



Assessing Asiatic black bear (*Ursus thibetanus*) temporal overlap and co-occurrence with sympatric species in the temperate zone of the Hindu Raj Mountain range

Faizan Ahmad^{1,4} · Muhammad Rehan¹ · Eve Bohnett² · Ammar Hassan¹ · Sami Ullah¹ · Shah Zeb¹ · Hammad Ali Mian³ · Muhammad Kabir¹

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Abstract

Ecological research focused on Asiatic black bears (*Ursus thibetanus*) sympatric interactions is critical for understanding not only species coexistence, but also for devising effective conservation strategies. We studied the temporal overlap and co-occurrence patterns of the Asiatic black bear and ten of its sympatric species. Asiatic black bears and Asiatic jackals exhibited bimodal diel activity patterns, with activity peaks occurring during dusk and the night. The diel activity pattern of Asiatic black bear was significantly distinct from its sympatric species ($P < 0.001$). We found the highest temporal overlap of Asiatic black bear with red fox ($\Delta t = 0.78$, 95% CI = 0.68 – 0.89) followed by stone marten ($\Delta t = 0.76$, 95% CI = 0.64 – 0.87) and Indian crested porcupine ($\Delta t = 0.74$, 95% CI = 0.62 – 0.85). The lowest temporal overlap of the Asiatic black bear was recorded with rhesus monkey ($\Delta t = 0.38$, 95% CI = 0.27 – 0.50). Asiatic black bears avoided human activity times and had little activity overlap ($\Delta t = 0.29$, 95% CI = 0.19 – 0.39). Asiatic black bear was more likely to co-occur ($P_{gt} < 0.05$) with six other species than what we observed. This study's comprehensive insights into the adaptable behavior of Asiatic black bears, including their spatial and temporal overlap with sympatric species and the influence of environmental variables like forest cover and altitude, provide crucial guidance for wildlife managers and conservationists in designing effective conservation measures to protect habitat and mitigate human-wildlife conflicts, thereby ensuring the sustainable management and conservation of Asiatic black bears and the broader biodiversity of their temperate habitats.

Keywords Asiatic black bear · Activity overlap · Camera trapping · Coexistence · Sympatric species · Conservation

Introduction

Interactions between sympatric species and intraguild competition can significantly affect the structure and function of ecological communities (Soulé et al. 2003; Ripple

et al. 2014; Elbroch et al. 2015; Harvey et al. 2017). In competitive interactions, resources can be partitioned, and characters can be displaced, which may affect the dynamics of the species involved and the structure and function of ecological communities (Schoener 1974; Schluter and

✉ Muhammad Kabir
kabir_ajk@hotmail.com

Faizan Ahmad
faizanqandil99@gmail.com

Muhammad Rehan
mrehanswaat@gmail.com

Eve Bohnett
evebohnnett@ufl.edu

Ammar Hassan
ammar.pride1@gmail.com

Sami Ullah
samiullahghaznavi03@gmail.com

Shah Zeb
shahzebk085@gmail.com

Hammad Ali Mian
h143alimian@gmail.com

¹ Wildlife Ecology Lab, Department of Forestry & Wildlife Management, The University of Haripur, Khyber Pakhtunkhwa, Pakistan

² Department of Landscape Architecture, University of Florida, Gainesville, US

³ Pir Mehr Ali Shah Arid Agriculture University Rawalpindi, Rawalpindi, Pakistan

⁴ Pakistan Forest Institute, Peshawar, Pakistan

McPhail 1992). For a number of different taxa, separation of sympatric species in space or time is known to reduce the intensity of species interactions (e.g., Schuette et al. 2013; Karanth et al. 2017; Krohner and Ausband 2019; Li et al. 2022), hence enhancing coexistence and species richness (Vanak et al. 2013; Sladeczek et al. 2017; Prat-Guitart et al. 2020). This information is important to the conservation and management of biological communities as anthropogenic disturbances and climate change intensifies (Li et al. 2019; Dai et al. 2020; Sévêque et al. 2020).

Humans, as the only predators of apex carnivores, have a profound ecological impact on the ecosystem (Ripple et al. 2014; Oriol-Cotterill et al. 2015). Anthropogenic disturbance poses a new hazard to social predators since it can alter group dynamics and endanger the survival of their young (Creel and Rotella 2010; Ausband et al. 2015). In human populated regions, social predators may restrict the size of their groups to avoid being detected (Oriol-Cotterill et al. 2015). In any habitat impacted by anthropogenic factors, humans have become the primary competition for wildlife species (Krohner and Ausband 2019).

Variations in wildlife diel activity patterns originate from competition, prey, predators, or other disruptions (Ayres et al. 1986; Olson et al. 1998; Laundré et al. 2001; Neale and Sacks 2001; Kronfeld-Schor and Dayan 2003). As a result, diel activities may provide insight into some of the underlying factors that ultimately determine life histories (Bunnell and Harestad 1990). This suggests that diel activities could be important in the establishment of threatened species conservation programs. The competing and resource-sharing strategies of sympatric species can be better understood with an understanding of their temporal and spatial activity patterns (Schoener 1974). Managers can conserve and manage natural ecosystems more effectively if they have a thorough understanding of how species niches differ and how they coexist (HilleRisLambers et al. 2012).

The study of species co-occurrence patterns is critical to understand the role of evolution, history, coexistence mechanisms, competition, and the environment in shaping community structure and assembly (Griffith et al. 2016). Patterns of co-occurrence among various species are an important component of ecological research (Letten et al. 2017; Croose et al. 2019; Carvalho and Cardoso 2020; Nickel et al. 2020; Farris et al. 2020). Interspecific interactions provide the basis for species coexistence, community structure and assembly, and the maintenance of genetic diversity (Griffith et al. 2016; Prat-Guitart et al. 2020). Even the earliest Clementsian and Gleasonian theories on the structure of plant communities can be interpreted in terms of species co-occurrence (Hoagland and Collins 1997). Positive, negative, or random associations exist between two species on a fundamental level. However pairwise approaches are designed to identify species pairs with positive, negative, or random

associations (Sfenthourakis et al. 2006; Gotelli and Ulrich 2010; Veech 2013). Co-occurrence between two species can be quantified. The observed co-occurrence can be compared with the expected co-occurrence, which is the product of the co-occurrence probability of the two species multiplied by the number of sample locations (Griffith et al. 2016).

In the past decade, camera trapping has made it possible to systematically study activity patterns and niche overlap over time. One of the most common and straightforward approaches to analyze Asiatic black bear behavior over a wide range of environments and climates is the use of thermal infrared camera traps (Akbaba and Ayaş 2012). Recent research has examined whether overlapping activity patterns among species are indicative of competition or predation (Linkie and Ridout 2011; Carver et al. 2011; Ramesh et al. 2012; Ross et al. 2013; Azevedo et al. 2018; Havmøller et al. 2020; Kamler et al. 2020). In order to gain a better understanding of the diel activity patterns and coexistence of species, camera trap detections provided valuable data for both these aspects (Krohner and Ausband 2019; Zhang et al. 2019; Prat-Guitart et al. 2020; Zahoor et al. 2021; Li et al. 2022) (Table 1).

Using camera trap data, the temporal overlap and co-occurrence of the Asiatic black bear (hereafter “bear”) and its sympatric species were assessed in the temperate zone of Pakistan’s Hindu Raj Mountain range. In the Hindu Raj Mountain range, there is no published information on mammalian activity and co-occurrence. To acquire a better knowledge of bear ecology and conservation in disturbed habitats, researchers must measure the impact of humans and other sympatric species on the diel activity and co-occurrence patterns of bears. Although no such study has ever been conducted in the Hindu Raj Mountain range, the findings of this study will serve as a foundation and provide baseline data, for future, in-depth research.

Materials and methods

Study area

This study was conducted in the Hindu Raj Mountain range (35°02'0" N-35°60'0" N; 72°10'0"E-72°55'15" E) covering an area of 3025 km². This region features moist temperate, dry temperate, subalpine, alpine, and snowcap zones between 1,235 to 5,954 m above sea level (a.s.l) (Figs. 1 and 2). The Hindu Raj Mountain range is connected with Himalayan and Hindukush Mountain ranges (Hildebrand et al. 2000). The average annual temperature is 10.84 °C, with a high of 32.1 °C and a low of -12.2 °C; yearly rainfall is 1029.63 mm (Working Plan for Kalam Forests, 1987 – 1988 to 2001 – 2002; Rahman et al. 2022). In the study area, forests serve as the primary source of fuelwood during harsh winters and of building materials. However, this dependency, coupled with uncontrolled grazing and increasing

Table 1 Body size, diet habits, diel activity pattern and IUCN / National red list status of the Asiatic black bear and its sympatric species

Species	Body size (kg)	Diet habits	Diel activity pattern	IUCN Status / National Red list Status	Source
Asiatic black bear	90–115	Omnivores	Cathemeral	VU / VU	Ding et al. (2022), Sheikh and Molur (2003), Zahoor et al. (2021), Ngoprasert et al. (2022), Ali et al. (2017), Prater (1980)
Leopard cat	1.5–5	Carnivore	Cathemeral ^a	LC / DD	Ding et al. (2022), Sheikh and Molur (2003), Bu et al. (2016), Shehzad et al. (2012)
Rhesus monkey	5–10	Insectivores, Frugivores, Granivores, Herbivores	Diurnal	LC / NT	Ding et al. (2022), Sheikh and Molur (2003), Goldstein and Richard (1989), Zhdanova et al. (2011)
Grey wolf	28–40	Carnivores	Cathemeral	LC / EN	Ding et al. (2022), Sheikh and Molur (2003), Shabbir et al. (2013)
Asiatic jackal	6.5–9.8	Omnivores	Cathemeral	LC / NT	Ding et al. (2022), Sheikh and Molur (2003), Mahmood et al. (2013), Roberts (1997)
Red fox	3.6–7	Omnivores	Cathemeral	LC / NT	Ding et al. (2022), Sheikh and Molur (2003), Reshamwala et al. (2018), Sidorovich et al. (2006)
Stone marten	0.8–1.6	Omnivores	Nocturnal	LC / DD	Ding et al. (2022), Sheikh and Molur (2003), Roy et al. (2019), Monterroso et al. (2014), Bischof et al. (2014), Torretta et al. (2017), Padial et al. (2002)
Indian crested porcupine	11–15	Frugivores, Herbivores	Nocturnal	LC / NT	Hagen et al. (2019), Sheikh and Molur (2003), Fattorini and Pokheral (2012); Mukherjee et al. (2017), Hafeez et al. (2011), Khan et al. (2014)
Feral dog	Variable	Omnivores	Cathemeral		Vanak and Gompper (2009), Zanin et al. (2019)
Yellow throated marten	0.8–2.8	Omnivores	Diurnal	LC / DD	Ding et al. (2022), Sheikh and Molur (2003), Grassman et al. (2005), Li et al. (2022)

^aBashir et al. (2014) and Mukherjee et al. (2019) reported the leopard cat as nocturnal from the eastern Himalaya and northeast India. These differences in results may be due to geographical differences and the influence of climates, as some species may be active longer in warm regions than in cold regions (Kowalczyk et al. 2003; Goszczynski et al. 2005)

livestock population, significantly hampers forest regrowth, thereby degrading the ecosystem (Qasim et al. 2013).

Field survey

Camera trapping

In order to systematically explore the research area with camera traps, we used ArcGIS version 10.8 to create a map of the area (ESRI 2011; Kabir et al. 2017; Hameed et al.

