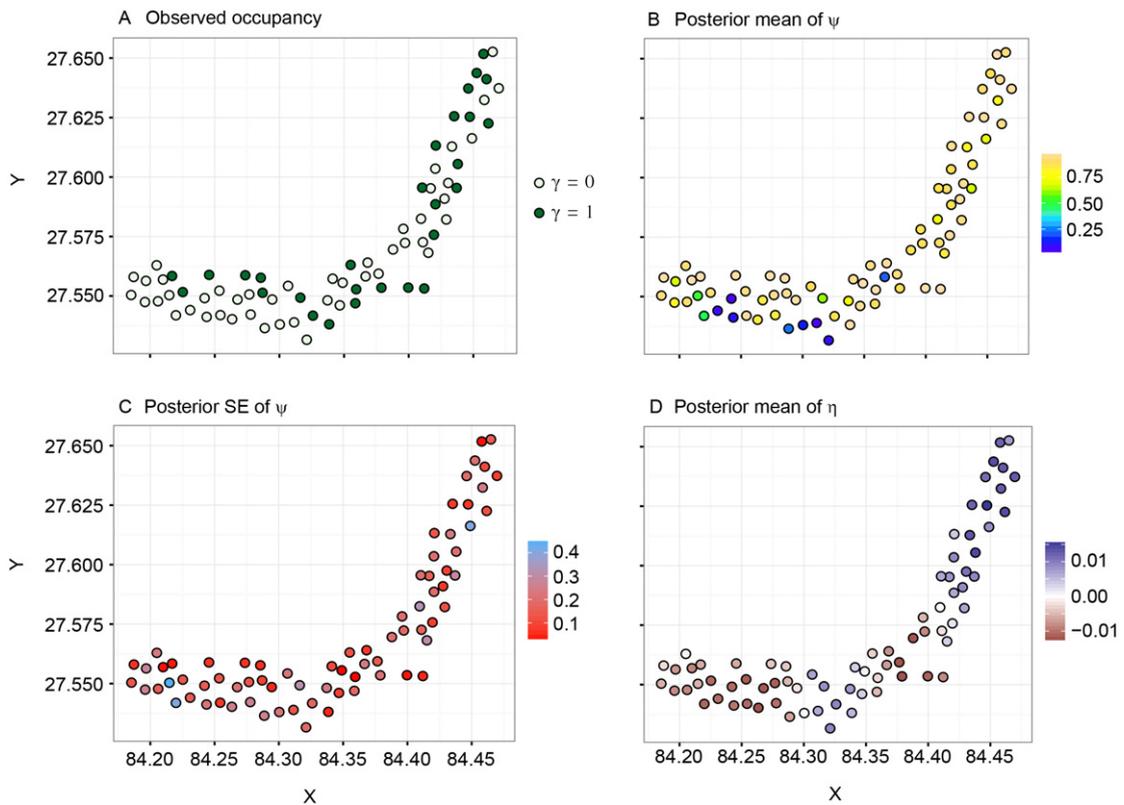
Fig. 3. Maps of leopard observations and occupancy (space use) model results across the study site for 2010. A, illustrates sample locations (camera traps) where leopards were not observed (grey circles) and observed (green circles). B, represents the posterior mean of ψ (the space use probability) for each sample location. C, is the posterior standard error of the mean of ψ for each sample location. D, shows the posterior mean of the η process (spatially correlated random effect) for each sample location. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

Leopard temporal activity differed somewhat with respect to year and whether they were found inside or outside the park. In 2010, leopard temporal activity inside the park peaked at ~6:00 and ~18:00 (Fig. 5) and nearly 60% of their temporal activity occurred during those daytime hours. In 2011, leopards inside the park were also active throughout the day (45%) with peaks at ~5:00, ~11:00, and ~20:00 (Fig. 6). Leopards outside the park were predominately active at night with peaks at ~3:00 and ~20:00 in both years (Figs. 5, 6). Leopard temporal activity outside the park between 6:00 and 18:00 was a quarter (15.7%) and third (18.5%) of leopard temporal activity inside the park in 2010 and 2011, respectively (Figs. 5, 6).

