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Posted Date: September 29th, 2026

DOI: https://doi.org/10.21203/rs.3.rs-10826412/v1

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Additional Declarations: No competing interests reported.

Chronoecology of sympatric wildlife: Niche segregation of the Ratel (*Mellivora capensis*) in Mitiyala Wildlife Sanctuary, Gujarat, India

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Abstract

Temporal segregation reduces the interspecific and intraspecific competition, enhancing the survival of sympatric species sharing spatial overlap. This study investigates the diel activity patterns of the Ratel (*Mellivora* capensis) and evaluates its temporal niche segregation relative to sympatric ungulates and large carnivores in the Mitiyala Wildlife Sanctuary. Using camera traps data collected across the sanctuary, we recorded independent detections of Ratels and potential competitors. We analysed activity patterns using circular Kernel density estimation and calculated temporal overlap coefficients alongside Watson's circular statistics (U^2) to test significant differences in activity timing. The Ratels was found to be predominantly nocturnal, with peak activity concentrated between 21:00 h and 03:00 h. We observed low to moderate temporal overlap with large ungulates, such as Chital (*Axis axis*, $\Delta = 0.22, p < 0.001$), Sambar (*Rusa unicolor*, $\Delta = 0.16, p < 0.001$) and Wild Boar (*Sus scrofa,* $\Delta = 0.34, p < 0.001$). While in the case of large carnivores, in comparison with the Asiatic Lion (*Panthera leo persica*, $\Delta = 0.36, p < 0.001$), there was less overlap with the Ratel, while Watson's circular statistics state $U^2 = 1.89$, and it was $\Delta = 0.39, p < 0.001;$ $U^2 = 1.23$ for the Indian leopard (*Panthera pardus fusca*). These findings demonstrate that the Ratel employs strict nocturnal temporal partitioning to minimise direct encounters with dominant carnivores and large ungulates. Such niche segregation plays a crucial role in facilitating sympatric coexistence and reducing competition in semi-arid protected ecosystems.

Keywords: Camera trapping; Coexistence; Diel activity; Hierarchical clustering; Intraguild avoidance

Behavioural adjustments, Camera trapping, Circular statistics, Diel segregation, Niche complementarity.

Introduction

The mechanisms that allow sympatric species to coexist in complex ecological communities continue to be a major focus for evolutionary ecologists and conservation biologists. Based on the classical concept and Gause's competition exclusion principle, two or more species have no chance at a stable long-term coexistence if they occupy exactly identical ecological niches and share limited resources (Weber and Strauss, 2016). In order to avoid competitive exclusion or predation, sympatric wildlife species usually segregate along one or more of the three main niche axes (spatial, dietary or temporal). Although there has been considerable interest in

spatial and dietary segregation, recent technological advances, such as non-invasive monitoring devices, have focused attention on temporally-based resource use behaviour (the 24-hour diel cycle) as a flexible dynamic axis by which species can manipulate their co-occurrence (Ferreiro-Arias et al., 2021; Proudman and Allen, 2025; Watabe et al., 2022). For most semi-arid organisms, this seasonal nature of recurrence can create an array of environmental challenges, such as high seasonal temperatures, high levels of environmental degradation, etc., which influence the potential extent to which the organism will receive its resources (Luzuriaga et al., 2012). Also, with apex predators being the primary top-down force acting on these semi-arid landscapes, they pose an extreme modern-day dynamic pressure for smaller and more vulnerable mammals living within that same ecosystem. Consequently, those organisms that may be subject to top-down forcing will undergo extremely flexible behaviour, by employing both fine-scale temporal shifts and very rigid nocturnal foraging strategies to optimise their foraging efforts or decrease their frequency of interaction with the apex predators that would exploit them due to their competitors or prey (Burgos et al., 2026; Ferretti et al., 2023; Palomo-Munoz et al., 2024).

The Saurashtra peninsula in Gujarat is a remarkable area of western India and provides a unique landscape with many opportunities to examine the behavioural dynamics present in this semi-arid ecosystem. This region is home to the only extant population of Asiatic Lion (*Panthera leo persica*); as such, there is a large area of the region with a growing population of its wildlife as they begin to expand their range into smaller, fragmented protected areas and satellite habitats surrounding the core of their area, i.e., Gir National Park and Wildlife Sanctuary. In addition, these smaller protected areas are now acting as critical structural corridors between the core habitats, thereby creating a very high density of various mammals coexisting in a very small geographic area. In addition to this compact spatial conformation, the availability of large areas of space between the top-tier felids, various mesocarnivores and a diverse range of prey categories has been reduced in size, creating the physical constraints necessary for large-scale spatial avoidance (Cong et al., 2024). As a consequence of this, wildlife residing in the satellite forests will need to rely more on fine-scale, behavioural adjustments and temporal niche adjustments to reduce competition and conflict than wildlife in the core environments, and therefore, this area is considered one of the suitable areas for chronoecological studies.

Honey Badgers (*Mellivora capensis*), also known as Ratel in some areas, are an appealing species for assessing fine-scale trade-offs in behaviour. Ratel populations are found all over Africa and extending into the Middle East and India; they represent a widely diverse group of highly adaptable, fossorial mesocarnivores that rely on a large spectrum of food sources (opportunistic feeders) and defend themselves very aggressively. Although Ratels are remarkably strong with physical resilience, they co-occur in habitats populated with large carnivores such as lions and leopards in the small, closely packed landscapes of the Saurashtra satellite zone of India, as well as a dense guild of competing mesocarnivores and diverse prey species. However, because of their elusive nature and naturally low densities, there has been little research conducted on the community-level relationships of Ratels within protected areas in India using quantitative methods. The compact size and unique ecosystem of the Mitiyala Wildlife Sanctuary (hereafter Mitiyala) make it an important region for filling this research

gap. Mitiyala is also a critical wildlife corridor and satellite habitat that supports a high density of sympatric vertebrates within its area. The high spatial density increases the potential for overlap, and therefore, species depend on fine-scale behavioural evolutions instead of using broad spatial avoidance to avoid each other. This study, with the help of camera trapping, aims to determine the chronological structure of Mitiyala Wildlife Sanctuary (Jiang et al., 2025). This also fills the gap of how the daily activity pattern of the Ratel is structured, focusing on the interaction and avoidance with competing nocturnal and diurnal guilds. This research provides important empirical data on behavioural mechanisms that drive community stability across high-priority conservation areas within Western India.

Study area

The Mitiyala Wildlife Sanctuary is an important protected area in Amreli district of the Saurashtra region of Gujarat, covering 1822 ha of protected habitat, located in the semi-arid biogeographic zone of Western India. The sanctuary includes rough, hilly terrain with dry seasonal streams spanning over (21°9′30″– 21°12′0″E and 71°13′30″– 71°18′0″N). The climate of this region is semi-arid and tropical with three main seasons, i.e., hot and dry summer (March to June), variable monsoon (July to September), and mild winter (October to February). The temperature ranges from 8°C in winter to approximately 50°C during the peak summer, with the average annual rainfall between 500mm and 700mm. Mitiyala consists primarily of two forest types: northern tropical dry deciduous forest and southern thorn forests. The dominant trees in the canopy include *Senegalia senegal, Anogeissus latifolia, Ziziphus mauritiana*, *and Butea monosperma,* along with the areas of dense thorn scrub and large areas of seasonal grasslands. This unique mixture of plant life provides structural diversity in terms of habitats that support an array of wildlife species. Also, it functions as an important environmental link, or corridor, between other fragmented patches, facilitating wildlife movement towards suitable habitats, helping to ensure the continued genetic and spatial flow of species to all regions of the Saurashtra peninsula within the larger Gir conservation area (Kaushal et al. 2026).

