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Leopard (*Panthera pardus*) density and diet in a forest corridor of Terai: implications for conservation and conflict management

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Abstract

Context. Increasing forest fragmentation and degradation has forced wildlife to live in close proximity to humans, increasing the chances of human–wildlife conflict. Leopard (*Panthera pardus*) typifies the problem faced by large carnivores. It is a threatened species with a wide distribution, with a large part of their range outside protected areas, leaving them vulnerable to human–leopard conflict. Understanding their status and diet in such non-protected forests is necessary for their long-term conservation.

Aims. The present study aimed to estimate leopard density and assess their diet in a non-protected forest.

Methods. A camera-trapping survey was carried out in the Kamdi forest corridor outside of protected areas, covering 791.29 km^2 in the western part of Terai Arc Landscape (TAL) in Nepal. Leopard density was estimated based on the photographs obtained in camera traps, using Bayesian Explicit Capture–recapture (B-SECR) models. Scats of leopards were opportunistically collected ($n = 60$) and their diet analysed through micro-histological characters of hair remains. The frequency of occurrence and relative biomass of different prey species consumed by leopard was calculated.

Key results. Leopard density was estimated to be 1.50 ($\pm$ 0.49 s.e.) 100 km^{-2} in the survey area. Similarly, we identified 13 prey species in the leopard scats. Wild prey contributed the majority (67.8%) of leopard diet, including 23.2% of wild boar (*Sus scrofa*) and 18.3% of spotted deer (*Axis axis*). Nearly one-third of leopard diet consists of domestic livestock (cattle, goat, sheep) and dog.

Conclusions. Leopard density was found to be relatively low in the forest corridor compared with protected areas. Nearly one-third of leopard diet from domestic livestock and dogs suggests that human–leopard conflict could be problematic in the survey area.

Implications. Increasing prey density in the forest corridor and improving livestock husbandry in the periphery will contribute to increase leopard density, reduce the human–leopard conflict and enhance the functionality of the corridor.

Additional keywords: density, diet, Kamdi, Nepal, Terai Arc Landscape.

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Introduction

The ongoing fragmentation and degradation of natural areas to meet growing human needs has confined wildlife species to small (and sometimes insular) patches in the increasingly human-dominated landscape (Fischer and Lindenmayer 2007). Wildlife species are thus forced to live in close proximity to humans, increasing the chances of human–wildlife conflict. This poses a serious threat to wildlife, especially bigger carnivores, due to their large range and dietary requirements (Inskip and Zimmermann 2009). Most large carnivore species are globally threatened, primarily due to habitat loss, depletion of prey base, poaching (Raza *et al.* 2012) and retaliatory killing (Lamichhane *et al.* 2019). The common leopard (*Panthera pardus*, called 'leopard' hereafter) typifies the threats faced by big carnivores. In a large part of their range, especially within protected areas, leopards occur with more powerful carnivores such as tigers (*Panthera tigris*) and lions (*Panthera leo*). As a result, within protected areas, leopards tend to live in the periphery or marginal habitats because of interspecific competition (Odden *et al.* 2010; Lamichhane *et al.* 2019), which increases the chances of human–leopard conflict (Lamichhane *et al.* 2018; Upadhyaya *et al.* 2019). Understanding leopard status and their diet in periphery of the protected areas and biological corridors is important for reducing such conflicts and supporting their conservation.

Despite a wide distribution throughout Asia, Africa and the Middle East in various habitat types (Jacobson *et al.* 2016; Sunquist and Sunquist 2017), leopards are globally threatened ('Vulnerable' in the IUCN Redlist, Stein *et al.* 2016), and populations have been declining (Nowell and Jackson 1996;

