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Factors associated with co-occurrence of large carnivores in a human-dominated landscape

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Abstract

We investigated the factors facilitating co-occurrence of two large carnivores, tigers (*Panthera tigris*) and common leopards (*Panthera pardus*), within a human-dominated landscape. We estimated their density and population size using camera-trap photographs and examined spatial segregation of habitats, temporal activity pattern, and diets in Chitwan National Park, Nepal. A Bayesian spatially-explicit capture-recapture model estimated densities of 3.2–4.6 (3.94 ± 0.37) tigers and 2.6–4.1 (3.31 ± 0.4) leopards per 100 km^2 with abundance of 70–102 tigers and 66–105 leopards. Tigers occupied the prime habitats (grasslands and riverine forests) in alluvial floodplains of the Park whereas leopards appeared in Sal forests and marginal areas where livestock are present. Both tigers and leopards showed crepuscular activity patterns with a high overlap but tigers were less active during the day compared to leopards. Leopards' activity in the day increased in the presence of tigers. Tiger and leopard diet overlapped considerably (90%). Compared to leopards, tigers consumed a higher proportion of the large prey and a smaller proportion of livestock. Our study demonstrates that sympatric large carnivores can coexist in high densities in prey rich areas that contain a mosaics of habitats. To increase the resilience and size of the Chitwan carnivore population, strategies are needed to increase prey biomass and prevent livestock depredation in adjacent forests. Long-term monitoring is also required to obtain a detailed understanding of the interaction between the large carnivores and their effects on local communities living in forest fringes within the landscape.

Keywords Tiger (*Panthera tigris*) · Common leopard (*Panthera pardus*) · Abundance and density · Diet · Activity pattern · Chitwan National Park (Nepal)

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Introduction

Large carnivores have a relatively greater influence on the community structure through resource facilitation and trophic cascades, although they remain in low densities naturally due to energetic constraints (Ripple et al. 2014; Schmitz et al. 2000). They are threatened globally by habitat fragmentation and loss, poaching and illegal trade for their body parts, declining prey and conflict with humans (Karanth and Chellam 2009). Because survival of large carnivores is conservation dependent in increasingly human-dominated landscapes (Weber and Rabinowitz 1996; Linnell et al. 2001; Wikramanayake et al. 2004), conservation strategies should focus on the protection of core breeding areas (or source sites) which have the potential to repopulate neighboring areas when embedded in larger landscapes (Kenney et al. 2014). The Terai Arc Landscape (TAL) in Nepal and India is one of such landscapes for conservation of large mammals including top-predators tigers and common leopards (hereafter called 'leopards') (Chanchani et al. 2014).

Tigers and leopards are the two largest sympatric felids in Asian forests for a long time (Simcharoen et al. 2014; Goodrich et al. 2015; Jacobson et al. 2016; Stein et al. 2018). Paleontological and molecular studies suggest leopards evolved in Africa and dispersed to Asia ca. 2 million years ago whereas tigers are endemic to Asia; they appear in the fossil record ca. 1.5 million years ago (Turner and Anton 1997; Lovari et al. 2015). Both are obligate meat-eaters and solitary hunters. However, they differ in body size; an adult tiger (65–306 kg) is approximately four times the body weight of adult leopard (28–90 kg) (Seidensticker 1976).

Interference and inter-guild competition of large carnivores resulting in the displacement of the subordinate by dominant is common (Holt and Polis 1997; Linnell and Strand 2000). Such competition by tigers (dominant) towards leopards (sub-ordinate) has been widely observed (Odden et al. 2010; Harihar et al. 2011). However, Karanth and Sunquist (2000) found high dietary overlap in India and Simcharoen et al. (2018) found both dietary and spatial overlap in Southeast Asia with no evidence of displacement. High dietary and spatial overlap suggests that both interference and resource competition may occur (Simcharoen et al. 2018; Lovari et al. 2015). Ultimately, prey composition and density as well as habitat types play a key role in determining the nature of tiger–leopard interactions (Carter et al. 2015).

Lovari et al. (2015) reported a large overlap in tiger and leopard diet in the western part of TAL indicating no prey partitioning. They suggested additional research was needed to examine if spatial and/or temporal partitioning occurs between these large cats. We selected Chitwan National Park (CNP) situated in the eastern part of TAL for this study to examine the factors facilitating the co-occurrence of these large carnivores. CNP holds one of the largest populations of tigers and leopards in TAL (Thapa 2011; Karki et al. 2015). Tigers and leopard co-occur in CNP with a large overlap in their home ranges (Seidensticker 1976). Co-occurrence could be facilitated by high prey biomass, diversity of prey sizes and dense vegetation that may reduce tiger leopard encounter rate (Bhattarai and Kindlmann 2012a; Simcharoen et al. 2018). However, McDougal (1998) recorded intra-guild predation of at least five leopards by tigers in less than 2 years in the western part of CNP when the tiger population was recovering there. Since the tiger density has increased in CNP, the impact on the spatial dynamics of leopards remains unknown. Given the relatively small size of CNP and the adjoining forests in the human-dominated landscape, an understanding of these competitive dynamics is critical to ensure conservation of both tigers and leopards. Although tigers are relatively well studied in CNP (Sunquist 1981; Smith and McDougal

1991; Smith 1993; McDougal et al. 2016), few studies have been conducted on leopards (Thapa 2011). Establishing baseline ecological, behavioral and demographic data is also important for future management strategies.

This study examined how two sympatric large carnivores, tigers and leopards, co-occur in CNP, a global biodiversity hotspot (Carter et al. 2015). Our research questions are (1) what is the density and population size of tigers and leopards, (2) what factors influence the spatial distribution of tigers and leopards (3) do their diurnal activity patterns differs, and (4) what is their dietary composition and overlap. We tested the broad hypothesis that co-occurrence of tigers and leopards in Chitwan is facilitated by the temporal and spatial segregation of habitats with varying degree of prey and human disturbances. Our results will have implications on conservation of these large carnivores in human-dominated landscapes.