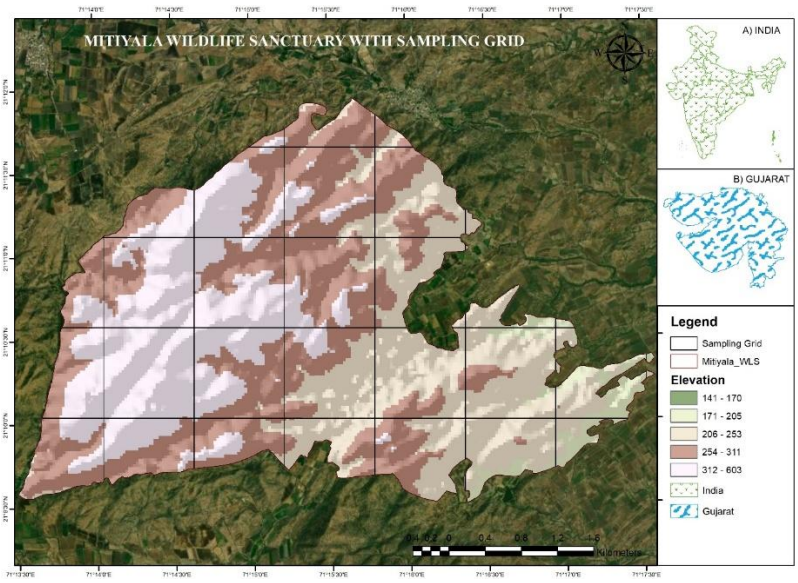


Figure 1 Mitiyala Wildlife Sanctuary with sampling grids; map insets A) India and B) Gujarat

The Mitiyala is home to many higher vertebrates, including apex predators such as the Asiatic Lion (*Panthera leo persica*) and Indian leopard (*Panthera pardus fusca*), that coexist with a group of mesocarnivores, including the study species (Ratel/Honey Badger *Mellivora capensis*), the Striped Hyaena (*Hyaena hyaena*), the Jungle Cat (*Felis chaus*), the Small Indian Civet (*Viverricula indica*) and three mongoose species (*Urva spp*.). Additionally, herbivores as prey are represented by structured populations of Chital (*Axis axis*), Sambar (*Rusa unicolor*), Nilgai (*Boselaphus tragocamelus*), Wild Boar (*Sus scrofa*) and Indian Crested Porcupine (*Hystrix indica*) and the vulnerable Chausingha or Four-horned Antelope (*Tetracerus quadricornis*). It also harbours the endangered scaly anteater, the Indian Pangolin (*Manis crassicaudata*). Avian species, specifically the Indian Peafowl (*Pavo cristatus*), also utilise the understory and canopy strata within the sanctuary area and also serve as prey base for leopards (Sehgal et al., 2022). Due to the sanctuary being small, with a high density of sympatric predators and prey, Mitiyala is an appropriate landscape to investigate the fine-scale temporal niche partitioning and behavioural coexistence mechanisms of mesocarnivores.

Methodology

To systematically capture the fine-scale activity patterns of the Ratel (*Mellivora capensis*) and its sympatric community, an intensive gridded camera-trapping methodological approach was implemented across a 1822 ha landscape of the Mitiyala Wildlife Sanctuary. The sampling was conducted from April 2024 to August 2025. The entire study area was overlaid with a standardised grid system consisting of 1 km×1 km sampling blocks. Within each grid, a Cuddeback (C1 and IR20) passive motion-triggered infrared camera trap unit was deployed at or as close as topographically feasible to the geometric centroid of the grid cell to ensure even and unbiased spatial coverage (Kühl et al., 2023; Woodgate et al., 2023). To maximise detection probabilities for elusive, low-density and nocturnal species, this systematic grid array was augmented by placing additional camera traps strategically at highly frequented wildlife features, including perennial and seasonal water points. All camera traps were securely tightened to the sturdy tree trunks at a uniform height of 30-40cm above the ground, adjusted parallel to the substrate to guarantee the effective capture of varying animal body sizes ranging from the small rodents and mesocarnivores to the large apex felids and ungulates (Cusack et al., 2015; Tanwar et al., 2021). The camera traps were set to operate continuously for 24 hours a day, and each unit was placed for at least 10 days at a location. If the detection rate was found to be higher at any single location, the sampling was increased to 5±2 days based on the species and detection probability. Camera traps were set to trigger at FAP mode with a delay of ½ seconds between each capture, the sequence at burst mode of 3 consecutive photos upon detection, followed by 20-30 second videos while maintaining data management efficiency to minimise the missing probabilities (Forrester et al., 2016; Lepard et al., 2018; Palencia et al., 2021).

To reduce the probability of data loss, memory cards and raw image repositories were retrieved from the deployed camera traps at regular intervals or upon completion of the sampling period. To automate the extraction of rigorous structural metadata embedded within thousands of raw media files, we utilised the *exif* and *camtrapR* packages within R programming software RStudio ($version$ 4.3.1) (Niedballa et al., 2016). This automated pipeline extracted the exact

image captured dates and timestamps ($00:00 - 24:00$ h) and unique camera trap IDs in the subfolders of each location separately, directly from the Exchangeable Image File Format (EXIF) headers of each graphic file, eliminating manual human entry data loss (Ivan and Newkirk, 2015). Following the metadata extraction, the massive image database was processed through a machine learning computer vision workflow to accelerate and refine species classification (Blair et al., 2024). We deployed MegaDetector (v5), a deep learning convolutional neural network (CNN) optimised specifically for wildlife camera trap datasets, to automatically filter out empty frames (false triggers caused by vegetation movement or sun glints) and isolate frames containing animals (Vélez et al., 2022). Once animal presence was flagged, the images were run through an open-source object detection and classification model framework (YOLOv8) to generate initial taxonomic identity tags. All automated computer vision classifications were subsequently subjected to double-blind manual review by the researcher to assure 100% taxonomic accuracy before downstream statistical computation (Dave et al., 2023).



Figure 2 Graphical representation of the methodology

To satisfy the underlying assumptions of circular statistical models and eliminate the severe inflation of the sampling metrics caused by stationary individuals or animals resting in front of the camera traps, the verified species dataset was subjected to temporal independence filtering (Lee et. al., 2022). Photographic captures of a given species at any single camera station were compressed into a single independent observation event if they satisfied at least one of the following strict criteria:

- Consecutive photographs of different individuals that could be clearly and unambiguously distinguished via unique natural markings or morphological traits.
- Consecutive photographs of the same individual separated by a minimum threshold interval of 30 minutes.
- Accumulative photographs captured after a prolonged, verified absence of activity by that species at the specific camera location.

The resulting filtered dataset comprising independent records with precise timestamps linked to verified species identities was structured into a clean community matrix model (Niedballa et al., 2019; Treilibs et al., 2016).

Data Analysis

All quantitative assessments of temporal niche ecology and community-wide interactions were executed using RStudio (v 4.3.1; $RCoreTeam$). Structural image metadata extraction with exact data, timestamps and identified species with chronological data filtering was streamlined via the $tidyverse$ suite (primarily $dplyr$ and $lubridate$) (Moeller and Lukacs, 2021). Non-parametric kernel density schedules and continuous daily activity budgets were modelled using the $overlap$ package. Inferential statistics for testing differences in circular distribution shapes and locations were calculated using the $circular$ package (Ferretti et. al., 2012; Rowcliffe et al., 2014). Finally, two-way hierarchical clustering computations and distance matrices were processed using the core $stats$ package, with advanced multi-panel visual representations and matrices generated via $ggplot2$.

To reconstruct and visualise the daily activity curves of individual species without imposing arbitrary parametric constraints, we applied non-parametric kernel density estimation. Because time is periodic, a standard linear Gaussian kernel causes a boundary at midnight (Gilbert and Dominoni, 2025). Therefore, we utilised the von Mises kernel (the circular equivalent of the normal distribution) to model the continuous 24-hour activity probability density function $\hat{f}(t)$:

$$\hat{f}(t) = \frac{1}{2\pi n I_0(\kappa)} \sum_{i=1}^{n} \exp[\kappa \cos(t - \theta_i)]$$

Where n is the number of independent photographic captures for the target species, θ_i represents the individual independent capture timestamps transformed into radians ($0 \leq \theta_i < 2\pi$), κ is the smoothing parameter functioning as the circular bandwidth, and $I_0(\kappa)$ is the modified Bessel function of the first kind of order zero acting as the normalising constant (Rowcliffe et al., 2014). To evaluate the central tendency and temporal predictability of these daily budgets, circular data vectors were tracked. We calculate the mean circular direction (μ) to identify the absolute peak activity hour, alongside the mean vector length (r). The r statistic ranges from 0 to 1; values approaching 1 signify an extremely tight, highly predictable concentration of animal activity around a specific hour, whereas values near 0 indicate completely uniform, cathemeral distribution across the diel cycle (Blanco et. al., 2016).