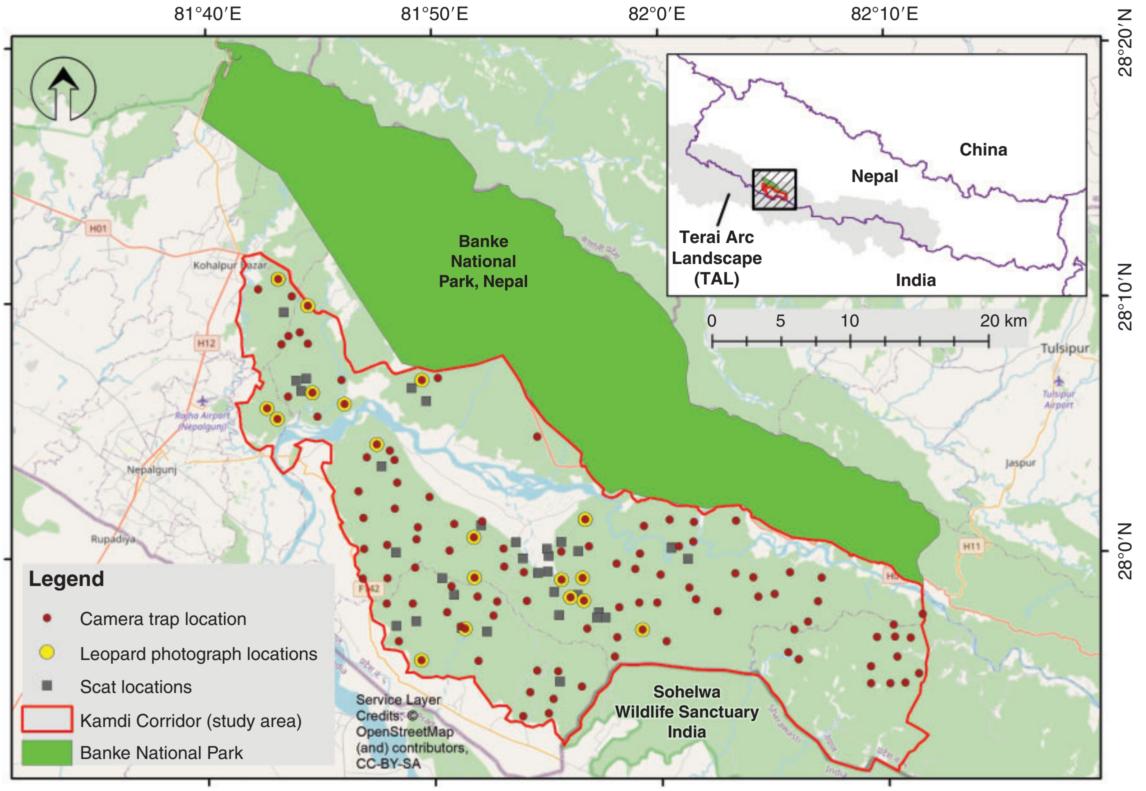

Fig. 1. Study area with camera and leopard photograph locations. Rivers and streams are indicated by curved lines and forested areas are shaded.

Ray *et al.* 2005; Stein *et al.* 2016). Leopard range has collapsed by 63–75% globally, 83–87% in Asia and 48–67% in Africa (Jacobson *et al.* 2016). Only 17% of remaining habitat falls within Protected Areas (PAs). Most of the habitats of subspecies found in South Asia (i.e. *P. pardus fusca*) fall outside PA (89%) (Jacobson *et al.* 2016).

Behavioural plasticity of leopards makes them more dispersed compared with other big cats. Their density varies highly, from 0.1 individuals 100 km^{-2} on Ghanzi commercial farmland in north-west Botswana (Boast and Houser 2012) to 30.9 individuals 100 km^{-2} in Bori wildlife sanctuary and Satpura National Park, in India (Edgaonkar 2008). Such variation in density throughout the range is supported by variation in habitats and its diverse range of diet (Hayward *et al.* 2006). They even persist in the human-dominated landscape, where the natural prey base is low, feeding on domestic livestock (Athreya *et al.* 2016). In Nepal, leopards are widely distributed across the country up to an altitude of 4400 m, with an estimated population of around 1000 matured individuals (Jnawali *et al.* 2011). A large portion of their range falls outside the protected areas, where prey density is very low (Shrestha 2004). To meet their dietary needs, leopards frequently kill livestock (Khorozyan *et al.* 2015) and occasionally attack humans. Such conflict occasionally results in retaliatory killing or translocation of the leopard (Thapa 2015).

We selected Kamdi forest corridor in Nepal, a part of transboundary Terai Arc Landscape (TAL), to study leopards because it typifies subtropical forests interspersed with cultivated areas and settlements, where leopards occur along with other large predators. Kamdi is one of the forest corridors of transboundary importance that connects Banke National Park (BaNP) in Nepal with Suhelwa Wildlife Sanctuary in India. Moreover, there is an information gap on the leopard in the western part of the TAL; previous studies have focused only on the eastern part of the TAL (Thapa 2011; Thapa *et al.* 2014; Lamichhane *et al.* 2019).

Materials and methods

Study area

The present study was conducted in the Kamdi biological corridor of Nepal (28°9′16″–27°53′5″N, 81°42′7″–81°56′26″E), which has an area of ~791.29 km^2 (Fig. 1). The corridor lies in the western part of the TAL, a transboundary landscape that spreads over 51 000 km^2 of Terai and Churia hills of Nepal and India (MoFSC 2015). The Kamdi has transboundary importance, facilitating the movement of wide-ranging animals like tiger, leopard and elephant (*Elephas maximus*) between BaNP and Suhelwa Wildlife Sanctuary.

Rapti is the major river that bisects the corridor (Fig. 1). Most of the streams (tributaries of Rapti) in the study area have highly permeable boulder and debris deposited, which makes them wider, but water flows during the rainy season (monsoon) only. In other seasons, the water infiltrates and flows underground, appearing on the surface downstream (outside the corridor, near settlements). The climate of the study area is monsoon-dominated subtropical with usually three distinct seasons in the annual cycle: summer (March–June), monsoon (July–October) and winter (November–February). More than 80% of the precipitation occurs in monsoon (CBS 2013).

The majority of the corridor is covered by sal (*Shorea robusta*)-dominated mixed forest. Occurring along the rivers are khair (*Senegalia catechu*), simal (*Bombax ceiba*), saj (*Terninalia elliptica*), bamboo (*Bombusa spp*) and sisso (*Dalbergia sissoo*). Prey species present in the corridor are spotted deer (*Axis axis*), wild boar (*Sus scrofa*), hog deer (*Axis porcinus*), barking deer (*Muntiacus vaginalis*), sambar (*Cervus unicolor*), four horned antelope (*Tetracerus quadricornis*), nilgai (*Boselaphus tragocamelus*) and porcupine (*Hystrix indica*) (WWF Nepal 2017).

Agricultural land and settlements are interspersed with the forest in the corridor. The majority of the people are *Tharu* (ethnic group of Terai), followed by *Chhetri* and *Magar*. Other castes include *Brahmin–hill*, *Tamang*, *Kami*, *Newar* and *Yadav*. Most people here depend on subsistence agriculture for their livelihood, with an increasing attraction among youths towards service careers and foreign employment. Carnivores, primarily leopards, occasionally kill domestic livestock, affecting the livelihood of the subsistence farmers (Kandel 2018). Kamdi corridor is highly susceptible to both natural and anthropogenic threats such as encroachment, stone and gravel extraction, poaching, deforestation or habitat degradation, intensive grazing by livestock, uncontrolled forest fire, drought and linear infrastructures such as roads, canals and proposed railway (MoFSC 2015).

