

# Multi-dimensional Temporal Risk Partitioning Among Tigers, Prey, and Human Activity in South-Central Bhutan

Wangdi<sup>1</sup> & Rupesh Subedi<sup>2</sup>

<sup>1</sup>Forest Resources Planning and Management Division, Department of Forests and Park Services

<sup>2</sup>College of Natural Resources, Royal University of Bhutan

## Abstract

1. Predators and anthropogenic disturbance jointly structure prey behaviour, yet few studies evaluate multiple temporal risk dimensions within the same landscape. Understanding the temporal dimensions of predator–prey–human coexistence is essential for managing large carnivore landscapes where wildlife and people share space.
2. Camera-trap data from 149 stations spanning 12,835 trap-nights across three adjoining management units in south-central Bhutan (Royal Manas National Park, Phipsoo Wildlife Sanctuary, and Sarpang Forest Division) were used to quantify temporal risk partitioning among tigers (*Panthera tigris*), five focal prey species, and human activity. Temporal overlap was estimated using the coefficient of overlapping (Dhat4), median post-tiger prey re-detection intervals (RT50) were quantified, beta regression models of tiger nocturnality against local human-use rates were fitted, and diel activity patterns were compared at tiger-present versus tiger-absent stations.
3. Tiger–prey temporal overlap varied substantially among species (Dhat4 range: 0.671–0.909), with wild boar (*Sus scrofa*) showing the highest exploratory temporal-exposure score (Dhat4 = 0.671, RT50 = 272 min) and gaur (*Bos gaurus*) the lowest (Dhat4 = 0.909, RT50 = 582 min). Tiger–human temporal separation was pronounced (Dhat4 = 0.397, 95% CI: 0.370–0.490). Tiger nocturnality showed a positive but statistically uncertain association with human-use rates (beta = 0.087,  $p = 0.088$ , pseudo- $R^2 = 0.19$ ), based on a limited station-level sample ( $n = 13$ ). Conditional diel analysis suggested that dhole (*Cuon alpinus*) showed the strongest apparent temporal shift at tiger-present stations (Dhat4 = 0.809), whereas ungulates maintained largely stable activity patterns.
4. These results suggest that temporal exposure in tiger landscapes is species-specific and multi-dimensional, requiring joint consideration of temporal overlap and station-level re-detection behaviour. The strong tiger–human temporal separation observed in this relatively undisturbed Himalayan landscape provides an initial behavioural reference condition against which future anthropogenic encroachment can be assessed.

**Keywords:** activity overlap, camera trapping, Dhat4, landscape of fear, nocturnality, predator–prey interactions, temporal partitioning, tiger

## Introduction

Predation risk fundamentally structures animal communities through both direct mortality and non-consumptive effects that alter prey behaviour, habitat use, and fitness (Lima & Dill, 1990; Creel & Christianson, 2008). The landscape-of-fear framework posits that prey perceive and respond to spatially heterogeneous predation risk, adjusting their temporal activity, space use, and vigilance to reduce encounter rates with predators (Laundre et al., 2010). Although originally conceived as a spatial concept, the landscape of fear has an equally important temporal dimension: prey may avoid periods of peak predator activity, generating diel partitioning that facilitates coexistence (Frid & Dill, 2002; Kohl et al., 2018). Quantifying this temporal risk landscape is critical for understanding how prey communities persist alongside large carnivores and, increasingly, alongside intensifying human activity.

Camera-trap surveys have emerged as the principal tool for estimating diel activity patterns of cryptic terrestrial mammals (Sollmann, 2018; Rovero & Zimmermann, 2016). Kernel density estimation of detection timestamps, combined with the non-parametric coefficient of overlapping (Dhat; Ridout & Linkie, 2009), enables pairwise quantification of temporal niche similarity between predators and prey. The Dhat4 estimator is recommended for sample sizes exceeding 75 observations and provides a bounded metric (0–1) interpretable as the shared area under two circular activity density curves (Meredith & Ridout, 2014). Although temporal overlap is now routinely reported in camera-trap studies (Lira-Torres & Briones-Salas, 2012; Ramesh et al., 2012), it captures only one dimension of temporal risk. Species that show high temporal overlap with a predator may nonetheless mitigate risk through delayed station re-use after predator detections. Conversely, species with moderate overlap but short re-detection intervals may face elevated temporal exposure. Thus, a comprehensive assessment of temporal exposure requires integrating overlap coefficients with post-predator re-detection dynamics.

Anthropogenic disturbance adds a second, increasingly dominant risk axis. A global meta-analysis reported that mammals worldwide are shifting toward increased nocturnality in response to human activity, with effect sizes comparable to those induced by natural predators (Gaynor et al., 2018). For large carnivores, human disturbance can compress activity into narrow temporal windows, potentially intensifying competitive and predatory interactions during nocturnal hours (Carter et al., 2012; Nickel et al., 2020). Understanding how human presence modulates carnivore diel behaviour is therefore integral to predicting cascading effects on prey communities and to designing effective conservation interventions.

Tiger (*Panthera tigris*) landscapes present a particularly compelling system for studying multi-axis temporal risk. As apex predators occupying diverse habitats from lowland tropical forests to montane subtropical ecosystems, tigers impose strong top-down effects on ungulate prey communities (Karanth & Sunquist, 1995; Ramesh et al., 2012). Tiger–prey temporal dynamics have been studied across South and Southeast Asia, with evidence for both high overlap (suggesting shared habitat constraints) and temporal avoidance (suggesting active risk mitigation) depending on prey species and landscape context (Carter et al., 2015; Kafley et al., 2019). However, studies simultaneously quantifying tiger–prey temporal overlap, post-tiger prey re-detection intervals, and the modulating influence of human activity remain scarce (Botts et al., 2020). Most existing work addresses these dimensions in isolation, limiting inference about how multiple temporal risk dimensions shape prey exposure.