2020). From October 2020 to December 2021, 81 camera trap sites with motion-sensitive thermal infrared cameras (ZopuCam, SL122C-2) were placed for 616 trap nights in the study area. Camera traps were set up in the locations where we suspected the presence of Asiatic black bears after conducting a preliminary surveys comprised of signs survey and group discussion with indigenous communities. Except for sites separated by roads, rivers, or nearly vertical cliffs, we set up a camera trapping station at least one kilometer apart. With the use of a Global Positioning System, we were

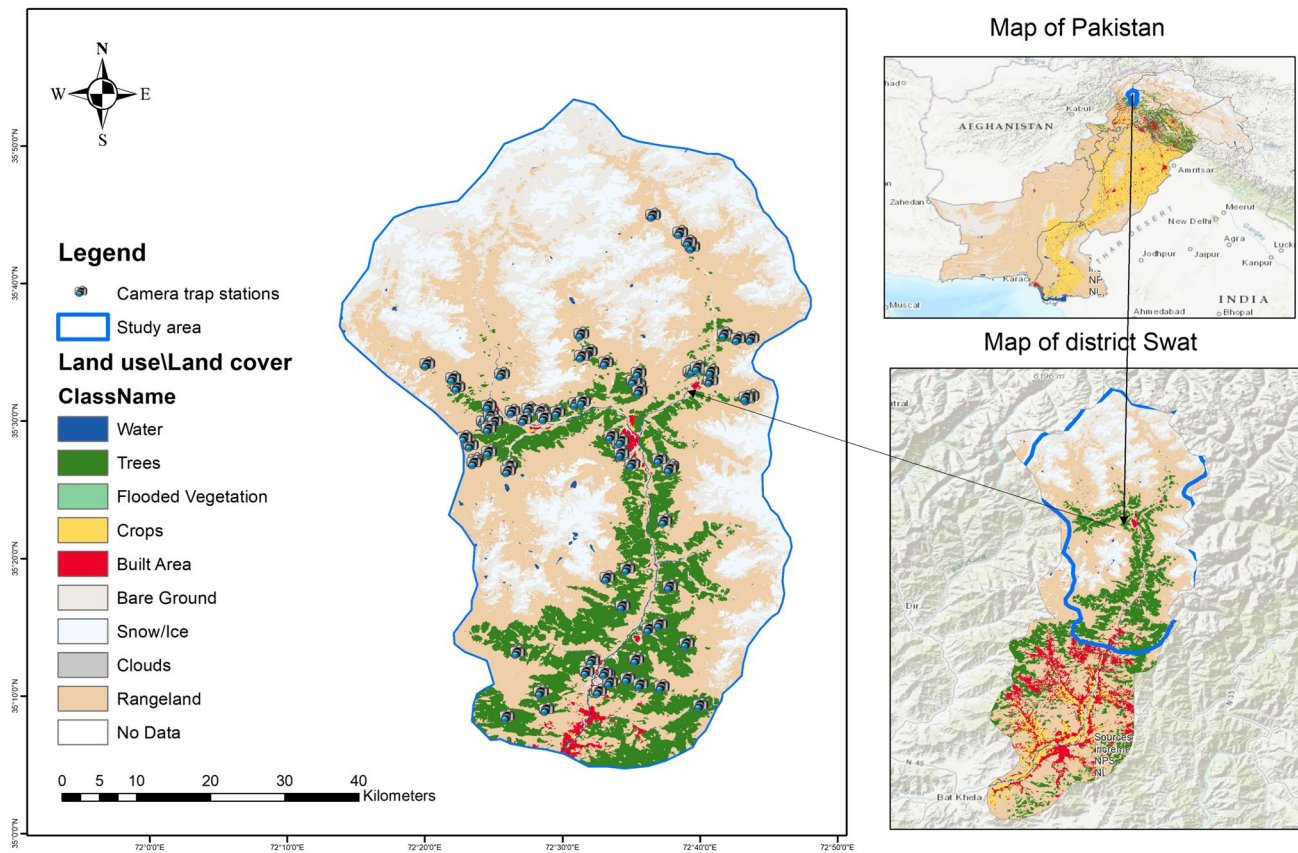


Fig. 1 The location of the study area is in the district of Swat in Khyber Pakhtunkhwa Province, northwestern Pakistan. The map insets show the locations of the study area in Swat district and Pakistan

able to record the altitude and coordinates of every camera trapping station. The cameras were positioned to avoid triggering by foreground foliage (Apps and McNutt 2018). We improvised in a few locations by placing the camera higher or lower than the typical height of 40 to 60 cm due to concerns about theft.

Data analysis

Species activity and overlap patterns

During data analysis process, only detections that happened within 30 min of the previous image at the same camera station were considered (Linkie and Ridout 2011). We determined the diel pattern and coefficient of overlapping, a quantitative measure ranging from 0 (no overlap) to 1 (identical activity patterns), by fitting a kernel density function to periods of observations of animals (Ridout and Linkie 2009). We used a von Mises kernel instead of the more common Gaussian kernel since it represents a circular distribution. For a spiky kernel density curve, we have chosen the default value of 1 for argument adjustment. For samples with fewer than 50 observations, we utilized Dhat1, the

best non-parametric estimate of the overlapping coefficient, and when both samples were larger than 50, we used Dhat4 estimate. We performed 10,000 smoothed bootstrap estimations to obtain a 95 percent confidence interval (CI). The significance of two curves was determined using Watson's two-sample homogeneity test. The "overlap" package in R (R Core Team 2016) was used to conduct diel activity pattern and temporal overlap analysis (further details in the Supplementary Materials, Appendix 2) (Meredith and Ridout 2021).

The following formula was used to figure out the selection ratios for each species and each time period (Manly et al. 2007; Bu et al. 2016; Li et al. 2022).

$$w_i = o_i / \pi_i$$

where w_i is the selection ratio for the period in question, o_i is the proportion of independent detections in the relevant period, and π_i is the proportion of length in the relevant period to the total length of all the periods. If $w_i > 1$, the time period is preferentially preferred, but if $w_i < 1$ the time period is avoided. At last, we analyzed hourly temperature variations using data gleaned from the bear photos to see if there was a temperature threshold for bear activity.

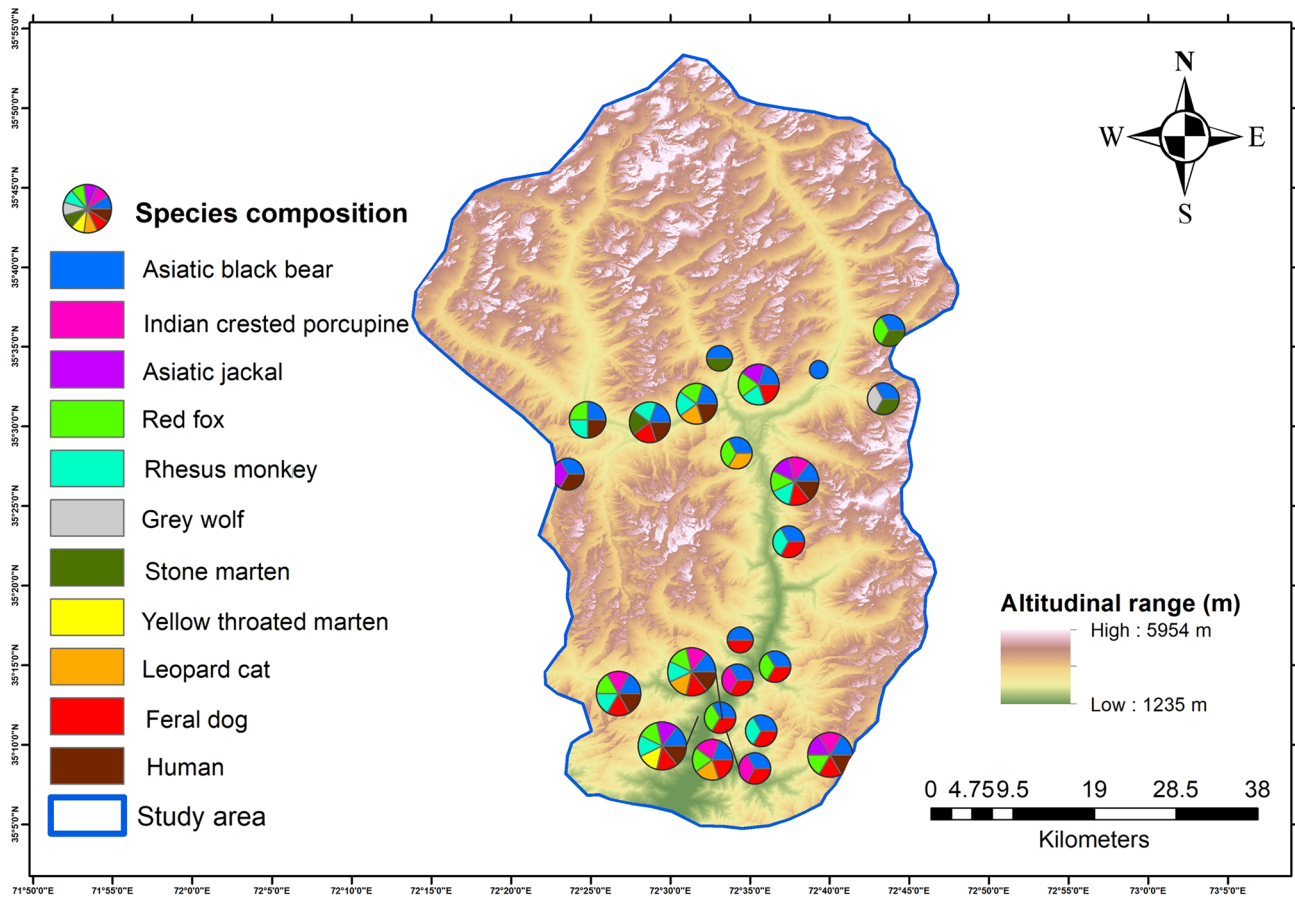


Fig. 2 Species captured along with bear at each camera trap station

Species co-occurrence patterns

We assessed how many sampling sites had two species co-occurring using the probabilistic model of species co-occurrence (Veech 2013; Pulver et al. 2016; Watabe et al. 2022). We used pairwise techniques to determine if species pairs reflect positive, negative, or random associations (Sfenthourakis et al. 2006; Gotelli and Ulrich 2010; Veech 2013). In this study, we compared observed and expected co-occurrence. The probabilistic model uses combinatorics to ascertain whether the observed frequency of co-occurrence is significantly large and greater than expected (positive association), significantly lower and less than expected (negative association), or not significantly different and relatively close to expected (random association) (Veech 2013). Effect sizes were determined from the difference of the expected and observed co-occurrence rates, as described in the probabilistic co-occurrence study by Veech (2013). In R (R Core Team 2016), the "co-occur" package was used to do co-occurrence analyses (further details in the Supplementary Materials, Appendix 2) (Griffith et al. 2016).

Exploratory regression analysis

Exploratory Regression Analysis was conducted using ArcGIS 10.8, employing the Exploratory Regression tool to identify significant predictors of Asiatic black bear encounter rates at presence points (ESRI 2011; Fenglin et al. 2023). This tool is particularly useful for examining potential relationships while diagnosing issues of multicollinearity and ensuring that the assumptions of normality and homoscedasticity are met.

Digital elevation models (DEMs) provide data on altitude, aspect, slope, and roughness. These rasters were sourced from Open Topography, ensuring high-resolution and accurate topographic information (NASA Shuttle Radar Topography Mission (SRTM) 2013). Forest cover data was obtained from the Global Forest Change project, which provides insights into the extent and changes in forest cover over time (Hansen et al. 2013). Euclidean Distance to Built Areas was calculated using a raster developed from Esri's Land Use Land Cover data, identifying the proximity of each camera trap location to the nearest built environment (Karra et al. 2021). Initially included in

the study, bioclimatic variables from the CHELSA dataset were considered for their potential influence on bear habitats (Karger et al. 2017). However, due to high multicollinearity observed in the preliminary models, these variables were excluded from the final analysis (Feng and Tong 2017).

Models were iteratively built and refined. The final selection of variables and model configuration were determined based on optimal values for Adjusted R-Squared, AICc, and other statistical criteria that ensure a robust model. Initial models included a wide range of variables (bioclimatic, sympatric species encounter rates, and topographic variables). Through a process of model evaluation and refinement, variables causing multicollinearity were identified and excluded. This iterative process helped in pinpointing the most relevant explanatory variables without overstating the effects due to collinear variables.

Adjusted R-Squared was used to determine the explanatory power of the models, with higher values indicating better explanatory capabilities (Sheng et al. 2017; Sá et al. 2011). Akaike Information Criterion corrected (AICc), a key criterion for model comparison, with lower values indicating a model with a better fit (Akaike 1981). Variance Inflation Factor (VIF) was used to detect the presence of multicollinearity among explanatory variables. Variables with VIF values exceeding 7.5 were scrutinized and, if necessary, removed from the model (Sheng et al. 2017; Sá et al. 2011). The Jarque-Bera (JB) test for normality of residuals and Koenker (BP) statistic for homoscedasticity were used to validate the model fit (Sheng et al. 2017; Sá et al. 2011). Global Moran's *I* was conducted to assess spatial autocorrelation in the exploratory regression model.

This approach ensures that the findings are grounded in empirical data and statistically sound, providing a solid foundation for conservation and management strategies in the region (Sheng et al. 2017; Sá et al. 2011) (further details in the Supplementary Materials, Appendix 1).

Non-metric multidimensional scaling (NMDS)

Non-metric Multidimensional Scaling (NMDS) was employed to explore the ecological distances between species based on their presence and absence data (Steenweg et al. 2023). The Jaccard dissimilarity index was used as the distance measure for NMDS, appropriate for binary data as it emphasizes the proportion of shared presence between species pairs relative to the total presence across species pairs (de Abreu Pestana et al. 2023).

The “vegdist” function from the “vegan” package in R was used to compute the Jaccard dissimilarity matrix among all pairs of species (Oksanen et al. 2007; R Core Team 2016). Subsequently, the “metaMDS” function

from the same package was applied to perform the NMDS analysis with a configuration set to two dimensions and a maximum of 100 tries for a stable solution. The number of dimensions was chosen to balance the complexity of interpretation with the fidelity of representation of the dissimilarities among species.

The stress value, a measure of the goodness of fit of the NMDS configuration, was annotated on the plot to quantify the representation accuracy (further details in the Supplementary Materials, Appendix 2) (Dexter et al. 2018).