Materials and methods

Study area

Our study was conducted in Chitwan NP (27°16.56′–27°42.14′N and 83°50.23′–84°46.25′E; area 953 km^2), and adjoining forests (495 km^2). CNP, a World Heritage Site, is the flagship park in Nepal, well known for its biodiversity with species diversity of ~ 70 mammals, > 600 birds, 49 reptiles and amphibians, 156 butterflies, and 120 fish species (CNP 2013). The Park is contiguous to Parsa National Park on the east and Valmiki Tiger Reserve (India) on the south (UNESCO 2003). These three adjacent forests combined make it one of the largest intact forest patches (~ 3500 km^2) in the TAL (Lamichhane et al. 2018b). CNP is connected to the Hill forests of Mahabharat (outer Himalayas) on the north through a forest corridor called Barandabhar (Fig. 1). The Park is characterized by a monsoon-dominated sub-tropical climate with an average monthly maximum temperature of 24 °C–38 °C, monthly minimum temperature 11–26 °C, annual rainfall ~ 2250 mm and relative humidity 89–98% during 2000–2010 (Subedi et al. 2017). Sal (*Shorea robusta*) dominated forest is the climax vegetation covering nearly 70% of the Park where wildlife density is relatively low. Floodplain grasslands (9.6%) and riverine forests in different stages of succession (10%) support a high density of wildlife. Different waterbodies (rivers, streams, oxbow lakes) cover 3% of the Park (Thapa 2011).

CNP is recognized as one of the core breeding sites of the tigers globally (Walston et al. 2010) and contains a major population of leopards (Thapa 2011). Other carnivores such as Asiatic wild dog (*Cuon alpinus*), striped hyena (*Hyaena hyaena*), clouded leopard (*Neofelis nebulosa*) and three smaller cats (fishing cat *Prionailurus viverrinus*, Jungle cat *Felis chaus* and leopard cat *Prionailurus bengalensis*) (Lamichhane et al. 2014) also occur in the Park. A wide range of ungulates including chital (*Axis axis*), sambar (*Rusa unicolor*), hog deer (*Axis porcinus*), barking deer (*Muntiacus vaginalis*), wild boar (*Sus scrofa*), gaur (*Bos gaurus*), Nilgai (*Boselaphus tragocamelus*) and two primates (rhesus macaque *Macaca mulatta* and langur *Semnopithecus hector*) serve as prey species for the carnivores.

The Park is surrounded by a buffer zone (729 km^2) ~ 5 km from the boundary. About half of the buffer zone is covered by forests/grasslands, the remaining half includes human settlements and agricultural areas (Karki et al. 2015). These buffer zone forests have significantly higher human pressure but increasingly are managed for national and foreign ecotourism safaris (Carter et al. 2015; Wegge et al. 2018). In addition, the communities

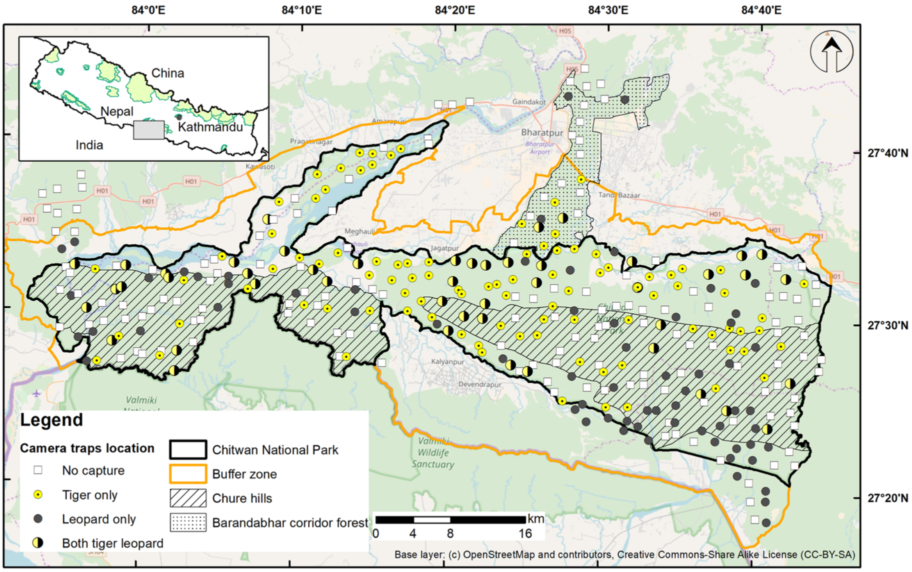


Fig. 1 Study area (Chitwan National Park and surrounding forests) showing locations of camera-traps and captures of tiger and leopard in 2013

exploit these forests for fodder, fuelwood, grazing and non-timber forest products following a regulated system of forest use. There are > 45,000 households living in the buffer zone spread over 12 municipalities belonging to four states (2, 3, Gandaki, 5) and five districts (Chitwan, Makawanpur, Nawalpurasi East, Nawalpurasi West and Parsa) (Lamichhane et al. 2019). The majority of people rely on subsistence agriculture but dependence on agriculture is decreasing as the younger generation prefers off-farm activities such as tourism (e.g. nature-guides, jobs in hotels), national and foreign employment. Livestock has been an integral part of subsistence agriculture and until the last decade, open grazing was common in the buffer zone. With the establishment of community managed forests and grazing restrictions in these forests, a gradual shift has occurred towards stall feeding (Gurung et al. 2009). These changes are driven in part by adoption of improved livestock, commercialization of the farms and shortage of labor (Lamichhane et al. 2018a). Adjoining forests outside of the buffer zone (including state managed forests and community forests) administered by the Department of Forests experience more human pressure from subsistence communities as timber exploitation is the focus of the management instead of wildlife conservation or tourism.