Data collection and analysis

Camera trap survey

A camera-trap-based photographic capture–recapture method was adopted to estimate the density of leopards. Systematic grid cells of 2×2 km^2 ($n = 112$) were overlaid across the study area. The survey was conducted in the cool–dry (winter) season during January and February 2018, following Thapa (2011) and Thapa *et al.* (2014). Within each grid cell, camera placement location (with the maximum probability of capturing leopards) was identified following the intensive survey of their signs such as faeces, scratches on trees, urine spray and pugmarks. A pair of motion sensor cameras (Cuddeback-C1, WI) was placed in each grid cells at the identified location. Cameras were placed at the height of 45 cm and clamped with the wooden poles at 5–7 m apart. Camera traps were operated 24 h a day for 15–18 days in the survey area (Thapa *et al.* 2014).

Density estimations using spatial capture–recapture methods

All the photos were sorted systematically in folders and the ones containing leopards were separated. Leopard individuals were identified based on the asymmetrical rosette pattern of both flanks and limbs (Miththapala *et al.* 1989; Thapa *et al.* 2014). Identification was done by two researchers independently. The individuals were finalised after comparing the identification done independently and both researchers agreed. Sex of the individuals was also identified from the photographs when possible.

Leopard density was estimated using Bayesian Spatially Explicit Capture–recapture (B-SECR) estimator, implemented using SPACECAP ver. 1.1.0 (Gopalaswamy *et al.* 2012) in R (R Core Team 2018). Standard data input files (potential home range centre file, trap deployment details file and animal captured details file) were prepared. Trap deployment records and animal capture details were obtained from the camera trap photos. For the home range centre file, we created continuous points at the interval of 580 m in and around 10 km (distance larger than the mean maximum distance moved (MMDM) by leopards) of the camera trap survey area. Each point representing an area of 0.3364 km^2 as the potential home range was coded '1' for habitats (forests, grasslands, riverbanks) and '0' for non-habitat (settlements, agriculture, reservoirs, etc.). Although leopards use agriculture and settlement areas occasionally, we indicated them as non-habitat because these areas are used only opportunistically (Odden *et al.* 2014), which disqualifies for leopard habitat, and the leopards in these areas face a greater threat of retaliatory killing (Thapa 2015). Spatial capture–recapture models were constructed with the combination of (1) trap response present (behavioural response of animal; the probability of encounter in a trap increases subsequent to initial capture) and (2) trap response absent, with (3) half normal and (4) negative exponential detection function and Bernoulli capture encounter process (Gopalaswamy *et al.* 2012). Markov Chain Monte Carlo (MCMC) simulation settings were performed using 115 000 iterations, burn-in period 15 000 and a thinning rate of 5. The data augmentation was set to 50 individuals (five times the number of individuals captured during the camera trap survey). Parameters estimates from the best performing model were presented.

Scat collection

Scats were collected opportunistically along the ridgeline, trails near water and passages between hills where leopards are likely to pass. Scats of leopard size (i.e. 2–4 cm diameter; Rostro-García *et al.* 2018; Ghoddousi *et al.* 2016) were collected after confirming the presence of leopard signs (pugmark and scrapes) within the proximity (around 10–15 m). Leopard pugmarks and scrapes were identified with the measurement pad width of pugmark (<6.5 cm) and length (<25 cm) and breadth (<15 cm) of scrapes (Simcharoen *et al.* 2018). We could not conduct the required DNA analysis to confirm that all scats originate from leopards due to a lack of funding and limited DNA analysis facilities in Nepal. Experienced field technicians accompanied the first author (SRK) during the scat collection to correctly identify the leopard scats and their signs. Based on a similar study in Bardia, 83% of the scats identified in the field were found to be correctly identified after DNA analysis (Upadhyaya *et al.* 2018). Tigers are known to occur in the corridor but during our field survey (January–February 2018), tigers were not detected, further suggesting that samples were restricted to leopards (DNPWC and DFSC 2018).

Diet analysis

Leopard diet was analysed through micro-histological characters of hair remains in the collected scat samples. Scats were dried and dipped into a solution of benzalkonium chloride to break them down them down for easy removal of hairs. Then the scats were washed using a 1.5-mm sieve to separate the hair from other organic matter (Ramakrishnan *et al.* 1999). From each scat a minimum of 20 hairs was taken (Mukherjee *et al.* 1994) and dipped in sodium hypochlorite for 30 min and ethanol for 30 min. The identification of the prey hair was based on the cuticle and medullar characteristics. The sample was dried in blotting paper. Air cavities present in the medulla (which could obstruct the actual structure) was removed by cutting the hair into small pieces and treating it with xylene for 24 h (Rostro-García *et al.* 2018). Slides of hair samples were prepared and examined using an Olympus microscope (Olympus, Tokyo, Japan) under magnification of ×40 and ×100, and microphotographs were taken. These photos were compared with the reference pictures maintained at NTNC laboratory as well as Bahuguna (2010), and prey species were identified. Frequency of occurrence was converted to biomass consumed (D) to correct the potential bias of overestimation of the small prey, following the leopard-specific model developed by Lumetsberger *et al.* (2017):

$$y = 2.242x/(4.976 + x)$$

where y is the weight (kg) of prey consumed per felid collectible scat and x is the body mass (kg) of prey species derived from (Khan *et al.* 1996) and Thapa (2011).

Table 1. Summary of camera trap photographs of individual leopards in Kamdi corridor, 2018

Parameters	Value
Number of camera trap stations	112.00
Sampling effort (trap days)	1799.00
Trapping occasion (days)	18.00
Number of independent detections	24.00
Leopard activity index (number of detections per 100 sampling effort)	0.96
Minimum number of leopard individuals caught in camera trap (M_{t+1})	10.00
Males	6.00
Females	2.00
Individuals with undetermined sex	2.00
Total number of captures of identified individuals	22.00
Number of individual animals caught once	5.00
Number of individual animals caught more than once	5.00

Results

Leopard density

In total, 77 leopard photographs were obtained from 24 independent detections over 1799 trap days. Analysing the photographs, we identified 10 individual leopards (Table 1). Photographs of two independent detections were put aside for further analysis because we were unable to confirm the identity of the individual in the photo. Of 10 individuals, two were females, six males and sex of two individuals could not be determined from the photographs.