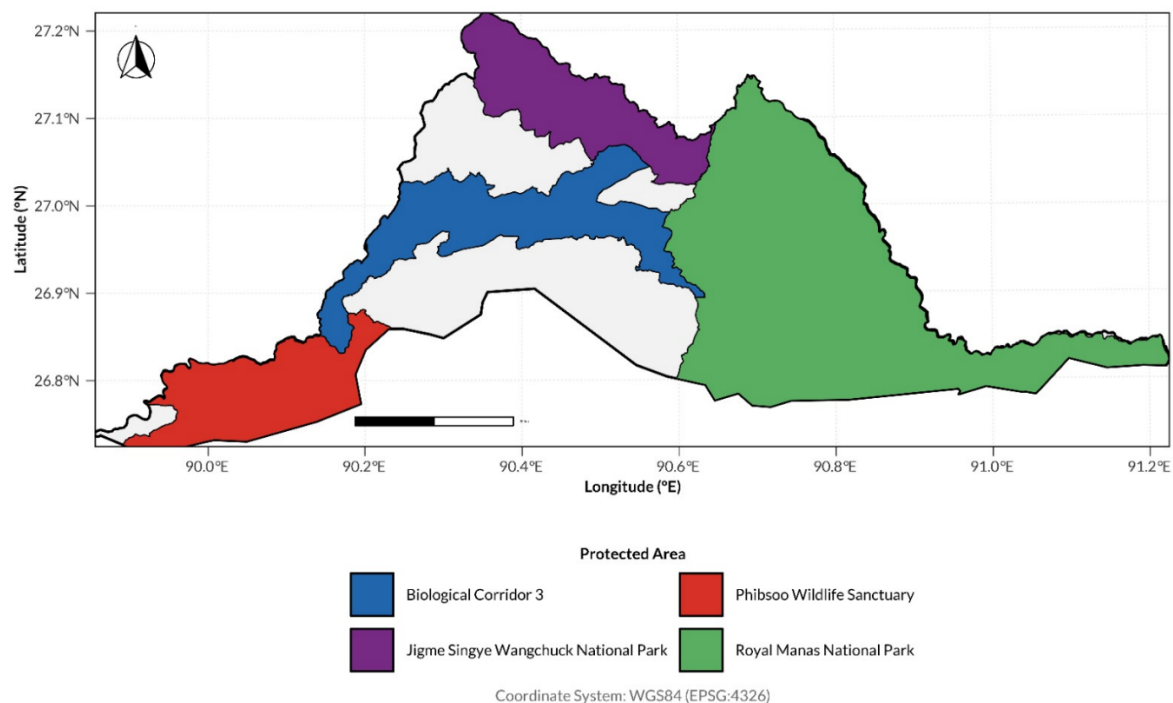
South-central Bhutan offers a unique setting for this investigation. The study region encompasses a contiguous forest corridor connecting Royal Manas National Park (RMNP), Phipsoo Wildlife Sanctuary (PWS), and Sarpang Forest Division (SFD), spanning an elevational gradient from 64 to 2,552 m. Unlike many tiger range countries where habitat fragmentation and high human density dominate, Bhutan retains extensive forest cover (>70% of national area) and maintains relatively low human population densities within protected area buffer zones (Wang et al., 2006; Tempa et al., 2019). This comparatively low-disturbance context allows investigation of predator–prey temporal dynamics under a reference condition relative to many human-dominated tiger landscapes.

Four research questions were addressed with directional predictions. First, prey temporal exposure to tigers was expected to be species-specific, with smaller-bodied prey of higher tiger dietary importance (wild boar, barking deer) predicted to show lower temporal overlap but shorter post-tiger re-detection intervals. Second, tiger nocturnality was expected to increase with local human-use intensity, consistent with human-induced temporal displacement. Third, post-tiger prey re-detection intervals were expected to vary among tiger-detection stations, with station-level return sequences revealing heterogeneity in temporal risk windows. Fourth, prey was expected to modify diel activity at tiger-present versus tiger-absent stations, with stronger conditional temporal shifts predicted in mesocarnivores (dhole) than in large ungulates, reflecting guild-specific anti-predator strategies.

## Methods

### Study area

The study was conducted across three adjoining management units in south-central Bhutan: Royal Manas National Park (RMNP; 1,057 km<sup>2</sup>), Phipsoo Wildlife Sanctuary (PWS; 278 km<sup>2</sup>), and Sarpang Forest Division (SFD), collectively spanning the southern foothills of the eastern Himalayas (Figure 1). The landscape is characterised by subtropical broadleaf and mixed coniferous forests along a steep elevational gradient (64–2,552 m a.s.l.), dissected by major river systems including the Manas, Phibsoo, and Sarpang rivers. The region experiences a monsoonal climate with pronounced wet (June–September) and dry (November–March) seasons. Land use is predominantly forested, with scattered agricultural settlements and livestock grazing areas along river valleys and forest margins. The study area forms part of the Transboundary Manas Conservation Area, which connects Bhutan's protected area network with Manas National Park in Assam, India.



*Figure 1: Study area in south-central Bhutan, showing Royal Manas National Park, Phipsoo Wildlife Sanctuary, and Sarpang Forest Division.*

### Camera trap survey design

Camera-trap sampling used 149 stations across the study area between January and December 2022, accumulating 12,835 trap-nights. Stations were positioned along wildlife trails, ridge lines, and riparian corridors to maximise detection probability for medium-to-large terrestrial mammals. Because cameras were placed primarily along wildlife trails, ridge lines, and riparian corridors, activity estimates represent detections along animal movement routes rather than unbiased landscape-wide activity. Each station comprised paired camera units mounted at approximately 40 cm height on trees flanking trails, with sensors oriented perpendicular to the expected direction of animal movement. Cameras were programmed to capture three consecutive images per trigger event with a minimum interval of 1 second between triggers. Station spacing

averaged approximately 2 km, consistent with recommended protocols for tiger density surveys (Karanth & Nichols, 1998). Station coordinates were recorded using handheld GPS units (WGS84 datum). Cameras were checked and maintained at approximately 3-month intervals throughout the survey period.

### ***Event independence filtering***

To minimise pseudo-replication from repeated photographs of the same individual during a single visit, a 20-minute independence threshold was applied within each species–station combination. Consecutive photographs of the same species at the same station within 20 minutes were collapsed into a single independent detection event. This threshold follows established protocols for camera-trap activity analyses (O’Brien et al., 2003; Meek et al., 2014) and balances the need to reduce pseudo-replication against the risk of discarding genuine re-visits by different individuals. The optimal independence interval is species- and context-dependent. Sensitivity analyses using 30- and 60-minute thresholds are reported in the Supporting Information and were used to assess whether the main activity-overlap rankings were robust to the independence threshold.

### ***Activity density estimation and temporal overlap***

For each focal species, diel activity density was estimated using non-parametric kernel density estimation on angular (circular) time-of-day data, implemented via the *overlap* package in R (Meredith & Ridout, 2014). Detection timestamps were converted to radians ( $0-2\pi$ ) for circular analysis. The Dhat4 estimator of the coefficient of overlapping was selected for all pairwise comparisons, as recommended when both samples exceed 75 observations (Ridout & Linkie, 2009). The Dhat4 coefficient ranges from 0 (no overlap) to 1 (identical activity patterns) and is calculated as the integral of the minimum of two estimated density functions. Dhat4 was used for consistency across comparisons; however, estimates involving fewer than 75 detections in one comparison group were interpreted cautiously.

Tiger–prey overlap was computed for five focal prey species selected based on dietary importance and sufficient sample sizes: wild boar (*Sus scrofa*,  $n = 858$  detections), barking deer (*Muntiacus muntjak*,  $n = 3,168$ ), sambar (*Rusa unicolor*,  $n = 2,961$ ), Himalayan serow (*Capricornis thar*,  $n = 232$ ), and gaur (*Bos gaurus*,  $n = 2,585$ ). Tiger detections totalled 183 independent events across 51 stations. Confidence intervals for Dhat4 were obtained via 10,000 bootstrap resamples from the smoothed activity distributions.

### ***Return-time modelling***

To complement overlap analysis, post-tiger prey re-detection intervals were quantified at stations where tigers were detected. For each tiger detection event, subsequent detections of each focal prey species at the same station within a 48-hour window were identified. The post-tiger re-detection interval (minutes) was calculated as the interval between a tiger detection and the next independent detection of a given prey species at the same station. The median re-detection interval (RT50) is reported for each species, along with the 10th and 90th percentiles (P10, P90) to characterise the distribution of intervals. The proportion of sequences with lags shorter than 6 hours (360 minutes) was also calculated as a measure of rapid site re-use following predator presence. Return-time estimates based on fewer than 10 tiger–prey sequences were treated as descriptive because percentile estimates are unstable at low sample sizes.