Leopards tended to avoid periods of high human temporal activity (between ~7:00 and ~15:00) in both years (Figs. 5, 6). In particular, leopards had significantly less temporal activity overlap with people on foot and vehicles outside the park than inside the park in 2010 (Fig. 5). Likewise, in 2011, leopards had significantly less temporal activity overlap with people on foot outside the park than inside the park (Fig. 6). Leopards did not appear to displace their temporal activity from tiger temporal activity in either year (Figs. 7, 8). Leopard temporal activity overlapped highest with boar and spotted deer inside the park in both years. Leopard temporal activity overlapped highest with boar and sambar outside the park in both years (Figs. 7, 8). Sambar were mostly active at night inside and outside the park in both years. Spotted deer and barking deer were predominantly active during the day inside and outside the park in both years. Boar were more active during the day inside the park in both years, but were more active at night outside the park in both years (Figs. 7, 8).

4. Discussion

Our findings suggest that leopards are adjusting their spatiotemporal activity patterns to both tigers and people, supporting hypothesis 1. However, the mechanism by which leopards were avoiding tigers was different than that of people. Leopards were spatially avoiding tigers in 2010, as evidenced by the occupancy models, but did not appear to avoid tigers in time. In contrast, people on foot and vehicles had no significant effect on leopard spatial detection and use, but leopard temporal activity was displaced from those periods of time with highest human activity.

As we were unable to directly observe tiger–leopard–prey interactions, it is uncertain if spatial segregation of tigers and leopards in 2010 was due primarily to distinct habitat preferences or caused directly by competition between the two predators. The negative effect of tigers on leopard space use may reflect leopard preference for more open habitat than tigers
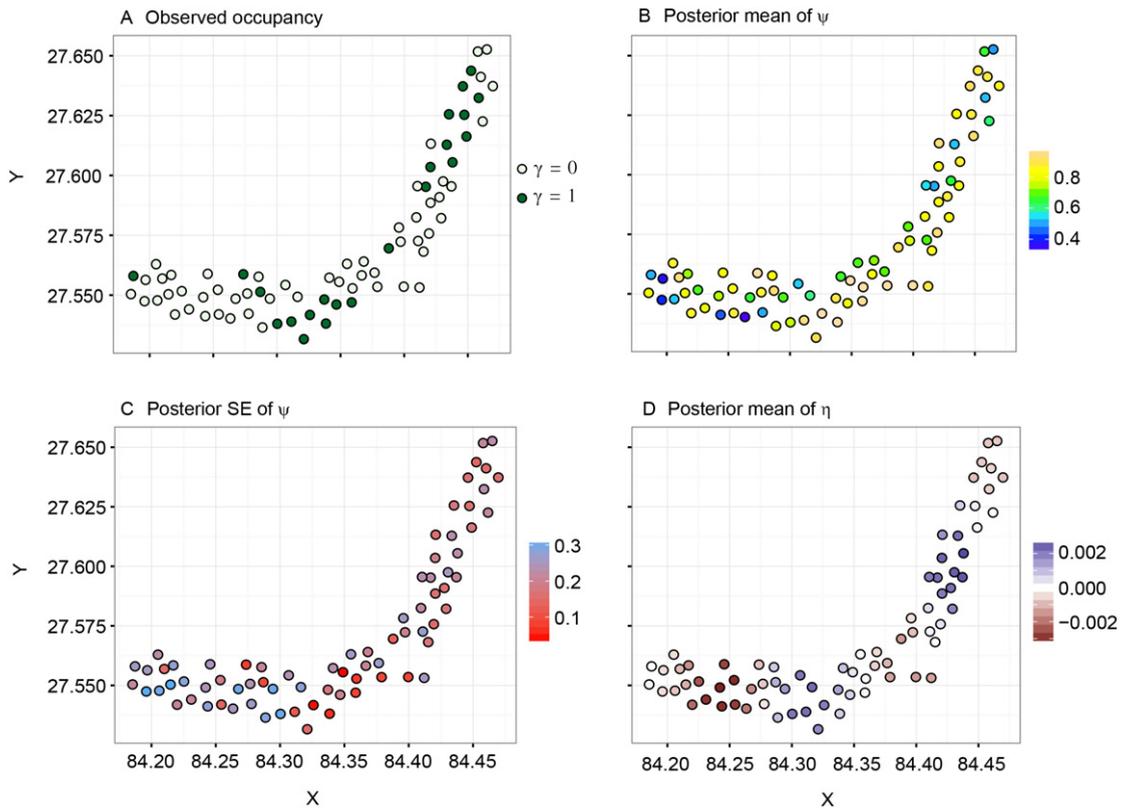
Fig. 4. Maps of leopard observations and occupancy (space use) model results across the study site for 2011. A, illustrates sample locations (camera traps) where leopards were not observed (grey circles) and observed (green circles). B, represents the posterior mean of ψ (the space use probability) for each sample location. C, is the posterior standard error of the mean of ψ for each sample location. D, shows the posterior mean of the η process (spatially correlated random effect) for each sample location. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