In the B-SECR, all the parameters were conserved on the Geweke diagnostic (Gopalaswamy *et al.* 2012) for the spatial capture–recapture model with trap response present (negative exponential detection function) (Table 2). This model produced the best model fit (Bayesian P-value based on individual encounter: 0.6236) among other candidate models (Table 3). Density was estimated to be 1.5 (±0.49) 100 km^{-2}. Density heatmap of leopards in Kamdi was prepared at the pixel size of 0.336 km^2 (Fig. 2).

Leopard diet

We collected 60 leopard scat samples and successfully identified 13 prey species. Almost 59% of the total scats constituted single prey taxa; 36% of total scat contained two prey taxa and the remaining 5% contained three prey items. Frequency of occurrence of wild ungulates and domestic livestock in leopard scats was 59.3% and 25.6% respectively (Table 3). Hair remains of a sample could not be identified because it did not match with any of our reference library. The wild ungulates include spotted deer, sambar, hog deer, barking deer and wild boar. The domestic animals consumed by leopards were cattle, goat, sheep and dog. Two prey items (4.7%) were primates – langur (*Semnopithecus hector*) and macaque (*Macaca mulatta*) (Table 3). Leopards also preyed on rodents (2.3%) and birds (7%) (Table 3). For birds, species-level identification was difficult, so they were all grouped as bird species, which made frequency of occurrence look higher in the present study.

Wild prey contributed more than two-thirds of leopard diet (67.8%). The livestock biomass consumed by leopards included cattle (19.9%), goat (4.6%) and sheep (0.9%). Dogs contributed 6.1% of leopard diet. Among the wild prey, more than one-third of the leopard diet (34.2%) was contributed by wild boar, followed by spotted deer (27.0.%) (Table 3).

Table 2. Summary of the model selected parameters from Bayesian spatially explicit capture–recapture (B-SECRC) from Kamdi corridor 2018, with Geweke's statistics

Sigma, the range parameter of the species; lam0, the intercept of expected frequency; psi, the ratio of the number of animals present within the state space; S, to the maximum allowable number; n, the number of activity centre in S. Density is expressed in 100 km^{-2}, which is N divided by S and | z-score | greater than 1.6 implies lack of convergence. HPD, highest posterior density

Parameter	Posterior mean	Posterior s.d.	95% lower HPD level	95% upper HPD level	Geweke's statistics | z-score |
Sigma	4012.60	729.534	2859.84000	5471.36000	0.4075
lam0	0.02708	0.01806	0.00239	0.06224	0.6720
Psi	0.40440	0.14061	−0.15151	0.68564	−0.7269
N	24.0863	7.88026	12.00000	40.00000	−0.6135
Density 100 km^{-2}	1.50864	0.49357	0.75161	2.50539	

Discussion

The present study is the first to estimate the density and diet of leopards outside the protected area in Nepal. We used the B-SECR model in SPACECAP because of its robustness with smaller datasets (Srivathsa *et al.* 2015). The design of the present study was based on that of Thapa *et al.* (2014), who surveyed in Parsa National Park (Nepal), putting camera traps in each station for 16 days. Unfortunately, we attained a very low recapture rate (only five out of 10 leopards photographed more than once). Although all the model parameters were conserved, shorter sampling duration and lower recapture rate might have affected our density estimates. Duration of survey was probably short for

Table 3. Composition of leopard scats ($n = 60$), with relative frequency of preys consumed and estimated relative biomass from Kamdi corridor, 2018

D (biomass consumed) was calculated based on a leopard-specific model developed by Lumetsberger *et al.* (2017)

Prey species	Frequency of occurrence	Relative frequency of occurrence (%)	Average body mass (kg)	Biomass consumed *D* (kg)	Relative biomass consumed *D* (%)
Spotted deer	15	17.4	53.0	30.7	18.3
Sambar	3	3.5	212.0	6.6	9.0
Hog deer	1	1.2	33.0	1.9	1.0
Barking deer	10	11.6	18.0	17.6	8.3
Wild boar	22	25.6	38.0	43.6	23.2
Langur	1	1.2	8.0	1.4	0.7
Macaque	3	3.5	6.0	3.7	2.1
Cattle	8	9.3	167.0	17.4	19.9
Goat	5	5.8	26.0	9.4	4.6
Sheep	1	1.2	27.0	1.9	0.9
Dog	8	9.3	12.0	12.7	6.1
Mouse	2	2.3	0.5	0.4	1.3
Birds	6	7.0	1.8	3.6	3.9
Unknown	1	1.2	10.0	1.5	0.7

