SPATIOTEMPORAL OVERLAP OF COMMON LEOPARD (PANTHERA PARDUS) AND PREY SPECIES IN A MODERATELY HILLY REGION OF NEPAL

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Abstract. The common leopard (*Panthera pardus*) is a large carnivore species primarily ranging in the protected areas within the flat plains of Nepal. Facing competition from tigers (*Panthera tigris*) and decline prey population within these areas, the leopards venture into the mid-hills, leading to increased conflicts with local people. This study was designed to identify the predator and determine the spatiotemporal interactions between predators and potential prey species in the Chhatradev Rural Municipality (CRM) of Arghakhanchi, Nepal. The study utilized 18 camera traps in two phases: from March 2nd to August 3rd, 2021 and from August 5th to January 6th, 2022, with a total sampling effort of 2,402 trap night. Two common leopards and individuals of six prey species were identified. The findings indicated that common leopard activities were primarily nocturnal, with distinct crepuscular peaks at dawn and dusk, when the highest spatiotemporal overlaps were seen with wild boar and barking deer. Composite scores indicated that wild boars and barking deer had relatively higher scores, suggesting that they are the main prey species for common leopards. Our study confirmed the presence of common leopards in the mid-hill regions of Nepal, emphasizing the importance of maintaining a healthy prey population for leopard conservation and human conflict reduction.

Keywords: activity pattern, camera trap, Chhatradev rural municipality, human–wildlife conflict, predator–prey relationship

Introduction

Predator-prey interactions are an integral part of community ecology, and understanding these relations enables the understanding of ecosystem functions and ecological niches (Allen et al., 2021; Havmoller et al., 2020). The spatiotemporal overlap between predators and prey reflects the encounter frequency, and may indicate predator preferences for prey species (de Matos Dias et al., 2018; Fortin et al., 2015). Understanding this overlap can assist in the identification of patterns of interspecific interaction, and provide insights into ecosystem functions and conservation requirements of studied species (Allen et al., 2021; Ramesh et al., 2015).

The study of predator–prey interactions is complex, but is vital for the identification of niche preferences (Ripple et al., 2014). Recently, the use of camera traps has greatly facilitated the study of large carnivores such as the common leopard, allowing research into ecological traits such as their occurrence, distribution, activity patterns, and population density (Singh and Macdonald, 2017). Such data have been used to identify temporal patterns of species behavior, interactions, and the spatiotemporal overlap between predator and prey presence (Centore et al., 2018; Mori et al., 2020). This knowledge is especially valuable because in some regions, large carnivores frequently come into conflict through livestock predations. Understanding the spatiotemporal activity pattern of predators can contribute to reducing the overlap between their presence and domestic prey species, potentially mitigating conflict by adjusting and regulating the timing of livestock movements (Puls et al., 2021).

The common leopard (*Panthera pardus*) is a medium-sized predator weighing 17–65 kg (Hunter et al., 2013), occurring in tropical, forested landscapes of varying elevations in Asia and Africa (Jacobson et al., 2016). In Nepal, it occurs mostly in protected areas in the southern lowlands and Himalayan foothills, where it may coexist with the Royal Bengal tiger (*Panthera tigris*) (Subedi et al., 2021). The common leopard exhibits behavioral plasticity, with an activity pattern that can be diurnal (Ngoprasert et al., 2017), nocturnal (Martins and Harris, 2013), or cathemeral (active evenly throughout the 24 h of daily cycle) (Tattersall, 1987). The hog deer (*Axis porcinus*), chital (*Axis axis*), barking deer (*Muntiacus muntjak*), and wild boar (*Sus scrofa*) are its major prey species in Nepal, with occasional predation on domestic cattle and dogs (Dhungana et al., 2019; Kunwar and Koju, 2019).

In Nepal, studies of common leopard density, abundance, and prey preferences have been focused on the Terai and the Chure range, at 75–1,200 m ASL (Dhungana et al., 2019; Lamichhane et al., 2021; Thapa et al., 2014). However, its occurrence is poorly recorded for moderately hilly regions (Baral et al., 2021; Kunwar and Koju, 2019). Notably, recent report on the increased livestock depredation and rising instances of human-wildlife conflict have drawn attention to the Chhatradev Rural Municipality (CRM, Arghakhanchi district). Prior to this study, the residence of this region remained uncertain about the identity of predator responsible for these incidents. However, the results of our initial animal-tracking survey (including pugmarks, scat, pellets, and other signs), and interviews suggested that the common leopard is the species involved.

Hence, our study was designed to 1) identify the primary predator species 2) determine the activity pattern of predator species; 3) estimate the spatiotemporal overlap between predator and potential prey species presence; and 4) calculate the composite score for predicting predator–prey encounter rate. The findings may provide information on livestock protection for the local inhabitants, and support national project managers in their efforts to reduce human–wildlife conflicts, while maintaining healthy populations of wild prey species.

Materials and methods

Study area

The study was conducted in the CRM (northeastern Arghakhanchi district; 28°00'-28°07' N, 83°13'-83°34' E) (*Fig. 1*), within an area of 87.62 km². This rural

municipality has a moderately hilly topography (720–1,800 m ASL) with a subtropical climate, and a human population of 25,425 (Sapkota, 2018). The primary occupation of the inhabitants is agriculture, which provides a living for > 80% of the local population, with the remainder employed by the government, businesses, or in other countries (Sapkota, 2018). The temperature range is 14.9–25.8°C and the average annual rainfall is 1627.7 mm (Department of Hydrology and Meterology, 2017).