An exploratory composite temporal-exposure index was computed for each prey species by combining three components: Dhat4 overlap, inverse median post-tiger re-detection interval, and the proportion of short-lag sequences. Each component was standardised using z-scores. The mean standardised score was then min–max rescaled across species to produce a comparative index ranging from 0 to 1. Because no established weighting scheme exists for these components, the index was treated as exploratory rather than as a validated estimate of predation risk.

### ***Beta regression modelling of nocturnality***

To test whether tiger diel activity shifts toward nocturnality in response to human disturbance, station-level tiger nocturnality was modelled as a function of local human-use rate using beta regression (Ferrari & Cribari-Neto, 2004). Nocturnality was defined as the proportion of a station’s tiger detections occurring between 18:00 and 06:00 hours, bounded on the open interval (0, 1). Human-use rate was calculated as the number of independent human detection events per 100 trap-days at each station. Analysis was restricted to stations with a minimum of 5 independent tiger detections ( $n = 13$  stations) to ensure reliable estimation of the nocturnality proportion. The model was fitted using maximum likelihood with a logit link function and identity-linked precision parameter, implemented via the *betareg* package in R (Cribari-Neto & Zeileis, 2010). The coefficient estimate, standard error, z-statistic, associated *p*-value, and pseudo- $R^2$  are reported. This analysis was treated as exploratory because only 13 stations met the minimum threshold of five independent tiger detections.

### ***Conditional diel activity analysis***

To assess whether prey species modify their diel activity in response to tiger presence, stations were classified as tiger-present (at least one tiger detection during the survey) or tiger-absent (no tiger detections). This binary classification captures coarse tiger occurrence rather than continuous variation in predation risk and was therefore interpreted as a station-level contrast rather than a direct measure of predation pressure. For each of five focal species (common leopard, dhole, barking deer, sambar, gaur), detection timestamps were pooled separately for tiger-present and tiger-absent stations and Dhat4 was estimated between the two resulting activity distributions. A Dhat4 value near 1.0 indicates that the species maintains the same diel pattern regardless of tiger presence, whereas lower values indicate temporal displacement at sites with tiger activity.

### ***Moon phase correlation***

Moon-phase effects were treated as a secondary analysis and are reported in the Supporting Information. Moon phase was approximated using a sinusoidal model referenced to the nearest new moon (3 January 2022), yielding a continuous illumination index from 0 (new moon) to 1 (full moon). For each nocturnal or crepuscular species with sufficient detections, mean lunar illumination across detection nights was calculated and the correlation between nightly detection frequency and moon illumination was tested using Spearman’s rank correlation.

### ***Reproducibility and software***

All analyses were conducted in R version 4.4.0 (R Core Team, 2024) using a reproducible pipeline managed by the *targets* package (Landau, 2021) with package dependencies tracked via *renv* (Ushey, 2024). Random number generation was initialised with `set.seed(42)` prior to all stochastic procedures. Key packages included *overlap* (Meredith & Ridout, 2014) for activity estimation, *betareg* (Cribari-Neto & Zeileis, 2010) for beta regression, and *circular* (Agostinelli & Lund, 2022) for circular statistics. The complete analytical pipeline, including all scripts,

configuration files, and package versions, is archived in the project repository at [https://github.com/wangdiues/camtrap\\_ecology\\_analytics](https://github.com/wangdiues/camtrap_ecology_analytics). Processed detection tables required to reproduce the analyses are available in the project repository where disclosure does not compromise sensitive species-location information; raw images and exact sensitive-location records are available only through data-governance approval from the Department of Forests and Park Services.

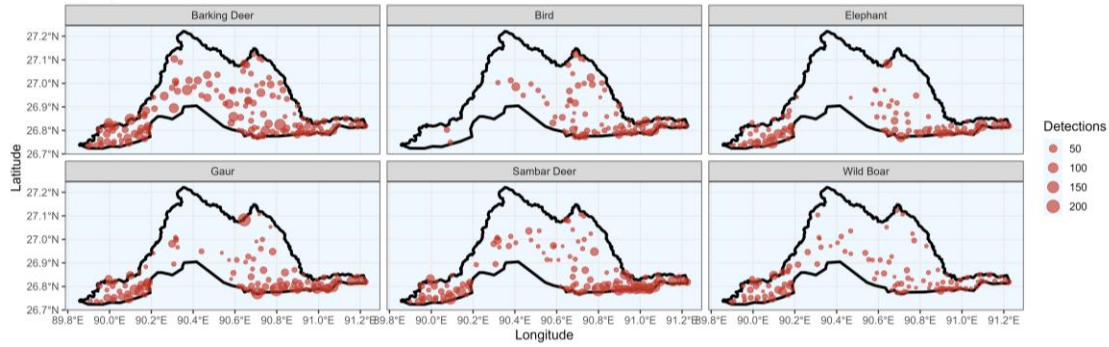
## Results

### Survey summary

The 149 camera-trap stations accumulated 12,835 trap-nights over the 2022 survey period (range per station: 41–350 days) (Figure 2). Tigers were detected at 51 of 149 stations (34.2%), yielding 183 independent detection events after application of the 20-minute independence filter. The five focal prey species were widely distributed: barking deer occurred at 145 stations (3,168 detections), sambar at 113 stations (2,961 detections), gaur at 105 stations (2,585 detections), wild boar at 110 stations (858 detections), and Himalayan serow at 55 stations (232 detections). Human detections totalled 1,503 independent events across the study area (Table 1).

**Table 1.** Survey effort summary for focal species detected across 149 camera-trap stations in south-central Bhutan, 2022. Stations indicate the number of stations at which each species was independently detected. Total detections are independent events after applying the 20-minute independence filter. Mean RAI represents the mean station-level relative abundance index, calculated as independent detections per 100 trap-nights at occupied stations.

Species	Stations	Total detections	Mean RAI
Barking Deer ( <i>Muntiacus muntjak</i> )	145	3,168	69.51
Sambar ( <i>Rusa unicolor</i> )	113	2,961	217.86
Gaur ( <i>Bos gaurus</i> )	105	2,585	166.21
Wild Boar ( <i>Sus scrofa</i> )	110	858	33.06
Asian Elephant ( <i>Elephas maximus</i> )	92	–	60.47
Himalayan Serow ( <i>Capricornis thar</i> )	55	232	4.72
Tiger ( <i>Panthera tigris</i> )	51	183	21.46
Common Leopard ( <i>Panthera pardus</i> )	72	–	21.33
Dhole ( <i>Cuon alpinus</i> )	59	–	4.15
Human activity	149	1,503	10.56



**Figure 2.** Camera-trap stations across Royal Manas National Park, Phipsoo Wildlife Sanctuary, and Sarpang Forest Division in south-central Bhutan.