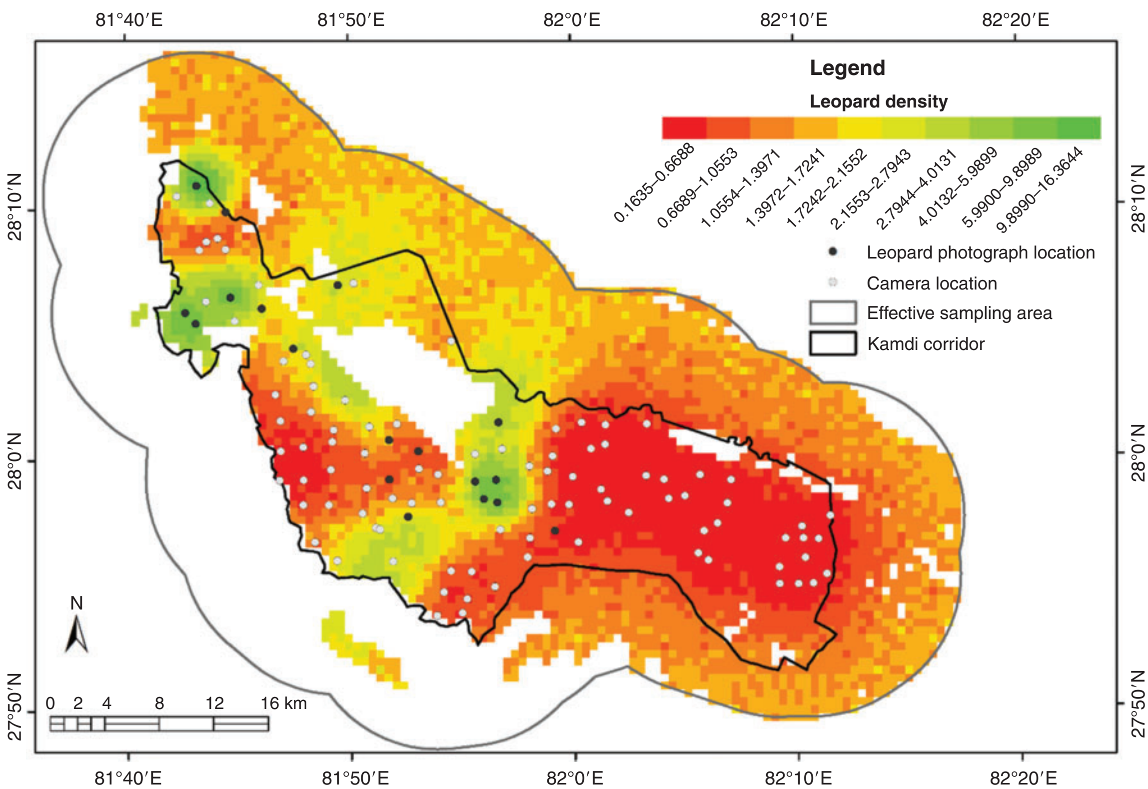

Fig. 2. A pixelated density map showing relative leopard density.

low density areas like Kamdi. We suggest longer survey periods in future to increase the recapture and get more accurate density estimates from the capture–recapture models.

Our results of comparatively lower density of leopards in Kamdi corridor was expected. Leopard density in the corridor is probably limited by the low prey density and high anthropogenic pressure. Density of carnivores primarily depends on the availability of prey. Comparatively higher proportion (more than one-quarter) of leopard diet from livestock also suggests that there is not enough wild prey in the corridor (Khorozyan *et al.* 2015). Also, leopard density is also negatively affected in areas where leopard and people frequently interact (Carter *et al.* 2015).

There is a high variation in reported leopard density among various studies conducted in South Asia (Nepal, India and Bhutan). Factors include prey density and level of human disturbance, along with topography and habitat type (Thapa *et al.* 2014; Lamichhane *et al.* 2019). In human-dominated land from Akole Tahsil, Maharastra, India, Athreya *et al.* (2013) reported a density of 4.8 ($\pm$1.2) 100 km^{-2}, which was higher than the present study in a multi-use landscape. The lower leopard density in the present study might be associated with lower prey density and high anthropogenic pressure, *viz.* grazing, encroachment, resource extraction and ongoing construction of linear infrastructures such as the sikta irrigation canal and a highway fragmenting the corridor habitat. Such linear infrastructures might have long-term impacts on large-mammal populations in the area (Espinosa *et al.* 2018). Additional research is required to fully understand the impacts of anthropogenic intrusion in Kamdi corridor.

Studies inside protected areas in Nepal show comparatively higher density than that of the present study in the corridor forest. In the alluvial floodplain of Chitwan National Park, densities of 3.45 ($\pm$0.49) and 3.31 ($\pm$0.4) leopards 100 km^{-2} were reported by Thapa (2011) and Lamichhane *et al.* (2019) respectively. Similarly, Thapa *et al.* (2014) estimated leopard density in the Bhabar zone in Parsa National Park at 3.48 ($\pm$0.83). Some studies have reported that recovering tiger populations dominate the core area of protected areas, displacing the leopard (Harihar *et al.* 2011; Mondal *et al.* 2012). The tiger population in Bardia NP and BaNP is increasing, which may push leopards into a marginal habitat like Kamdi corridor (DNPWC and DFSC 2018). However, the short survey period of the present study (18 days) cannot provide reliable evidence of leopards being pushed to the fringe areas for this reason (Barlow *et al.* 2009).

Breeding females play a crucial role in the population stability of large carnivores (Barlow *et al.* 2009). Low leopard density in Kamdi might be associated with a smaller population of adult females (Williams *et al.* 2017), or on the male-biased sex ratio of 3 : 1 (male : female), based on eight individuals whose sex could be determined. More females would be expected in a healthy population, based on social organisation of cats, where the small home range of females is overlapped by the large home range of males (Nowell and Jackson 1996). A skewed sex ratio (male-biased) might be associated with a higher number of dispersing and transient male leopards passing by the corridor in search of territory (Foster 2008). Distribution of male carnivores is generally determined by prey availability and size of female population, whereas the distribution of residential females is a function of resource availability. The smaller number of females in the present study indicates the poor habitat quality of Kamdi corridor. Continued monitoring is necessary in the Kamdi forest to depict the actual constitution of the population, including number of adults, subadults, sex and migration.