Figure 1. Geographical location of the Chhatradev Rural Municipality (CRM), Arghakhanchi, Nepal, and the location and numbers of camera traps in the intensive-study area. Camera trap locations with encircles represent common leopard capture sites

In this region, the forest covers an area of 37.1%, which had increased by 2.2% from 2000 to 2019, whereas the agricultural land cover had decreased by 2.1% in the same period (Aryal, 2021). The region has many floral species, including chilaune (*Schima wallichii*), chir pine (*Pinus roxburghii*), kaphal (*Myrica esculenta*), katus (*Castanopsis hystrx*), Nepalese alder (*Alnus nepalensis*), mahua (*Madhuca longifolia*), and fig (*Ficus*). The main potential prey species for the common leopard are the barking deer (*Muntiacus muntjak*), wild boar (*Sus scrofa*), rhesus monkey (*Macaca mulatta*), Indian hare (*Lepus nigricollis*), Himalayan crestless porcupine (*Hystrix brachyura*), red jungle fowl (*Gallus gallus*), and the kaliz pheasant (*Lophura leucomelanos*). Other carnivores beside the common leopard include the leopard cat (*Prionailurus bengalensis*), and the small Asian mongoose (*Herpestes palustris*) (Kunwar and Koju, 2019; Paudel et al., 2017).

Camera trapping

A preliminary animal-tracking survey was performed to determine the potential routes of movement. Infrared-triggered camera traps (Bushwhacker, ROBOT D30, Shenzhen, China, 1080P resolution) were deployed in 18 locations at elevations from 792 to 1399 m asl (*Fig. 1*). For habitat type coverage i.e., grassland, forest, riverbeds,

and other water resources, we established 2×2 km grids to guide the placement of camera traps. Camera trapping was first performed using 18 infrared-triggered cameras placed in pairs at nine locations from March 2nd to August 3rd, 2021. Additional camera trapping was performed at the remaining nine locations from August 5th to January 6th, 2022, to cover the entire study area. At each location, two camera traps were set up 3–4 m from the path on either side of the trail to photograph the passing leopard. Camera were set up perpendicular to the trail, affixed to a metal post at a height of 0.3 m. No bait or lure were used. We followed the guide by WildCAM, a Canadian network of camera trap researchers, to set up camera traps that accounted for the issue of imperfect detection (available at https://wildcams.ca/protocols). The cameras were set to take photographs and videos when triggered and operated 24 h each day. The camera batteries and memory cards were checked weekly, and the camera was moved if required.

Species identification was based on the timed and dated photographs. Records were considered independent when the interval between consecutive captures of one species at a site was 45 min or greater (Linkie and Ridout, 2011; O' Brien et al., 2003). When two distinguishable individuals of the same species were captured, we classified these as separate records. Common leopards were individually identified by their coat color and spot patterns, as suggested by Henschel and Ray (2003); Kittle et al. (2017). Individual spot patterns can vary according to the size of the muzzle, the number of spots present, and the position of spots relative to each other (Miththapala et al., 1989; Wattegedera et al., 2022).

Data analysis

We fitted a non-parametric circular kernel density model (Linkie and Ridout, 2011) to determine common leopard activity patterns and to quantify temporal overlap with the prey species presence. The overlapping coefficient (Δ), a quantitative measure ranging from 0 (no overlap) to 1 (complete overlap), was calculated for the common leopards and prey species using the 'overlap' package (Ridout and Linkie, 2009) in R-studio (R Development Core Team, 2017; version 3.0.1). We used two estimators of Δ (adjusted for different sample sizes), labeled Δ 1 for small samples (<75 records) and Δ 4 for large samples (>75 records) (Meredith and Ridout, 2018). The 95% confidence interval for each coefficient was determined using a bootstrap method (bootCI and bootEst in R) with 10,000 iterations from a representative sample (Meredith and Ridout, 2018).

We divided the observations into nocturnal (night), diurnal (day), crepuscular (dawn and dusk), and cathemeral (irregular intervals during day or night) (Ikeda et al., 2016). The packages 'circular' (Lund et al., 2017), and 'overlap' (Ridout and Linkie, 2009) were used to implement these tasks in R. The smoothing parameter was set to 1.0 to determine the overlapping coefficient.

We used a relative abundance index (RAI) as a proxy for leopards and its prey species abundance. The RAI was calculated using the formulae shown in *Equation 1*.

$$RAI = \left(\sum_{i=1}^{n} TE_{i} / \sum_{i=1}^{n} TN_{i}\right) * 100$$
 (Eq.1)

where TN and TE represent the number of successful trap nights and trap events, respectively, at i location (Mohd-Azlan and Sharma, 2006; Rovero et al., 2014; Ogurtsov et al., 2018). RAI estimates the mean number of animals trapped, based on the total number of photos and effort (i.e., events per 100 days of camera tapping).

We used the method suggested by Allen et al. (2021) to determine spatial overlap. At each camera trap site, the relative abundance index (RAI; "trap success"), was calculated for leopard and its prey species and then scaled to continuous probability values ranging from 0 to 1 (Ngoprasert et al., 2012). We conducted a logistic regression analysis using the number of trapped common leopards as the dependent variable and the numbers of trapped prey species as the independent variables. To assess spatial overlap, we used the area under the curve (AUC) of receiver operating characteristic (ROC) plots (Jiménez-Valverde, 2012). AUC ranges from 0.5 (reflecting a random distribution) to 1.0 (reflecting a perfect fit). We applied the Hermans-Rasson test to the dataset for each species to determine whether there was random overlap of activity over the circadian cycle (Landler et al., 2019).

To identify the preferred prey species, we plotted the spatiotemporal overlap. Species falling into the upper-right quadrant of the plot (reflecting high spatial and temporal overlap) were considered to have a high overlap with the common leopard. Those species in the upper-left quadrant (high spatial and low temporal overlap) and lower-right quadrant (high temporal and low spatial overlap) were classified as having intermediate overlap with the common leopard. Species in the lower left quadrant were assigned low overlap (low spatial and low temporal overlap).