(Seidensticker, 1976; Seidensticker et al., 1990). However, most studies indicate that tigers and leopard spatiotemporal activities are influenced largely by either exploitative or interference competition with each other. Exploitative competition is the result of sympatric carnivores adversely affecting each other due to their limited effect on shared prey resources (Begon et al., 2006). Interference competition is the result of one carnivore species limiting the foraging ability (e.g., by agonistic interactions) of an inferior competitor (Norris and Johnstone, 1998). Our results indicate that our study site supports high numbers of prey of different sizes, thus leopards and tigers are unlikely to be competitively excluding one another from locations due to a low abundance of shared resources. Rather, we suspect that leopards were spatially segregated from tigers at a fine spatial scale (i.e., camera trap locations) in 2010 in order to avoid negative encounters with tigers (i.e., interference competition). A similar process between leopards and tigers was observed in Bardia National Park, Nepal (Odden et al., 2010). As with Odden et al. (2010), our findings suggest that behavioral factors, not prey abundance *per se*, play an important role in tiger–leopard interactions and spatiotemporal activity patterns.

Unlike 2010, leopard space use in 2011 was unrelated to the presence of tigers. It is unclear why this is the case. It is possible that the substantial increase in human presence from 2010 to 2011 across our study site altered the spatial interactions between leopards and tigers, such that tigers became less influential on leopard space use. However, this explanation lacks strong support because leopard space use did not appear strongly related to human presence in either year. Another possible explanation may relate to the high turnover in leopards from 2010 to 2011. Very few of the leopards observed in 2011 were also observed in 2010, suggesting that the residents in 2010 either died or dispersed thus leaving vacant territories. Several of the leopards we observed in 2011 may have been transients that were temporarily passing through the area to find vacant territories, and consequently had space use patterns that differed from the resident animals in 2010. This influx of new leopards in 2011, and their distinct space use patterns, may have also inflated density estimates across our study site compared to 2010.

Although we did find some support for spatial displacement between leopards and tigers, tiger–leopard interactions in our study site do not appear to be characterized by temporal niche partitioning. It has been suggested that leopards may be more diurnal when tigers are present in the same area (Azlan and Sharma, 2006). As our study site was characterized by high levels of human presence, it is possible that temporal niche partitioning between leopards and tigers would have been more pronounced had people been absent. However, several studies at different sites with comparatively low human
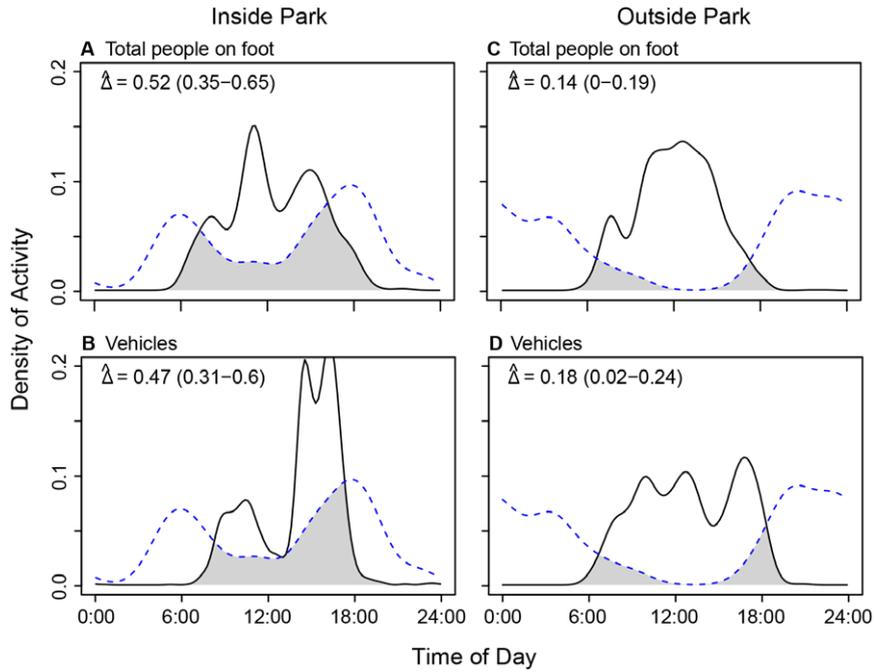
Inside Park