Results

Our surveys accumulated 428 independent detections of 14 different mammal species throughout 616 trap nights (Fig. 3). The analysis omitted the species (Persian leopard, Giant flying squirrel, Jungle cat, Indian pika) with ten or fewer independent detections, but included the calculated overlap of the Leopard cat (6) and Yellow-throated marten (4) with bear.

Diel activity pattern

Bears do not hibernate in the southern portion of our study region, which is situated at a lower altitude and accumulates less snow in winters than the northern portion. Bear hibernation patterns also vary with the ruggedness of landscapes and the amount and depth of snowfall (Moll et al. 2021). Diel activity patterns of bears varied considerably between periods (crepuscular, diurnal, nocturnal) ($X^2 = 55.98$, $df = 2$, p -value < 0.001).



Fig. 3 A camera trap acquired photo of the Asiatic black bear and the Indian crested porcupine at the same time and location in the research area

Table 2 Summary of the number of independent detections n (selection ratio: w_i) and Chi-square test results for diurnal, nocturnal, and crepuscular time periods for bear and sympatric species in the Hindu Raj mountain range

Species	n (w_i) in time period			Chi-square tests (χ^2 , $df=2$)
	diurnal	nocturnal	crepuscular	
Asiatic black bear	13(0.28)	66 (1.54)	16 (2.10)	$\chi^2=55.98$, $P<0.001$
Asiatic black bear (before snowfall)	1(0.12)	13 (1.66)	5 (3.2)	$\chi^2=11.79$, $P=0.002$
Asiatic black bear (after snowfall)	12 (0.38)	53 (1.70)	11 (1.8)	$\chi^2=45.34$, $P<0.001$
Red fox	6 (0.19)	60 (1.97)	8 (1.35)	$\chi^2=76$, $P<0.001$
Feral dog	19 (1.54)	7 (0.56)	4 (1.60)	$\chi^2=12.6$, $P=0.001$
Indian crested porcupine	0 (0.00)	33 (2.2)	2 (0.71)	$\chi^2=58.68$, $P<0.001$
Stone marten	9 (0.54)	29 (1.76)	2 (0.62)	$\chi^2=29.45$, $P<0.001$
Asiatic jackal	4 (0.44)	9 (0.99)	9 (5.11)	$\chi^2=2.27$, $P=0.321$
Rhesus monkey	36 (1.87)	4 (0.20)	7 (1.86)	$\chi^2=39.87$, $P<0.001$
Grey wolf	1(0.20)	11 (2.23)	0 (0.00)	$\chi^2=18.5$, $P<0.001$
Human	46 (2.03)	1 (0.044)	8 (1.81)	$\chi^2=63.96$, $P<0.001$

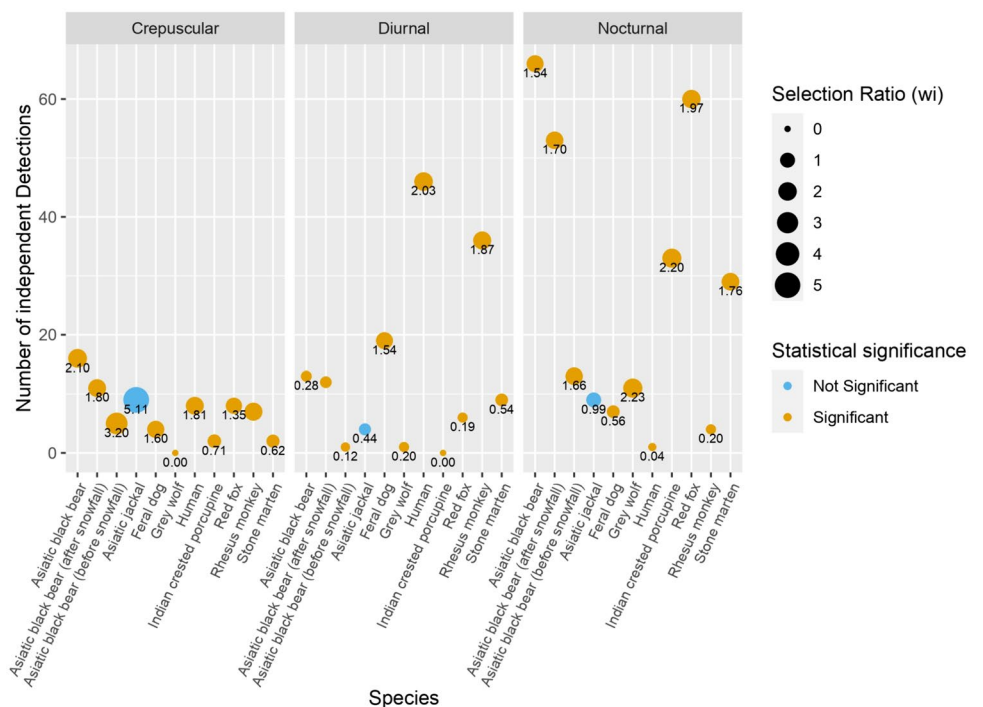
Based on the selection ratios formula and kernel density analysis (Table 2, Fig. 4), the bear and the Asiatic jackal had a bimodal activity pattern with peaks during the crepuscular period ($w_i=2.10$ and 5.11 , respectively) and the nocturnal period ($w_i=1.54$ and 0.99 , respectively), and low levels of activity during the day ($w_i=0.28$ and 0.44). Independent crepuscular bear detections occurred primarily after sunset rather than before daybreak. The activity patterns of the red fox, Indian crested porcupine, stone marten, and the grey wolf all exhibited a higher degree of nocturnal activity ($w_i=1.97$, 2.2 , 1.76 , and 2.23 respectively) than crepuscular ($w_i=1.35$, 0.71 , 0.62 , and 0.00 respectively) or diurnal ($w_i=0.19$, 0.00 , 0.54 , and 0.20 respectively). During a 24-h period, feral dogs

displayed cathemeral behavior with multiple activity peaks, including crepuscular ($w_i=1.60$), diurnal ($w_i=1.54$), and nocturnal ($w_i=0.56$). Rhesus monkeys and humans were most active during the diurnal ($w_i=1.87$ and 2.03 respectively) and crepuscular hours ($w_i=1.86$ and 1.81 respectively) and had minimal nocturnal activity ($w_i=0.20$ and 0.04 respectively).

Activity pattern overlap

Bears exhibited considerable distinct diel activity patterns compared to those of their sympatric species ($P<0.001$). Bear with red fox had the greatest temporal overlap ($\Delta t=0.78$, 95%

Fig. 4 Independent detections and selection ratio of Asiatic black bear and other sympatric species across crepuscular, diurnal, and nocturnal periods



CI=0.68 – 0.89) followed by stone marten ($\Delta 1=0.76$, 95% CI=0.64 – 0.87), Indian crested porcupine ($\Delta 1=0.74$, 95% CI=0.62 – 0.85), Asiatic jackal ($\Delta 1=0.73$, 95% CI=0.59 – 0.87), feral dog ($\Delta 1=0.53$, 95% CI=0.41 – 0.66), and grey wolf ($\Delta 1=0.40$, 95% CI=0.22 – 0.55). Bear and rhesus monkey had the lowest temporal overlap ($\Delta 1=0.38$, 95% CI=0.27 – 0.50). Bears avoided the human activity and rarely overlapped with humans ($\Delta 4=0.29$, 95% CI=0.19 – 0.39). We only collected six and four independent detections of leopard cat and Yellow throated marten, respectively, for which we estimated activity overlap with bear, leopard cat ($\Delta 1=0.76$, 95% CI=0.40 – 1.03, $0.001 < P < 0.01$) and yellow throated marten ($\Delta 1=0.53$, 95% CI=0.22 – 0.84, $P < 0.001$). The bear activity after snowfall remained almost identical to before snowfall, but it was primarily photographed during the daytime after the snowfall ($\Delta 1=0.82$, 95% CI=0.68 – 0.97). This might have occurred because of fewer disturbances following the snowfall, when locals rarely visit the bear habitat. The maximum temperature recorded by camera traps for bear activity was 29 °C, and the lowest was -5 °C, while the mean maximum and mean minimum was 12.85 °C and -0.90 °C respectively (Figs. 5 and 7).

Species co-occurrence patterns

Bear had six significant positive, three random and zero negative associations with its sympatric species (Tables 3 and 4, Figs. 6 and 7).

There were no negative associations found with the Asiatic black bear; however, there were 66.67 and 33.33 percent of positive and random associations, respectively.

In addition, a co-occurrence analysis was conducted to assess the effect sizes (practical significance), which are the differences between the expected and observed co-occurrence rates (Fig. 8). To standardize their values, these differences were divided by the total number of sampling sites (81) in our dataset. In standardized form, these values range from -1 to 1, with positive values indicating positive associations and negative values indicating negative associations.

Results from the exploratory regression analysis

Initial models that included bioclimatic variables and additional species such as the leopard cat and Asiatic jackal were found to suffer from high multicollinearity, which obscured the individual effects of explanatory variables. Through systematic removal and retesting, it was determined that excluding these variables improved the clarity and performance of the models. Exploratory regression analysis using the final selected variables in different combinations from 2 to 12 variables resulted in 34 models in several variables

demonstrating varying degrees of significance and impact on bear encounter rates (further details in the Supplementary Materials, Appendix 1). Feral dog and rhesus monkey were significant 42.06% and 24.62% of the time, respectively, both showing a 100% positive effect on bear detections. Stone marten, appearing significant in 19.20% of cases, mostly affects detections positively (94.33%) with a small negative component (5.67%). Euclidean distance to villages is significant 15.93% of the time, predominantly negatively impacting detections (78.02%). Altitude, significant in 14.07% of cases, has a wholly negative influence. Forest cover and red fox, though less frequently significant at 2.20% and 0.88% respectively, generally had a positive association with bear, with forest cover having a minor negative impact (8.94%) and red fox almost entirely positive (98.83%). Indian crested porcupine and grey wolf show minimal significance but a balanced impact between negative and positive influences. Variables like human, roughness, and aspect, despite having no overall significance, display mixed effects, slightly favoring positive over negative impacts in detections (Fig. 9). This analysis captures the diverse roles these variables play in influencing bear detection probabilities, highlighting the complex interactions within their habitat. The final model included stone marten, feral dog, rhesus monkey and altitude as explanatory variables, and achieved an Adjusted R-Squared of 0.43, indicating that approximately 43% of the variability in Asiatic black bear detections could be explained by these variables. The AICc of the best model was 23.02, suggesting a balance between model complexity and explanatory power (further details in the Supplementary Materials, Appendix 1).

The Variance Inflation Factor (VIF) values were substantially reduced in the final models, with all remaining variables showing VIFs well below the threshold of 7.5, indicating minimal multicollinearity. The final models passed the Jarque-Bera test for normality of residuals, suggesting that the error terms were normally distributed, which is a critical assumption for the validity of regression analyses. The Koenker (BP) test results were also within acceptable limits, indicating that the models did not suffer from heteroscedasticity, and the error variance was constant across different levels of the independent variables. Global Moran's *I* result indicated no significant spatial autocorrelation in the residuals of the final models. This suggests that the models adequately captured the spatial structure of the data, and any spatial pattern in the bear detections was effectively explained by the models without leaving spatial dependencies unaccounted for.

NMDS ordination

This analysis illustrates how closely the two species are co-occurring based on the extent of their spatial patterns.