To quantify the descriptive degree of temporal niche sharing between the focal Ratel ($\hat{f}(t)$) and the remaining sympatric species ($\hat{g}(t)$), non-parametric coefficient of overlap (Δ) models were calculated using the $overlap$ package in R. The Δ_1 estimator was applied for species pairs where the smaller sample size was less than 75 independent records ($N < 75$), mapping the area under the minimum of the two estimated density functions:

$$\Delta_1 = \int_0^{2\pi} \min\left[\hat{f}(t), \hat{g}(t)\right] dt$$

Conversely, the Δ_4 estimator was utilised for pairs featuring large datasets ($N \geq 75$) calculated as:

$$\Delta_4 = \frac{1}{2}\left(\frac{1}{n}\sum_{i=1}^{n}\min\left[1, \frac{\hat{g}(\theta_i)}{\hat{f}(\theta_i)}\right] + \frac{1}{m}\sum_{j=1}^{m}\min\left[1, \frac{\hat{f}(\phi_j)}{\hat{g}(\phi_j)}\right]\right)$$

Where θ_i and ϕ_j are the radian observation vectors of species A (sample size n) and species B (sample size m) (Zanni et al., 2020), respectively. The resulting overlap coefficient ranges from 0 (absolute temporal segregation) to 1 (identical daily schedules). To determine whether these descriptive overlap scores represented statistically significant differences in underlying circular distributions rather than random sampling variations, Watson's Two-Sample Test of Homogeneity (U^2) was executed. This non-parametric test evaluates the null hypothesis that two independent circular distributions are drawn from the same population ($H_0: F(t) = G(t)$) by calculating the mean square deviation of the joint empirical cumulative distribution function:

$$U^2 = \frac{nm}{N^2}\left[\sum_{i=1}^{n}\left(d_i - \bar{d}\right)^2 + \sum_{j=1}^{m}\left(e_j - \bar{e}\right)^2\right]$$

Where $x_1, x_2, \ldots, x_n$ and $y_1, y_2, \ldots, y_m$ are the ranks of the combined observations ($N = n + m$) in clockwise order, $d_i \; and \; e_j$ represent the adjustments of the empirical step functions relative to the ranks of the combined observations around the perimeter of the circle, and $\bar{d}$ and $\bar{e}$ are the respective arithmetic means of those deviations. This adjustment ensures the static remains invariant regardless of which clock hour is selected as the origin ($00{:}\,00$ h) (Mutwiri et al., 2016). To interpret the overarching chronoecological organisation of the entire Mitiyala vertebrate community, a multi-dimensional scaling approach was used. A comprehensive distance matrix was built using pairwise Euclidean distances derived across the continuous temporal overlap densities of all recorded species. Using the matrix, a two-way hierarchical cluster analysis was performed via a complete-linkage algorithm. The output was mapped as a dual dendrogram similarity tree flanking an overlap intensity heatmap, allowing for the objective, mathematical classification of the wildlife community into distinct behavioural blocks and shared temporal guilds (Kyaw et al., 2021; Smith et al., 2023).

Results

The systematic camera trap-based study in Mitiyala helped in establishing a very distinct structure and specialisation of the diel schedule of activity of 19 sympatric vertebrate species (Wang et al., 2025) (Figure 1). The effective segregation of the wildlife community according to the circular distribution of activity and mean vector analysis resulted in three temporal guilds, namely nocturnal, diurnal, and cathemeral or crepuscular generalist species (Botts et al., 2020; Lucherini et al., 2009). In the case of the focal species of this study, Ratel (*Mellivora capensis*), the diel schedule of activity is almost completely nocturnal. The mean circular vector of *M. capensis* is oriented strictly towards midnight ($\mu \approx 00{:}00$ h), demonstrating high concentration (r), which indicates the temporal predictability of the schedule of activity and

total exclusion from day hours. The strictly nocturnal strategy of the Ratel coincides very precisely with several other key species of the mammalian community of the sanctuary (Grabowski et al., 2024). The Indian Crested Porcupine (*Hystrix indica*), Small Indian Civet (*Viverricula indica*), Indian Gerbil (*Tatera indica*) and Indian Pangolin (*Manis crassicaudata*) all revealed tightly concentrated activity schedules during $20{:}00 - 04{:}00$ h, and their mean vectors are concentrated on the midnight vector. On the other hand, there were distinctive directional differences in the vectors for their mean activity, with leopards showing strong tendencies towards late night and early morning, possibly indicating temporal segregation among species of the high-ranking carnivore guilds in order to reduce any interactions. In contrast with the nocturnal guild, a distinct diurnal guild was found during the day with complete temporal segregation from the nocturnal guilds. The Indian Peafowl (*Pavo cristatus*) is known to be diurnal in its pattern, as indicated by independent captures which started immediately after dawn ($\sim 06{:}00\ h$) and ended at dusk ($\sim 18{:}00h$), leading to a mean activity vector arrow directed into the early afternoon. Likewise, other examples of diurnal ungulates, such as Chausingha (*Tetracerus quadricornis*) and Nilgai (*Boselaphus tragocamelus*), had definite day activities. Their rose diagram is characterised by long, clear vectors directed towards the mid-morning and early afternoon, respectively (Figure 1).

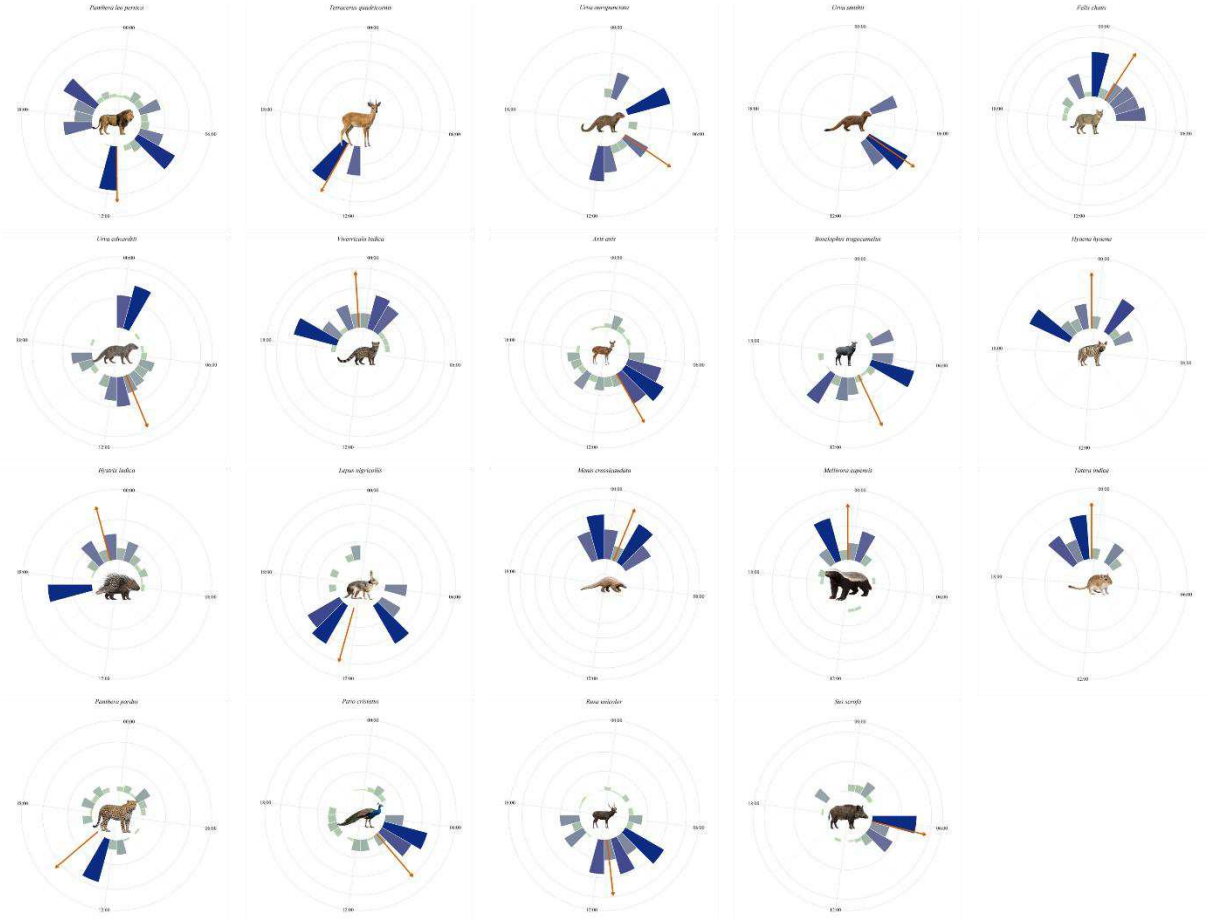


Figure 3 Diel activity patterns of the mammalian community in Mitiyala Wildlife Sanctuary