Camera-trap survey

We set 362 camera-trap grid cells with a spacing of 2 km in Chitwan National Park and adjoining forests (~ 1450 km^2) (Karanth and Nicholas 1998). A pair of motion sensor digital camera-traps (Reconyx 500 & 550, Bushnell Trophy Cam HD) were deployed in each cell during the dry season in 2013 (18 Feb–04 May). Cameras were set to take three pictures per trigger with no delay to ensure complete capture of animals within 15 m distance of the camera trap. Camera-traps were active 24 h in in each site for a minimum of 15 days and checked twice a week. Due to limited availability of camera-traps and logistical challenges, the survey area was divided into four blocks that ranged from 272 to 423 km^2; these were surveyed successively. Prior to camera deployment, intensive sign surveys helped us identify potential survey sites to increase the probability of photographing tigers/leopards and maximize camera safety. Camera-traps were mounted on trees or on wooden poles 45 cm above the ground, perpendicular to, and 5–7 m apart on either side of game trails, forest roads, and riverbeds without using lure. Tiger and leopard photographs obtained in camera-traps were systematically sorted in separate folders. Paired camera-traps at each sampling point obtained photos of both flanks of tigers and leopards in most of the events (~ 80%) which enabled us to identify individuals accurately based on their coat marking patterns (Karanth and Nicholas 1998; Thapa et al. 2014). Because paired cameras operated independently, ~ 20% of capture events were composed of photos of a single flank.

Individual identification was conducted by three independent observers and cross-verified collectively where 4–7 observers participated. We also used Extract-Compare Software to verify manually identified tiger and leopard individuals (Hiby et al. 2009).

Estimating population and density

We estimated density and population size of tigers and leopards through Baysean Spatially-Explicit Capture-Recapture Bayesian (B-SECR) models implemented in the package 'SPACECAP' (Gopalaswamy et al. 2012) in R 3.4.0 (R Core Team 2017). SPACECAP requires three input files i.e. (1) tiger capture history with location, animal ID and sampling occasion; (2) camera activity records (1—active and 0—not-active) for each camera-trap location and sampling occasion; and (3) home range centres. Around a 15 km buffer of the camera locations, equally spaced points (580 m apart, a grid size of 0.336 km^2) were generated to represent hypothetical home range centers ($n = 13{,}288$). This resulted in an area of 3854 km^2 of tiger and leopard habitat after removing the 2739 km^2 area of settlements. We ran the analysis with four different combinations (1) trap response present, (2) trap response absent, (3) half-normal and (4) negative-exponential detection functions and reported the density and population size obtained from the best-performing model (Gopalaswamy et al. 2012). We ran a Markov Chain Monte Carlo (MCMC) over 100,000 iterations with a burn-in of 10,000 and a thinning rate of 5. An augmentation value of 400 and 350 (more than five times the number of animals captured or $Mt + 1$) was set for tigers and leopards respectively. We produced a pixelated map of tiger and leopard density at the size of home range center (0.336 km^2) and calculated average density within each survey grid (2×2 km^2) using QGIS (QGIS Development Team 2016).

We estimated the tiger and leopard abundance by multiplying the estimated density from B-SECR models with the respective effective sampled areas (Srivathsa et al. 2015). Effective sampling area was calculated following Srivathsa et al. (2015). Estimated sigma (σ) value was derived from converged B-SCR models for tigers and leopards and a buffer of sigma (σ) × sqrt (5.99) was added to the camera trap array (Thapa and Kelly 2017). Effective sampling area was obtained by removing the non-habitat (settlement and agriculture) from the buffer area. For abundance and density estimates, we reported the 95% credible intervals around the point estimate.

Factors associated with tiger and leopard distribution

We used a binomial logistic regression by constructing a Generalized Liner Model (GLM) to analyze the variables associated with tiger and leopard occurrence in a location measured as detection in camera-traps (Zuur et al. 2009). In the GLM, occurrence of tigers or leopards within each camera trapping grid was used as response variable. Fourteen explanatory variables representing environmental parameters, prey distribution and anthropogenic pressure were defined. The environmental variables included coverage area of four habitat types (grassland, Sal forest, riverine forests and waterbodies) within grid, physiography (flat or churia hills) and average ruggedness of the terrain. The ruggedness index was calculated in QGIS from the 30 m resolution digital elevation model of ASTER satellite images (QGIS Development Team 2016). Land cover data obtained from classification of 30 m resolution landsite satellite images was grouped into four habitat types and area of the habitat in each cell was calculated in QGIS (Thapa 2011).

Similarly we used the independent detection frequency of three major prey species (chital, sambar and muntjac) (Karanth and Sunquist 1995) in camera trap photos as explanatory variables. Photographs of a prey species or people captured within an hour was recorded as one independent detection. Anthropogenic pressure was represented by the number of independent detections of local people and livestock in the camera trap photos. Distance to forest edge (assuming closer the edges, higher the anthropogenic activities) and management type (assuming low human pressure in Park core areas and high pressure in forests outside) were also used as a measure for anthropogenic pressure. In addition, average density of other large cat within grid cell obtained from the pixelated density output of SPACECAP was also used as an explanatory variables. Using multi-model inference in ‘MuMIn’ package in R (Grueber et al. 2011), we ranked the best models based on AIC value (lower AIC value indicates higher model ranking). Final models for the tiger and leopard were obtained by averaging the top candidate models supporting the data equally well (AICc ≤ 2, Burnham and Anderson 2003). Analysis was done in R (R Core Team 2017). All the analyses can be reproduced using the R-script and the associated data provided in the Supplementary Files (S1–S8).