Based on scat analysis, leopard diet was dominated by wild ungulates (i.e. 60%; Table 3). Similar results have been reported by former studies of leopard diet in Nepal (Thapa 2011; Bhattarai and Kindlmann 2012; Lamichhane *et al.* 2019). In the present study, five different wild ungulate species were identified as part of the leopard diet in Kamdi, and among them, wild boar was the most abundant. Hayward *et al.* (2006) reported that leopards avoid wild boar when other easier prey is available. Therefore, the highest contribution of wildboar in leopard diet indicates the depletion of other prey species in the corridor and that leopards have been switching to suboptimal prey (Ghoddousi *et al.* 2017). The leopard diet in the Bandipur Tiger Reserve, India, is mostly composed of spotted deer and wild boar combined (65%; Andheria *et al.* 2007). Prey availability was not within the scope of the present study. In BaNP, which is adjacent to Kamdi and has a similar (but less anthropogenic) habitat, prey availability was 10 animals km^{-2}, including eight prey species (Dhakal *et al.* 2014). Among them, chital (*Axis axis*) had the highest density with 4.7 animals km^{-2} followed by wild boar (Dhakal *et al.* 2014). High numbers of livestock grazing, local people's pressure for fodder, fuelwood and non-timber forest product collection in the corridor forest were observed during the field survey. Such disturbances from people and their livestock might have hindered the increase in the prey base number in the corridor.

From the forest area in Nepal, India and Bhutan (where leopards are found to occur in human-dominated landscapes) leopards meet their nutritional needs partially by feeding on livestock (Athreya *et al.* 2016). Leopards' diet consists of a large proportion of domestic animals, small mammals and birds (Odden *et al.* 2010). Leopards can adaptively reside close to humans, where wild prey is scarce (Singh 2005; Athreya *et al.* 2013), and are compelled to feed on livestock (Khorozyan *et al.* 2015). We also recorded leopards using the habitat close to the settlements. Stray dogs and free-ranging livestock might have been attracting them. This could be the reason why 31.5% of biomass of leopard diet in Kamdi was contributed by livestock and dogs in the present study. We assume that inexperienced juveniles and infirm adults (especially dispersing or transient males) might have taken advantage of available livestock (Lamichhane *et al.* 2017; Saberwal *et al.* 1994) because domestic animals are easier to kill (Linnell *et al.* 1999).

Conclusion

We documented a relatively low density of leopard in Kamdi corridor. However, this corridor forest area has the potential to conserve leopard population in a meta-population approach in the landscape. The contribution of nearly one-third of the leopard's diet by domestic stock suggests that there is high human–leopard conflict in the corridor. Therefore, measures to manage human–leopard conflict and increase the community's tolerance to the large carnivores are required. Improving livestock husbandry practice, quickly compensating for livestock killed and raising community awareness are all necessary to reduce the threat of leopard retaliation. A quantitative study on prey density and disturbance level is essential in Kamdi corridor.

Conflicts of interest

The authors declare no conflicts of interest.

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References

Andheria, A., Karanth, K., and Kumar, N. (2007). Diet and prey profiles of three sympatric large carnivores in Bandipur Tiger Reserve, India. *Journal of Zoology* **273**(2), 169–175. doi:10.1111/j.1469-7998.2007.00310.x

Athreya, V., Odden, M., Linnell, J. D., Krishnaswamy, J., and Karanth, U. (2013). Big cats in our backyards: persistence of large carnivores in a human dominated landscape in India. *PLoS One* **8**(3), e57872. doi:10.1371/journal.pone.0057872

Athreya, V., Odden, M., Linnell, J. D., Krishnaswamy, J., and Karanth, K. U. (2016). A cat among the dogs: leopard *Panthera pardus* diet in a human-dominated landscape in western Maharashtra, India. *Oryx* **50**(1), 156–162. doi:10.1017/S0030605314000106

Bahuguna, A. (2010). 'Species Identification from Guard Hair of Selected Indian Mammals: a Reference Guide.' (Wildlife Institute of India: Dehradun, India.)

Barlow, A. C., McDougal, C., Smith, J. L., Gurung, B., Bhatta, S. R., Kumal, S., and Tamang, D. B. (2009). Temporal variation in tiger (*Panthera tigris*) populations and its implications for monitoring. *Journal of Mammalogy* **90**(2), 472–478. doi:10.1644/07-MAMM-A-415.1

Bhattarai, B. P., and Kindlmann, P. (2012). Interactions between Bengal tiger (*Panthera tigris*) and leopard (*Panthera pardus*): implications for their conservation. *Biodiversity and Conservation* **21**(8), 2075–2094. doi:10.1007/s10531-012-0298-y

Boast, L. K., and Houser, A. (2012). Density of large predators on commercial farmland in Ghanzi, Botswana. *African Journal of Wildlife Research* **42**(2), 138–143. doi:10.3957/056.042.0202

Carter, N., Jasny, M., Gurung, B., and Liu, J. (2015). Impacts of people and tigers on leopard spatiotemporal activity patterns in a global biodiversity hotspot. *Global Ecology and Conservation* **3**, 149–162. doi:10.1016/j.gecco.2014.11.013

CBS (2013). 'Environment statistics of Nepal 2013.' (Central Bureau of Statistics: Kathmandu, Nepal.)

Dhakal, M., Karki, M., Jnawali, S., Subedi, N., Pradhan, N., Malla, S., and Oglethorpe, J. (2014). 'Status of Tigers and Prey in Nepal.' (Department of National Park and Wildlife Conservation: Kathmandu, Nepal.)

DNPWC, DFSC (2018). 'Status of Tigers and Prey in Nepal.' (Department of National Parks and Wildlife Conservation and Department of Forests and Soil Conservation: Kathmandu, Nepal.)

Edgaonkar, A. (2008). Ecology of the leopard (*Panthera pardus*) in Bori Wildlife Sanctuary and Satpura National Park, India. Ph.D. Thesis, University of Florida, Gainesville, FL, USA.

Espinosa, S., Celis, G., and Branch, L. C. (2018). When roads appear jaguars decline: increased access to an Amazonian wilderness area reduces potential for jaguar conservation. *PLoS One* **13**(1), e0189740. doi:10.1371/journal.pone.0189740

Fischer, J., and Lindenmayer, D. B. (2007). Landscape modification and habitat fragmentation: a synthesis. *Global Ecology and Biogeography* **16**(3), 265–280. doi:10.1111/j.1466-8238.2007.00287.x

Foster, R. (2008). The ecology of jaguars (*Panthera onca*) in a human-influenced landscape. Ph.D. Thesis, University of Southampton, UK.