A number of species showed a more flexible behaviour, characterised by multi-peaks and cathemeral activity, linking together the guilds of day-active and night-active mammals. The

mongoose guild, consisting of the ruddy mongoose (*Urva smithii*), Indian Grey Mongoose (Urva edwardsii) and Small Indian Mongoose (*Urva auropunctata*), had different levels of crepuscular and diurnal activity, and their mean vectors were directed at different angles in the middle morning and late afternoon periods. The Jungle Cat (*Felis chaus*) had a distributed cathemeral activity, with a distinct peak at dawn and dusk. In parallel, the large herbivores such as Chital (*Axis axis*), Sambar (*Rusa unicolor*) and Wild Boar (*Sus scrofa*) also had a broad multi-peak activity pattern. *Sus scrofa* specifically had a very diverse distribution of captures during the night and twilight, ending with an early morning mean vector ($\sim 06{:}00\,h$) indicating a short dependence on crepuscular activity peaks.

Temporal niche differentiation between the *Mellivora capensis* and the other species of vertebrates at Mitiyala was achieved through pairwise kernel density estimations and with the non-parametric overlap calculations (Δ) (Figure 2). The highly inflexible nocturnal behaviour of the Ratel formed very high temporal segregation from most diurnal animals. Temporal pairwise analysis of the Ratel with the diurnal ungulates, including the Chausingha (*Tetracerus quadricornis,* $\Delta = 0.02$) and Nilgai (*Boselaphus tragocamelus,* $\Delta = 0.13$) and the diurnal Indian Peafowl (*Pavo cristatus,* $\Delta = 0.21$), indicated very little similarity in their activity patterns, Watson's two sample tests on comparison with these groups yielded highly significant results ($p < 0.001$), clearly indicating that these groups have complete segregation in their diurnal niches. In a similar way, the Ratel showed a very high degree of temporal segregation as compared to the mongoose guild in the sanctuary that occupies the crepuscular and daytime period. Low to moderate levels of overlap were observed in case of the Ruddy Mongoose (*Urva smithii*, $\Delta = 0.11$), Indian Grey Mongoose (*Urva edwardsii,* $\Delta = 0.41$) and Small Indian mongoose (*Urva auropunctata,* $\Delta = 0.3$). all three cases displayed very high degree of deviation from their underlying circular distribution by Watson's U^2 test statistics ($p < 0.001$). The mongooses have strong peaks during the mid-morning and late afternoon periods, whereas the Ratel moves only during the nighttime. However, the Ratel was observed having a large temporal overlap and synchronicity with other nocturnal carnivores and herbivores found in the sanctuary. The highest overlap value was recorded for the association between the Ratel and the Small Indian Civet (*Viverricula indica,* $\Delta = 0.72$), which was closely followed by the Indian Crested Porcupine (*Hystrix indica,* $\Delta = 0.71$) and the Indian Gerbil (*Tatera indica*, $\Delta = 0.86$). In this case, the circular distributions of the aforementioned pairs did not differ significantly from each other ($p > 0.05$), thus showing that all three species have the same activity period centred at midnight. Besides that, the Ratel had a high to moderate

temporal symmetry with the Jungle Cat (*Felis chaus,* $\Delta = 0.66, p < 0.01$) and the Striped Hyaena (*Hyaena hyaena*, $\Delta = 0.68, p > 0.05$).

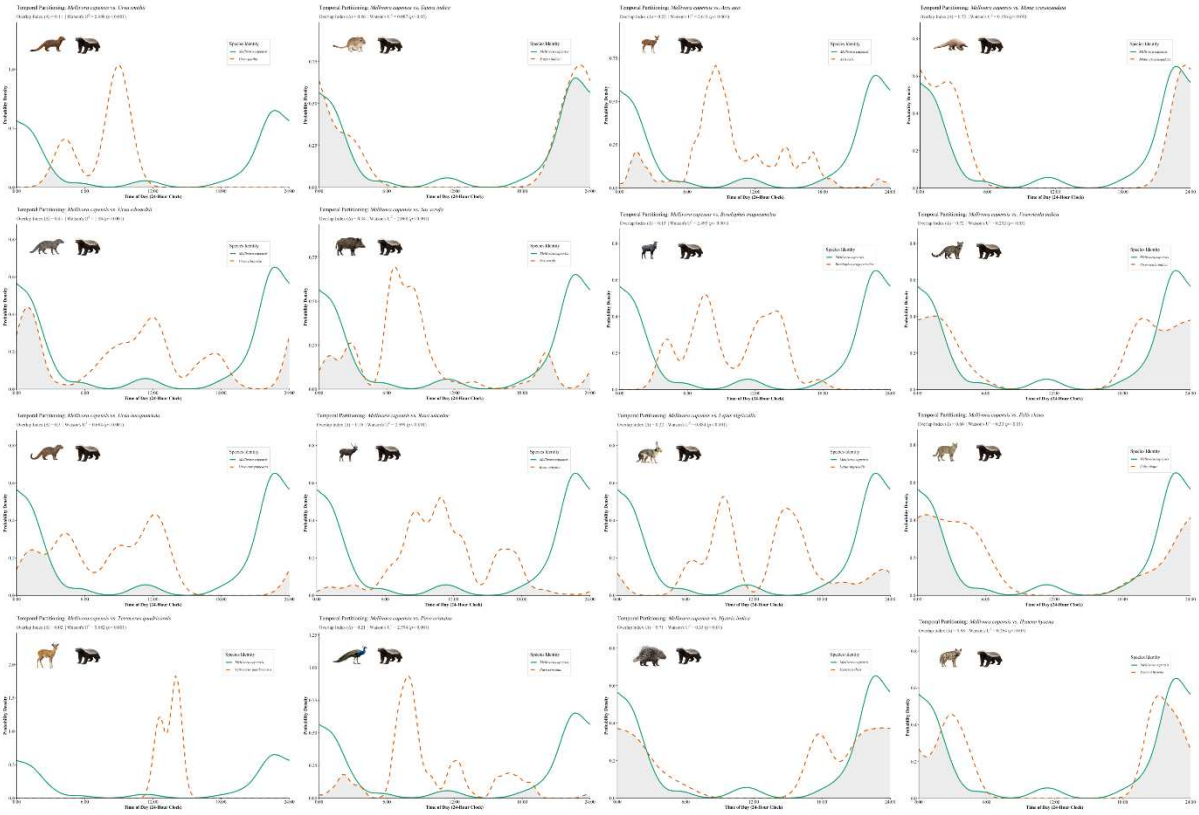


Figure 4 Temporal overlap comparison between Ratel and the mammalian community

Thus, the nocturnal behaviour of these species overlaps with that of the Ratel, suggesting their niche overlap is achieved through space use and diet divergence. Various levels of partial overlap and differential patterns of activity were noted with respect to cathemeral or broadly distributed species. Low to moderate temporal overlap was observed between the Ratel and the large ungulates such as Chital (*Axis axis*, $\Delta = 0.22, p < 0.001$), Sambar (*Rusa unicolor*, $\Delta = 0.16, p < 0.001$) and Wild Boar (*Sus scrofa,* $\Delta = 0.34, p < 0.001$). Although these ungulates displayed the multi-modal pattern of activity that included daytime periods, there was direct overlap between their nighttime foraging activities and the active period of the Ratel. There was a high overlap between the Indian Pangolin (*Manis crassicaudata*, $\Delta = 0.72, p > 0.05$). Both species are strictly nocturnal, elusive, and rare, but their dietary niches are totally different from each other, as pangolins are strict anteaters, being toothless mammals.