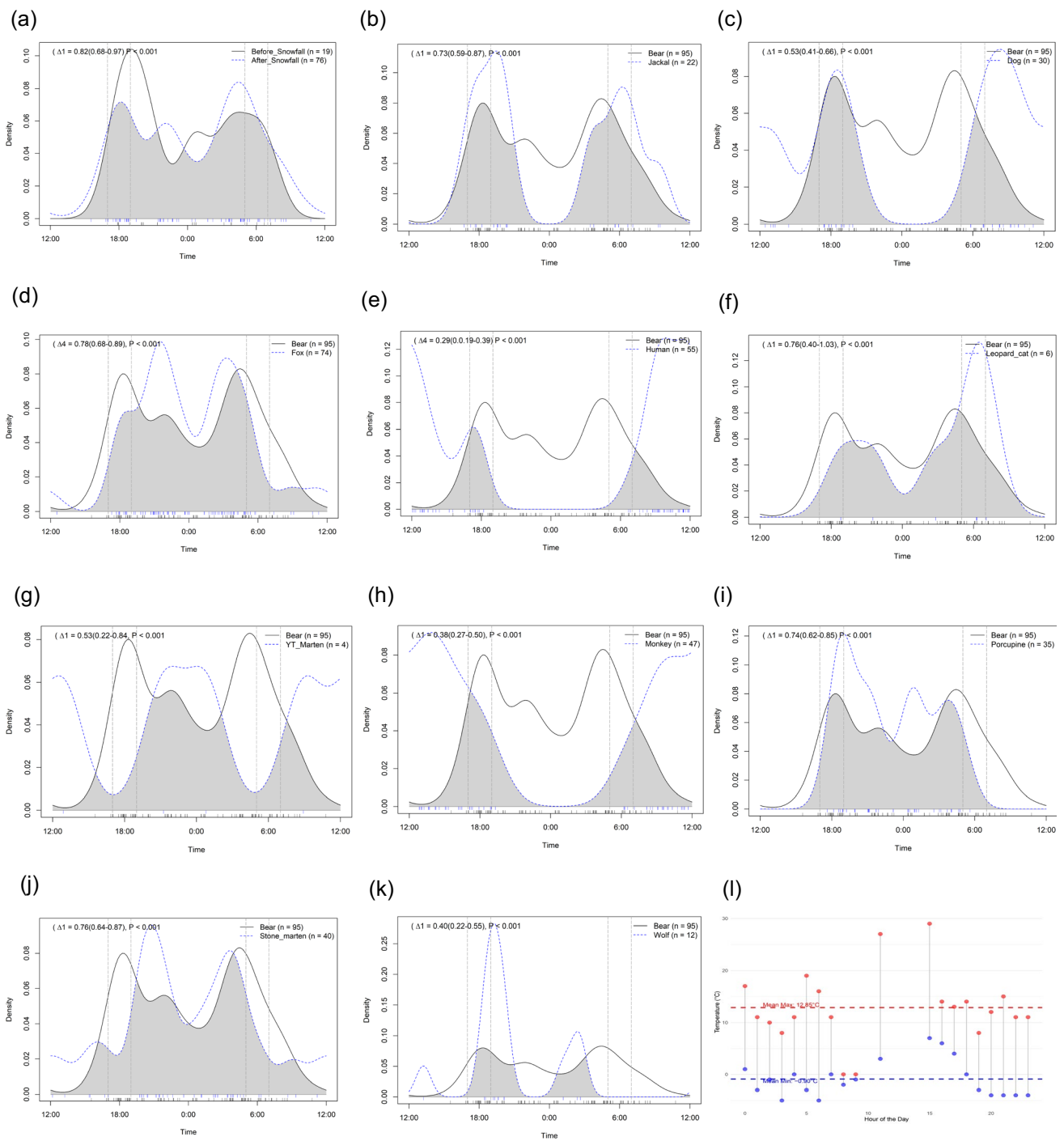


Fig. 5 a–k Kernel density estimations (Y axis) are plotted against time (X axis) and the overlap is illustrated by a shaded grey area. Sunrise and sunset times are depicted by the dashed vertical lines on the X axis, and midnight is located at the 0 o'clock position. The

lines at the bottom of the graphs represent the number of independent detections for each species. **l** Minimum and maximum temperatures recorded for all independent Asiatic black bear detections are grouped by hour of the day

The notion of interspecific interactions provides the foundation for analyzing whether two species' spatial patterns overlap. The greater the degree of overlap, the more likely it is that the species inhabit the same niche. We

used NMDS to evaluate the similarity of Asiatic black bear spatial distribution with sympatric species. The species ordinated close to bear have comparatively similar spatial patterns to bear and vice versa (Fig. 10).

Table 3 A summary of probabilistic co-occurrence analysis of the bear with its sympatric species

Sp1	Sp2	Sp1_inc	Sp2_inc	Obs_cooccur	Prob_cooccur	Exp_cooccur	P_it	P_gt
Bear	Indian crested porcupine	23	13	7	0.046	3.7	0.992	0.033
Bear	Red fox	23	31	13	0.109	8.8	0.990	0.031
Bear	Rhesus monkey	23	16	10	0.056	4.5	0.999	0.001
Bear	Leopard cat	23	5	4	0.018	1.4	0.998	0.021
Bear	Feral dog	23	22	15	0.077	6.2	1.000	0.000
Bear	Human	23	17	9	0.060	4.8	0.996	0.015
Bear	Grey wolf	23	10	1	0.035	2.8	0.158	0.972
Bear	Asiatic Jackal	23	10	5	0.035	2.8	0.972	0.109
Bear	Stone marten	23	22	4	0.077	6.2	0.167	0.940
Bear	Yellow throated marten ^a							

Sp1 = Species 1, Sp2 = Species 2, Sp1_inc = Total number of locations where species 1 was photographed, Sp2_inc = Total number of locations at which species 2 was photographed, obs_cooccur = The number of locations that were observed to have both species, prob_cooccur = The probability that both species will be found at a location, exp_cooccur = The expected number of locations that contain both species, p_it = If the two species were distributed randomly (independently), the probability that they would co-occur at a frequency less than the reported number of co-occurrence sites, p_gt = Co-occurrence probability at a frequency greater than the observed frequency

The figures in bold represent statistically significant positive associations, while the remaining are random associations

^aThe expected co-occurrence was < 1 for the Yellow throated marten pair with the bear and was not included in the co-occurrence analysis

Discussion

This study demonstrates for the first time how the bear shares the habitat with humans and other sympatric species, providing crucial information for the bear's conservation efforts in the Hindu Raj mountain range. In subtropical and temperate habitats, the bear has long been considered an "umbrella species," meaning that conserving its habitat will also maintain sufficient habitat for co-occurring species (Fleishman et al. 2000; Seddon and Leech 2008; Yamamoto et al. 2012).

Bears followed a fairly comparable diurnal activity pattern before and after the onset of snowfall, but the majority of daylight photographs were captured after the onset of snowfall. The reduced activity of humans (forest product

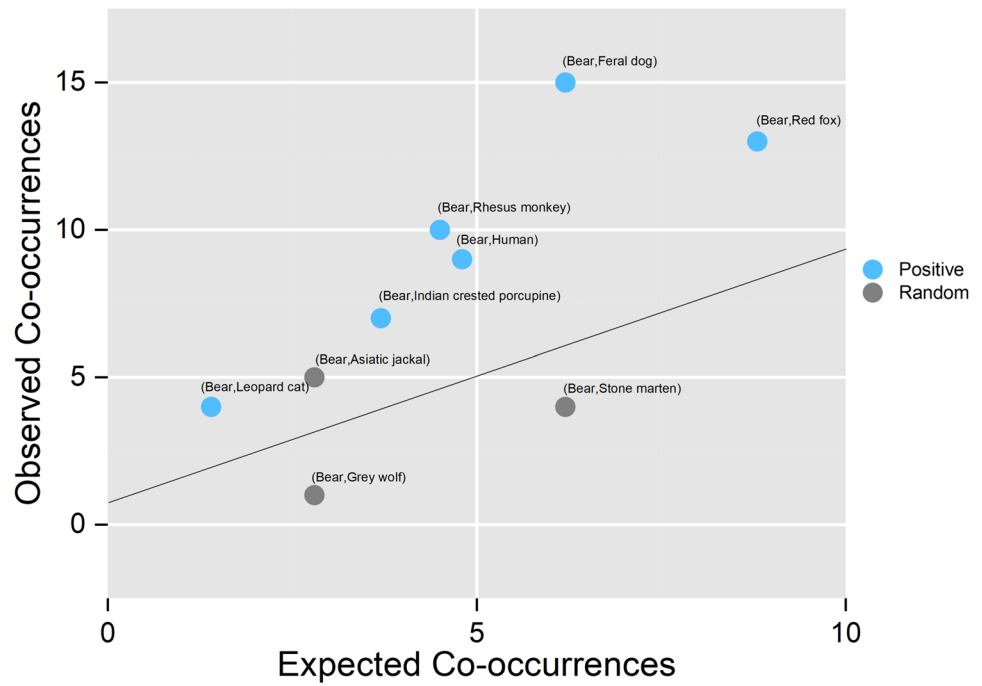
collectors, grazers, etc.) following a snowstorm may be an additional reason, as they are less likely to enter the forest. Overall bears showed a bimodal diel pattern with activity peaks just after the sunset and in the night hours. This may be because most of the capture events in our study were recorded in autumn and winter, and autumn food sources like *Quercus* species acorns are densely present, making nighttime foraging easier for bears. In autumn, both Asiatic and American black bears become more active at night (Reid et al. 1991; Garshelis and Pelton 1980). Nighttime activity has been attributed to increased foraging to prepare for winter denning (Nelson et al. 1983) or the avoidance of diurnal disturbances or threats by humans (e.g., hunters) (Swanson 1990; Bridges et al. 2004). It is thought to be

Table 4 Summary of the Probability of co-occurrence and co-efficient of overlap of bears with its sympatric species in the Hindu Raj mountain range

Other species	Asiatic black bear	
	Probability of co-occurrence (Pgt)	Co-efficient of overlap (95% CI) (P-value)
Indian crested porcupine	0.046 (0.0334)	0.74 (0.62 – 0.85) (P < 0.001)
Red fox	0.109 (0.0312)	0.78 (0.68 – 0.89) (P < 0.001)
Rhesus monkey	0.056 (0.0015)	0.38 (0.27 – 0.50) (P < 0.001)
Leopard cat	0.018 (0.0213)	0.76 (0.40 – 1.03) (P < 0.001)
Feral dog	0.077 (0.0000)	0.53 (0.41 – 0.66) (P < 0.001)
Human	0.060 (0.0153)	0.29 (0.19 – 0.39) (P < 0.001)
Asiatic jackal	0.035 (0.1093)	0.73 (0.59 – 0.87) (P < 0.001)
Grey wolf	0.035 (0.9722)	0.40 (0.22 – 0.55) (P < 0.001)
Stone marten	0.077 (0.9401)	0.76 (0.64 – 0.87) (P < 0.001)
Yellow throated marten^a		0.53 (0.22 – 0.84) (P < 0.001)

^aThe expected co-occurrence was < 1 for the Yellow throated marten pair with the bear and was not included in the co-occurrence analysis

Fig. 6 The plot shows probabilistic co-occurrence model determined positive and random associations for the bear and its sympatric species

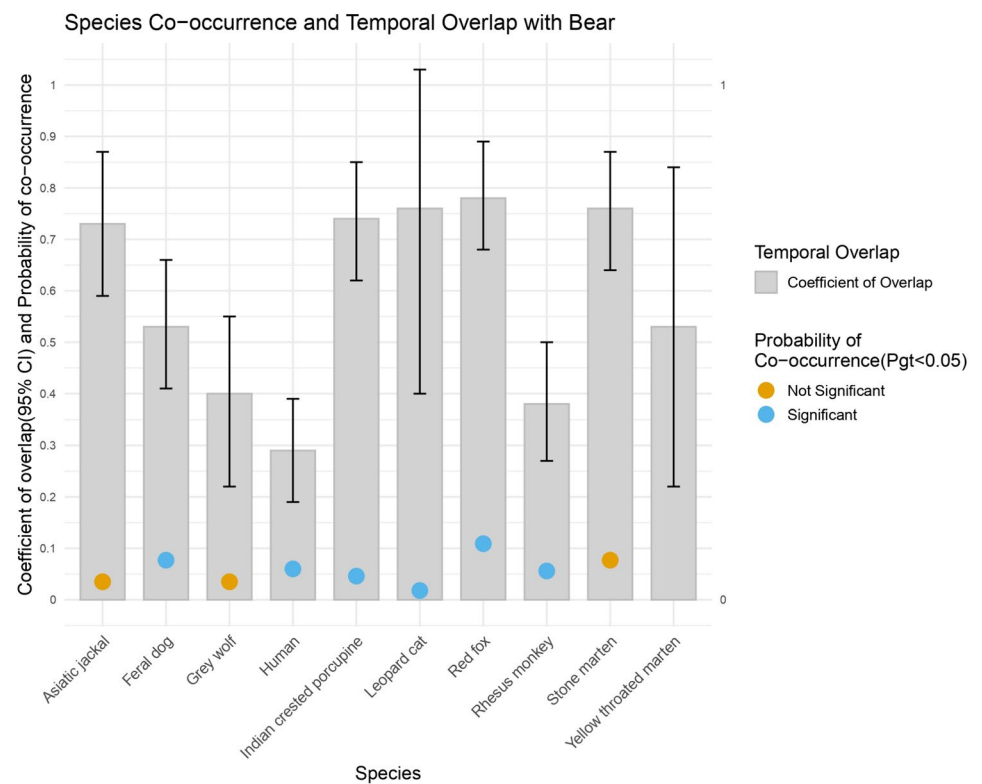


primarily nocturnal, although daylight sightings have been documented (Zahoor et al. 2021).