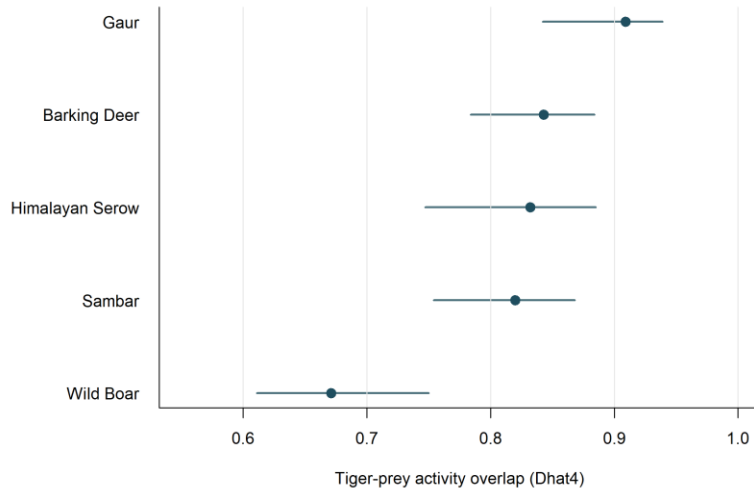
### *Tiger–prey temporal overlap*

Temporal overlap between tigers and focal prey species varied substantially (Dhat4 range: 0.671–0.909; Table 2, Figure 3). Wild boar exhibited the lowest overlap with tiger activity (Dhat4 = 0.671, 95% CI: 0.611–0.750), indicating the greatest degree of temporal separation. Barking deer (Dhat4 = 0.843, 95% CI: 0.784–0.884) and Himalayan serow (Dhat4 = 0.832, 95% CI: 0.747–0.885) showed intermediate overlap, while sambar (Dhat4 = 0.820, 95% CI: 0.754–0.868) was marginally lower. Gaur exhibited the highest temporal overlap with tigers (Dhat4 = 0.909, 95% CI: 0.842–0.939), suggesting minimal temporal avoidance. Bootstrap confidence intervals indicated moderate to high overlap for all prey species, but these intervals should not be interpreted as formal hypothesis tests against complete temporal segregation.

**Table 2.** Tiger–prey temporal overlap coefficients (Dhat4) with 95% bootstrap confidence intervals, median post-tiger prey re-detection interval (RT50, minutes), proportion of sequences occurring within 6 hours of a tiger detection, and exploratory temporal-exposure index for five focal prey species. Species are ordered by temporal-exposure index (highest to lowest).

Prey species	<i>n</i> prey	Dhat4	95% CI	RT50 (min)	Prop. short-lag	Temporal-exposure index
Wild Boar	858	0.671	0.611–0.750	271.9	0.600	0.667
Barking Deer	3,168	0.843	0.784–0.884	438.8	0.500	0.575
Sambar	2,961	0.820	0.754–0.868	458.6	0.424	0.453
Himalayan Serow	232	0.832	0.747–0.885	434.5	0.333	0.404
Gaur	2,585	0.909	0.842–0.939	582.2	0.250	0.333

Note: Tiger detections  $n = 183$ . Dhat4 = coefficient of overlapping. RT50 = median post-tiger prey re-detection interval within a 48-h window. The temporal-exposure index is an exploratory composite score based on standardized Dhat4, inverse RT50, and short-lag proportion, min-max rescaled from 0 to 1 across species.



**Figure 3.** Tiger-prey temporal overlap estimates for five focal prey species in south-central Bhutan. Points show Dhat4 coefficients and horizontal lines show 95% bootstrap confidence intervals.

### Prey return-time dynamics

Median post-tiger prey re-detection intervals revealed a consistent gradient that complemented the overlap results (Table 3). Wild boar was re-detected most rapidly (RT50 = 271.9 min,  $n = 10$  sequences), followed by Himalayan serow (RT50 = 434.5 min,  $n = 3$ ), barking deer (RT50 = 438.8 min,  $n = 6$ ), sambar (RT50 = 458.6 min,  $n = 33$ ), and gaur (RT50 = 582.2 min,  $n = 32$ ). The proportion of sequences occurring within 6 hours of a tiger detection showed a parallel pattern: wild boar had the highest proportion of short-lag re-detections (60.0%), whereas gaur had the lowest (25.0%). Notably, wild boar combined the lowest temporal overlap with the shortest re-detection interval, suggesting that although wild boar activity peaks diverge from tiger activity, wild boar detections reoccurred rapidly at tiger-detection stations. Return-time estimates for Himalayan serow and barking deer should be interpreted descriptively because sequence counts were low. Return-time curves showed faster re-detection of wild boar than other focal prey species following tiger detections (Figure 4).

**Table 3.** Prey re-detection interval statistics following tiger detections at the same camera-trap station within a 48-hour window. RT50 = median post-tiger prey re-detection interval (minutes); P10 and P90 = 10th and 90th percentile re-detection intervals;  $n$  = number of tiger-prey sequences.

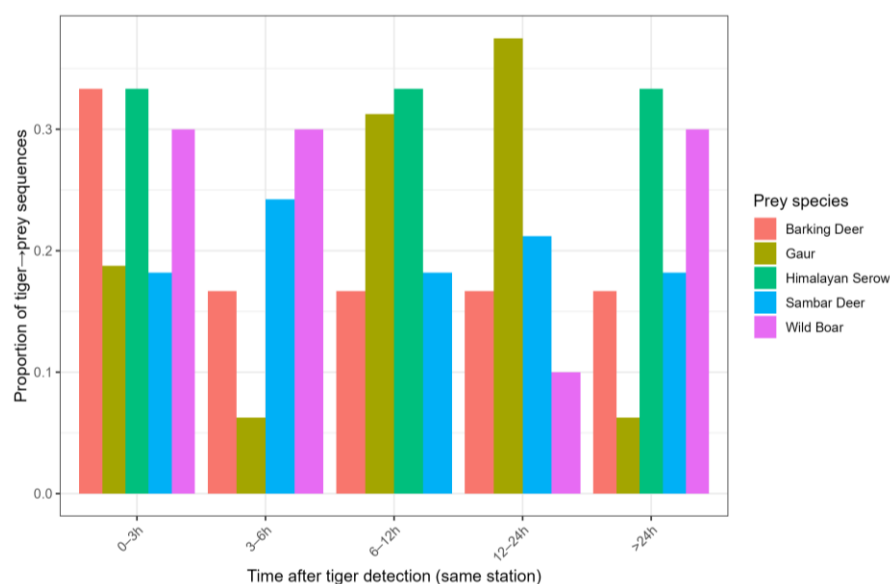
Prey species	$n$ sequences	RT50 (min)	P10 (min)	P90 (min)	Mean lag (min)
Wild Boar	10	271.9	23.1	2,222.4	785.7
Himalayan Serow	3	434.5	88.1	1,710.4	821.8

Prey species	<i>n</i> sequences	RT50 (min)	P10 (min)	P90 (min)	Mean lag (min)
Barking Deer	6	438.8	82.6	1,654.3	725.2
Sambar	33	458.6	78.7	1,887.1	783.8
Gaur	32	582.2	90.7	1,340.5	709.0

*Note:* Estimates based on fewer than 10 sequences should be interpreted descriptively because percentile estimates are unstable at low sample sizes.