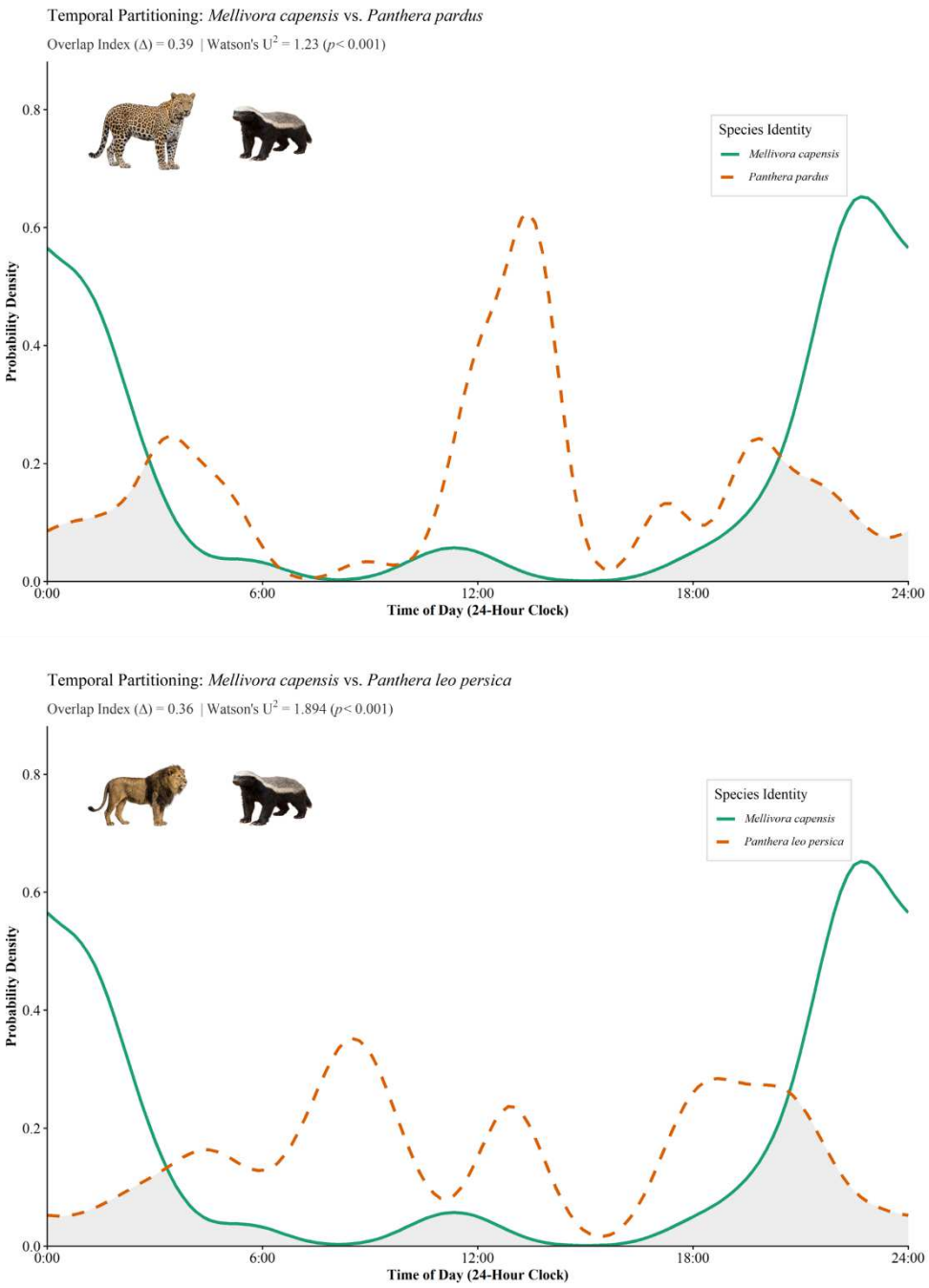


Figure 5 Temporal overlap of Ratel with Indian Leopard and Asiatic Lion

Pairwise temporal overlap and non-parametric circular analysis showed an extremely structured and highly significant behavioural avoidance mechanism between the Ratel and the sanctuary's apex predator species (Figure 3). While the Ratel, Leopard (*Panthera pardus fusca*) and the Asiatic Lion (*Panther leo persica*) are all well-established species of the nocturnal and crepuscular segments of the Mitiyala wildlife ecosystem, they show highly marked temporal segregation. Pairwise comparisons between the temporal distributions of the Ratel and the leopard showed very low overlap coefficients ($\Delta = 0.39$), with Watson's two-sample circular test confirming that their respective temporal distribution are actually very different from each other ($U^2 = 1.23, p < 0.001$). where the leopard was highly adaptive and multimodal in its

activity pattern, showing dominance over the late afternoon, dusk and midday periods, the Ratel was highly constrained in its activity pattern to a single major wave between $21{:}00\ h$ and $03{:}00\ h$. In the case of the Asiatic Lion (*Panthera leo persica*, $\Delta = 0.36, p < 0.001$), there was less overlap with the Ratel, while Watson's circular statistics state $U^2 = 1.89$, as lions were more active during early morning and late evening in the sanctuary. Ratel was found to be intentionally avoiding the locations with the apex predator's presence to avoid lethal competition with them.

As compared to the other seven strictly nocturnal mammalian species, which were compared separately, the resulting matrix showed very high temporal convergence and strict behavioural clustering in the dark period (Figure 4), so that the competition to Ratel can be assessed. The Ratel showed strong temporal overlap with the *Tatera indica* in such a way that the significant difference between the core hours of activity of the four species did not exceed the probability level of $p > 0.05$ according to Watson's U^2 test.