Temporal activity patterns

Temporal activity pattern and extent of overlap between tiger and leopard were calculated using (1) a non-parametric kernel density function of activity detected by camera-traps (Ridout and Linkie 2009), (2) coefficient of overlaps, $\hat{\Delta}$, ranging from 0 (no overlap) to 1 (complete overlap) and (3) a non-parametric Kolmogorov–Smirnov test to compare activity distributions. The time stamp of each independent detection (photograph taken at least 30 min apart at the same camera-trap station) was used to fit the density function of the activity pattern. We used 10,000 bootstrap samples to measure $\hat{\Delta}$ 95% confidence intervals (CI) (Ridout and Linkie 2009). We compared the activity pattern and calculated the overlap coefficient between tigers and leopards for locations (a) where both tigers and leopards occurred and (b) where either tiger or leopards occurred. The analysis was conducted using the ‘overlap’ package in R (R Core Team 2017).

Diet of tigers and leopards

Scat samples of tigers and leopards (all that were found intact and carnivore species could be verified) were collected along the roads, trails and streambeds in Chitwan National Park and Barandabhar corridor forest between January and March 2017. Although there was 4 years gap between the camera-trap survey and the diet study, we assume no substantial change in prey availability. Experienced observers can make the distinction between tiger and leopard scats fairly accurately based on size and morphology as well as the presence of secondary signs such as scrape marks and pugmarks (Simcharoen et al. 2018; Bhattarai and Kindlmann 2012b). Tiger tracks (>8 cm pad width) and scrapes (>35 cm long and >19 cm wide) are larger than leopard tracks (<6.5 cm pad width) and scrape (<25 cm long and <15 cm wide). In a similar study in Bardia NP, using molecular identification of the carnivore, Upadhyaya et al. (2018) reported high accuracy of field identification of scats ($n=101$). Prey remains in the scat such as hairs, feathers, bones, hooves and teeth were separated. Prey species in the scat were primarily identified through microscopic analysis of medullary and cuticular hair structures as described by Mukherjee et al. (1994). Microscopic analysis of hair was carried out at the laboratory of NTNC's Biodiversity Conservation Center, Chitwan. Prey species present in the scat were identified by comparisons of hair structure with reference samples maintained at NTNC and the Wildlife Institute of India (Bahuguna 2010). We used the non-linear (asymptotic) model developed by Chakrabarti et al. (2016) for calculation of the biomass consumed by tigers and leopards following Simcharoen et al. (2018). We also evaluated tiger-leopard diet overlap by using Pianka's index (O) which ranges between 0 (total separation) and 1 (total overlap) (Gotelli 2001).

Results

Density and abundance of tigers and leopards

A total sampling effort of 6085 trap-nights yielded 2950 tiger and 1453 leopard photographs in 329 and 209 independent detections respectively. Of the 362 sampling locations, tigers were detected from 143 locations; leopards from 110, including 47 locations where both species were photographed. Out of 78 tiger and 71 leopard individuals identified, we included in our analysis 71 tigers and 65 leopards identified from photos showing either both flanks or right flank for capture-recapture analysis and excluded 7 tigers and 6 leopards showing only the left flank in photos to avoid possible duplication (Table 1).

All model parameters in Bayesian spatial capture-recapture (in program SPACECAP) for both tigers and leopards converged based on Geweke diagnostic statistics (z scores less than 1.6) on the best performing models (trap-response present with negative exponential detection function for tiger and trap response present with half normal detection function for leopard). The tiger density was estimated 3.2 – 4.6 ($\text{mean}=3.94$, $\text{SE}=0.37$) individuals per 100 km^2. Tiger density was highly concentrated in the floodplain areas close to the rivers in the northern part of the Park (Fig. 2a, c). Similarly, leopard density was estimated 2.6–4.1 ($\text{mean}=3.31$, $\text{SE}=0.39$) animals per 100 km^2 in CNP and adjoining forests. We estimated population size of tiger between 70 and 102 (86 ± 8) and leopard between 66 and 105 (85 ± 10) based on density and effective sampled area (2142.2 km^2 for tiger and

Table 1 Details of tiger and leopard capture in camera-traps in Chitwan National Park, Nepal during survey between February and May 2013 (*M* males, *F* females, *U* sex undetermined)

Parameters	Tiger	Leopard
Number of camera stations with capture	143	110
Number of independent detections	329	207
Capture rate (number of detections per 100 trap days)	5.4	3.4
Number of individuals captured	78 (50 F, 18 M, 10 U)	71 (32 F, 27 M, 11 U)
Both flanks	61	58
Right flank only	10	7
Left flank only	7[a]	6[a]

[a] These individuals were excluded from capture-recapture analysis to avoid any duplication

2571.1 km^2 for leopard) (Table 2). We also generated surface density maps (Gopalaswamy et al. 2012) to visually depict posterior estimates of pixel-level densities of tigers and leopards in the landscape at the scale of 0.3364 km^2 (Fig. 2a, b). Density of leopards was higher close to the forest edges and decreased with increasing distance (Fig. 2b, c).

Factors related to tiger and leopard occurrence

Based on the averaged value of the top candidate models, tiger detection in the camera trap survey grid cell was positively related to the area of grassland and riverine forest, detection of chital and core areas of the Park but negatively related to livestock presence (Table 3). In contrast to tigers, the leopards were more likely to be detected in the grids containing larger areas of sal forest as well as presence of chital and livestock (Table 3).

Activity pattern

Both tigers and leopards showed a crepuscular activity pattern, although this was more pronounced in tigers (Fig. 3). There was a high overlap $\hat{\Delta} = 0.83(0.78-0.91)$) in temporal activity of both species across all habitats. Activity overlap was $\hat{\Delta} = 0.72(0.61-0.82)$ in the locations where tiger and leopard co-occurred and it was $\hat{\Delta} = 0.87(0.84-0.95)$ where tigers and leopards were captured separately (Fig. 3a, b). Activity density of tigers peaked just before sunrise and after sunset whereas, leopard activity peaked exactly at the sunrise and sunset. Comparatively leopards were more active during the day in the areas where they co-occurred with tigers. A Kolmogorov–Smirnov test showed the activity distribution of tigers and leopards differ significantly ($p = 0.011$) at locations where both species were photographed. However, their activity distribution did not differ ($p = 0.478$) at locations where just one species was detected in a camera trap.