The mean of the spatial and temporal overlap value was then determined to calculate the spatial and temporal composite scores (Allen et al., 2021). Species with a higher composite score may be more likely to be prey. The spatial overlap value was given extra weight in order to calculate the spatially adjusted composite score because it is a fundamental aspects of resource partitioning and niche selection between leopard and their potential prey species (Banjade et al., 2022; Sehgal et al., 2022). The spatial adjusted composite score was calculated as follows: spatial overlap \times 0.6 + temporal overlap \times 0.4.

We then considered a score to measure the size of potential prey species. We assigned a higher mass-adjustment weight (spatial and temporal composite score \times 1.1) to the overlap for potential prey within the common leopard's preferred size range (10–40 kg), and a lower weight (spatial and temporal composite score \times 0.9) to the overlap for potential prey outside of this range. The prey mass values were obtained from Kshettry et al. (2018). The mass-adjusted composite score was calculated as follows: (spatial overlap \times temporal overlap) \times mass adjustment. Based on Allen et al. (2021), we then calculated the final adjusted composite score as follows: ((spatial overlap \times 0.6)) \times mass-adjustment weight.

After calculating the composite scores for each potential prey species, we ranked the species based on their scores. Higher composite scores indicated higher encounter rates, which potentially indicated the more preferred prey.

Results

Identification of prey species in the CRM

During the 309 days of camera trapping, the total sampling effort was 2,402 trap nights, and the mean number of trapping nights per station was 151.9 ± 4.0 (n = 18). Altogether, 992 individuals of seven species were detected. In order of frequency, the ranking was rhesus monkey (32.3%), kaliz pheasant (24.6%), wild boar (14.1%), barking deer (10.7%), Himalayan crestless porcupine (7.4%), small Asian mongoose (6.0%), and the common leopard (4.5%) (*Fig. 2*). The rhesus monkey was the most

abundant (RAI = 13.36 captures per 100 trap nights), was photographed at all stations while the common leopard the least abundant (RAI = 1.61 captures per 100 trap nights) photographed at two stations (*Figure A1* in the *Appendix*). Some photographs were of poor quality, and inadequate for accurate species-level identification. Therefore, the number of potential prey species may be greater than identified. Beside leopard no other predatory species were photographed.



Figure 2. Prey species of common leopard captured using camera traps in the Chhatradev Rural Municipality (CRM), Arghakhanchi, Nepal

Predator identification in the CRM

Common leopards were identified based on coat color and rosette pattern. Altogether, 43 photographs of the common leopard were captured, at two stations (station no. #7 and #13, at Thulapokhara $(28^{\circ}02'N-83^{\circ}11'E, 1032 \text{ m})$ and Balkot $(28^{\circ}00'N - 83^{\circ}14'E, 986 \text{ m})$, respectively, approximately 8 km apart; *Fig. 1*). Among these 43 photographs, two distinct individuals were detected, based on body size and rosette patterns (*Fig. 3*). Individual A was recorded multiple times at station #7, whereas individual B was only recorded 9 times at station #13. Both individuals seemed to be adult, but the sex could not be determined. This indicated that the CRM could be a home range of at least two common leopards.

Temporal activity

Activity patterns of the common leopard and its potential prey species were analyzed continuously at all the camera-trap survey sites. The common leopards were most active during twilight $(6:00 \pm 1 \text{ h} \text{ and } 19:00 \pm 1 \text{ h})$ and less active at night with 83% of the records occurring during these periods, and least active during the day (*Fig. 4*). Some of

the prey species, kaliz pheasant (83.4%), rhesus monkey (78.8%), and the small Asian mongoose (69.2%), exhibited diurnal activity, while others (Himalayan crestless porcupine, wild boar, and barking deer) were nocturnal, with detection percentage of 93.2%, 62.4%, and 58.2%, respectively (*Fig. 4*).



Figure 3. Camera trap image showing distinct rosette patterns along the thighs of two different individuals of common leopard in the Chhatradev Rural Municipality (CRM), Arghakhanchi, Nepal



Figure 4. Temporal overlap, indicated via kernel density estimates, between common leopard and its prey species in the Chhatradev Rural Municipality (CRM), Arghakhanchi, Nepal. Solid line: common leopard, dashed line: prey species

Hermans-Rasson tests showed that all species had temporal overlap with the common leopard that was statistically different from random (*Table 1*). Temporal overlap of the common leopard and its prey was highest for wild boar [0.71 (0.49–0.83)] and barking deer [0.67 (0.50–0.81)]. Small Asian mongoose [0.45 (0.38–0.70)], Himalayan crestless porcupine [0.42 (0.26–0.66)], and kaliz pheasant [0.40 (0.23–0.62)] exhibited intermediate temporal overlap, and rhesus monkey [0.30 (0.24–0.57)] exhibited the least overlap (*Fig. 4; Table 2*).

Table 1. Hermans-Rasson uniformity tests to determine whether random activity overlap between common leopard and its prey species occurred during a circadian cycle, in the Chhatradev Rural Municipality (CRM), Arghakhanchi, Nepal

| Encoder | Hermans-Rasson test | | | | | |
|-------------------------------|---------------------|--------|-----------------|--|--|--|
| Species | Ν | Т | <i>P</i> < 0.01 | | | |
| Common leopard | 43 | 53.21 | 0.0010 | | | |
| Wild boar | 140 | 192.15 | 0.0010 | | | |
| Barking deer | 106 | 112.1 | 0.0010 | | | |
| Small Asian mongoose | 63 | 67.25 | 0.0010 | | | |
| Himalayan crestless porcupine | 74 | 86.14 | 0.0010 | | | |
| Kaliz pheasant | 245 | 298.64 | 0.0001 | | | |
| Rhesus monkey | 321 | 352.16 | 0.0001 | | | |

N: number of independent events (\leq 45 min interval between events). The threshold for significance is $P \leq 0.01$