Outside Park

A Total people on foot

$\hat{\Delta} = 0.52\ (0.35{-}0.65)$

C Total people on foot

$\hat{\Delta} = 0.14\ (0{-}0.19)$

B Vehicles

$\hat{\Delta} = 0.47\ (0.31{-}0.6)$

D Vehicles

$\hat{\Delta} = 0.18\ (0.02{-}0.24)$

Fig. 5. Activity patterns of leopard (dashed lines) and human presence types (solid lines) inside (A, B) and outside (C, D) Chitwan National Park, Nepal in 2010. A,C, total people on foot; and B,D, vehicles. The estimate of temporal overlap, $\hat{\Delta}$ [from 0 (no overlap) to 1 (complete overlap)], is indicated by the grey area, and is shown in each panel. Overlap was defined as the area under the curve formed by taking the minimum of the two activity patterns at each point in time. Approximate 95% bootstrap confidence intervals of overlap estimates are indicated in parentheses. Average time of sunrise was 6:00 and average time of sunset was 18:00 during the study.
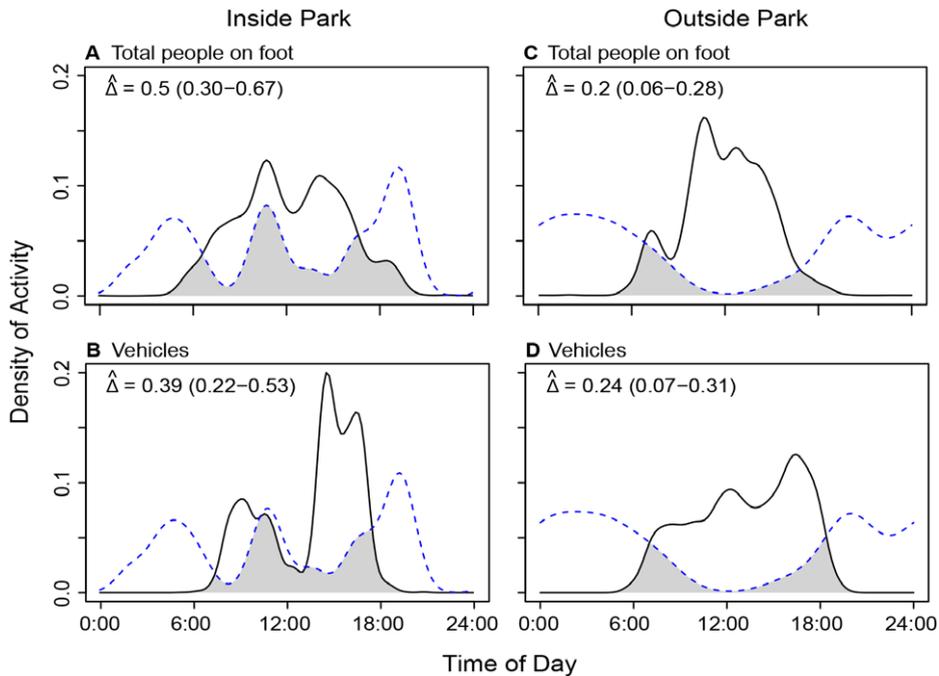
Inside Park