Diet of tiger and leopard

Among the prey species, chital contributed the highest biomass in the diet of tigers (38%) and leopards (48%). Tigers, however, consumed a greater biomass of the large prey such as sambar (22%) and gaur (2.3%) compared with leopards (12% and 0% respectively). Estimated consumed biomass of livestock was higher in leopard diet (15%) compared with tiger (3%) (Fig. 4a). Analysis using Pianka's prey overlap index demonstrated a 90.0% overlap in tiger and leopard diet.

Discussion

We documented a relatively high density of two sympatric carnivores in a national park and adjoining forests interspersed in a human-dominated landscape. We also observed spatial and temporal segregation between tigers and leopards, thus supporting our hypothesis. Tiger distribution was positively related to the habitats in the river floodplain (alluvial grasslands and riverine forests) and prey, but were negatively related to the disturbance (livestock presence and forests outside of CNP). In contrast, leopard distribution was positively related to less productive habitat i.e. sal forests, locations with livestock presence (disturbance) and prey species (chital). Leopards also adjusted their activity (increased in the daytime when tigers are less active) in locations where they co-occur with tigers. Both tiger and leopard occurrence showed a significant positive relationship with detection of chital in camera traps which was expected as chital constitutes a major portion of tiger and leopard diet. However, habitat type was different for tigers and leopards. The mosaic of habitats and different levels of anthropogenic pressures in these habitats have facilitated co-occurrence of tigers and leopards as they are able to occupy different niches in time and space (Karanth et al. 2017).

Tiger-leopard density

Our density estimates of tigers and leopards are comparable with those reported in previous studies (Thapa 2011; Karki et al. 2015). Karki et al. (2015) estimated 4.5 tigers per 100 km^2 in CNP. In India, tiger densities (SECR based) range between 1.15 and 8.9 animals per 100 km^2 (Kalle et al. 2011). Much lower tiger densities (individuals 100 km^2) are reported from other tiger range countries like Lao PDR (0.2–0.7; Johnson et al. 2006), Bhutan (0.52; Wang and Macdonald 2009), Malaysia (1.1–1.8; Kawanishi and Sunquist 2004) and Thailand (2.0; Duangchantrasiri et al. 2016). Tiger density in Chitwan NP is also high when compared to that recorded in other parks in Nepal (Bardia NP—3.3, Shuklaphanta NP—3.4, Parsa NP– 1.4, Banke NP—0.16; Dhakal et al. 2014; Lamichhane et al. 2018a).

Leopard density in our study is also close to the estimates reported by Thapa (2011) for CNP (3.4 leopards per 100 km^2) and Thapa et al. (2014) for Parsa NP (3.5 per 100 km^2). The density estimate of 3.9 individuals per 100 km^2 in a protected forest in Cambodia (Gray and Prum 2012) is comparable to our estimates. But the mountainous terrain in Bhutan has a much lower leopard density (1.04 individuals per 100 km^2). In India, the leopard density varied in parks between 2.07 and 13.1 individuals per 100 km^2 (Harihar et al. 2011; Kalle et al. 2011; Thapa et al. 2014).

A decrease in leopard density (9.76 to 2.07 individuals per 100 km^2) with an increase of tiger density (2.67 to 5.8 individuals per 100 km^2) has been reported from India (Harihar et al. 2011). In contrast we found both tiger and leopard densities increased over the last decade in CNP and remained relatively stable in few years before the survey (2010–2013) (Thapa 2011; Karki et al. 2015). Similar observations of leopards (in high density) that

Fig. 2 Density heat map obtained from SECR-B implemented in SPACECAP for **a** tiger; **b** leopard in Chitwan NP and surrounding forests; and **c** Average tiger/leopard density in each survey grid (calculated from modeled density surface created using pixel density obtained from SPACECAP) in relation to the distance to forest edge ▶