Table 2. Potential prey species of common leopard, with relative abundance, temporal overlap, spatial overlap, and composite scores

| Species | Relative abundance | Temporal overlap | Spatial overlap | Composite scores ^a | | | |
|-------------------------------|-----------------------|---------------------|--------------------|-------------------------------|---------------------|-----------------------|-----------------------------------|
| | | | | Spatial and temporal | Spatial adjusted | Prey mass adjusted | Spatial and prey mass adjusted |
| Wild boar | 5.80 | 0.71 | 0.83 | 0.77 | 0.78 | 0.69 | 0.70 |
| Barking deer | 4.41 | 0.67 | 0.70 | 0.68 | 0.68 | 0.74 | 0.74 |
| Small Asian mongoose | 2.62 | 0.45 | 0.62 | 0.53 | 0.55 | 0.47 | 0.49 |
| Himalayan crestless porcupine | 3.08 | 0.42 | 0.37 | 0.39 | 0.38 | 0.35 | 0.34 |
| Kaliz pheasant | 10.19 | 0.40 | 0.30 | 0.35 | 0.34 | 0.31 | 0.30 |
| Rhesus monkey | 13.36 | 0.30 | 0.26 | 0.28 | 0.27 | 0.30 | 0.29 |

^aHigher value composite scores indicate higher encounter rates and potentially higher prey preference

Spatial and composite overlap

Spatial overlap with the common leopard was the highest for wild boar (0.83), followed by barking deer (0.70), small Asian mongoose (0.62), Himalayan crestless porcupine (0.37), kaliz pheasant (0.30), and rhesus monkey (0.26) (*Table 2*). Spatiotemporal overlap was the highest (upper right quadrant, *Fig. 5*) for wild boar and barking deer, suggesting that they are potentially preferred prey. The small Asian mongoose exhibited high spatial but low temporal overlap (upper left quadrant, *Fig. 5*),

suggesting that it has intermediate potential as a prey species. The Himalayan crestless porcupine, kaliz pheasant, and rhesus monkey, exhibiting low spatial and temporal overlap (lower left quadrant, *Fig. 5*), are likely to be alternate prey species. Four different composite scores were estimated to determine preferred prey species. Wild boar, barking deer, and small Asian mongoose had the highest spatial and temporal composite scores, spatially adjusted composite scores, and spatially and mass-adjusted composite score (*Table 2*).



Figure 5. Spatiotemporal overlap of common leopard and its potential prey species in the Chhatradev Rural Municipality (CRM), Arghakhanchi, Nepal. The high level of overlap with wild boar and barking deer suggests that it is the most encountered prey species. The high spatial and low temporal overlap with small Asian mongoose suggests that it is a minor prey species. The low spatiotemporal overlap with the other species suggests that are rarely encountered with common leopard

Discussion

Our study aimed to determine the spatiotemporal activity patterns of the common leopard and its potential prey species in the CRM. Camera trapping over 309 d confirmed the presence of two common leopards, which were primarily active during twilight and at night, with peak activity at sunrise and sunset. Of the six potential prey species identified, rhesus monkeys, kaliz pheasant, and wild boar were the most common. Barking deer and wild boar exhibited the greatest spatiotemporal overlap with the common leopards, possibly indicating major prey species status. In the mid-hill regions of Nepal, the barking deer is the dominant deer species (Kandel, 2019) and constituting a major portion of the common leopard diet (Kandel, 2019; Koirala et al., 2012).

Early ecological studies considered temporal overlap to be a reliable method of determining prey preferences. However, Linkie and Ridout (2011) and O'Brien et al.

(2003) found that combining temporal and spatial overlap was more effective. High spatiotemporal overlap may not always signify prey preference, but indicates a high encounter rate (Allen et al., 2021; Fortin et al., 2015). The biomass of common leopard is significantly correlated with that of prey weighing 15–60 kg (Stander, 1997). Common leopards tend to disproportionately target prey within this weight range, as such prey species are both abundant and relatively easy to hunt (Bothma and Coertze, 2004). For this reason, common leopards commonly predate medium-sized ungulates like barking deer and wild boar, although this may vary across study areas (Hayward et al., 2006).

Our four composite spatiotemporal overlap scores produced similar rankings of potential prey species. Wild boar was consistently ranked the highest, followed by barking deer, potentially reflecting the higher abundance of wild boar (*Table 2*). More abundant species may be more widely distributed, potentially increasing their spatial overlap with predators. However, this may also contribute to overestimations of their preferability as prey (Allen et al., 2021). For the small Asian mongoose, the intermediate composite overlap score, with low temporal but high spatial overlap, identifies it is as a potential alternative prey species (*Fig. 3*). Moreover, in light of the crucial ecological theories pertaining to carnivore intraguild killing, the ecological dynamics of this potential predator-prey interaction need careful consideration. For Himalayan crestless porcupine, kaliz pheasant, and rhesus monkey, the low spatial and temporal overlap suggest that they are minor prey species.

The two common leopards were captured near permanent water sources in rugged forested terrain. Both leopard individuals were photographed in mixed forest having thick undergrowth. They were primarily crepuscular and nocturnal, consistent with earlier findings (Chaudhary et al., 2020; Rafiq et al., 2020) and observed in other felids such as the leopard cat (Austin et al., 2007), cheetah (Rafig et al., 2020), tiger (Wang et al., 2016; Yang et al., 2018), and lion (Chaudhary et al., 2020). Their heightened activity during twilight and at night is likely due to activity of their prey species (Jenny and Zuberbühler, 2005; Sunquist and Sunquist, 2002). Barking deer and wild boar, its primary prey species in this region (Kunwar and Koju, 2019), are most active during twilight and at night (Fig. 4). Reduced diurnal activity of common leopards may be due to anthropogenic disturbances, such as firewood and grass collection, which tend to occur more frequently during the day. Distance to a potential source of disturbance is the most influential factor affecting common leopard activity and density (Havmoller et al., 2020). For instance, in Thailand, leopards were more active during the day when there was less human activity (Ngoprasert et al., 2012). Further, leopards probably prefer to be active when it is cooler, avoiding activity during the hottest part of the day (Bailey, 2005), 9:00–15:00 in the CRM. These leopards must travel long distances to cover their large home ranges which is between 30-78 km² in male and 15-16 km² for females (Odden and Wegge, 2005).