Outside Park

A Total people on foot

$\hat{\Delta} = 0.5\ (0.30{-}0.67)$

C Total people on foot

$\hat{\Delta} = 0.2\ (0.06{-}0.28)$

B Vehicles

$\hat{\Delta} = 0.39\ (0.22{-}0.53)$

D Vehicles

$\hat{\Delta} = 0.24\ (0.07{-}0.31)$

Fig. 6. Activity patterns of leopard (dashed lines) and human presence types (solid lines) inside (A, B) and outside (C, D) Chitwan National Park, Nepal in 2011. A,C, total people on foot; and B,D, vehicles. The estimate of temporal overlap, $\hat{\Delta}$ [from 0 (no overlap) to 1 (complete overlap)], is indicated by the grey area, and is shown in each panel. Overlap was defined as the area under the curve formed by taking the minimum of the two activity patterns at each point in time. Approximate 95% bootstrap confidence intervals of overlap estimates are indicated in parentheses. Average time of sunrise was 6:00 and average time of sunset was 18:00 during the study.
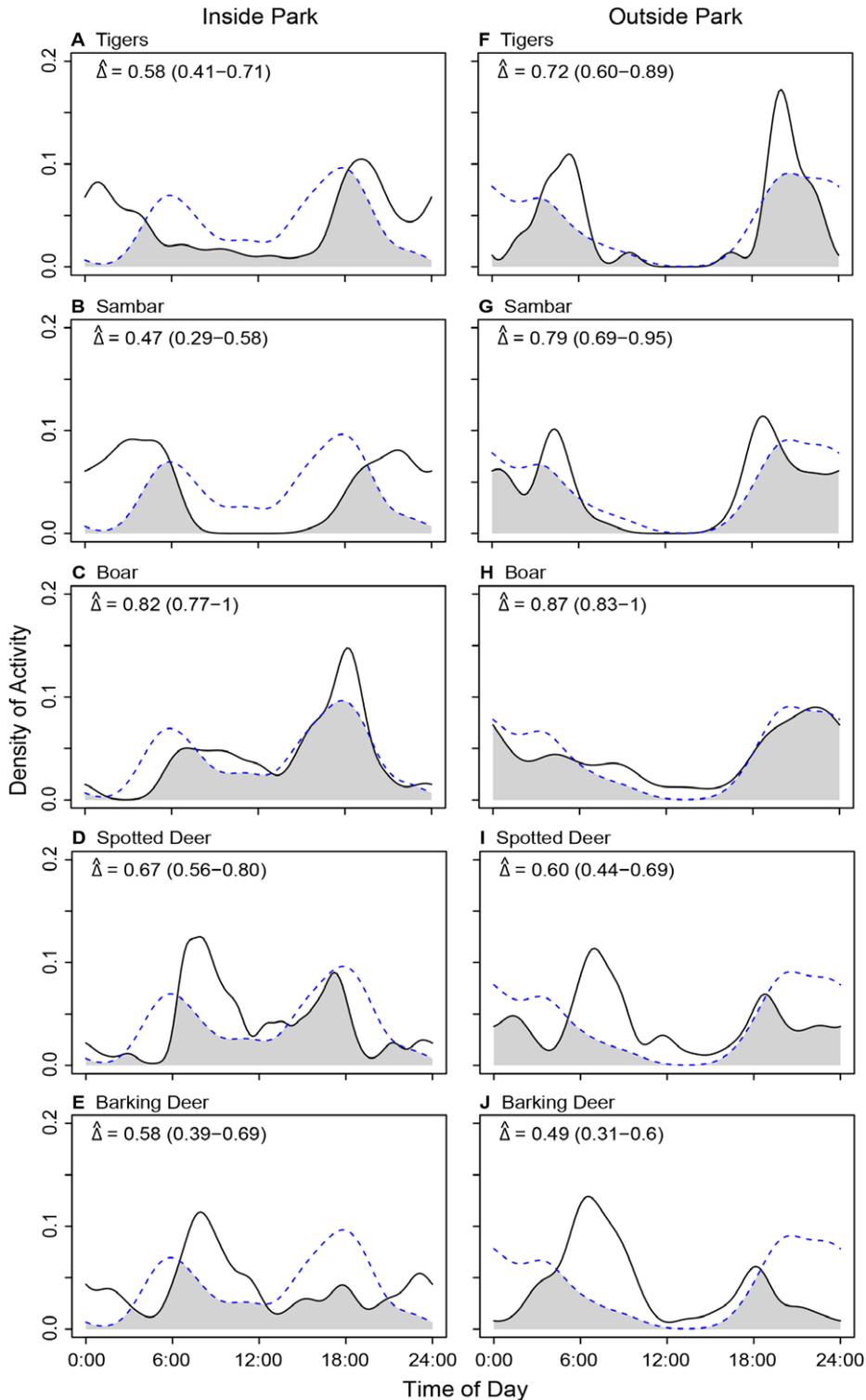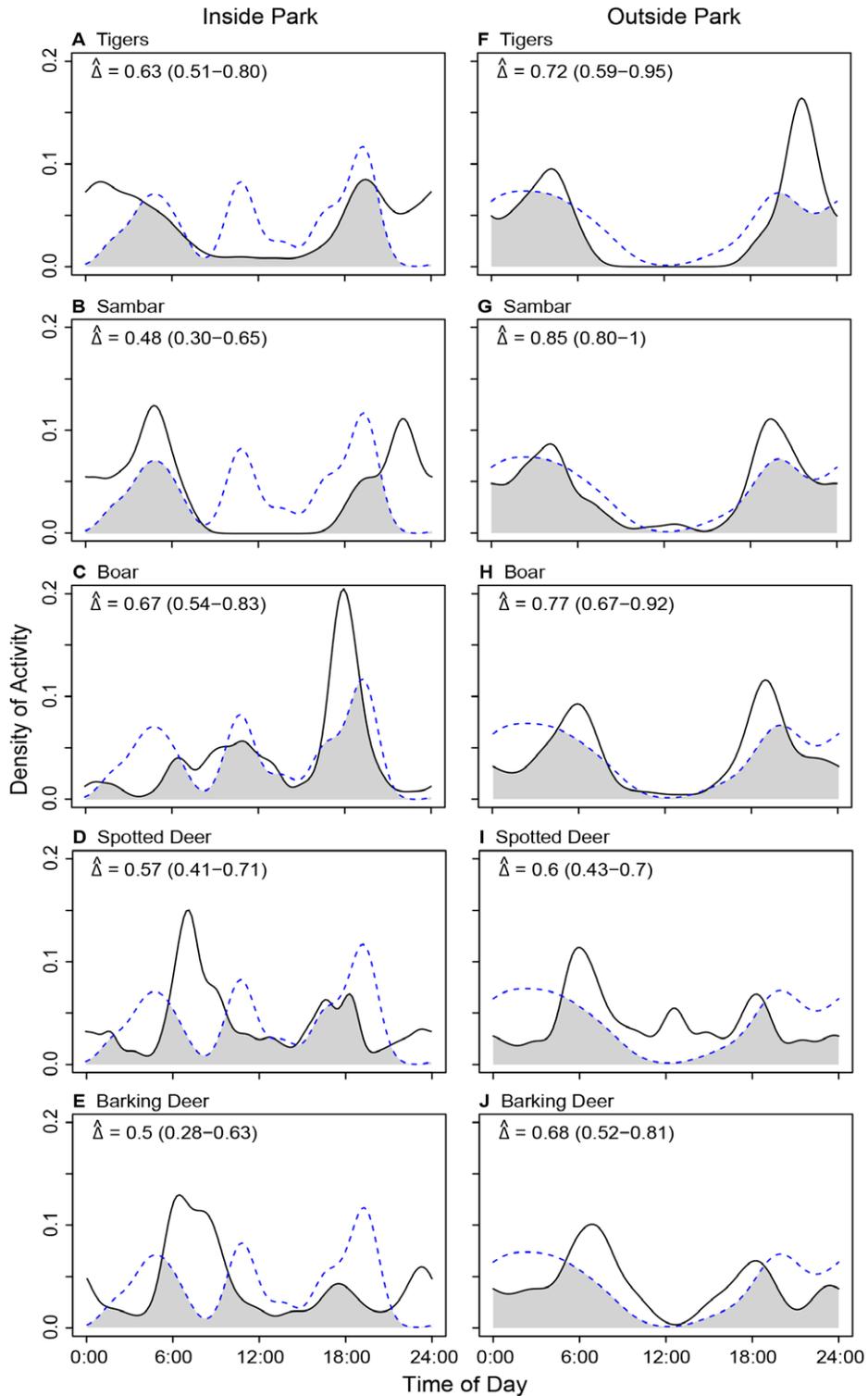
Fig. 7. Activity patterns of leopard (dashed lines) and tiger and prey species (solid lines) inside (A–E) and outside (F–J) Chitwan National Park, Nepal in 2010. A,F, tigers; B,G, sambar; C,H, boar; D,I, spotted deer; and E,J, barking deer. Gaur and hog deer were not included as they did not occur outside the park. The estimate of temporal overlap, $\hat{\Delta}$ [from 0 (no overlap) to 1 (complete overlap)], is indicated by the grey area, and is shown in each panel. Overlap was defined as the area under the curve formed by taking the minimum of the two activity patterns at each point in time. Approximate 95% bootstrap confidence intervals of overlap estimates are indicated in parentheses. Average time of sunrise was 6:00 and average time of sunset was 18:00 during the study.