Our data analysis suggest that bears are adjusting their temporal activity patterns, increasing nocturnal activities to avoid human presence while still occupying the same

areas. Similar avoidance behaviors have been observed in other large carnivores in Nepal (Carter et al. 2015). Our exploratory regression analysis shows that in most locations, bear detections increase with proximity to anthropogenic features, likely due to the scarcity of natural

Fig. 7 Asiatic black bear co-occurrence and temporal overlap with other sympatric species in the Hindu Raj Mountain range. The expected co-occurrence was < 1 for the Yellow throated marten pair with the bear and was not included in the co-occurrence analysis



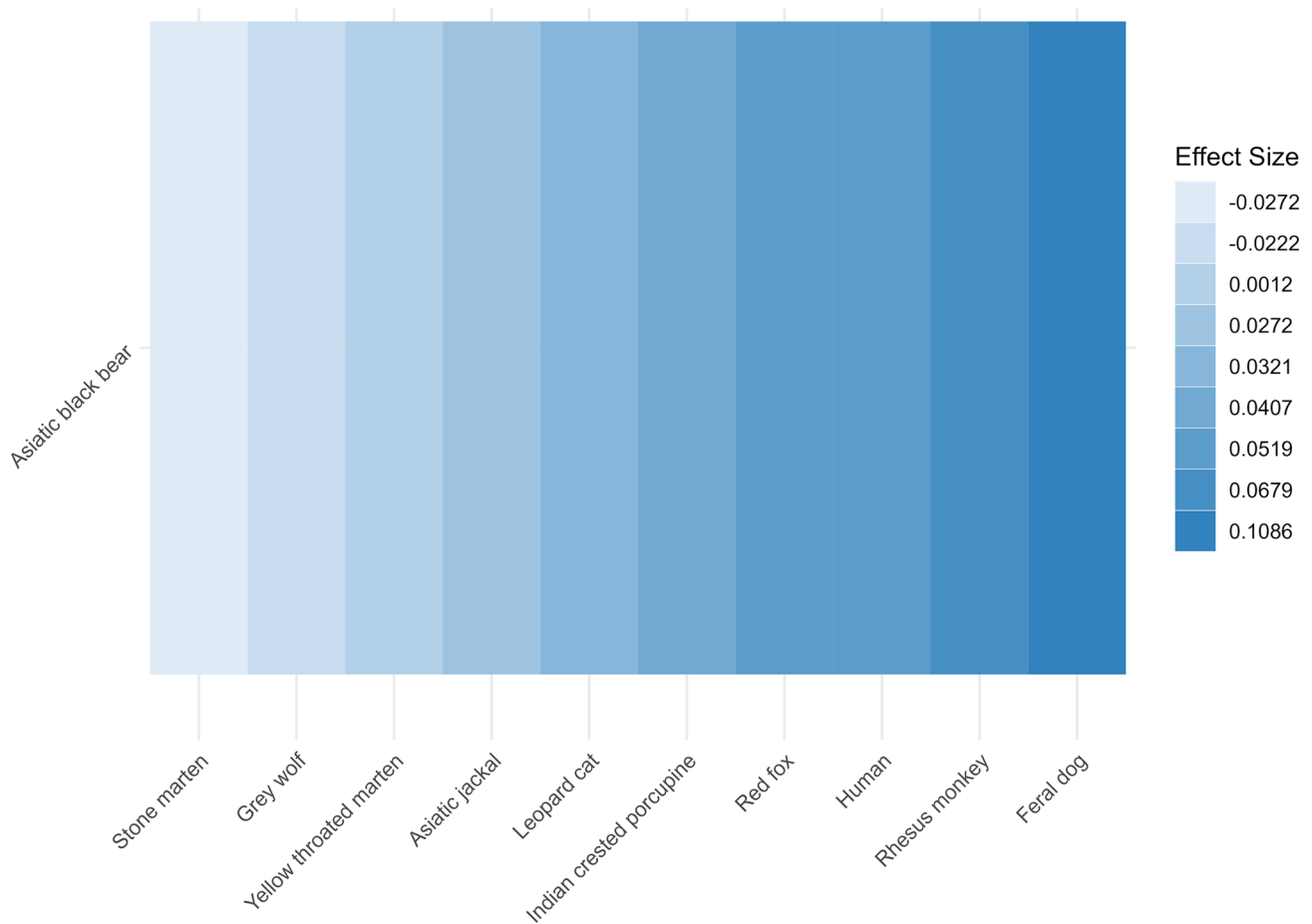


Fig. 8 Heat map of the effect sizes for all species pairs with the Asiatic black bear

food resources and the easy availability of anthropogenic sources. Conversely, in some areas, bear detection rates decrease as the distance from these anthropogenic features increases, which may be attributed to the availability of abundant natural food sources. In northern Pakistan and the autonomous state of Azad and Jammu Kashmir, bears frequently inhabit dense temperate forests at altitudes ranging from 1,500 m to 3,000 m above sea level, though they also intermittently occupy human-modified habitats at lower altitudes (Abbas et al. 2015; Awan et al. 2021; Ahmad et al. 2022). In areas where bears are heavily disturbed by human activities or rely on human food sources, they exhibit more nocturnal behavior and stay close to anthropogenic features (Ayres et al. 1986; Beckmann and Berger 2003; Matthews et al. 2006; Schwartz et al. 2010).

During autumn and winter, bears migrate to lower altitude Oak forests to feed on acorns and raid agricultural crops, resulting in significant geographical overlap with human populations (Ahmad et al. 2022). As generalists regarding habitat and diet, Asiatic black bears can adapt to various environmental conditions, including proximity to

human settlements (Escobar et al. 2015). Altitude consistently shows a negative effect on bear activity, with bears preferring Oak forest habitats at lower altitudes. Forest cover remains a significant predictor of bear detections, underscoring that Asiatic black bears primarily inhabit forested areas and rarely venture into open spaces or meadows (Ahmad et al. 2022).

Camera trapping surveys in our study area have captured images of solitary feral dogs and packs of two to six dogs, which pose potential threats to large carnivores like bears. Our analysis indicates a greater likelihood of co-occurrence between feral dogs and bears than expected, with significant associations suggesting a serious threat, especially to bear cubs. Feral dogs impact native wildlife through direct predation (Gatti et al. 2018; Khattak et al. 2021; Zamora-Nasca et al. 2021), competition for resources (Young et al. 2011; Vanak and Gompper 2009; Hughes and Macdonald 2013), and the spread of diseases such as canine distemper virus (CDV), which has significantly affected wildlife populations globally (Furtado et al. 2016; Czupryna et al. 2016; Wang et al. 2022; Terio and Craft 2013; Roelke-Parker et al.

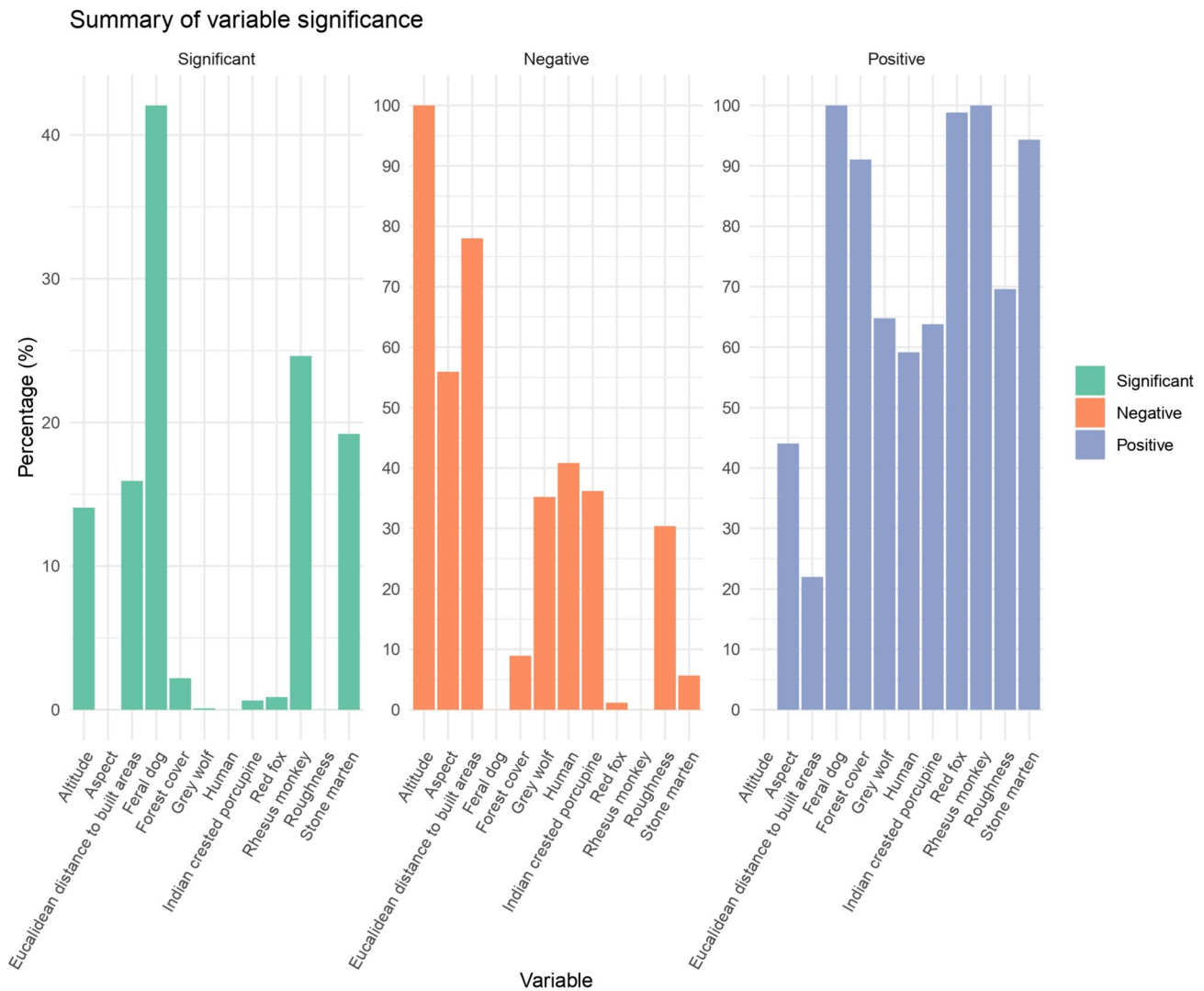


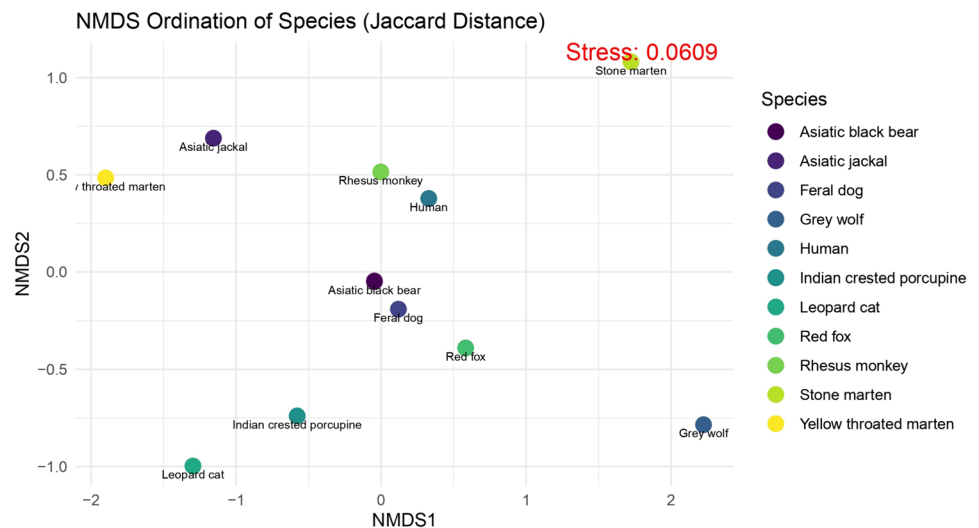
Fig. 9 The percentage of significance in all models with final selected explanatory variables, and their negative and positive on Asiatic black bear presence, as determined through exploratory regression analysis

1996; Mulia et al. 2021; Gordon et al. 2015; Timm et al. 2009). Notably, there is comparatively less overlap in the nocturnal activities of bears and dogs, which may reduce direct encounters. The frequent visits of dogs to bear habitats may also be influenced by the fact that in our study area, bear detections increase as the distance to anthropogenic features decreases. To adapt, bears tend to be mostly nocturnal, whereas dogs in our study area are primarily active during the day. Given their widespread presence and role as apex predators in areas lacking natural predators, feral dogs require effective management strategies to mitigate their negative impacts on ecosystem health (Vanak and Gompper 2009; Vanak et al. 2013; Zanin et al. 2019; Zapata-Ríos and Branch 2018; Tiwari et al. 2019; Khattak et al. 2021).

Our results show that bears and the Indian crested porcupine have a higher frequency of co-occurrence and a higher

temporal overlap. The Indian crested porcupine is predominantly nocturnal, with a unimodal activity pattern. Both species are known to extensively feed on *Quercus* acorns and damage crops across their distribution range (Naeem Awan et al. 2016; Ali et al. 2017; Hafeez et al. 2011; Waseem et al. 2020; Ashraf et al. 2021; Khan et al. 2021; Ahmad et al. 2022). In Pakistan, Indian crested porcupines are considered pests due to their substantial crop and plantation damage (Khan et al. 2000; Ashraf et al. 2021; Akhtar et al. 2021; Khan et al. 2021; Mushtaq et al. 2013). People's perceptions of individual species may be influenced by the behavior of other species in ecosystems where multiple species cause damage (Farhadinia et al. 2017). While this phenomenon is sometimes disregarded in conservation efforts, it is of critical importance in maintaining public acceptance of threatened mammals (Farhadinia et al. 2017). Similarly, rhesus

Fig. 10 Species which have a similar co-occurrence pattern to that of Asiatic black bear are ordinated near to Asiatic black bear



monkeys, which are active primarily during the day and consume large amounts of *Quercus* acorns in the fall, are more feared than bears for their crop damage. This species, although of least concern according to the IUCN, causes significant damage in orchards and agricultural areas, exacerbating local resentment towards wildlife (Pirta et al. 1997; Ahmad et al. 2022; Saraswat et al. 2015; Anand et al. 2018; Koirala et al. 2021).