In Nepal, most of the wildlife is found in human-dominated landscapes. Common leopards are more likely to attack and kill humans and livestock in human settlements and agricultural land than elsewhere (Acharya et al., 2016). More than 75% of such attacks occur within 1 km of the nearest forest (Baral et al., 2021). In terms of leopard attacks, Arghakhanchi is one of the hardest hit regions. As young people migrate to urban areas or travel internationally for education and employment, much of the agricultural land near villages is left abandoned and overgrown with secondary vegetation (Childs et al., 2014). This conversion of cultivated land, which previously

was a buffer between forests and human settlements, may contribute to human–wildlife conflict. In the last five years, common leopards have killed domestic animals and livestock, especially cattle and dogs (Kunwar and Koju, 2019). Despite numerous leopard attacks occurring in CRM, a significant portion of these incidents remains unknown and unrecorded. With increasing population of predators, including the common leopard, it is necessary to maintain healthy prey populations to reduce human–wildlife conflict (Adhikari and Thapa, 2013).

The common leopard is fairly common and widely distributed in the plain lowlands and Chure region of Nepal (Sharma et al., 2019; Subedi et al., 2021), and its habitat has recently expanded towards moderately hilly regions. Its population in the CRM and surrounding rural municipality may represent home-range expansion from the Chure range. The southern region of Arghakhanchi is within the Chure range (Pokhrel, 2013). Tigers and leopards have recently undergone range expansion in districts adjoining Arghakhanchi, including Kapilvastu, Palpa, and Rupendehi (Subedi et al., 2021). The tiger population in Nepal has doubled since 2010 (Thapa et al., 2017), requiring an increased home range in the Terai and Chure region. This may force leopards to shift into the moderately hilly region (Kafley et al., 2019; Lamichhane et al., 2019). Community forests in hilly regions are increasing, providing suitable habitat for large sized predators and their prey species. Deforestation and habitat fragmentation of Chure forests, under intensive human population growth and land use, may contribute to changes in predator ecology. Our study aims to elucidate the implications of these landscape changes on the common leopard, exploring the dynamics of its range expansion into the moderately hilly or even mountainous regions and its co-occurrence with diverse prey species in response to changing environment conditions.

Our study focused only on the CMR, which is a small part of the moderately hilly region of Nepal where leopards are found. Therefore, our results may not reflect the spatiotemporal overlap and activity pattern of leopard in other region of the country, which may vary depending on the prey availability and habitat characteristics. Further study should expand the spatial and temporal coverage of camera trapping to obtain a more comprehensive picture of leopard ecology in Nepal. Moreover, we acknowledge that the activity patterns derived from camera trap data may be influenced by the number of detections, as suggested by (Lashley et al., 2018). Some of the species in our study area, such as common leopard, small Asian mongoose and Himalayan crestless porcupine had low detections rates, which may affect the reliability of their activity estimates. Thus, we advise caution when interpreting the activity patterns of these species and recommend further data collection to increase the sample size.

These findings reveal that the common leopard occurs in the Terai and Chure range, and over wider areas in the moderately hilly regions of Nepal. Through camera trapping, we identified their primarily nocturnal behavior, with notable crepuscular activity peaks during dawn and dusk, corresponding to interactions with medium-sized prey species. Our assessment of composite scores highlights the essential role of wild boars and barking deer as the primary prey species for common leopards in this region. This highlights the importance of maintaining a robust prey population to ensure the conservation of apex predators. Further research is required into the behavioral and ecological factors for leopard attacks on humans and livestock predation. These findings extend our understanding of the relationships between common leopards and their prey, with potential conservation implications. **Author contributions.** M.B and P.A conceptualization, manuscript design and writing original draft, A.K and P.A performed the field visit and data collection, M.H.C and S.H.H supported the research design. D.H.L reviewed the manuscript and coordinated the overall research. The authors have read and agreed to the published version of the manuscript.

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Conflict of interests. The authors declare no competing interest.

Data availability. The data that supports the results of the study are accessible upon request from the corresponding author.