### *Composite temporal-exposure index*

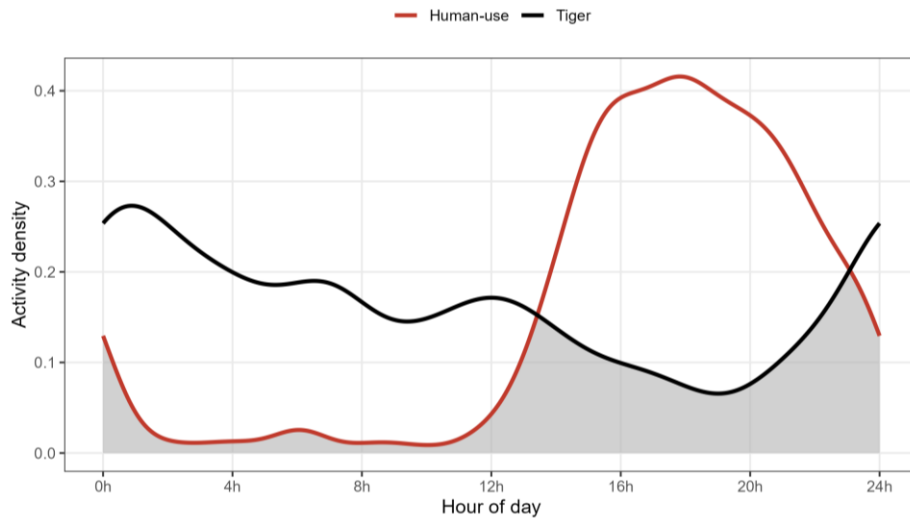
The exploratory composite temporal-exposure index, integrating standardised overlap, inverse post-tiger re-detection interval, and proportion of short-lag sequences, ranked wild boar as the species with the highest exploratory temporal-exposure score (index = 0.667), followed by barking deer (0.575), sambar (0.453), Himalayan serow (0.404), and gaur (0.333) (Table 2).



**Figure 4.** Tiger–prey risk windows showing prey re-detection intervals following tiger detections at the same camera-trap station within a 48-hour window. Each panel represents one focal prey species. The x-axis shows elapsed time since tiger detection; the y-axis shows the cumulative proportion of prey re-detection events.

### *Tiger–human temporal separation*

Tiger and human activity showed pronounced temporal segregation (Dhat4 = 0.397, 95% CI: 0.370–0.490; Figure 5). Human activity was concentrated during daylight hours, while tiger activity was predominantly crepuscular and nocturnal, producing a bimodal non-overlap pattern centred on dawn and dusk transitions. The low overlap coefficient indicates that tigers in this landscape maintain strong diel separation from human activity, with the estimated overlap between tiger and human activity-density curves below 0.40. Full tiger–human overlap statistics are provided in Table S1.



**Figure 5.** Diel activity overlap between tigers (*Panthera tigris*;  $n = 183$  detections) and human activity ( $n = 1,503$  detections) in south-central Bhutan. Kernel density curves show relative activity density across the 24-h diel cycle. The shaded area represents the coefficient of overlapping ( $Dhat4 = 0.397$ , 95% CI: 0.370–0.490).

#### *Nocturnality and human disturbance*

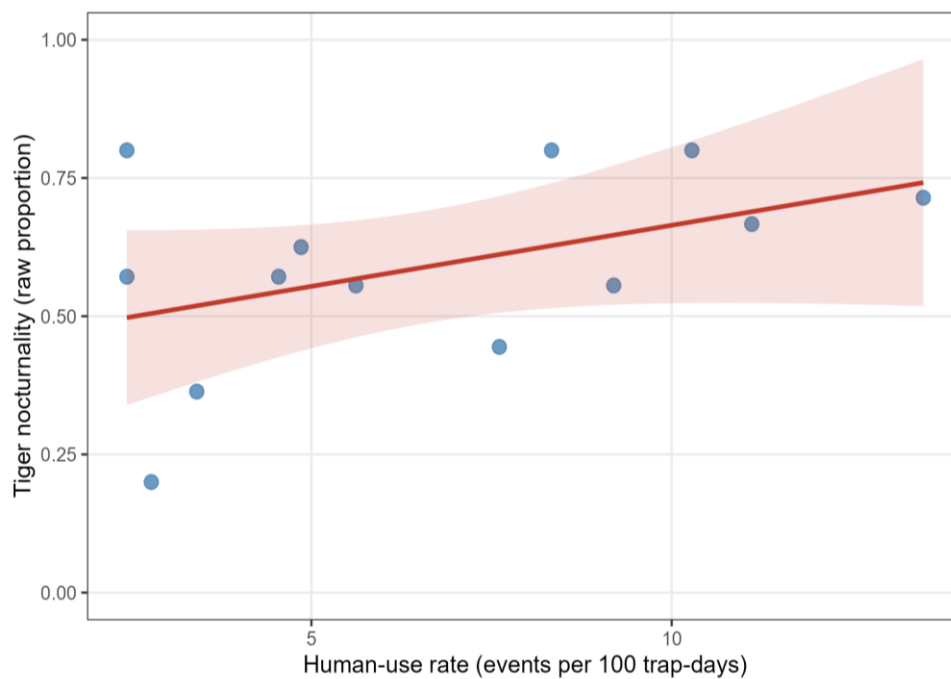
Among the 13 stations meeting the minimum threshold of 5 tiger detections, station-level tiger nocturnality (proportion of detections between 18:00–06:00) ranged from 0.200 to 0.800 (mean = 0.588). Human-use rates at these stations ranged from 2.44 to 13.49 events per 100 trap-days. Beta regression suggested a positive but statistically uncertain association between human-use rate and tiger nocturnality (beta = 0.087, SE = 0.051,  $z = 1.705$ ,  $p = 0.088$ ; Figure 6). The model explained approximately 19.4% of the variation in nocturnality (pseudo- $R^2 = 0.194$ ), and the precision parameter was well-estimated ( $\phi = 9.34$ ,  $p = 0.008$ ). Although the regression coefficient did not reach conventional significance at  $\alpha = 0.05$ , the direction of the association was consistent with the predicted effect of human disturbance on mammal nocturnality, but the small station-level sample prevents confirmatory inference. Larger station-level samples will be required to test this relationship with adequate statistical power. Station-level nocturnality and human-use rates varied substantially among the 13 stations retained for beta regression (Table 4).

**Table 4.** Station-level tiger nocturnality and human-use rates at 13 camera-trap stations with  $\geq 5$  independent tiger detections. Nocturnality = proportion of tiger detections occurring between 18:00–06:00. Human rate = independent human detections per 100 trap-days. Stations are ordered from west (PWS) to east (RMNP).

Station	Tiger detections	Nocturnality	Human rate	Trap-days
PWS_015_Pinkhawashir	9	0.444	7.61	92
PWS_019_Phibsoorateykhari	5	0.800	8.33	108
PWS_023_Kapurkhola	8	0.625	4.86	350
PWS_026_Kapurshir	5	0.200	2.78	108
PWS_028_Sukundeorali	5	0.800	10.28	107
RMNP_021_Badamkhola	11	0.364	3.41	88

Station	Tiger detections	Nocturnality	Human rate	Trap-days
RMNP_025_Bisuki	7	0.571	2.44	82
RMNP_032_Kukulung	9	0.667	11.11	90
RMNP_051_Sukunjan_Top	9	0.556	5.62	89
RMNP_071_Baluakhola	7	0.714	13.49	126
RMNP_074_Zomrong	9	0.556	9.20	87
RMNP_075_Gayhati	5	0.800	2.44	41
RMNP_088_Gelongpani	7	0.571	4.55	88

*Note:* Beta regression results – intercept: -0.225 (SE = 0.373,  $p = 0.547$ ); human\_rate: 0.087 (SE = 0.051,  $z = 1.705$ ,  $p = 0.088$ ); phi = 9.34 (SE = 3.49,  $p = 0.008$ ); pseudo- $R^2 = 0.194$ .