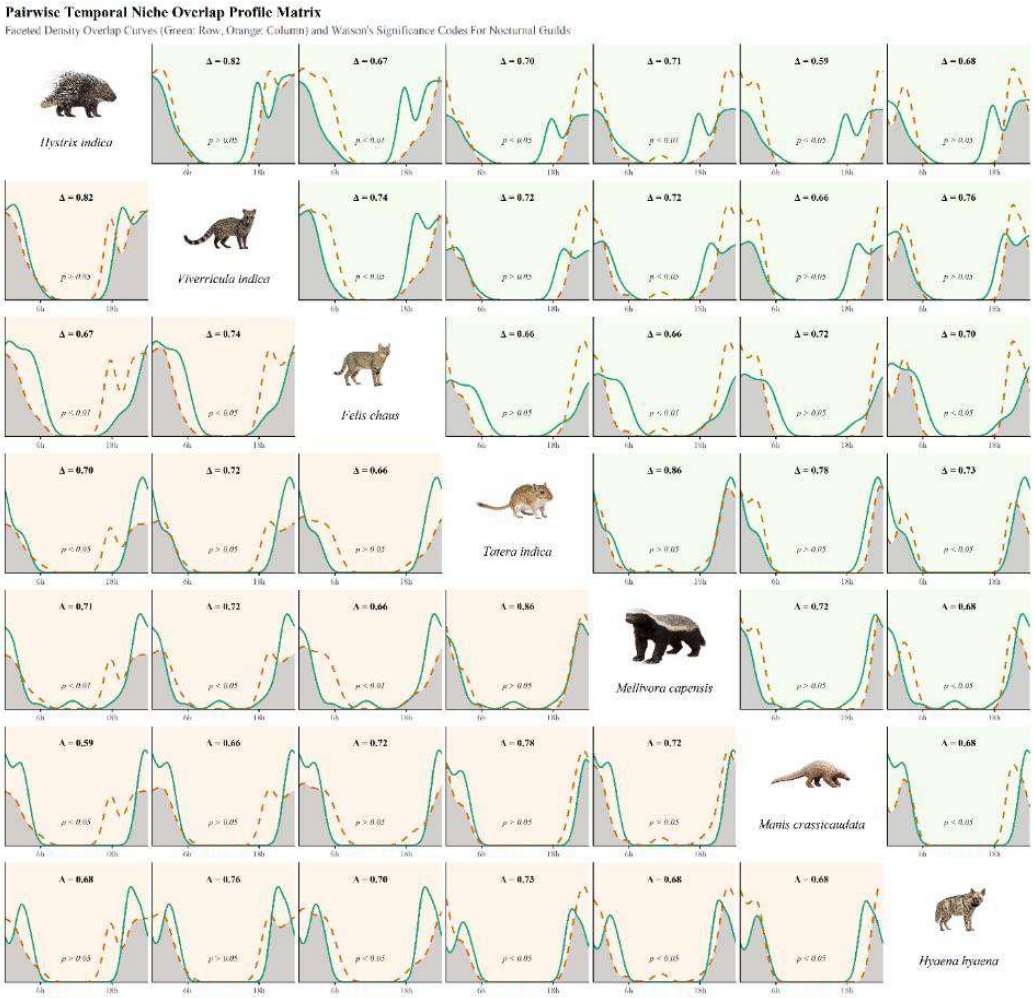


Figure 6 Nocturnal mammalian species temporal overlap

Two-way hierarchical cluster analysis successfully represented the macro structure of the Mitiyala wildlife community from the perspective of their chronological ecology, automatically grouping the 19 sympatric species into well-organised blocks according to the similarity of temporal niche behaviour (Figure 5). Complete linkage hierarchical cluster

dendrogram branching clearly split the community into two major clusters, one consisting of a strongly associated nocturnal guild and another of a highly spread-out diurnal/crepuscular guild. The nocturnal cluster made up a large, highly synchronised block in the lower left of the matrix that included specialised foragers such as the Ratel, Indian Gerbil, Small Indian Civet and Indian Crested Porcupine in conjunction with the apex predators such as the Asiatic Lion and Indian Leopard. This high-density cluster shows a high temporal symmetry ($\Delta > 0.65$). In contrast, the top and right-most branches of the dendrogram identified the purely diurnal and crepuscular species of the community as being distinct from the nocturnal specialists and exhibiting full niche divergence from them.

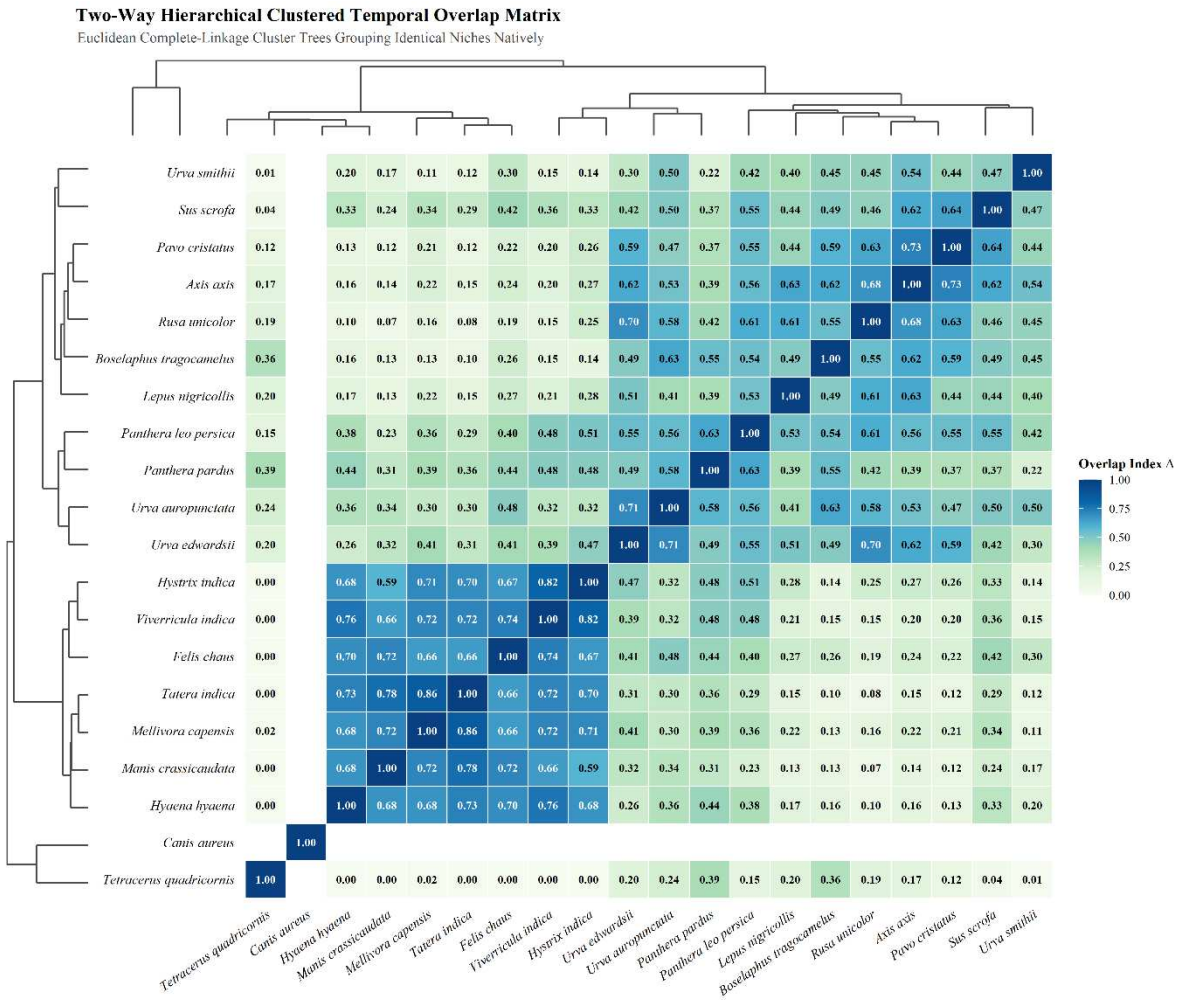


Figure 7 Two-way hierarchical cluster analysis of the Mammalian community in Mitiyala Wildlife Sanctuary

Species such as the Indian Peafowl, Chausingha and the Nilgai were grouped on separate branches of the similarity tree, due to the low degree of temporal overlap between them and the midnight feeders. Notably, the mongoose guild, along with the cathemeral animals, including the Wild Boar, occupied intermediary or sub-clustered bridge locations on the dendrogram. Through the classification of the whole community hierarchically, the clustering pattern offers strong statistical proof of organised temporal segregation in Mitiyala, rather than just random segregation of the animal species.

Discussion

The chronoecology map of Mitiyala Wildlife Sanctuary highlights the use of a highly structured and fundamental temporal niche partitioning principle, which allows the coexistence of a variety of sympatric vertebrates in the community by Altering The times of activity along the 24-hour clock scale. Species involved in competition or under threat minimise chances of interaction, thus decreasing competition and the need for spatial segregation. (Nakabayashi et al., 2021; Durán-Antonio et al., 2020; Tsunoda et al., 2025). The macro-scale structure of the community presented by the two-way hierarchical clustering matrix (Figure 5) makes it evident that temporal structure in the community of the semi-arid landscape is not a product of randomness but rather reflects a clear classification of the community into separate groups in terms of behaviour. Specifically, there is a separation between Daytime and a highly coordinated nighttime for any communities in this network. Ratel *Mellivora capensis* plays an important role in the midnight community and adjusts its behaviour to the need for foraging together with other competing and apex predator species (Allen et al., 2018; Cox et al., 2021). The conspicuous temporal segregation observed between the Ratel and the two apex predators in the sanctuary, namely the Leopard (*Panthera pardus fusca*) and the Asiatic lion (*Panthera leo persica*), serves as statistical evidence of the Ratel's behavioural avoidance of these large carnivores (Figure 4). Even though both the felines and the Ratel are broadly classified as nocturnal or crepuscular, the minimum coefficient of temporal overlap ($\Delta = 0.39$ for the leopard; $\Delta = 0.36$ for the Asiatic lion), along with highly significant results in Watson's U^2 test, demonstrate a precise temporal adjustment mechanism. It is clear from the density curves that the Ratel avoids being active during the post-dusk and pre-dawn periods, which is exactly the period when the hunting activities of the large feline predators reach their peaks (Karanth et al., 2017). Then, the Ratel accelerates quickly to make use of the midnight period, which represents a period of rest for the apex predators. Furthermore, understanding such patterns gives us great insights into the pressures that have made the behaviour of mesocarnivores plastic. In cases where the pressure from the apex predators is strong, small carnivores have to pay the energy price, such as feeding at suboptimal temperatures or limiting themselves to a certain window of movement, in order to prevent fatal interactions with the apex predators. From the analysis of the behaviour of the Ratel in the Mitiyala, it becomes clear that behaviours are favoured rather than spatial avoidance. The Ratel doesn't leave the area, which is highly occupied by the lions and leopards; instead, it uses time as a mechanism to evade interactions (Zhao et al., 2019). On the contrary, the extremely high synchronisation shown by the nocturnal mammal group is indicative of yet another ecosystem adaptation niche complementarity (Figure 5). Here, the Ratel shows excellent temporal symmetries and overlaps with the midnight activity of the Small Indian Civet, Indian Crested Porcupine and Indian Gerbil; Watson's homogeneity test has established that these major activity periods do not significantly differ. Since these organisms share exactly the same period of time, coexistence among them can only be achieved on dimensions other than time, either spatial microhabitat selection or feeding specialisation (Ramesh et al., 2012). In the case of the Ratel and the porcupine, though both have their activity peaks at the same hour, their lack of any feeding overlap means that competition between them is absent, as Ratel are generalist feeders but are less classified as herbivores, and porcupines are strictly herbivores feeding on the roots or fruits, seeds, etc. The