REFERENCES

- [1] Acharya, K. P., Paudel, P. K., Neupane, P. R., Köhl, M. (2016): Human-wildlife conflicts in Nepal: patterns of human fatalities and injuries caused by large mammals. PLoS ONE 11(9): e0161717.Mi.
- [2] Adhikari, P., Thapa, T. B. (2013): Estimating abundance of large mammalian prey in Suklaphanta Wildlife Reserve, Nepal. – Journal of Institute of Science and Technology 18(2): 84-89.
- [3] Allen, M. L., Sibarani, M. C., Krofel, M. (2021): Predicting preferred pry of Sumatran tigers *Panthera tigris sumatrae* via spatio-temporal overlap. Oryx 55(2): 197-203.
- [4] Aryal, R. R. (2021): Land cover of Nepal based on the regional database system. ICIMOD. https://rds.icimod.org/Home/DataDetail?metadataId=1972729.
- [5] Austin, S. C., Tewes, M. E., Grassman, L. I., Silvy, N. (2007): Ecology and conservation of the leopard cat *Prionailurus bengalensis* and clouded leopard *Neofelis nebulosa* in KhaoYaiNational Park, Thailand. Acta Zoologica Sinica 53: 1-14.
- [6] Bailey, T. (2005): The African Leopard: Ecology and Behavior of a Solitary Felid. Blackburn Press, Caldwell, NJ.
- [7] Banjade, M., Jeong, Y. H., Jin, S. D., Son, S. H., Kunwar, A., Park, S. M., Lee, J. W., Choi, S. H., Oh, H. S. (2022): Spatiotemporal overlap between Siberian roe deer (*Capreolus pygargus tianschanicus*) and sympatric mammalian species on Jeju Island, South Korea. – Mammalia 87(2): 101-109.
- [8] Baral, K., Sharma, H. P., Rimal, B., Thapa-Magar, K., Bhattarai, R., Kunwar, R. M., Aryal, A., Ji, W. (2021): Characterization and management of human-wildlife conflicts in mid-hills outside protected areas of Gandaki province, Nepal. – PLoS ONE 16(11): 1-17.
- [9] Bothma, J. D. P., Coertze, R. J. (2004): Motherhood increases hunting success in southern Kalahari leopards. Journal of Mammalogy 85(4): 756-760.
- [10] Centore, L., Ugarkovic, D., Scaravelli, D., Safner, T., Panduric, K., Sprem, N. (2018): Locomotor activity pattern of two recently introduced non-native ungulate species in a Mediterranean habitat. – Folia Zool 67(1): 17-24.
- [11] Chaudhary, R., Zehra, N., Musavi, A., Khan, J. A. (2020): Spatio-temporal partitioning and coexistence between leopard (*Panthera pardus fusca*) and Asiatic lion (*Panthera leo persica*) in Gir protected area, Gujarat, India. PLoS ONE 15(3): 1-14.
- [12] Childs, G., Craig, S., Beall, C. M., Basnyat, B. (2014): Depopulating the himalayan highlands: education and outmigration from ethnically Tibetan communities of Nepal. – Mountain Research and Development 34(2): 85-94.
- [13] de Matos Dias, D., de Campos, C. B., Guimarães Rodrigues, F. H. (2018): Behavioural ecology in a predator-prey system. Mammalian Biology 92: 30-36.
- [14] Department of Hydrology and Meterology. (2017): Observed Climate Trend Analysis in the Districts and Physiographic Region of Nepal (1971-2014). Department of Hydrology and Meteorology, Kathmandu, Nepal. http://www.dhm.gov.np/.

- [15] Dhungana, R., Lamichhane, B. R., Savini, T., Dhakal, M., Poudel, B. S., Karki, J. B. (2019): Livestock depredation by leopards around Chitwan National Park, Nepal. – Mammalian Biology 96: 7-13.
- [16] Fortin, D., Buono, P. L., Schmitz, O. J., Courbin, N., Losier, C., St-Laurent, M. H., Drapeau, P., Heppell, S., Dussault, C., Brodeur, V., Mainguy, J. (2015): A spatial theory for characterizing predator—multiprey interactions in heterogeneous landscapes. – Proceedings of the Royal Society B: Biological Sciences 282(1812): 20150973.
- [17] Havmoller, R. W., Jacobsen, N. S., Scharff, N., Rovero, F., Zimmermann, F. (2020): Assessing the activity pattern overlap among leopards (*Panthera pardus*): potential prey and competitors in a complex landscape in Tanzania. – Journal of Zoology 311(3): 175-182.
- [18] Hayward, M. W., Henschel, P., O'Brien, J., Hofmeyr, M., Balme, G., Kerley, G. I. H. (2006): Prey preferences of the leopard (*Panthera pardus*). – Journal of Zoology 270(2): 298-313.
- [19] Henschel, P., Ray, J. (2003): Leopards in African rainforests: survey and monitoring techniques. Wildlife Conservation Society 33: 54.
- [20] Hunter, L., Henschel, P., Ray, J. (2013): *Panthera pardus.* In: Kingdon, J. S., Hoffmann, M. (eds.) Mammals of Africa Volume V: Carnivores, Pangolins, Equids and Rhinoceroses. Bloomsbury, London.
- [21] Ikeda, T., Uchida, K., Matsuura, Y., Takahashi, H., Yoshida, T., Kaji, K., Koizumi, I. (2016): Seasonal and diel activity patterns of eight sympatric mammals in northern Japan revealed by an intensive camera-trap survey. – PLoS ONE 11(10): e0163602.
- [22] Jacobson, A. P., Gerngross, P., Lemeris, J. R., Schoonover, R. F., Anco, C., Breitenmoser-Würsten, C., Durant, S. M., Farhadinia, M. S., Henschel, P., Kamler, J. F., Laguardia, A., Rostro-García, S., Stein, A. B., Dollar, L. (2016): Leopard (*Panthera pardus*) status, distribution, and the research efforts across its range. – PeerJ 4(5): e1974.
- [23] Jenny, D., Zuberbühler, K. (2005): Hunting behaviour in West African forest leopards. African Journal of Ecology 43(3): 197-200.
- [24] Jiménez-Valverde, A. (2012): Insights into the area under the receiver operating characteristic curve (AUC) as a discrimination measure in species distribution modelling.
 Global Ecology and Biogeography 21(4): 498-507.
- [25] Kafley, H., Lamichhane, B. R., Maharjan, R., Khadka, M., Bhattarai, N., Gompper, M. E. (2019): Tiger and leopard co-occurrence: intraguild interactions in response to human and livestock disturbance. – Basic and Applied Ecology 40: 78-89.
- [26] Kandel, S. R. (2019): *Panthera pardus fusca* (Family: Felidae) diet composition from lamjung, nepal. Environment and Ecology Research 7(4): 253-258.
- [27] Kittle, A. M., Watson, A. C., Fernando, T. S. P. (2017): The ecology and behaviour of a protected area Sri Lankan leopard (*Panthera pardus kotiya*) population. Tropical Ecology 58(1): 71-86.
- [28] Koirala, R. K., Raubenheimer, D., Adhikari, B., Aryal, A., Amiot, C., Karmacharya, D. (2012): Genetic identification of carnivore scat: implication of dietary information for human–carnivore conflict in the Annapurna Conservation Area, Nepal. – Zoology and Ecology 22(3-4): 137-143.
- [29] Kshettry, A., Vaidyanathan, S., Athreya, V. (2018): Diet selection of leopards (*Panthera pardus*) in a human-use landscape in North-Eastern India. Tropical Conservation Science 11: 1940082918764635.
- [30] Kunwar, A., Koju, N. P. (2019): Prey diversity of common leopard and factors affecting human-common leopard conflict in community forests of Arghakhanchi District Nepal. Journal of Advanced Academic Research 6(1): 84-100.
- [31] Lamichhane, B. R., Leirs, H., Persoon, G. A., Subedi, N., Dhakal, M., Oli, B. N., Reynaert, S., Sluydts, V., Pokheral, C. P., Poudyal, L. P., Malla, S., de Iongh, H. H. (2019): Factors associated with co-occurrence of large carnivores in a human-dominated landscape. – Biodiversity and Conservation 28(6): 1473-1491.