**Figure 6.** Association between station-level human-use rate and tiger nocturnality at 13 camera-trap stations with at least five independent tiger detections. The fitted line represents the beta regression model ( $\beta = 0.087$ ,  $p = 0.088$ , pseudo- $R^2 = 0.194$ ). The positive fitted slope indicates a statistically uncertain trend toward increased tiger nocturnality at stations with higher human activity.

#### **Conditional diel activity at tiger-present versus tiger-absent stations**

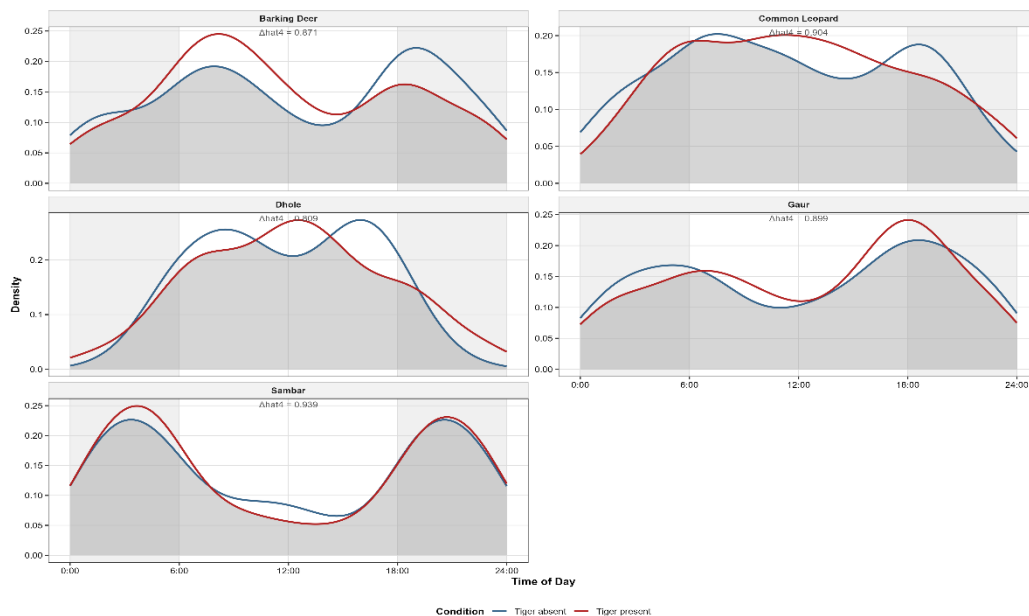
Comparison of diel activity patterns at tiger-present versus tiger-absent stations suggested species-specific responses (Table 5, Figure 7). Dhole showed the strongest apparent temporal shift, with a Dhat4 of 0.809 between tiger-present ( $n = 43$  detections at 21 stations) and tiger-absent station groups ( $n = 80$  detections at 38 stations), indicating moderate divergence in activity patterns in the presence of tigers. This pattern is consistent with, but does not confirm, possible interference avoidance between sympatric carnivores.

In contrast, ungulate prey showed limited conditional temporal adjustment. Sambar maintained highly similar activity patterns regardless of tiger presence (Dhat4 = 0.939,  $n_{\text{present}} = 1,961$ ,  $n_{\text{absent}}$

= 1,000), as did gaur (Dhat4 = 0.899,  $n_{\text{present}} = 1,830$ ,  $n_{\text{absent}} = 755$ ) and barking deer (Dhat4 = 0.871,  $n_{\text{present}} = 1,086$ ,  $n_{\text{absent}} = 2,082$ ). Common leopard, as a subordinate carnivore, showed high overlap between tiger-present and tiger-absent stations (Dhat4 = 0.904,  $n_{\text{present}} = 97$ ,  $n_{\text{absent}} = 125$ ), suggesting that leopard diel activity is relatively insensitive to tiger co-occurrence at the station level.

**Table 5.** Conditional diel activity overlap (Dhat4) comparing activity patterns of five focal species at tiger-present versus tiger-absent camera-trap stations. Dhat4 near 1.0 indicates identical activity patterns regardless of tiger presence; lower values indicate temporal displacement. Species are ordered by degree of temporal shift (lowest Dhat4 first).

Species	Tiger-present stations	Tiger-absent stations	$n$ detections (present)	$n$ detections (absent)	Dhat4	Interpretation
Dhole	21	38	43	80	0.809	Moderate temporal shift
Barking Deer	50	95	1,086	2,082	0.871	Slight temporal shift
Gaur	50	55	1,830	755	0.899	Similar activity
Common Leopard	30	42	97	125	0.904	Similar activity
Sambar	47	66	1,961	1,000	0.939	Highly similar activity



**Figure 7.** Conditional diel activity patterns of five focal species at tiger-present and tiger-absent camera-trap stations. Kernel density curves show relative activity density across the 24-h diel cycle. Dhat4 values indicate the overlap between activity distributions at tiger-present and tiger-absent stations.

### *Moon phase effects and Seasonal community shift*

Moon phase showed no detectable association with nightly detection frequency for nocturnal or crepuscular species (Table S2; Fig. S1). Because this analysis was secondary to the main tiger–prey–human risk-partitioning questions, detailed species-level results are provided in the Supporting Information.

Community-wide activity patterns differed between dry and monsoon-adjacent periods. Shannon diversity was higher during the dry season ( $H' = 2.77$ , 73 species, 16,175 detections) than during monsoon-adjacent months ( $H' = 2.67$ , 43 species, 779 detections). This seasonal contrast likely reflects both genuine changes in animal activity and reduced camera operability during the monsoon. These seasonal summaries are provided as survey context and were not used to infer tiger–prey risk partitioning.

## **Discussion**

### *Multi-dimensional temporal exposure*

The composite index should be interpreted as an exploratory synthesis of temporal exposure, not as a direct estimate of predation risk. The integration of temporal overlap (Dhat4) with post-tiger re-detection intervals (RT50) suggests a nuanced temporal-exposure gradient in which species-specific strategies produce distinct profiles. Wild boar, despite exhibiting the lowest temporal overlap with tigers (Dhat4 = 0.671), was re-detected at tiger-detection stations most rapidly (RT50 = 272 min) and had the highest proportion of short-lag sequences (60%). This pattern – temporal avoidance coupled with rapid station-level re-detection – suggests diel displacement combined with strong station re-use, possibly driven by localised resource dependence on rooting substrates and seasonal food patches. A similar pattern of temporal avoidance with spatial persistence has been documented for wild boar in relation to wolves in European systems (Keuling et al., 2008), suggesting a potentially comparable response across predator systems.

Gaur, by contrast, exhibited the highest temporal overlap (Dhat4 = 0.909) and longest re-detection intervals (RT50 = 582 min). This pattern is consistent with the predation-risk allocation hypothesis (Lima & Bednekoff, 1999), whereby large-bodied prey with lower per-encounter mortality risk tolerate greater temporal co-occurrence with predators while maintaining longer station-level re-detection intervals that reduce cumulative exposure. Gaur body mass (700–1,000 kg) may make adults less exposed to tiger predation than smaller wild boar (50–100 kg), and the energetic costs of temporal displacement may outweigh the marginal reduction in predation risk for such large-bodied species (Creel & Christianson, 2008).