Ghoddousi, A., Soofi, M., Hamidi, A. K., Lumetsberger, T., Egli, L., Khorozyan, I., and Waltert, M. (2016). Assessing the role of livestock in big cat prey choice using spatiotemporal availability patterns. *PLoS One* **11**(4), e0153439. doi:10.1371/journal.pone.0153439

Ghoddousi, A., Soofi, M., Hamidi, A. K., Lumetsberger, T., Egli, L., Ashayeri, S., and Waltert, M. (2017). When pork is not on the menu: assessing trophic competition between large carnivores and poachers. *Biological Conservation* **209**, 223–229. doi:10.1016/j.biocon.2017.02.032

Gopalaswamy, A. M., Royle, J. A., Hines, J. E., Singh, P., Jathanna, D., Kumar, N. S., and Karanth, K. U. (2012). Program SPACECAP: software for estimating animal density using spatially explicit capture–recapture models. *Methods in Ecology and Evolution* **3**(6), 1067–1072. doi:10.1111/j.2041-210X.2012.00241.x

Harihar, A., Pandav, B., and Goyal, S. P. (2011). Responses of leopard *Panthera pardus* to the recovery of a tiger *Panthera tigris* population. *Journal of Applied Ecology* **48**(3), 806–814. doi:10.1111/j.1365-2664.2011.01981.x

Hayward, M. W., Henschel, P., O'brien, J., Hofmeyr, M., Balme, G., and Kerley, G. I. H. (2006). Prey preferences of the leopard (*Panthera pardus*). *Journal of Zoology* **270**(2), 298–313. doi:10.1111/j.1469-7998.2006.00139.x

Inskip, C., and Zimmermann, A. (2009). Human–felid conflict: a review of patterns and priorities worldwide. *Oryx* **43**(1), 18–34. doi:10.1017/S003060530899030X

Jacobson, A. P., Gerngross, P., Lemeris, J. R., Jr, Schoonover, R. F., Anco, C., Breitenmoser-Würsten, C., and Kamler, J. F. (2016). Leopard (*Panthera pardus*) status, distribution, and the research efforts across its range. *PeerJ* **4**, e1974. doi:10.7717/peerj.1974

Jnawali, S., Baral, H., Lee, S., Acharya, K., Upadhyay, G., Pandey, M., and Griffiths, J. (2011). 'The Status of Nepal Mammals: The National Red List Series.' (Department of National Parks and Wildlife Conservation: Kathmandu, Nepal.)

Kandel, S. R. (2018). Status and prey preference of leopard (*Panthera pardus*) in Kamdi Corridor Banke, Nepal. M.Sc. Thesis, Tribhuvan University, Kathmandu, Nepal.

Khan, J. A., Chellam, R., Rodgers, W., and Johnsingh, A. (1996). Ungulate densities and biomass in the tropical dry deciduous forests of Gir, Gujarat, India. *Journal of Tropical Ecology* **12**(1), 149–162. doi:10.1017/S0266467400009366

Khorozyan, I., Ghoddousi, A., Soofi, M., and Waltert, M. (2015). Big cats kill more livestock when wild prey reaches a minimum threshold. *Biological Conservation* **192**, 268–275. doi:10.1016/j.biocon.2015.09.031

Lamichhane, B. R., Persoon, G. A., Leirs, H., Musters, C. J. M., Subedi, N., Gairhe, K. P., Pokheral, C. P., Poudel, S., Mishra, R., Dhakal, M., and Smith, J. L. D. (2017). Are conflict-causing tigers different? Another perspective for understanding human–tiger conflict in Chitwan National Park, Nepal. *Global Ecology and Conservation* **11**, 177–187. doi:10.1016/j.gecco.2017.06.003

Lamichhane, B. R., Persoon, G. A., Leirs, H., Poudel, S., Subedi, N., Pokheral, C. P., and De Iongh, H. H. (2018). Spatio-temporal patterns of attacks on human and economic losses from wildlife in Chitwan National Park, Nepal. *PLoS One* **13**(4), e0195373. doi:10.1371/journal.pone.0195373

Lamichhane, B. R., Leirs, H., Persoon, G. A., Subedi, N., Dhakal, M., Oli, B. N., and Malla, S. (2019). Factors associated with co-occurrence of large carnivores in a human-dominated landscape. *Biodiversity and Conservation* **28**(6), 1473–1491. doi:10.1007/s10531-019-01737-4

Linnell, J. D., Odden, J., Smith, M. E., Aanes, R., and Swenson, J. E. (1999). Large carnivores that kill livestock: do "problem individuals" really exist? *Wildlife Society Bulletin* **27**(3), 698–705.

Lumetsberger, T., Ghoddousi, A., Appel, A., Khorozyan, I., Waltert, M., and Kiffner, C. (2017). Re-evaluating models for estimating prey consumption by leopards. *Journal of Zoology* **302**(3), 201–210. doi:10.1111/jzo.12449

Miththapala, S., Seidensticker, J., Phillips, L., Fernando, S., and Smallwood, J. (1989). Identification of individual leopards (*Panthera pardus kotiya*) using spot pattern variation. *Journal of Zoology* **218**(4), 527–536. doi:10.1111/j.1469-7998.1989.tb04996.x

MoFSC (2015). 'Strategy and Action Plan 2015–2025, Terai Arc Landscape, Nepal.' (Ministry of Forests and Soil Conservation: Kathmandu, Nepal.)