- [32] Lamichhane, B. R., Lamichhane, S., Regmi, R., Dhungana, M., Thapa, S. K., Prasai, A., Gurung, A., Bhattarai, S., Paudel, R. P., Subedi, N. (2021): Leopard (*Panthera pardus*) occupancy in the Chure range of Nepal. – Ecology and Evolution 11(20): 13641-13660.
- [33] Landler, L., Ruxton, G. D., Malkemper, E. P. (2019): The Hermans-Rasson test as a powerful alternative to the Rayleigh test for circular statistics in biology. BMC Ecology 19(1): 4-11.
- [34] Lashley, M. A., Cove, M. V., Chitwood, M. C., Penido, G., Gardner, B., Deperno, C. S., Moorman, C. E. (2018): Estimating wildlife activity curves: comparison of methods and sample size. – Scientific Reports 8(1): 1-11.
- [35] Linkie, M., Ridout, M. S. (2011): Assessing tiger-prey interactions in Sumatran rainforests. Journal of Zoology 284(3): 224-229.
- [36] Lund, U., Claudio, A., Hiroyoshi, A., Alessando, G., Portugues, E. G., Giunchi, D., Irisson, J.-O., Pocernich, M., Rotolo, F. (2017): Circular statistics. R package version 0.4-93. – https://cran.r-project.org/package=circular.
- [37] Martins, Q., Harris, S. (2013): Movement, activity and hunting behaviour of leopards in the Cederberg mountains, South Africa. African Journal of Ecology 51(4): 571-579.
- [38] Meredith, M., Ridout, M. (2018): Estimates of coefficient of overlapping for animal activity patterns. R package version 0.3.2. https://cran.r-project.org package=overlap.
- [39] Miththapala, S., Seidensticker, J., Phillips, L., Fernando, S. B. U., Smallwood, J. A. (1989): Identification of individual leopards (*Panthera pardus kotiya*) using spot pattern variation. – Journal of Zoology 218(4): 527-536.
- [40] Mohd-Azlan, J., Sharma, D. S. K. (2006): The diversity and activity patterns of wild felids in a secondary forest in Peninsular Malaysia. Oryx 40(1): 36-41.
- [41] Mori, E., Bagnato, S., Serroni, P., Sangiuliano, A., Rotondaro, F., Marchianò, V., Cascini, V., Poerio, L., Ferretti, F. (2020): Spatiotemporal mechanisms of coexistence in an European mammal community in a protected area of southern Italy. – Journal of Zoology 310(3): 232-245.
- [42] Ngoprasert, D., Lynam, A. J., Ronglarp, S., Naruemon, T., Wanlop, C., Robert, S., Kate, E., George, A. G., Lon, I. G., Shumpei, K., JoGayle, H., David, H. R. (2012): Occurance of three felids across a network of protected areas in Thailand: prey, intraguild and habitat association. Biotropica 44(46): 810-817.
- [43] Ngoprasert, D., Lynam, A. J., Gale, G. A. (2017): Effects of temporary closure of a national park on leopard movement and behaviour in tropical Asia. Mammalian Biology 82: 65-73.
- [44] O'Brien, T. G., Kinnaird, M. F., Wibisono, H. T. (2003): Crouching tigers, hidden prey: Sumatran tiger and prey populations in a tropical forest landscape. – Animal Conservation 6(2): 131-139.
- [45] Odden, M., Wegge, P. (2005): Spacing and capacity pattern of Leopard (Panther pardus) in the Royal Bardia National Park, Nepal. Wildlife Biology 1(2): 50-56.
- [46] Ogurtsov, S. S., Zheltukhin, A. S., Kotlov, I. P. (2018): Daily activity patterns of large and medium-sized mammals based on camera traps data in the central forest nature reserve, Valdai Upland, Russia. Nature Conservation Research 3(2): 68-88.
- [47] Paudel, N., Paudel, L. P., Ghimire, U., Das, B. D. (2017): Archichlamydae and sympetalae flora of Arghakhanchi District, Western Nepal. International Journal of Life Sciences Research 5(3): 73-81.
- [48] Pokhrel, kabi P. (2013): Chure forestry conservation and management plan: a case study of Arghakhanchi district, Nepal. Journal of Geography and Regional Planning 6(5): 172-183.
- [49] Puls, S., Teichman, K. J., Jansen, C., O'Riain, M. J., Cristescu, B. (2021): Activity patterns of leopards (*Panthera pardus*) and temporal overlap with their prey in an arid depredation hotspot of southern Africa. – Journal of Arid Environments 187: 104430.
- [50] R Development Core Team (2017): R: A Language and Environment for Statistical Computing. https://www.R-project.org.