overlap of the Indian Gerbil and Ratel is beneficial for the Ratel, as they feed on the rodents, which are easy and small prey. Ratel digs the gerbil's burrows very easily. Gerbils, which used to roam mostly in the open space, become an easy target as prey.

Moreover, subtle sub-guild refinements persist even in this nocturnal cluster; the Indian Pangolin (*Manis crassicaudata*) shows the same activity hours but starts its activity late in the middle of the night, while Ratels start their activity a little earlier. This can avoid the interactions to some extent. They both have different feeding classes, as pangolins are a strict anteater, so they didn't compete for the same feeding resources. Another peculiar behaviour of the pangolin is that they roll up their body when feeling threatened, so feeding or fatal interactions are also not possible for them. This significant amount of clustering among many species during nighttime shows that being active in the dark of night results in many benefits for creatures living in habitats with both warm and dry conditions, and for creatures living in an environment where they are often hunted down by sight (i.e., visual predators). Additionally, the fact that all these organisms come together during such a small period of time means that they are competing with each other across a broad, diffuse network (Wooster et al., 2026). For instance, because the activity schedule of a Ratel overlaps temporally with other nocturnal insectivores or small mammal hunters, such as jungle cat and Small Indian Civet, there is likely to be much fine-scale spatial segregation or micro-habitats used within the immediate habitat (e.g., the utilisation of different layers of the canopy, different rock crevices, or the lower growth of the scrub). The concept of multi-dimensional niche will allow the presence of temporally overlapping species to coexist without the exclusion of competing species in their environment. In conclusion, these interrelated findings indicate that temporal partitioning within the Mitiyala Wildlife Sanctuary serves as an important stabilising force for the whole vertebrate community (Ferreiro-Arias et al., 2021). By dividing the diurnal community (e.g., Chausingha, Indian Peafowl) from the high-risk nocturnal period, the animals can use the fine scale of the clock to track apex cats without interfering with each other's foraging success (Ramesh et al., 2012).

These insights are very useful for conservation efforts on the larger Gir landscape through identifying that elusive species, such as Ratels, require protection by ensuring that not only are they provided habitat, but also the undisturbed structural integrity of their natural diel activity cycle. Therefore, any human-mediated disturbances, including ecotourism or externally driven artificial lighting management plans, should consider these behavioural windows in order to avoid compressing these critical temporal refuges (Lee et al., 2024).

Acknowledgements
We would like to thank the Principal Chief Conservator of Forest and Chief Wildlife Warden, Gujarat, for issuing the permission to conduct this study (Permit No. WLP/RTC/TE-1/C/725-26/2023). We would like to thank Shri. Pratap N. Chandu (R.F.O., Savarkundla) for his support and for arranging logistics during the study period. We would extend our thanks to Mr. P. V. Chavda (Forester); Mr. Dhawal Ranani, Mr. L.G. Gohil for helping in the field. We would especially thanks Mr. Dadhubhai M. Kamaliya, Mr. Rahimbhai U. Savat, Mr. Ahmadbhai Parmar, Mr. Peerbhai Laliya for their continuous support in completing this study.

Competing Interest
The authors declare no conflict of interest.

Data availability
The datasets generated and/or analysed during the current study are not publicly available due to strict non-disclosure conditions of the research permit and severe conservation concerns regarding the precise locations of critically endangered species. Data are however available from the corresponding author on reasonable request, strictly subject to prior approval and clearance from the permitting forest department authority.

Ethical Statement
This study employed non-invasive camera trapping without the use of bait, scent lures, or attractants. Animals were neither captured, handled, nor disturbed during the study; therefore, ethical approval was not required.

Supplementary material
The authors declare that no supplementary material is attached to this manuscript.

Authors' Contribution
S.K.K. wrote the main manuscript text, S.K.K. prepared the map, performed the analysis and prepared all the figures. A.M.K. supervised the study and reviewed the first draft. S.K.K. and A.M.K. reviewed and edited the final draft. Both the author read final manuscript.

Funding
Not Applicable**.**

Consent for publications
Both authors consented to the publication of this manuscript in *Scientific Reports.*

References

Allen, M.L., Peterson, B. and Krofel, M., 2018. No respect for apex carnivores: distribution and activity patterns of honey badgers in the Serengeti. *Mammalian Biology*, *89*(1), pp.90-94.

Amir, Z., Sovie, A. and Luskin, M.S., 2022. Inferring predator–prey interactions from camera traps: A Bayesian co-abundance modeling approach. *Ecology and Evolution*, *12*(12), p.e9627.

Blair, J.D., Gaynor, K.M., Palmer, M.S. and Marshall, K.E., 2024. A gentle introduction to computer vision-based specimen classification in ecological datasets. *Journal of Animal Ecology*, *93*(2), pp.147-158.

Botts, R.T., Eppert, A.A., Wiegman, T.J., Rodriguez, A., Blankenship, S.R., Asselin, E.M., Garley, W.M., Wagner, A.P., Ullrich, S.E., Allen, G.R. and Mooring, M.S., 2020. Circadian activity patterns of mammalian predators and prey in Costa Rica. *Journal of mammalogy*, *101*(5), pp.1313-1331.

Burgos Díaz-Guerra, T., Escribano-Ávila, G., Fedriani, J.M. and Virgós, E., 2026. Cascading Effects of Apex Predator Recovery on Rodent Foraging Activity and Seed Predation. Ecosystems (2026) 29:19. pp. 1-16

Cong, W., Li, J., Hacker, C., Li, Y., Zhang, Y., Jin, L., Zhang, Y., Li, D., Xue, Y. and Zhang, Y., 2024. Different coexistence patterns between apex carnivores and mesocarnivores based on temporal, spatial, and dietary niche partitioning analysis in Qilian Mountain National Park, China. *Elife*, *13*, p.RP90559.

Cox, D.T.C., Gardner, A.S. and Gaston, K.J., 2021. Diel niche variation in mammals associated with expanded trait space. *Nature communications*, *12*(1), p.1753.

Dave, B., Mori, M., Bathani, A. and Goel, P., 2023. Wild animal detection using YOLOv8. *Procedia Computer Science*, *230*, pp.100-111.

Di Blanco, Y.E., Spørring, K.L. and Di Bitetti, M.S., 2017. Daily activity pattern of reintroduced giant anteaters (Myrmecophaga tridactyla): effects of seasonality and experience. *Mammalia*, *81*(1), pp.11-21.

Durán-Antonio, J., González-Romero, A. and Sosa, V.J., 2020. Activity overlap of carnivores, their potential wild prey, and temporal segregation, with livestock in a Biosphere Reserve in the Chihuahuan Desert. *Journal of Mammalogy*, *101*(6), pp.1609-1621.