Martens, like bears, are generalist omnivores that primarily consume the same foods (Serafini and Lovari 1993; Padial et al. 2002; Monterroso et al. 2014; Grassman et al. 2005; Ali et al. 2017; Ding et al. 2022). Our study found a very high temporal overlap between stone martens and bears, suggesting spatial adaptations that allow coexistence. However, the research did not show any significant or random associations between bears and stone martens at the sample sites. But our analysis of co-occurrence effect sizes indicated that bears and stone martens generally avoid each other in space.

For yellow-throated martens, our limited sample revealed that their association with bears appears random. Like other martens, yellow-throated martens can adapt to changes in food availability, which supports their extensive biogeographic range (Ben-David et al. 1997; Rodel and Stubbe 2006; Zhou et al. 2011). Nonetheless, more detailed and prolonged studies involving diet, activity patterns, and spatial usage are necessary to gain a clearer understanding of how yellow-throated martens coexist within this ecosystem.

After bears, red foxes were the second most frequently recorded species in our camera trap surveys. Temporal overlap analysis indicated that bears had the highest overlap with red foxes and a significant, though lesser, overlap with Asiatic jackals. Our effect size estimations and probabilistic

co-occurrence analysis revealed that red foxes have a considerably positive relationship with bears, co-occurring more frequently than expected. They also displayed a random association with Asiatic jackals. The likely reasons for this co-occurrence with bears could be the scavenging opportunities provided by bear prey, as observed in our camera trapping survey, or to avoid predation from larger predators like wolves and leopards. Recent research suggests that the presence of top predators can benefit mesocarnivores by increasing their scavenging opportunities and offering protection from other predators, though this hypothesis warrants further exploration (Sivy et al. 2017; Moll et al. 2021).

Grey wolves and bears exhibit significant spatial and temporal separation, likely because wolves prefer higher altitudes in subalpine and alpine meadows and are specialist carnivores, while bears are omnivores inhabiting temperate forests. During their active seasons in autumn and winter, bears frequent *Quercus* forests to consume acorns and raid nearby maize crops and *Diospyros lotus* (Din et al. 2013; Rehman et al. 2021; Werhahn et al. 2018; Ahmad et al. 2022).

Although our sample size for leopard cats is small, results suggest a significant temporal overlap with bears but with a wider confidence interval, with leopard cats most active just before sunrise, a period of lower bear activity. Despite this, leopard cats have a significant positive relationship with bears, co-occurring more frequently than expected, as shown by probabilistic co-occurrence analysis and effect size calculations. However, NMDS ordination indicates significant spatial dissimilarity between the two species, suggesting that leopard cats might share space with bears but avoid temporal interaction as they have high temporal overlap, but their peak activity times are different. While bears have a broad omnivorous diet, leopard cats are specialized carnivores primarily

preying on murids. Both species prefer dense cover and habitats below the tree line (Bashir et al. 2014; Ali et al. 2017; Escobar et al. 2015; Ahmad et al. 2022).

Conclusion

The Asiatic black bear serves as a focal point for conservation in the Hindu Raj Mountain range, acting as an umbrella species whose habitat requirements encompass those of many sympatric species. This study provides detailed insights into the adaptable nature of the Asiatic black bear, explaining varied levels of spatial and temporal overlap with sympatric species in the study area. The bears' increased nocturnal activity, particularly in areas with higher human activity and easier access to anthropogenic food sources, underscores their ability to adapt to changing environmental conditions. This adaptation, however, also brings them into closer contact with humans and other species such as feral dogs, which poses additional risks including increased potential for conflict, retaliatory killings, and disease transmission. This research highlights the importance of habitat features such as forest cover and altitude, especially the Oak forests located at lower altitude close to human settlements which significantly influence bear detections. These environmental variables are crucial for designing effective conservation measures, ensuring the preservation of habitat that supports not only the Asiatic black bear but also the broader biodiversity of the region. While the research provides valuable insights into bear ecology and interspecies relationships, it did not include an analysis of food availability. Future studies should incorporate food availability assessments, prey-predator dynamics, and other niche dimensions not included in this study to enhance our understanding of bear ecology and inform conservation efforts. Continuing such detailed ecological investigations is crucial for the sustainable management and conservation of Asiatic black bears and the ecological balance of their temperate habitats.

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Data availability All relevant data are within the paper and supplementary materials.

Declarations

Competing interests The authors declare no competing interests.

References

- Abbas FI, Bhatti ZI, Haider J, Mian A (2015) Bears in Pakistan: distribution, population biology, and human conflicts. *J Biosour Manag* 2(2):1
- Ahmad F, Nawaz MA, Salim M, Rehan M, Farhadinia M, Bosso L, Kabir M (2022) Patterns of spatial distribution, diel activity, and human-bear conflict of *Ursus thibetanus* in the Hindu Kush mountains. *Pak Glob Ecol Conserv* 37:e02145
- Akaike H (1981) Likelihood of a model and information criteria. *J Econom* 16(1):3–14
- Akbaba B, Ayaş Z (2012) Camera trap study on inventory and daily activity patterns of large mammals in a mixed forest in north-western Turkey. *Mammalia* 76(1):43–48. <https://doi.org/10.1515/mamm.2011.102>
- Akhtar A, Khan KA, Iqbal M, Bano SA, Hussain M, Munawar N, Habiba U (2021) Identification and crop damage assessment of Indian crested porcupine (*Hystrix indica*) in selected zones of Abbottabad, Pakistan. *Braz J Biol* 82:e242635
- Ali A, Zhou Z, Waseem M, Khan MF, Ali I, Asad M, Qashqaei AT (2017) An assessment of food habits and altitudinal distribution of the Asiatic black bear (*Ursus thibetanus*) in the Western Himalayas. *Pak J Nat Hist* 51(11–12):689–701
- Anand S, Binoy VV, Radhakrishna S (2018) The monkey is not always a God: Attitudinal differences toward crop-raiding macaques and why it matters for conflict mitigation. *Ambio* 47(6):711–720
- Apps PJ, McNutt JW (2018) How camera traps work and how to work them. *Afr J Ecol* 56(4):702–709
- Ashraf RZ, Ahmad B, Shafique F, Hassan MU, Asim N, Muhammad MW, Khawaja S, Butt S, Akbar N, Sheikh N (2021) Evaluation of economic loss caused by Indian crested porcupine (*Hystrix indica*) in agricultural land of district Muzaffarabad, Azad Jammu and Kashmir, Pakistan. *Braz J Biol* 83:e249847
- Ausbund DE, Stansbury CR, Stenglein JL, Struthers JL, Waits LP (2015) Recruitment in a social carnivore before and after harvest. *Anim Conserv* 18(5):415–423
- Awan MN, Awan MS, Nawaz MA, Hameed S, Kabir M, Lee DC (2021) Landscape associations of Asiatic black bears in Kashmir Himalaya Pakistan. *Ursus* 2021(32e23):1–10
- Ayres LA, Chow LS, Graber DM (1986) Black bear activity patterns and human induced modifications in Sequoia National Park. *Bears: Their Biology and Management* 6:151–154
- Azevedo FC, Lemos FG, Freitas-Junior MC, Rocha DG, Azevedo FCC (2018) Puma activity patterns and temporal overlap with prey in a human-modified landscape at Southeastern Brazil. *J Zool* 305(4):246–255
- Bashir T, Bhattacharya T, Poudyal K, Sathyakumar S, Qureshi Q (2014) Integrating aspects of ecology and predictive modelling: implications for the conservation of the leopard cat (*Prionailurus bengalensis*) in the Eastern Himalaya. *Acta Theriol* 59(1):35–47
- Beckmann JP, Berger J (2003) Rapid ecological and behavioural changes in carnivores: the responses of black bears (*Ursus americanus*) to altered food. *J Zool* 261(2):207–212
- Ben-David M, Flynn RW, Schell DM (1997) Annual and seasonal changes in diets of martens: evidence from stable isotope analysis. *Oecologia* 111(2):280–291
- Bischof R, Ali H, Kabir M, Hameed S, Nawaz MA (2014) Being the underdog: an elusive small carnivore uses space with prey and time without enemies. *J Zool* 293(1):40–48
- Bridges AS, Vaughan MR, Klenzendorf S (2004) Seasonal variation in American black bear *Ursus americanus* activity patterns: quantification via remote photography. *Wildl Biol* 10(1):277–284
- Bu H, Wang F, McShea WJ, Lu Z, Wang D, Li S (2016) Spatial co-occurrence and activity patterns of mesocarnivores in the temperate forests of Southwest China. *PLoS ONE* 11(10):e0164271

- Bunnell FL, Harestad AS (1990) Activity budgets and body weight in mammals. How sloppy can mammals be? *Current Mammalogy* 2:245–305
- Carter N, Jasny M, Gurung B, 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
- Carvalho JC, Cardoso P (2020) Decomposing the causes for niche differentiation between species using hypervolumes. *Front Ecol Evol* 8:243
- Carver BD, Kennedy ML, Houston AE, Franklin SB (2011) Assessment of temporal partitioning in foraging patterns of syntopic Virginia opossums and raccoons. *J Mammal* 92(1):134–139
- Creel S, Rotella JJ (2010) Meta-analysis of relationships between human off-take, total mortality and population dynamics of gray wolves (*Canis lupus*). *PLoS ONE* 5(9):e12918
- Croose E, Bled F, Fowler NL, Beyer DE Jr, Belant JL (2019) American marten and fisher do not segregate in space and time during winter in a mixed-forest system. *Ecol Evol* 9(8):4906–4916
- Czupryna AM, Brown JS, Bigambo MA, Whelan CJ, Mehta SD, Santymire RM, Lankester FJ, Faust LJ (2016) Ecology and demography of free-roaming domestic dogs in rural villages near Serengeti National Park in Tanzania. *PLoS One* 11(11):e0167092
- Dai Y, Hacker CE, Zhang Y, Li Y, Li J, Xue Y, Li D (2020) Conflicts of human with the Tibetan brown bear (*Ursus arctos pruinosus*) in the Sanjiangyuan region. *China Global Ecology and Conservation* 22:e01039
- de Abreu Pestana LF, Martello F, Fonseca RCB (2023) Richness and composition of terrestrial mammals vary in eucalyptus plantations due to stand age. *Austral Ecol* 48(4):743–760
- Dexter E, Rollwagen-Bollens G, Bollens SM (2018) The trouble with stress: A flexible method for the evaluation of non-metric multidimensional scaling. *Limnol Oceanogr Methods* 16(7):434–443
- Din JU, Hameed S, Shah KA, Khan MA, Khan S, Ali M, Nawaz MA (2013) Assessment of canid abundance and conflict with humans in the Hindu Kush Mountain Range of Pakistan. *Wildl Biol Pract* 9(2):20–29
- Ding C, Liang D, Xin W, Li C, Ameica EI, Jiang Z (2022) A dataset on the morphological, life-history and ecological traits of the mammals in China. *Biodiversity Science* 30(2):21520
- Elbroch LM, Lendrum PE, Allen ML, Wittmer HU (2015) Nowhere to hide: pumas, black bears, and competition refuges. *Behav Ecol* 26(1):247–254
- Escobar LE, Awan MN, Qiao H (2015) Anthropogenic disturbance and habitat loss for the red-listed Asiatic black bear (*Ursus thibetanus*): Using ecological niche modeling and nighttime light satellite imagery. *Biol Cons* 191:400–407
- ESRI (2011) ArcGIS desktop: Release 10. Environmental Systems Research Institute, Redlands. Available at <https://www.esri.com/en-us/arcgis/products/arcgis-desktop/resources>
- Farhadinia MS, Johnson PJ, Hunter LT, Macdonald DW (2017) Wolves can suppress goodwill for leopards: Patterns of human-predator coexistence in northeastern Iran. *Biol Cons* 213:210–217
- Farris ZJ, Gerber BD, Karpanty S, Murphy A, Wampole E, Ratelolahy F, Kelly MJ (2020) Exploring and interpreting spatiotemporal interactions between native and invasive carnivores across a gradient of rainforest degradation. *Biol Invasions* 22(6):2033–2047
- Fattorini N, Pokheral CP (2012) Activity and habitat selection of the Indian crested porcupine. *Ethol Ecol Evol* 24(4):377–387
- Feng Y, Tong X (2017) Using exploratory regression to identify optimal driving factors for cellular automaton modeling of land use change. *Environ Monit Assess* 189:1–17
- Fenglin W, Ahmad I, Zelenakova M, Fenta A, Dar MA, Teka AH, Belew AZ, Damtie M, Berhan M, Shafi SN (2023) Exploratory regression modeling for flood susceptibility mapping in the GIS environment. *Sci Rep* 13(1):247
- Fleishman E, Murphy DD, Brussard PF (2000) A new method for selection of umbrella species for conservation planning. *Ecol Appl* 10:569–579
- Furtado MM, Hayashi EMK, Allendorf SD, Coelho CJ, de Almeida Jacomo AT, Megid J, Ramos Filho JD, Silveira L, Torres NM, Ferreira Neto JS (2016) Exposure of free-ranging wild carnivores and domestic dogs to canine distemper virus and parvovirus in the cerrado of central Brazil. *EcoHealth* 13:549–557
- Garshelis DL, Pelton MR (1980) Activity of black bears in the great smoky mountains national park. *J Mammal* 61(1):8–19
- Gatti A, Seibert JB, Moreira DD (2018) A predation event by free-ranging dogs on the lowland tapir in the Brazilian Atlantic Forest. *Anim Biodiv Conserv* 41(2):311–314
- Goldstein SJ, Richard AF (1989) Ecology of rhesus macaques (*Macaca mulatta*) in northwest Pakistan. *Int J Primatol* 10(6):531–567
- Gordon CH, Banyard AC, Hussein A, Laurenson MK, Malcolm JR, Marino J, Regassa F, Stewart AME, Fooks AR, Sillero-Zubiri C (2015) Canine distemper in endangered Ethiopian wolves. *Emerg Infect Dis* 21(5):824
- Goszczyński J, Juszko S, Pacia A, Skoczyńska J (2005) Activity of badgers (*Meles meles*) in Central Poland. *Mamm Biol* 70(1):1–11
- Gotelli NJ, Ulrich W (2010) The empirical Bayes approach as a tool to identify non-random species associations. *Oecologia* 162(2):463–477
- Grassman LI, Tewes ME, Silvy NJ (2005) Ranging, habitat use and activity patterns of binturong *Arctictis binturong* and yellow-throated marten *Martes flavigula* in north-central Thailand. *Wildl Biol* 11(1):49–57
- Griffith DM, Veech JA, Marsh CJ (2016) Cooccur: probabilistic species co-occurrence analysis in R. *J Stat Softw* 69:1–17
- Hafeez S, Khan GS, Ashfaq M, Khan ZH (2011) Food habits of the Indian crested porcupine (*Hystrix indica*) in Faisalabad. *Pakistan Pak J Agric Sci* 48(3):205–210
- Hagen KB, Hammer S, Frei S, Ortmann S, Głogowski R, Kreuzer M (2019) Digestive physiology, resting metabolism and methane production of captive Indian crested porcupine (*Hystrix indica*). *Journal of Animal and Feed Sciences* 28:69–77
- Hameed S, Din JU, Ali H, Kabir M, Younas M, Ur Rehman E, Bari F, Hao W, Bischof R, Nawaz MA (2020) Identifying priority landscapes for conservation of snow leopards in Pakistan. *PLoS ONE* 15(11):e0228832
- Hansen MC, Potapov PV, Moore R, Hancher M, Turubanova SA, Tyukavina A, Thau D, Stehman SV, Goetz SJ, Loveland TR, Komareddy A (2013) High-resolution global maps of 21st-century forest cover change. *Science* 342(6160):850–853
- Harvey E, Gounand I, Ward CL, Altermatt F (2017) Bridging ecology and conservation: from ecological networks to ecosystem function. *J Appl Ecol* 54(2):371–379
- Havmøller RW, Jacobsen NS, 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. *J Zool* 311(3):175–182
- Hildebrand PR, Searle MP, Khan Z, Van Heijst HJ (2000) Geological evolution of the Hindu Kush, NW Frontier Pakistan: active margin to continent-continent collision zone. Geological Society, London, Special Publications 170(1):277–293
- HilleRisLambers J, Adler PB, Harpole WS, Levine JM, Mayfield MM (2012) Rethinking community assembly through the lens of coexistence theory. *Annu Rev Ecol Evol Syst* 43:227–248