The intermediate positions of barking deer, sambar, and Himalayan serow along both the overlap and return-time gradients suggest a continuum of anti-predator temporal strategies scaled to body size and dietary ecology. Sambar, a preferred tiger prey species across South Asian landscapes (Karanth & Sunquist, 1995), showed moderate overlap (Dhat4 = 0.820) and intermediate return times (RT50 = 459 min), consistent with behavioural flexibility that balances predation avoidance against the costs of altered foraging schedules. These findings align with multi-species studies from central India (Ramesh et al., 2012) and Nepal (Kafley et al., 2019), which reported species-specific variation in temporal overlap with tigers, although direct comparison is complicated by differences in community composition and landscape context.

### *Tiger–human temporal segregation*

The strong temporal separation between tiger and human activity ( $D_{hat4} = 0.397$ ) was lower than several published estimates from more human-dominated tiger landscapes. Carter et al. (2012) reported tiger–human overlap coefficients of 0.50–0.65 in Chitwan National Park, Nepal, where human settlements abut park boundaries and people regularly enter forests for resource extraction. The lower overlap value in south-central Bhutan likely reflects the comparatively limited human presence within Bhutan’s protected area interiors, where permanent settlements are sparse and anthropogenic activity is largely restricted to patrol routes, livestock grazing corridors, and seasonal resource collection.

The beta regression analysis provided suggestive evidence that tiger nocturnality may increase with local human-use intensity (beta = 0.087,  $p = 0.088$ , pseudo- $R^2 = 0.19$ ), a pattern consistent with the global meta-analysis of Gaynor et al. (2018), who reported a mean 1.36-fold increase in nocturnality across 62 mammal species in response to human disturbance. The effect was in the predicted direction but did not reach conventional significance, reflecting the limited number of stations ( $n = 13$ ) with sufficient tiger detections for reliable nocturnality estimation. This result should be interpreted as directionally consistent with human-induced nocturnality, with confirmation requiring either expanded spatial sampling or multi-season data to increase the number of stations meeting minimum detection thresholds.

The observed range of station-level nocturnality (0.20–0.80) is notable in itself, suggesting substantial local variation in tiger diel behaviour that may be driven by a combination of human disturbance, prey availability, and microhabitat characteristics. Stations at the extremes of this range – PWS\_026\_Kapurshir (nocturnality = 0.20) and three stations at 0.80 – present contrasting behavioural profiles that merit investigation in future site-level analyses incorporating habitat covariates.

### *Conditional diel responses: guild-specific strategies*

The conditional diel analysis suggested a distinction between carnivore and ungulate responses to tiger presence. Dhole showed the strongest apparent temporal shift at tiger-present stations ( $D_{hat4} = 0.809$ ), consistent with intraguild interference avoidance. As cooperative pack hunters occupying a similar trophic position to tigers, dhole face both direct mortality risk and competitive displacement at shared prey resources (Kamler et al., 2015). The observed temporal shift suggests that dhole may adjust activity timing in landscapes shared with tigers, a pattern previously documented in central India where dhole shifted to more diurnal activity in zones of high tiger density (Ramesh et al., 2012).

Ungulate prey species – barking deer, sambar, and gaur – showed minimal conditional temporal adjustment ( $D_{hat4} = 0.871$ – $0.939$ ), suggesting that these species maintain relatively fixed diel activity patterns regardless of local tiger presence. This stability may reflect phylogenetic constraint on circadian rhythms, the high energetic cost of temporal displacement for large herbivores, or the fact that station-level tiger presence (a binary classification) is too coarse a metric to capture the fine-scale temporal risk perception that might trigger behavioural shifts. Alternative explanations include the possibility that ungulates employ spatial rather than temporal avoidance at fine scales, adjusting microhabitat use rather than activity timing in response to predator cues (Fortin et al., 2005).

Common leopard showed high activity overlap between tiger-present and tiger-absent stations ( $D_{hat4} = 0.904$ ), consistent with findings from other South Asian landscapes where leopards exhibit temporal flexibility but do not strongly partition activity in response to tiger co-occurrence (Harihar et al., 2011). The relatively high overlap may reflect spatial partitioning (leopards using different microhabitats within the same station grid cell) rather than temporal displacement as the primary mechanism of coexistence.

### *Moon phase as a minor influence*

Moon phase showed no detectable relationship with nocturnal detection frequency in this dataset. One possible explanation is that closed-canopy forest reduces biologically relevant variation in lunar illumination, although canopy-level light availability was not measured.

### *Comparison with other tiger landscapes*

The temporal dynamics observed in south-central Bhutan share broad similarities with other tiger range landscapes while exhibiting distinctive features. Tiger–prey overlap values in this study ( $D_{hat4} = 0.671–0.909$ ) span a wider range than those reported from Chitwan (0.60–0.85; Carter et al., 2015) or central India (0.65–0.80; Ramesh et al., 2012), likely reflecting the greater diversity of prey body sizes in this study system, which includes both small-bodied wild boar and megaherbivore gaur. The relatively low tiger–human overlap (0.397) distinguishes this landscape from more human-dominated tiger habitats in India and Southeast Asia, where overlap values frequently exceed 0.50 (Carter et al., 2012; Nickel et al., 2020). This contrast underscores the conservation significance of Bhutan’s protected area network in maintaining conditions under which tiger–human temporal segregation can persist without the severe activity compression observed in more degraded landscapes.

### **Conservation Implications**

The temporal risk partitioning documented here carries direct implications for tiger conservation and human–wildlife coexistence planning in Bhutan’s protected area network. First, the strong tiger–human temporal segregation ( $D_{hat4} = 0.397$ ) indicates that current human activity levels have not eliminated strong tiger–human diel segregation, but the suggestive nocturnality–human-use relationship warns that incremental increases in human activity could progressively compress tiger activity into narrower nocturnal windows. Future monitoring could evaluate whether increasing human-use rates correspond to measurable tiger activity compression and could inform site-specific access management.

Second, the species-specific temporal-exposure rankings identify wild boar as the prey species with the highest exploratory temporal-exposure score, a finding with implications for both tiger diet studies and ungulate management. Wild boar population monitoring should be prioritised alongside preferred prey species (sambar, barking deer) to ensure that the prey base supporting tiger populations remains adequate.

Third, the dhole temporal shift at tiger-present stations highlights the potential for intraguild effects to cascade through the carnivore community. Conservation planning that focuses exclusively on tiger–prey dynamics may overlook important competitive interactions that structure mesocarnivore behaviour and, ultimately, community composition.

Finally, the initial behavioural reference condition established by this study provides a temporal reference for a relatively undisturbed Himalayan tiger landscape. As anthropogenic pressures intensify across Bhutan’s southern border zone, repeat surveys using identical methods will

enable detection of temporal niche compression, altered prey exposure rankings, or erosion of tiger–human temporal segregation – each serving as an early-warning indicator of declining habitat quality.

### **Limitations**

Several limitations constrain the scope of inference. First, this study represents a single survey season (2022), precluding analysis of inter-annual variation in temporal dynamics or assessment of population closure. Multi-season data would enable dynamic occupancy modelling and permit evaluation of whether observed temporal patterns are stable or responsive to annual fluctuations in prey density, human activity, or climate. Results are framed as a cross-sectional behavioural snapshot under the assumption of population closure within the survey period (MacKenzie et al., 2002).

Second, the beta regression of tiger nocturnality against human-use rate was limited to 13 stations meeting the minimum detection threshold, substantially constraining statistical power. The marginal significance ( $p = 0.088$ ) and moderate explanatory power (pseudo- $R^2 = 0.19$ ) should be interpreted as hypothesis-generating rather than confirmatory. Future studies should aim to increase the number of high-detection stations through optimised camera placement and extended survey duration.