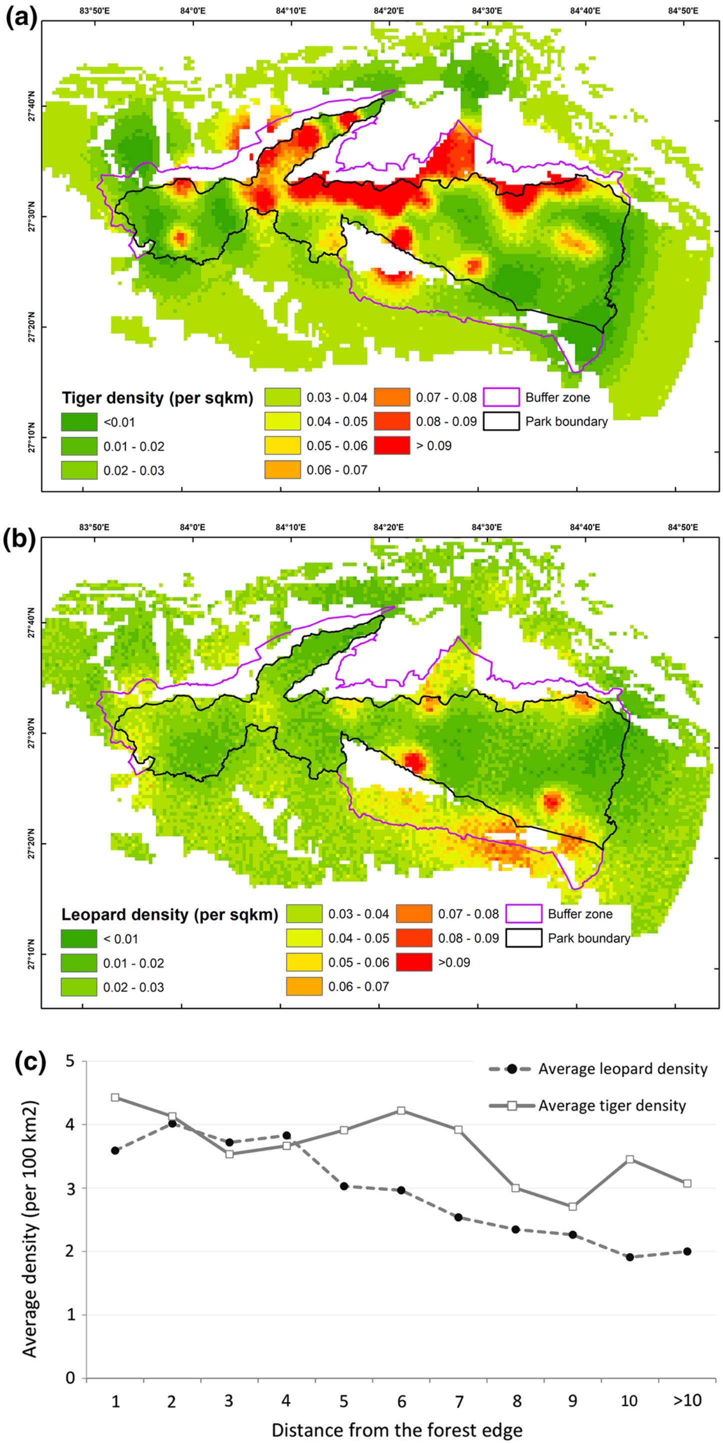
were unaffected by interference from lions, another apex predator, was reported from Sabi Sand Game Reserve in South Africa (Balme et al. 2017). For a multiple decades, tigers and leopards have co-occurred with a large overlap of home range and diet (Seidensticker 1976). Factors facilitating the high density of these two large cats in Chitwan may be a combination of high density of ungulates (73 prey per km^2, Dhakal et al. 2014), mosaics of the habitats (Bhattarai and Kindlmann 2012a), control of hunting with enhanced protection, habitat restoration in the buffer zone (Gurung et al. 2008) and support from local communities (Nepal and Spiteri 2011; Lamichhane et al. 2019).

Spatial distribution of tiger and leopard densities

Carnivore density is not evenly distributed in CNP but concentrated in certain patches. Contrary to the general expectation, both tiger and leopard densities were estimated to be relatively higher near the Park boundary. The Park is bordered by three major rivers which creates highly productive floodplains with alluvial grasslands and riverine forests that harbor a high density of ungulates and lie in proximity to these rivers (Lehmkuhl 1994; Shrestha 2004). Thus, a high tiger density close to the Park edges is a function of ecological factors (highly productive alluvial grasslands and riverine forests) (Sunquist 1981; Smith 1993). Similarly, leopard density was also higher close to the Park boundary or forest edge and decreased with increasing distance. Such a pattern of leopards using fringe areas has also been documented in Bardia and Shuklaphanta National Parks of TAL Nepal (Odden et al. 2010; Pokheral and Wegge 2018) and Rajaji of TAL India (Harihar et al. 2011). High densities of large carnivores (both tigers and leopards) and their prey in close proximity to the Park boundaries may help to explain the high incidence of human-wildlife conflict in CNP (Average annual 9.3 ± SD 5.7 human death, 31.3 ± SD 11.8 human injury and 122.94 ± SD 80.97 livestock depredation) compared with other parks in Nepal (Bhattarai and Fischer 2014; Lamichhane et al. 2018a).

The physiography of the Park may also have facilitated the uneven density distribution of tigers and leopards. The Churia Hills, covering $>60\%$ of the Park (Thapa and Kelly 2017), stretch east to west in the middle of the Park. Lower prey density in these Hills resulted in lower use of higher elevations by tigers (Smith et al. 1989). Recent studies have documented both tigers and leopards occupying this habitat (Karki et al. 2015) but in lower densities i.e. 1.5 tigers and 2.1 leopards per 100 km^2 (Thapa and Kelly 2017).

Tigers were concentrated in the prime habitats having a high density of prey species and leopards in comparatively marginal habitats. A higher proportion of livestock in the diet of leopards compared to that in tiger diet also supports the leopard use of the boundary of CNP and buffer zone area where local communities graze their cattle occasionally. We assume that interference competition by tigers led to habitat segregation by these two species (Seidensticker 1976; Carter et al. 2015). The density heatmap shows that high density areas of tigers and leopards are mostly separated from each other except for a small overlapping areas in the northern portion of the study area (Barandabhar Corridor Forest). A high number of livestock attacked by leopards has been reported by communities in recent years near the corridor forest where such a concentration of carnivores was observed


(a)
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27°40'N
27°30'N
27°20'N
27°10'N
Tiger density (per sqkm)
<0.01
0.01 - 0.02
0.02 - 0.03
0.03 - 0.04
0.04 - 0.05
0.05 - 0.06
0.06 - 0.07
0.07 - 0.08
0.08 - 0.09
> 0.09
Buffer zone
Park boundary
(b)
Leopard density (per sqkm)
< 0.01
0.01 - 0.02
0.02 - 0.03
0.03 - 0.04
0.04 - 0.05
0.05 - 0.06
0.06 - 0.07
0.07 - 0.08
0.08 - 0.09
>0.09
Buffer zone
Park boundary
(c)
Average leopard density
Average tiger density
Average density (per 100 km2)
0
1
2
3
4
5
1
2
3
4
5
6
7
8
9
10
>10
Distance from the forest edge

Table 2 Estimates of tiger and leopards density (animals 100 km^{-2}) and abundance (N) for Chitwan National Park, Nepal obtained from Bayesian spatially explicit capture–recapture (B-SCR) implemented in SPACECAP (Gopalaswamy et al. 2012) along with the posterior summaries of model parameters (sigma, lamda, beta, psi, p1 and p2)