Mondal, K., Gupta, S., Bhattacharjee, S., Qureshi, Q., and Sankar, K. (2012). Response of leopards to re-introduced tigers in Sariska Tiger Reserve, Western India. *International Journal of Biodeversity and Conservation* **4**(5), 228–236. doi:10.5897/IJBC12.014

Mukherjee, S., Goyal, S., and Chellam, R. (1994). Standardisation of scat analysis techniques for leopard (*Panthera pardus*) in Gir National Park, Western India. *Mammalia* **58**(1), 139–144. doi:10.1515/mamm.1994.58.1.139

Nowell, K., and Jackson, P. (1996). 'Wild Cats: Status Survey and Conservation Action Plan (Vol. 382)'. (IUCN: Gland, Switzerland.)

Odden, M., Wegge, P., and Fredriksen, T. (2010). Do tigers displace leopards? If so, why? *Ecological Research* **25**(4), 875–881. doi:10.1007/s11284-010-0723-1

Odden, M., Athreya, V., Rattan, S., and Linnell, J. D. (2014). Adaptable neighbours: movement patterns of GPS-collared leopards in human dominated landscapes in India. *PLoS One* **9**(11), e112044. doi:10.1371/journal.pone.0112044

Ramakrishnan, U., Coss, R. G., and Pelkey, N. W. (1999). Tiger decline caused by the reduction of large ungulate prey: evidence from a study of leopard diets in southern India. *Biological Conservation* **89**(2), 113–120. doi:10.1016/S0006-3207(98)00159-1

Ray, J. C., Hunter, L., and Zigouris, J. (2005). Setting conservation and research priorities for larger African carnivores. Working paper 24, Wildlife Conservation Society, Bronx, New York, NY, USA.

Raza, R. H., Chauhan, D. S., Pasha, M., and Sinha, S. (2012). Illuminating the blind spot: a study on illegal trade in leopard parts in India (2001–2010). TRAFFIC India/WWF India, New Delhi, India.

R Core Team (2018). 'R: A language and environment for statistical computing.' (R Foundation for Statistical Computing: Vienna, Austria.) Available at https://www.R-project.org/ [verified May 2020].

Rostro-García, S., Kamler, J. F., Crouthers, R., Sopheak, K., Prum, S., In, V., and Macdonald, D. W. (2018). An adaptable but threatened big cat: density, diet and prey selection of the Indochinese leopard (*Panthera pardus delacouri*) in eastern Cambodia. *Royal Society Open Science* **5**(2), 171187. doi:10.1098/rsos.171187

Saberwal, V. K., Gibbs, J. P., Chellam, R., and Johnsingh, A. (1994). Lion-human conflict in the Gir Forest, India. *Conservation Biology* **8**(2), 501–507. doi:10.1046/j.1523-1739.1994.08020501.x

Shrestha, M. K. (2004). Relative ungulate abundance in a fragmented landscape: implications for tiger conservation. Ph.D. Thesis, University of Minnesota, St. Paul, MN, USA.

Simcharoen, A., Simcharoen, S., Duangchantrasiri, S., Bump, J., and Smith, J. L. (2018). Tiger and leopard diets in western Thailand: evidence for overlap and potential consequences. *Food Webs* **15**, e00085. doi:10.1016/j.fooweb.2018.e00085

Singh, H. (2005). Status of leopard (*Panthera parnus fusca*) in India. *Indian Forester* **131**(10), 1353–1362.

Srivathsa, A., Parameshwaran, R., Sharma, S., and Karanth, K. U. (2015). Estimating population sizes of leopard cats in the Western Ghats using camera surveys. *Journal of Mammalogy* **96**(4), 742–750. doi:10.1093/jmammal/gyv079

Stein, A., Athreya, V., Gerngross, P., Balme, G., Henschel, P., Karanth, U., and Laguardia, A. (2016). *Panthera pardus*. The IUCN Red List of Threatened Species. Paper e.T15954A50659089. IUCN, Gland, Switzerland.

Sunquist, M., and Sunquist, F. (2017). 'Wild Cats of the World.' (University of Chicago Press: Chicago, IL, USA.)

Thapa, T. B. (2011). Habitat suitability evaluation for leopard (*Panthera pardus*) using remote sensing and GIS in and around Chitwan National Park, Nepal. Ph.D. Thesis, Saurashtra University, Rajkot, India.

Thapa, T. B. (2015). Human caused mortality in the leopard (*Panthera pardus*) population of Nepal. *Journal of Institute of Science and Technology* **19**(1), 155–159. doi:10.3126/jist.v19i1.13842

Thapa, K., Shrestha, R., Karki, J., Thapa, G. J., Subedi, N., Pradhan, N. M. B., and Kelly, M. J. (2014). Leopard *Panthera pardus fusca* density in the seasonally dry, subtropical forest in the Bhabhar of Terai Arc, Nepal. *Advances in Ecology* **2014**, 286949. doi:10.1155/2014/286949

Upadhyaya, S. K., Musters, C. J. M., Lamichhane, B. R., De Snoo, G. R., Thapa, P., Dhakal, M., and De Iongh, H. H. (2018). An insight into the diet and prey preference of tigers in Bardia National Park, Nepal. *Tropical Conservation Science* **11**. doi:10.1177/1940082918799476

Upadhyaya, S. K., Musters, C. J. M., Lamichhane, B. R., De Snoo, G. R., Dhakal, M., and De Iongh, H. H. (2019). Determining the risk of predator attacks around protected areas: the case of Bardia National Park, Nepal. *Oryx* . doi:10.1017/S0030605318001436

Williams, S. T., Williams, K. S., Lewis, B. P., and Hill, R. A. (2017). Population dynamics and threats to an apex predator outside protected areas: implications for carnivore management. *Royal Society Open Science* **4**(4), 161090. doi:10.1098/rsos.161090

WWF Nepal (2017). 'Assessment of Poaching and Illegal Wildlife Trafficking in Banke-Kamdi Complex.' (WWF Nepal: Kathmandu, Nepal.)

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