Third, temporal overlap (Dhat4) quantifies the similarity of activity distributions but does not directly measure encounter probability or predation risk. High overlap between a predator and prey species indicates temporal co-activity but does not account for spatial segregation at scales finer than the camera-trap station, habitat-mediated encounter rates, or individual-level variation in behaviour. The return-time analysis partially addresses this limitation by capturing a finer temporal resolution of predator–prey sequences, but inference about predation risk from camera-trap data alone remains correlative.

Fourth, the composite temporal-exposure index is exploratory and has not been externally validated as a predation-risk metric. Therefore, species rankings should be interpreted as comparative exposure patterns rather than direct estimates of mortality risk.

Fifth, the tiger-present versus tiger-absent classification is a coarse station-level contrast and does not measure continuous predation risk, tiger density, or fine-scale encounter probability.

Sixth, the 20-minute independence threshold, while consistent with standard protocols, may not be optimal for all species. Larger-bodied species with slower movement rates may require longer intervals to ensure independence, whereas highly mobile species may achieve independence more rapidly. Sensitivity analyses at 30- and 60-minute thresholds are presented in the Supporting Information.

Seventh, camera-trap detection probability is species-specific and may be influenced by body size, movement speed, and habitat use, potentially biasing activity density estimates. This issue was partially addressed by restricting analysis to species with sample sizes exceeding the minimum recommended for Dhat4 estimation (Ridout & Linkie, 2009) and by reporting bootstrap confidence intervals that incorporate sampling uncertainty.

## Conclusion

This study suggests that temporal risk partitioning among tigers, prey, and human activity in south-central Bhutan is species-specific, multi-dimensional, and structured by both natural predation dynamics and anthropogenic influence. The integration of temporal overlap analysis with post-tiger re-detection intervals suggests that prey temporal exposure cannot be reduced to a single axis: wild boar combine low temporal overlap with rapid station-level re-detection, while gaur tolerate high overlap but show longer re-detection intervals. Tiger–human temporal segregation remains strong in this comparatively undisturbed landscape, though the positive relationship between human-use intensity and tiger nocturnality signals a potential mechanism for behavioural compression under future development scenarios. The whole temporal shift at tiger-present stations highlights intraguild dynamics as an underappreciated component of carnivore community structure.

These findings contribute to a growing body of evidence that temporal niche dynamics are central to predator–prey coexistence and that camera-trap-derived activity data, when analysed through complementary statistical lenses, can reveal behavioural mechanisms operating below the resolution of traditional occupancy or density estimation. The initial behavioural reference condition established here for a Himalayan tiger landscape provides a reference for long-term monitoring and positions south-central Bhutan as a priority landscape for multi-season studies of temporal coexistence dynamics.

## Data Availability

Data and analytical code supporting this study are archived in the project repository at [https://github.com/wangdiues/camtrap\\_ecology\\_analytics](https://github.com/wangdiues/camtrap_ecology_analytics). The reproducible pipeline includes camera-trap processing scripts, statistical analysis code, figure generation scripts, and package dependency files necessary to reproduce the results reported here. Processed detection tables required to reproduce the analyses are available where disclosure does not compromise sensitive species-location information; raw camera-trap images and exact sensitive-location records are available only through data-governance approval from the Department of Forests and Park Services, Royal Government of Bhutan.

## Author Contributions

All authors contributed to study design, field logistics, data collection, analysis, interpretation, and manuscript revision. The lead author conceived the study, processed the camera-trap data, performed the statistical analyses, and drafted the manuscript. All authors approved the final version for submission.

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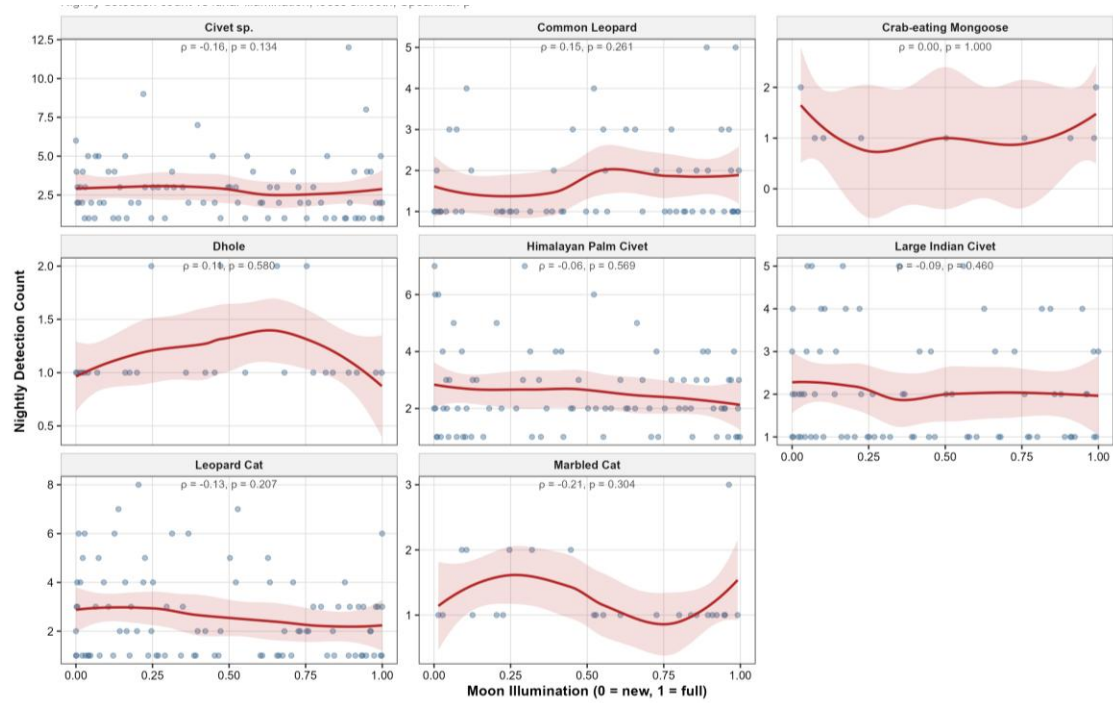
### Supporting Information

**Table S1.** Tiger–human temporal overlap summary. Dhat4 = coefficient of overlapping estimated from kernel density functions of detection timestamps.

Species pair	<i>n</i> tiger	<i>n</i> human	Estimator	Dhat4	95% CI lower	95% CI upper
Tiger – Human	183	1,503	Dhat4	0.397	0.370	0.490

**Table S2.** Spearman rank correlations between nightly detection frequency and lunar illumination index for eight nocturnal and crepuscular mammal species. Rho = Spearman’s correlation coefficient; *n* = number of detection-nights. No correlations were statistically significant at alpha = 0.05.

Species	Rho	<i>p</i> -value	<i>n</i> detection-nights
Common Leopard	0.204	0.131	56
Dhole	0.114	0.580	26
Crab-eating Mongoose	0.000	1.000	9
Himalayan Palm Civet	-0.063	0.569	83
Leopard Cat	-0.083	0.444	88
Large Indian Civet	-0.086	0.460	76
Civet sp.	-0.164	0.134	85
Marbled Cat	-0.214	0.304	25



**Figure S1.** Relationship between lunar illumination and nightly detection frequency for nocturnal and crepuscular mammal species. No significant correlations were detected.