Fig. 8. Activity patterns of leopard (dashed lines) and tiger and prey species (solid lines) inside (A–E) and outside (F–J) Chitwan National Park, Nepal in 2011. A,F, tigers; B,G, sambar; C,H, boar; D,I, spotted deer; and E,J, barking deer. Gaur and hog deer were not included as they did not occur outside the park. The estimate of temporal overlap, $\hat{\Delta}$ [from 0 (no overlap) to 1 (complete overlap)], is indicated by the grey area, and is shown in each panel. Overlap was defined as the area under the curve formed by taking the minimum of the two activity patterns at each point in time. Approximate 95% bootstrap confidence intervals of overlap estimates are indicated in parentheses. Average time of sunrise was 6:00 and average time of sunset was 18:00 during the study.

presence, including Malaysia and India, found that leopards and tigers have overlapping temporal activity patterns (Karanth and Sunquist, 2000; Kawanishi and Sunquist, 2004; Ramesh et al., 2012; Lynam et al., 2013). Similarly, Foster et al. (2013) did not find strong evidence for temporal displacement between jaguars (*Panthera onca*) and pumas (*Puma concolor*) in four different sites across Brazil, but did find partitioning in space. Temporal overlap between leopards and tigers may be facilitated in areas with abundant prey of various sizes, such as our study site, because leopards and tigers can thrive by hunting prey of different sizes. For example, Seidensticker (1976) found that leopards in Chitwan usually killed prey ranging in size from 25 to 50 kg, while tigers in Chitwan primarily fed on prey weighing 50–100 kg.

Contrary to expectations, leopards did not spatially displace themselves from people on foot or vehicles at a fine spatial scale in both years. Ngoprasert et al. (2007) suggested that leopard avoidance of areas near human settlements in Kaeng Krachan National Park, Thailand, was likely associated with greater animal poaching activity in those areas. We observed no signs of poaching (e.g., person holding gun) of leopards in the study site based on the camera trap images, nor did we come across any snares while in the field. Instead it is possible that agonistic interactions with tigers may be relegating leopards to areas bordering tiger territories, which may happen to be close to human settlements along the border of the park and buffer zone forest outside the park (Odden et al., 2010; Bhattarai and Kindlmann, 2012). This is further evidenced by leopards being more likely to be detected outside the park in both years, while tigers were more likely to be detected inside the park based on an earlier study using the same dataset (Carter et al., 2012). The use of locations near human settlements and with human presence is also probably facilitated by high prey abundance distributed throughout the study site, including the buffer zone forest outside the park. Leopards were detected more often along forest roads as well, likely because roads serve as lower energy movement pathways than moving through the forest understory (Smith et al., 1989; Bhattarai and Kindlmann, 2012; Carter et al., 2012).

Leopard use of areas visited frequently by people on foot and vehicles may have been facilitated by leopards using the night instead to avoid human disturbance associated with local resource collection. A similar pattern of temporal avoidance was observed in Thailand (Ngoprasert et al., 2007). Local people were active at more camera trap locations than tourists, who were taken on selected paths in the forest. As such, disturbance from local resource collection covered a larger portion of the study site. In addition, the extended period of time per day local people spend collecting forest products and the noise (cutting vegetation) they make in the forest while doing so may disrupt leopard behavior more so than the non-consumptive and short-lived human activities such as tourism within the park. There is a much greater prevalence of local resource collection just outside of the park in the buffer zone forest than inside the park (Carter et al., 2012). Leopards detected outside the park in Chitwan were one-third as active during the day than at sites in India, Malaysia, and Thailand, where human activity was considerably less (Kawanishi and Sunquist, 2004; Ngoprasert et al., 2007; Ramesh et al., 2012). A shift to more nocturnal behavior in areas with higher human activity was also found in brown bears (*Ursus arctos*). As human activity increased along streams used for food by brown bears, mid-day bear activity decreased while nocturnal activity (20:00–22:00) increased significantly (Olson et al., 1998). Another study in Southern California found that both bobcats (*Lynx rufus*) and coyotes (*Canis latrans*) reduced their mid-day activity in human fragmented habitats compared to non-fragmented habitats (Tigas et al., 2002). When using the same areas as people, African lions (*Panthera leo*) in Botswana avoided temporal overlap with people when they were most active (Valeix et al., 2012).