- [51] Rafiq, K., Hayward, M. W., Wilson, A. M., Meloro, C., Jordan, N. R., Wich, S. A., McNutt, J. W., Golabek, K. A. (2020): Spatial and temporal overlaps between leopards (*Panthera pardus*) and their competitors in the African large predator guild. – Journal of Zoology 311(4): 246-259.
- [52] Ramesh, T., Kalle, R., Sankar, K., Qureshi, Q. (2015): Role of body size in activity budgets of mammals in the Western Ghats of India. Journal of Tropical Ecology 31(4): 315-323.
- [53] Ridout, M. S., Linkie, M. (2009): Estimating overlap of daily activity patterns from camera trap data. Journal of Agricultural, Biological, and Environmental Statistics 14(3): 322-337.
- [54] Ripple, W. J., Estes, J. A., Beschta, R. L., Wilmers, C. C., Ritchie, E. G., Hebblewhite, M., Berger, J., Elmhagen, B., Letnic, M., Nelson, M. P., Schmitz, O. J., Smith, D. W., Wallach, A. D., Wirsing, A. J. (2014): Status and ecological effects of the world's largest carnivores. – Science 343(6167): 1241484.
- [55] Rovero, F., Martin, E., Rosa, M., Ahumada, J. A., Spitale, D. (2014): Estimating species richness and modelling habitat preferences of tropical forest mammals from camera trap data. PLoS ONE 9(7): e103300.
- [56] Sapkota, K. (2018): Seasonal labour migation and livelihood in the middle hill of Nepal: reflections from Arghakhanchi district. Research Nepal Journal of Development Studies 1(1): 42-57.
- [57] Sehgal, J. J., Kumar, D., Kalsi, R. S., Allen, M. L., Singh, R. (2022): Spatio-temporal overlap of leopard and prey species in the foothills of Shiwalik, Himalaya. European Journal of Wildlife Research 68.
- [58] Sharma, P., Adhikari, H., Tripathi, S., Ram, A. K., Bhattarai, R. (2019): Habitat suitability modeling of Asian Elephant *Elephas maximus* (Mammalia: Proboscidea: Elephantidae) in Parsa National Park, Nepal and its buffer zone. – Journal of Threatened Taxa 11(13): 14643-14654.
- [59] Singh, P., Macdonald, D. W. (2017): Populations and activity patterns of clouded leopards and marbled cats in Dampa Tiger Reserve, India. Journal of Mammalogy 98(5): 1453-1462.
- [60] Stander, P. E. (1997): Field age determination of leopards by tooth wear. African Journal of Ecology 35(2): 156-161.
- [61] Subedi, N., Bhattarai, S., Pandey, M., Kadariya, R., Thapa, S., Gurung, A., Prasai, A., Lamichane, S., Regmi, R., Dhungana, M., Regmi, P., Poudel, R., Rumpakha, B., Shrestha, B., Gautam, B., Baral, R., Poudel, U., Yadav, S., Pariyar, S., Lamichane, B. (2021): Report on Faunal Diversity in Chure Region of Nepal. – President Chure-Terai Madesh Conservation Development Board and National Trust for Nature Conservation, Kathmandu, Nepal.
- [62] Sunquist, M., Sunquist, F. (2002): Wild Cats of the World. The University of Chicago Press, Chicago. https://academic.oup.com/jmammal/article/85/2/365/2373563.
- [63] Tattersall, I. (1987): Cathemeral activity in primates: a definition. Folia Primatologica 49(3-4): 200-202.
- [64] Thapa, K., Shrestha, R., Karki, J., Thapa, G. J., Subedi, N., Pradhan, N. M. B., Dhakal, M., Khanal, P., 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: 1-12.
- [65] Thapa, K., Wikramanayake, E., Malla, S., Acharya, K. P., Lamichhane, B. R., Subedi, N., Pokharel, C. P., Thapa, G. J., Dhakal, M., Bista, A., Borah, J., Gupta, M., Maurya, K. K., Gurung, G. S., Jnawali, S. R., Pradhan, N. M. B., Bhata, S. R., Koirala, S., Ghose, D., Vattakaven, J. (2017): Tigers in the terai: strong evidence for meta-population dynamics contributing to tiger recovery and conservation in the terai arc landscape. – PLoS ONE 12(6): 1-15.

- [66] Wang, T., Feng, L., Mou, P., Wu, J., Smith, J. L. D., Xiao, W., Yang, H., Dou, H., Zhao, X., Cheng, Y., Zhou, B., Wu, H., Zhang, L., Tian, Y., Guo, Q., Kou, X., Han, X., Miquelle, D. G., Oliver, C. D., Ge, J. (2016): Amur tigers and leopards returning to China: direct evidence and a landscape conservation plan. Landscape Ecology 31(3): 491-503.
- [67] Wattegedera, M., Silva, D., Sooriyabandara, C., Wimaladasa, P., Siriwardena, R., Piyasena, M., Marasinghe, R. M., Hathurusinghe, B. M., Nilanthi, R. M. R., Gunawardena, S., Peiris, H., Seneviratne, P., Sendanayake, P. C., Dushmantha, C., Chandrasena, S., Gooneratne, S. S., Premaratne, P., Wickremaratne, S., Mahela, M. (2022): A multi-point identification approach for the recognition of individual leopards (*Panthera pardus kotiya*). Animals 12(5):660.
- [68] Yang, H., Han, S., Xie, B., Mou, P., Kou, X., Wang, T., Ge, J., Feng, L. (2018): Do prey availability, human disturbance and habitat structure drive the daily activity patterns of Amur tigers (*Panthera tigris altaica*). Journal of Zoology 307(2): 131-140.



APPENDIX

Figure A1. Spatial patterns of detection frequency for animal species in the camera-trapping study area form March 2021 to January 2022. Different color in each sites represent species and their size indicates detection frequency