Parameters	Tiger			Leopard		
	Estimate ± SD	95% CI	Gweke diagnostics|z score|	Estimate ± SD	95% CI	Gweke diagnostics|z score|
Sigma (σ)	5089.2 ± 191.0	4746–5475	1.2956	7002.52 ± 604.67	5841–8176	− 0.0716
Lamda ($\lambda 0$)	0.029 ± 0.004	0.021–0.038	− 1.2801	0.003 ± 0.001	0.003–0.004	− 0.1049
Beta (β)	1.33 ± 0.19	0.97–1.71	0.5596	3.28 ± 0.23	2.84–3.74	− 0.1471
Psi (ψ)	0.32 ± 0.04	0.25–0.39	− 0.4057	0.31 ± 0.04	0.23–0.39	0.989
N-super	152 ± 14	123–179	− 0.2921	128 ± 15	99–157	0.807
Density (D)	3.94 ± 0.37	3.19–4.64		3.31 ± 0.39	2.57–4.07	
p1	0.028 ± 0.004	0.02–0.037		0.003 ± 0.001	0.003–0.004	
p2	0.103 ± 0.014	0.076–0.131		0.072 ± 0.011	0.051–0.095	
Effective sampling area (km^2)	2142.2			2571.1		
Ñ	86 ± 8	70–102		85 ± 10	66–105	

(Lamichhane et al. 2018a). With the increasing number of tigers dispersing from parks to the corridor forests, leopards may have been pushed into the edges where they kill the livestock (Odden et al. 2010; Lamichhane et al. 2018a).

Daily activity pattern and diet

Both tiger and leopard showed nocturnal behavior with pronounced activities during dawn and dusk. Tiger activity intensity was less during daytime (6:00–18:30) (< 30% of total activity) compared to that of leopards (~ 40% of the activities during day). Both tiger and leopard activity coincides closely with higher overlap (0.87) in locations where only a single species was photographed. The activity overlap decreased (0.72) and activity distribution of the two species differed significantly in areas where both species occurred. Decrease in overlap is primarily due to leopards being more diurnal in the presence of tigers. More than 50% of the leopard activities were diurnal in locations overlapped with tigers and it declined to < 40% diurnal in areas where tigers were absent. Thus, leopards exhibited temporal avoidance of tigers. Kawanishi and Sunquist (2004) also observed a shift in leopard behavior to more nocturnal activity in the absence of tigers but Rayan and Linkie (2016) reported no temporal avoidance of leopard.

Scat analysis demonstrated that chital was the most important (estimate as biomass) species in the diet for both tigers and leopards as observed in other studies (Lovari et al. 2015; Wegge et al. 2018). Although there was a large overlap in prey of tigers and leopards, niche separation in the diet was observed with tigers preferring larger-sized prey (Bhattarai and Kindlmann 2012b). Rosenzweig (1966) showed coexistence between predator species is the result of size difference leading one species to hunt a different set of prey species. Wild prey contributed to most of the diets of tigers and leopards indicating that prey is not a limiting factor in the Park and buffer zone. Prey occurs in relatively high densities in CNP and

Table 3 Model averaged parameter values of individual variables (Supplementary Information S2 and S8) obtained from the GLM fitted to Tiger (A) and Leopard (B) occurrence in each camera trapping survey grids during a camera-trap survey in Chitwan National Park, 2013

Parameters	Estimate	Unconditional SE	Z value	Relative importance	Pr(> |z|)
(A) Tiger					
(Intercept)	−2.087	0.592	3.516	–	< 0.001***
Chital	0.064	0.027	2.326	1.00	0.020*
Grassland	0.006	0.003	1.992	1.00	0.046*
Livestock	−0.130	0.066	1.981	0.97	0.048*
Management_CNP	0.843	0.405	2.074	0.93	0.038*
Muntjac	0.082	0.047	1.732	0.92	0.083
Riverine_forest	0.942	0.353	2.658	0.75	0.008**
Sal_forest	0.180	0.111	1.611	0.70	0.107
Sambar	0.057	0.032	1.769	0.64	0.077
Physio_Lowland	0.452	0.299	1.508	0.44	0.132
Ruggedness	−0.003	0.003	1.010	0.24	0.313
Waterbodies	0.609	0.664	0.914	0.19	0.361
Local_people	−0.043	0.037	1.150	0.16	0.250
Leopard_density	−0.167	0.154	1.080	0.10	0.280
(B) Leopard					
(Intercept)	−1.613	0.378	4.258	–	< 0.001***
Chital	0.051	0.025	2.031	1.00	0.042*
Livestock	0.118	0.044	2.701	1.00	0.007**
Sal_forest	0.203	0.104	1.938	1.00	0.053*
Sambar	0.035	0.027	1.294	0.31	0.196
Waterbodies	0.773	0.639	1.206	0.29	0.228
Ruggedness	0.003	0.002	1.062	0.23	0.288
Tiger_density	−0.052	0.049	1.062	0.21	0.288
Grassland	0.002	0.002	0.934	0.10	0.350
Distance_forest_edge	−0.027	0.046	0.59	0.05	0.555
Management_CNP	0.179	0.310	0.574	0.05	0.566
Physio_Lowland	−0.136	0.254	0.535	0.05	0.593

*p between 0.05 and 0.01, **p between 0.01 and 0.001, ***p < 0.001

the buffer zone (73 prey animals/km^2; Dhakal et al. 2014) but density is very low in the forests outside these areas due to high anthropogenic pressure and possibly hunting (Shrestha 2004; NTNC unpublished data). Increasing wild prey density in these forests is important to sustain the high density of tigers/leopards and reduce livestock depredation especially from dispersing (or pushed out) large cats (Lamichhane et al. 2017; Kolipaka 2018).