The spatial segregation of leopards from tigers but not from people may create conditions in which leopards are more likely to encounter people than they would have if tigers were not present. In Rajaji National Park, India, the increasing presence of tigers caused leopards to supplement wild prey with domestic prey associated with nearby human settlements (Harihar et al., 2011). However, the increasing presence of leopards in human-dominated lands outside core protected areas does not necessarily lead to increasing human–leopard conflict. Athreya et al. (2013) reported that no fatal attacks on people by leopards had occurred in an agricultural area in western Maharashtra, India, despite high densities of people and leopards co-occurring there. Future research is needed to assess the degree to which leopards are consuming domestic prey and attacking people in Chitwan, and how these conflicts are related to competition with tigers and human disturbance. This is especially crucial information to obtain, because tiger numbers appear to be increasing in and around Chitwan National Park (WWF, 2013), not only increasing the likelihood of human–tiger conflicts (Gurung et al., 2008) but potentially increasing the likelihood of human–leopard conflicts as well (Bhattarai and Kindlmann, 2012).

Contrary to expectation, leopard space use was unrelated to prey covariates. With high numbers of prey inside and outside the park, it is likely that other factors, such as leopard social structure (e.g., female philopatry), territorial behavior, and competition with tigers, may influence leopard space use more so than fine-scale spatial heterogeneity of prey abundance (Mizutani and Jewell, 1998). In contrast, Steinmetz et al. (2013) found that space use by leopards in Kuiburi National Park, Thailand, was positively associated with prey but was negatively associated with tigers. Prey density in Kuiburi is lower than in Chitwan, which suggests that where prey numbers are high, the main concern of leopards is to avoid tigers (as in Chitwan), but where prey is scarce (as in Kuiburi) leopards must closely track prey as well as avoid tigers.

Leopards in our study site did exhibit relatively high temporal overlap with several prey species, especially boar, lending some support for hypothesis 2. It is likely that leopards are deliberately active when boar are active. In Bardia National Park, Nepal, Wegge et al. (2009) found that boar occurred in leopard scat significantly more often than expected, indicating the importance of boar in leopard diets. Wegge et al. (2009) also noted that increasing numbers of tigers but not leopards in Bardia, after being declared a national park, may have suppressed numbers of some ungulate species, such as boar. The 2 years of data collected from a relatively small area for our study during the dry season are insufficient to test arguments about longer-term, broader spatial scale patterns. Collecting information year-round, from a much larger area, and over a longer

time frame than 2 years will enable stronger inferences about the effects of people and tigers on leopard spatiotemporal activity patterns.

5. Conclusion

Our study demonstrates how leopards respond at fine scales to tigers and human presence inside and outside Nepal's Chitwan National Park: part of a global biodiversity hotspot. Leopards responded differently to tigers than to humans; leopards avoided tigers in space in 2010 but avoided people on foot and vehicles by being mostly active at night. This study illustrates the high adaptive capacity of leopards to human presence and settlements. Furthermore, our findings suggest that spatial co-occurrence with people is likely influenced by several factors, including competition with tigers, high prey numbers, and low poaching pressure. The effects of temporal displacement from people on leopard hunting success and population persistence, however, still needs to be determined. Furthermore, as leopards and tigers often occur in areas outside protected areas where human presence is ubiquitous, studies that evaluate the interconnections among leopards, tigers, and people across different land management regimes are needed to develop robust landscape-scale conservation strategies. For example, such information would provide insights on how tiger recovery efforts currently underway in Nepal (i.e., doubling tiger numbers from 2010 to 2022) may influence negative encounter rates with humans and leopards.

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