- Hoagland BW, Collins SL (1997) Gradient models, gradient analysis, and hierarchical structure in plant communities. *Oikos* 78(1):23–30. <https://doi.org/10.2307/3545796>
- Hughes J, Macdonald DW (2013) A review of the interactions between free-roaming domestic dogs and wildlife. *Biol Cons* 157:341–351
- Kabir M, Hameed S, Ali H, Bosso L, Din JU, Bischof R, Redpath S, Nawaz MA (2017) Habitat suitability and movement corridors of grey wolf (*Canis lupus*) in Northern Pakistan. *PLoS ONE* 12(11):e0187027
- Kamler JF, Inthapanya X, Rasphone A, Bousa A, Vongkhamheng C, Johnson A, Macdonald DW (2020) Diet, prey selection and activity of Asian golden cats and leopard cats in northern Laos. *J Mammal* 101(5):1267–1278
- Karantk K, Srivathsa A, Vasudev D, Puri M, Parameshwaran R, Kumar NS (2017) Spatio-temporal interactions facilitate large carnivore sympatry across a resource gradient. *Proceedings of the Royal Society B: Biological Sciences* 284(1848):20161860
- Karger DN, Conrad O, Böhrer J, Kawohl T, Kreft H, Soria-Auza RW, Zimmermann NE, Linder HP, Kessler M (2017) Climatologies at high resolution for the earth's land surface areas. *Scientific Data* 4(1):1–20
- Karra K, Kontgis C, Statman-Weil Z, Mazzariello J, Mathis M, Brumby SP (2021) Global land use/land cover with Sentinel 2 and deep learning. *IEEE International Geoscience and Remote Sensing Symposium*. Brussels, Belgium, pp 4704–4707. <https://doi.org/10.1109/IGARSS47720.2021.9553499>
- Khan AA, Ahmad S, Hussain I, Munir S (2000) Deterioration impact of Indian crested porcupine *Hystrix indica* on forestry and agricultural systems in Pakistan. *Int Biodeter Biodegr* 45(3–4):143–149
- Khan AA, Mian A, Hussain R (2014) Deterioration impact of Indian crested porcupine, *Hystrix indica*, on irrigated forest plantations in Punjab, Pakistan. *Pakistan Journal of Zoology* 46(6):1691–1696
- Khan MB, Irshad N, Ahmed B, Khan MR, Minhas RA, Ali U, Mahmood M, Muhammad A, Sheikh AA, Ashraf N (2021) Food habits of Indian crested porcupine (*Hystrix indica*) (Kerr, 1792) in district Bagh, Azad Jammu and Kashmir. *Braz J Biol* 82:e243063
- Khattak RH, Xin Z, Ahmad S, Bari F, Khan A, Nabi G, Shah AA, Khan S, Rehman EU (2021) Feral dogs in Chitral gol national park, Pakistan: a potential threat to the future of threatened Kashmir Markhor (*Capra falconeri cashmiriensis*). *Braz J Biol* 83:e245867
- Koirala S, Garber PA, Somasundaram D, Katuwal HB, Ren B, Huang C, Li M (2021) Factors affecting the crop raiding behavior of wild rhesus macaques in Nepal: Implications for wildlife management. *J Environ Manage* 297:113331
- Kowalczyk R, Jędrzejewska B, Zalewski A (2003) Annual and circadian activity patterns of badgers (*Meles meles*) in Białowieża Primeval Forest (eastern Poland) compared with other Palaearctic populations. *J Biogeogr* 30(3):463–472
- Krohner JM, Ausband DE (2019) Associations between sympatric apex predators across a diverse landscape. *Mammal Research* 64(2):203–212
- Kronfeld-Schor N, Dayan T (2003) Partitioning of time as an ecological resource. *Annu Rev Ecol Evol Syst* 34(1):153–181
- Laundré JW, Hernández L, Altendorf KB (2001) Wolves, elk, and bison: reestablishing the "landscape of fear" in Yellowstone National Park, USA. *Can J Zool* 79(8):1401–1409
- Letten AD, Ke PJ, Fukami T (2017) Linking modern coexistence theory and contemporary niche theory. *Ecol Monogr* 87(2):161–177
- Li Z, Wang T, Smith JL, Feng R, Feng L, Mou P, Ge J (2019) Coexistence of two sympatric flagship carnivores in the human-dominated forest landscapes of Northeast Asia. *Landscape Ecol* 34(2):291–305
- Li J, Li D, Hacker C, Dong W, Wu B, Xue Y (2022) Spatial co-occurrence and temporal activity patterns of sympatric mesocarnivores guild in Qinling Mountains. *Glob Ecol Conserv* 36:e02129
- Linkie M, Ridout MS (2011) Assessing tiger–prey interactions in Sumatran rainforests. *J Zool* 284(3):224–229
- Mahmood T, Niazi F, Nadeem MS (2013) Diet composition of asiatic jackal (*Canis aureus*) in margallah hills national park, Islamabad, Pakistan. *J Anim Plant Sci* 23(2):444–456
- Manly BFL, McDonald L, Thomas DL, McDonald TL, Erickson WP (2007) Resource selection by animals: statistical design and analysis for field studies. Springer Science & Business Media
- Matthews SM, Beecham JJ, Quigley H, Greenleaf SS, Leithhead HM (2006) Activity patterns of American black bears in Yosemite National Park. *Ursus* 17(1):30–40
- Meredith M, Ridout M (2021) Overview of the overlap package. www.cran.r-project.org/web/packages/overlap. Accessed 16 Nov 2022
- Moll RJ, Jackson PJ, Wakeling BF, Lackey CW, Beckmann JP, Mills-paugh JJ, Montgomery RA (2021) An apex carnivore's life history mediates a predator cascade. *Oecologia* 196(1):223–234
- Monterroso P, Alves PC, Ferreras P (2014) Plasticity in circadian activity patterns of mesocarnivores in Southwestern Europe: implications for species coexistence. *Behav Ecol Sociobiol* 68(9):1403–1417
- Mukherjee S, Singh P, Ri C, Kakati K, Borah B, Tapi T, Kadur S, Choudhary P, Srikant S, Nadig S, Navya R (2019) Activity patterns of the small and medium felid (Mammalia: Carnivora: Felidae) guild in northeastern India. *J Threat Taxa* 11(4):13432–13447
- Mukherjee A, Kumara HN, Bhupathy S (2017) Determinants of occupancy and burrow site selection by Indian crested porcupine in Keoladeo National Park, Bharatpur, Rajasthan, India. *Curr Sci* 112(12):2440–2448. <http://www.jstor.org/stable/26163993>
- Mulia BH, Mariya S, Bodgener J, Iskandriati D, Liwa SR, Sumampau T, Manansang J, Darusman HS, Osofsky SA, Techakriengkrai N, Gilbert M (2021) Exposure of wild sumatran tiger (*panthera tigris sumatrae*) to canine distemper virus. *J Wildl Dis* 57(2):464–466
- Mushtaq M, Hussain I, Mian A, Munir S, Ahmed I, Khan AA (2013) Field evaluation of some bait additives against Indian crested porcupine (*Hystrix indica*) (Rodentia: Hystricidae). *Integrative Zoology* 8(3):285–292
- Naeem Awan M, Karamanlidis AA, Siddique Awan M, Ali Nawaz M, Kabir M (2016) Preliminary survey on Asiatic black bear in Kashmir Himalaya, Pakistan: Implications for preservation. *Int J Conserv Sci* 7(3):719. ISSN: 2067-533X
- NASA Shuttle Radar Topography Mission (SRTM) (2013) Shuttle Radar Topography Mission (SRTM) Global. Distributed by OpenTopography. <https://doi.org/10.5069/G9445JDF>. Accessed 18 Dec 2022
- Neale JC, Sacks BN (2001) Resource utilization and interspecific relations of sympatric bobcats and coyotes. *Oikos* 94(2):236–249
- Nelson RA, Folk GE, Pfeiffer EW, Craighead JJ, Jonkel CJ, Steiger DL (1983) Behavior, biochemistry, and hibernation in black, grizzly, and polar bears. *Bear Biol Manag* 5:284–290. <https://doi.org/10.2307/3872551>
- Ngoprasert D, Steinmetz R, Sribuarod K et al (2022) The overlap of sympatric sun bears and Asiatic black bears in space and time. *Mamm Biol* 102:143–153. <https://doi.org/10.1007/s42991-021-00201-7>
- Nickel BA, Suraci JP, Allen ML, Wilmers CC (2020) Human presence and human footprint have non-equivalent effects on wildlife spatiotemporal habitat use. *Biol Cons* 241:108383