Livestock contributed to only a small portion of the big cats' diets in Chitwna NP; lower than the previously reported by Bhattarai and Kindlmann (2012b). Kapfer et al. (2011) also reported small contribution (< 1%) of livestock in big cat diet. Reduced availability of livestock in forests due to grazing restrictions in the Park and community managed buffer zone forests may have led to lower encounter of livestock by tigers and leopards (Gurung et al. 2009) which is also reflected in their diets. Annual average of 50.6 incidents of livestock depredation in the buffer zone of CNP during 2011–2016 (Lamichhane et al. 2018a) is

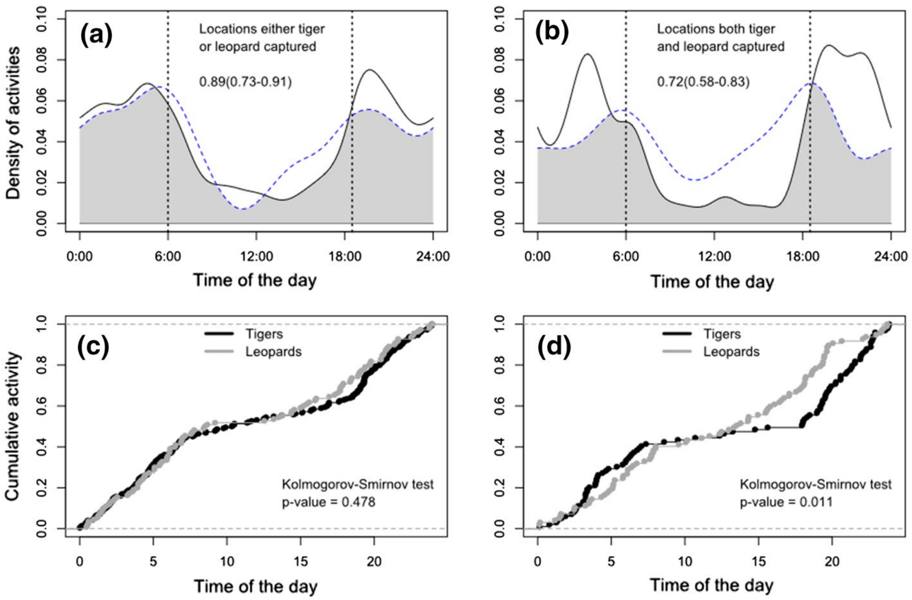

Fig. 3 Temporal activity pattern of Tigers and Leopards in locations where only tiger or leopard occurred (**a, c**) and locations where both tiger and leopard occurred (**b**, **d**). On the figures of first row (**a, b**), the shaded area represents the overlap, the continuous and dashed lines represent the activity of tigers and leopards respectively as detected in camera-traps. The vertical dotted line represents sunrise (6:00) and sunset (18:30) during the survey period. The figures on lower row (**c**, **d**) shows the cumulative activity over the hour of the day

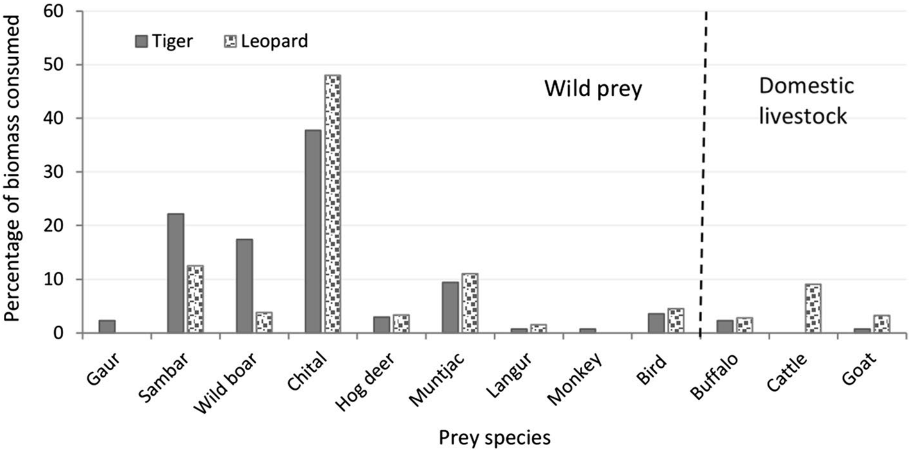

Fig. 4 Proportion of prey biomass consumed by tigers and leopards in Chitwan National Park and surrounding forests

low when compared to data from parks in India (462/year, Kanha NP; Miller et al. 2016) where free grazing is common. Lamichhane et al. (2018a) reported a higher frequency of livestock depredations caused by leopards versus tigers during 2014–2016. Comparatively more leopard scats were detected in the buffer zone or corridor forest (82%, n = 57) while more tiger scats were detected in the Park (53%, n = 148) suggesting leopards are being pushed out of the CNP (Bhattarai and Kindlmann 2012b).

Conservation implications

Our study documents a unique scenario of large carnivores co-occurring in high density with spatial and temporal segregation within a human-dominated landscape. The high density of large cats in alluvial floodplains close to the Park boundaries should be considered while designing strategies to conserve these carnivores and minimize their impacts on humans. Additionally, managing the mosaic of habitats will help to maintain the diversity and density of prey to support tigers and leopards. High and stable densities of tigers in the core areas of CNP in recent years may have increased recruitment of tigers and resulted in higher rates of dispersal. A result may be that more tigers are attempting to occupy buffer zone forests, ultimately exerting pressure on leopards to move into marginal habitats. With improved management in buffer zone forests (e.g. restoration of degraded forests, grasslands and wetland management), managers should expect higher densities of both tigers and leopards in these forests. Strategies to increase prey density and reduce livestock depredation should be adopted in buffer zones or outside forests to reduce potential conflict with humans. Regular monitoring of wildlife, especially in the fringe areas, will help improve understanding of the interactions between carnivores and humans. Monitoring will also help to reduce conflict by establishing an early warning of the vulnerable communities when tigers and leopards are in close proximity.

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Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

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