- Oksanen J, Kindt R, Legendre P, O'Hara B, Stevens MHH, Oksanen MJ, Suggests MASS (2007) The vegan package. *Community Ecology Package* 10(631–637):719
- Olson TL, Squibb RC, Gilbert BK (1998) Brown bear diurnal activity and human use: a comparison of two salmon streams. *Ursus* 10:547–555. <http://www.jstor.org/stable/3873167>
- Oriol-Cotterill A, Valeix M, Frank LG, Riginos C, Macdonald DW (2015) Landscapes of coexistence for terrestrial carnivores: the ecological consequences of being downgraded from ultimate to penultimate predator by humans. *Oikos* 124(10):1263–1273
- Padial JM, Avila E, Sanchez JM (2002) Feeding habits and overlap among red fox (*Vulpes vulpes*) and stone marten (*Martes foina*) in two Mediterranean mountain habitats. *Mammalian Biology-Zeitschrift für Säugetierkunde* 67(3):137–146
- Pirta RS, Gadgil M, Kharshikar AV (1997) Management of the rhesus monkey *Macaca mulatta* and Hanuman langur *Presbytis entellus* in Himachal Pradesh India. *Biol Conserv* 79(1):97–106
- Prat-Guitart M, Onorato DP, Hines JE, Oli MK (2020) Spatiotemporal pattern of interactions between an apex predator and sympatric species. *J Mammal* 101(5):1279–1288
- Prater SN (1980) *The book of Indian Animals*. Bombay Natural History Society and Oxford University Press, Bombay, India, p 324
- Pulver JR, Liu H, Scott-Denton E (2016) Modelling community structure and species co-occurrence using fishery observer data. *ICES J Mar Sci* 73(7):1750–1763
- Qasim M, Hubacek K, Termansen M (2013) Underlying and proximate driving causes of land use change in district Swat, Pakistan. *Land Use Policy* 34:146–157
- R Core Team (2016) R: a language and environment for statistical computing. R foundation for statistical Computing, Vienna, Austria. <https://www.R-project.org/>
- Rahman G, Rahman AU, Anwar MM, Dawood M, Miandad M (2022) Spatio-temporal analysis of climatic variability, trend detection, and drought assessment in Khyber Pakhtunkhwa Pakistan. *Arab J Geosci* 15(1):1–13
- Ramesh T, Kalle R, Sankar K, Qureshi Q (2012) Spatio-temporal partitioning among large carnivores in relation to major prey species in Western Ghats. *J Zool* 287(4):269–275
- Rehman EU, Din JU, Ahmad S, Hameed S, Shah KA, Mehmood T, Nawaz MA (2021) Insight into occupancy determinants and conflict dynamics of grey wolf (*Canis lupus*) in the dry temperate zone of Hindukush Range. *Glob Ecol Conserv* 25:e01402
- Reid D, Jiang M, Teng Q, Qin Z, Hu J (1991) Ecology of the Asiatic black bear (*Ursus thibetanus*) in Sichuan. *China Mammalia* 55(2):221–238
- Reshamwala HS, Shrotriya S, Bora B, Lyngdoh S, Dirzo R, Habib B (2018) Anthropogenic food subsidies change the pattern of red fox diet and occurrence across Trans-Himalayas, India. *J Arid Environ* 150:15–20
- Ridout MS, Linkie M (2009) Estimating overlap of daily activity patterns from camera trap data. *J Agric Biol Environ Stat* 14(3):322–337
- Ripple WJ, Estes JA, Beschta RL, Wilmers CC, Ritchie EG, Hebblewhite M, Berger J, Elmhagen B, Letnic M, Nelson MP, Schmitz OJ (2014) Status and ecological effects of the world's largest carnivores. *Science* 343(6167):1241484
- Roberts TJ (1997) *The mammals of Pakistan*, revised edn, vol 1. Oxford University Press, p 525 (ISBN 978-0-19-577760-4)
- Rodel HG, Stubbe M (2006) Shifts in food availability and associated shifts in space use and diet in stone marten. *Lutra* 49(1):67
- Roelke-Parker ME, Munson L, Packer C, Kock R, Cleaveland S, Carpenter M, O'Brien SJ, Pospischil A, Hofmann-Lehmann R, Lutz H, Mwamengele GL (1996) A canine distemper virus epidemic in Serengeti lions (*Panthera leo*). *Nature* 379(6564):441–445
- Ross J, Hearn AJ, Johnson PJ, Macdonald DW (2013) Activity patterns and temporal avoidance by prey in response to Sunda clouded leopard predation risk. *J Zool* 290(2):96–106
- Roy S, Ghoshal A, Bijoor A, Suryawanshi K (2019) Distribution and activity pattern of stone marten *Martes foina* in relation to prey and predators. *Mamm Biol* 96(1):110–117
- Sá ACL, Pereira JMC, Charlton ME, Mota B, Barbosa PM, Stewart Fotheringham A (2011) The pyrogeography of sub-Saharan Africa: a study of the spatial non-stationarity of fire–environment relationships using GWR. *J Geogr Syst* 13:227–248. <https://doi.org/10.1007/s10109-010-0123-7>
- Saraswat R, Sinha A, Radhakrishna S (2015) A god becomes a pest? Human-rhesus macaque interactions in Himachal Pradesh, northern India. *Eur J Wildl Res* 61(3):435–443
- Schluter D, McPhail JD (1992) Ecological character displacement and speciation in sticklebacks. *Am Nat* 140(1):85–108
- Schoener TW (1974) Resource Partitioning in Ecological Communities: Research on how similar species divide resources helps reveal the natural regulation of species diversity. *Science* 185(4145):27–39
- Schuetz P, Wagner AP, Wagner ME, Creel S (2013) Occupancy patterns and niche partitioning within a diverse carnivore community exposed to anthropogenic pressures. *Biol Conserv* 158:301–312
- Schwartz CC, Cain SL, Podruzny S, Cherry S, Frattaroli L (2010) Contrasting activity patterns of sympatric and allopatric black and grizzly bears. *J Wildl Manag* 74(8):1628–1638
- Seddon PJ, Leech T (2008) Conservation short cut, or long and winding road? A critique of umbrella species criteria. *Oryx* 42(2):240–245
- Serafini P, Lovari S (1993) Food habits and trophic niche overlap of the red fox and the stone marten in a Mediterranean rural area. *Acta Theriol* 38(3):233–244
- Sévêque A, Gentle LK, López-Bao JV, Yarnell RW, Uzal A (2020) Human disturbance has contrasting effects on niche partitioning within carnivore communities. *Biol Rev* 95(6):1689–1705
- Sfenthourakis S, Tzanatos E, Giokas S (2006) Species co-occurrence: the case of congeneric species and a causal approach to patterns of species association. *Glob Ecol Biogeogr* 15(1):39–49
- Shabbir S, Anwar M, Hussain I, Nawaz MA (2013) Food habits and diet overlap of two sympatric carnivore species in Chitral, Pakistan. *J Anim Plant Sci* 23(1):100–107
- Shehzad W, Riaz T, Nawaz MA, Miquel C, Poillot C, Shah SA, Pompanon F, Coissac E, Taberlet P (2012) Carnivore diet analysis based on next-generation sequencing: Application to the leopard cat (*Prionailurus bengalensis*) in Pakistan. *Mol Ecol* 21(8):1951–1965
- Sheikh KM, Molur S (eds) (2003) Status and red list of Pakistan's mammals. Based on the conservation assessment and management plan. IUCN Pakistan, p 312
- Sheng J, Han X, Zhou H (2017) Spatially varying patterns of afforestation/reforestation and socio-economic factors in China: a geographically weighted regression approach. *J Clean Prod* 153:362–371
- Sidorovich VE, Sidorovich AA, Izotova IV (2006) Variations in the diet and population density of the red fox *Vulpes vulpes* in the mixed woodlands of northern Belarus. *Mamm Biol* 71(2):74–89
- Sivy KJ, Pozzanghera CB, Grace JB, Prugh LR (2017) Fatal attraction? Intraguild facilitation and suppression among predators. *Am Nat* 190(5):663–679
- Sladeczek FXJ, Segar ST, Lee C, Wall R, Konvicka M (2017) Temporal segregation between dung-inhabiting beetle and fly species. *PLoS ONE* 12(1):e0170426
- Soulé ME, Estes JA, Berger J, Del Rio CM (2003) Ecological effectiveness: conservation goals for interactive species. *Conserv Biol* 17(5):1238–1250

- Steenweg R, Hebblewhite M, Burton C, Whittington J, Heim N, Fisher JT, Ladle A, Lowe W, Muhly T, Paczkowski J, Musiani M (2023) Testing umbrella species and food-web properties of large carnivores in the Rocky Mountains. *Biol Cons* 278:109888
- Swanson SAS (1990) Activities and habitat use of black bears in north-central Minnesota (Doctoral dissertation, University of Minnesota)
- Terio KA, Craft ME (2013) Canine distemper virus (CDV) in another big cat: should CDV be renamed carnivore distemper virus? *MBio* 4(5):10–1128
- Timm SF, Munson L, Summers BA, Terio KA, Dubovi EJ, Rupprecht CE, Kapil S, Garcelon DK (2009) A suspected canine distemper epidemic as the cause of a catastrophic decline in Santa Catalina Island foxes (*Urocyon littoralis catalinae*). *J Wildl Dis* 45(2):333–343
- Tiwari HK, Robertson ID, O’Dea M, Vanak AT (2019) Demographic characteristics of free-roaming dogs (FRD) in rural and urban India following a photographic sight-resight survey. *Sci Rep* 9(1):1–10
- Torretta E, Mosini A, Piana M, Tirozzi P, Serafini M, Puopolo F, Balestrieri A (2017) Time partitioning in mesocarnivore communities from different habitats of NW Italy: insights into martens’ competitive abilities. *Behaviour* 154(2):241–266
- Vanak AT, Thaker M, Gompper ME (2013) Experimental examination of behavioural interactions between free-ranging wild carnivores and domestic dogs in central India. *PLoS One* 8(1):e53313
- Vanak AT, Gompper ME (2009) Dogs *Canis familiaris* as carnivores: their role and function in intraguild competition. *Mammal Rev* 39(4):265–283
- Veech JA (2013) A probabilistic model for analysing species co-occurrence. *Glob Ecol Biogeogr* 22(2):252–260
- Wang R, Wang X, Zhai J, Zhang P, Irwin DM, Shen X, Chen W, Shen Y (2022) A new canine distemper virus lineage identified from red pandas in China. *Transbound Emerg Dis* 69(4):e944–e952
- Waseem M, Mahmood T, Hussain A, Hamid A, Akrim F, Andleeb S, Fatima H (2020) Ecology and Human Conflict of Asiatic Black Bear (*Ursus thibetanus laniger*) in Mansehra District Pakistan. *Pak J Zool* 52(4):1443
- Watabe R, Tsunoda H, Saito MU (2022) Evaluating the temporal and spatio-temporal niche partitioning between carnivores by different analytical method in northeastern Japan. *Sci Rep* 12(1):11987
- Werhahn G, Senn H, Ghazali M, Karmacharya D, Sherchan AM, Joshi J, Kusi N, López-Bao JV, Rosen T, Kachel S, Sillero-Zubiri C (2018) The unique genetic adaptation of the Himalayan wolf to high-altitudes and consequences for conservation. *Glob Ecol Conserv* 16:e00455
- Yamamoto T, Tamatani H, Tanaka J, Yokoyama S, Kamiike K, Koyama M, Seki K, Kakefuda S, Kato Y, Izawa N (2012) Annual and seasonal home range characteristics of female Asiatic black bears in Karuizawa, Nagano Prefecture. *Japan Ursus* 23(2):218–225
- Young JK, Olson KA, Reading RP, Amgalanbaatar S, Berger J (2011) Is wildlife going to the dogs? Impacts of feral and free-roaming dogs on wildlife populations. *Bioscience* 61(2):125–132
- Zahoor B, Liu X, Wu P, Sun W, Jia X, Lv Z, Zhao X, He X, He B, Cai Q, Songer M (2021) Activity pattern study of Asiatic black bear (*Ursus thibetanus*) in the Qinling Mountains, China, by using infrared camera traps. *Environ Sci Pollut Res* 28(20):25179–25186
- Zamora-Nasca LB, di Virgilio A, Lambertucci SA (2021) Online survey suggests that dog attacks on wildlife affect many species and every ecoregion of Argentina. *Biol Conserv* 256:109041
- Zanin M, Bergamaschi CL, Ferreira JR, Mendes SL, Oliveira Moreira D (2019) Dog days are just starting: the ecology invasion of free-ranging dogs (*Canis familiaris*) in a protected area of the Atlantic Forest. *Eur J Wildl Res* 65(5):1–10
- Zapata-Ríos G, Branch LC (2018) Mammalian carnivore occupancy is inversely related to presence of domestic dogs in the high Andes of Ecuador. *PLoS ONE* 13(2):e0192346
- Zhang Y, Liu X, Lv Z, Zhao X, Yang X, Jia X, Sun W, He X, He B, Cai Q, Zhu Y (2019) Animal diversity responding to different forest restoration schemes in the Qinling Mountains, China. *Ecol Eng* 136:23–29
- Zhdanova IV, Masuda K, Quasarano-Kourkoulis C, Rosene DL, Killiany RJ, Wang S (2011) Aging of intrinsic circadian rhythms and sleep in a diurnal nonhuman primate, *Macaca mulatta*. *J Biol Rhythms* 26(2):149–159
- Zhou YB, Newman C, Xu WT, Buesching CD, Zalewski A, Kaneko Y, Macdonald DW, Xie ZQ (2011) Biogeographical variation in the diet of Holarctic martens (genus *Martes*, Mammalia: Carnivora: Mustelidae): adaptive foraging in generalists. *J Biogeogr* 38(1):137–147

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