Ferreiro-Arias, I., Isla, J., Jordano, P. and Benítez-López, A., 2021. Fine-scale coexistence between Mediterranean mesocarnivores is mediated by spatial, temporal, and trophic resource partitioning. *Ecology and Evolution*, *11*(22), pp.15520-15533.

Ferretti, F., Oliveira, R., Rossa, M., Belardi, I., Pacini, G., Mugnai, S., Fattorini, N. and Lazzeri, L., 2023. Interactions between carnivore species: limited spatiotemporal partitioning between apex predator and smaller carnivores in a Mediterranean protected area. *Frontiers in zoology*, *20*(1), p.20.

Gilbert, N.A. and Dominoni, D.M., 2025. Robust analysis of diel activity patterns. *Journal of Animal Ecology*, *94*(2), pp.172-174.

Grabowski, K.L., Phillips, E.M. and Gaynor, K.M., 2024. Limited spatiotemporal niche partitioning among mesocarnivores in Gorongosa National Park, Mozambique. *Ecology and Evolution*, *14*(2), p.e10965.

Ivan, J.S. and Newkirk, E.S., 2016. CPW Photo Warehouse: a custom database to facilitate archiving, identifying, summarizing and managing photo data collected from camera traps. *Methods in Ecology and Evolution*, *7*(4), pp.499-504.

Jiang, Q., Xiao, H., Zhou, H., Li, Y., Fu, J., Meshach, A., Li, Q., Kang, L., Yan, L., Shu, Y. and Zhang, J., 2025. Spatiotemporal Niche Differentiation of Ungulates in the Southwest Mountains, China. *Animals*, *15*(23), p.3490.

Karanth, K.U., Srivathsa, A., Vasudev, D., Puri, M., Parameshwaran, R. and Kumar, N.S., 2017. Spatio-temporal interactions facilitate large carnivore sympatry across a resource gradient. *Proceedings of the Royal Society B: Biological Sciences*, *284*(1848), p.20161860.

Kaushal, S.K., Khan, A.M., Chandu, P.N., Jhala, R.S. and Srivastava, N., 2026. First camera trap photographic record of Four-horned Antelope (*Tetracerus quadricornis* de Blainville, 1816) in and around Mitiyala Wildlife Sanctuary, Gujarat, India. *Mammalia*, 90(6). 1-4 https://doi.org/10.1515/mammalia-2026-0002

Kheswa, E.Z., Ramesh, T., Kalle, R. and Downs, C.T., 2018. Habitat use by honey badgers and the influence of predators in iSimangaliso Wetland Park, South Africa. *Mammalian Biology*, *90*, pp.22-29.

Kyaw, P.P., Macdonald, D.W., Penjor, U., Htun, S., Naing, H., Burnham, D., Kaszta, Ż. and Cushman, S.A., 2021. Investigating carnivore guild structure: Spatial and temporal relationships amongst threatened felids in Myanmar. *ISPRS International Journal of Geo-Information*, *10*(12), p.808.

Lee, S.X.T., Amir, Z., Moore, J.H., Gaynor, K.M. and Luskin, M.S., 2024. Effects of human disturbances on wildlife behaviour and consequences for predator-prey overlap in Southeast Asia. *Nature Communications*, *15*(1), p.1521.

Lucherini, M., Reppucci, J.I., Walker, R.S., Villalba, M.L., Wurstten, A., Gallardo, G., Iriarte, A., Villalobos, R. and Perovic, P., 2009. Activity pattern segregation of carnivores in the high Andes. *Journal of Mammalogy*, *90*(6), pp.1404-1409.

Luzuriaga, A.L., Sánchez, A.M., Maestre, F.T. and Escudero, A., 2012. Assemblage of a semi-arid annual plant community: abiotic and biotic filters act hierarchically.

Moeller, A.K. and Lukacs, P.M., 2022. spaceNtime: an R package for estimating abundance of unmarked animals using camera-trap photographs. *Mammalian Biology*, *102*(3), pp.581-590.

Mutwiri, R.M., Mwambi, H. and Slotow, R., 2016. Approaches for testing uniformity hypothesis in angular data of mega-herbivores. *International Journal of Science and Research*, 5(3), pp.1202-1207

Nakabayashi, M., Kanamori, T., Matsukawa, A., Tangah, J., Tuuga, A., Malim, T.P., Bernard, H., Ahmad, A.H., Matsuda, I. and Hanya, G., 2021. Temporal Activity Patterns of Sympatric Bornean Carnivore Species: Implications for Niche Partitioning and Conservation.

Niedballa, J., Sollmann, R., Courtiol, A. and Wilting, A., 2016. camtrapR: an R package for efficient camera trap data management. *Methods in Ecology and Evolution*, *7*(12), pp.1457-1462.

Niedballa, J., Wilting, A., Sollmann, R., Hofer, H. and Courtiol, A., 2019. Assessing analytical methods for detecting spatiotemporal interactions between species from camera trapping data. *Remote Sensing in Ecology and Conservation*, *5*(3), pp.272-285.

Oliveira-Santos, L.G.R., Zucco, C.A. and Agostinelli, C., 2013. Using conditional circular kernel density functions to test hypotheses on animal circadian activity. *Animal Behaviour*, *85*(1), pp.269-280.

Palomo-Munoz, G., Fidino, M., Werdel, T.J., Piper, C.W., Gallo, T., Peek, M.S., Ricketts, A.M. and Ahlers, A.A., 2024. Mesopredators have differing influences on prey habitat use and diel activity in a multipredator landscape. *Ecosphere*, *15*(9), p.e70006.

Proudman, N.J. and Allen, M.L., 2025. Habitat features, coyotes, and humans drive diel activity variation among sympatric mammals. *Integrative Zoology*. 2025; 0:1–12 https://doi.org/10.1111/1749-4877.13000

Ramesh, T., Kalle, R., Sankar, K. and Qureshi, Q., 2012. Spatio-temporal partitioning among large carnivores in relation to major prey species in Western Ghats. *Journal of Zoology*, *287*(4), pp.269-275.

Rowcliffe, J.M., Kays, R., Kranstauber, B., Carbone, C. and Jansen, P.A., 2014. Quantifying levels of animal activity using camera trap data. *Methods in ecology and evolution*, *5*(11), pp.1170-1179.

Santos, T., Marinho, P.H., Venticinque, E.M. and Fonseca, C.R., 2024. Spatial and temporal ecology of Cerdocyon thous: a mesopredator canid coping with habitat loss, fragmentation, and chronic anthropogenic disturbances. *Landscape Ecology*, *39*(8), p.157.

Sehgal, J.J., Kumar, D., Kalsi, R.S., Allen, M.L. and Singh, R., 2022. Spatio-temporal overlap of leopard and prey species in the foothills of Shiwalik, Himalaya. *European Journal of Wildlife Research*, *68*(2), p.18.

Smith, K., Venter, J.A., Peel, M., Keith, M. and Somers, M.J., 2023. Temporal partitioning and the potential for avoidance behaviour within South African carnivore communities. *Ecology and Evolution*, *13*(8), p.e10380.

Tanwar, K.S., Sadhu, A. and Jhala, Y.V., 2021. Camera trap placement for evaluating species richness, abundance, and activity. Scientific Reports, 11(1), p.23050.

Treilibs, C.E., Pavey, C.R., Hutchinson, M.N. and Bull, C.M., 2016. Photographic identification of individuals of a free-ranging, small terrestrial vertebrate. *Ecology and Evolution*, *6*(3), pp.800-809.

Tsunoda, H., Peeva, S., Raichev, E. and Kaneko, Y., 2025. Ecological traits and intraguild competition mediate Spatial and Temporal overlaps among sympatric mesocarnivores. *Diversity*, *17*(2), p.108.

Vélez, J., McShea, W., Shamon, H., Castiblanco-Camacho, P.J., Tabak, M.A., Chalmers, C., Fergus, P. and Fieberg, J., 2023. An evaluation of platforms for processing camera-trap data using artificial intelligence. *Methods in Ecology and Evolution*, *14*(2), pp.459-477.

Wang, D., Li, Q., Gao, J., Su, X. and Lian, X., 2025. Increased Temporal Overlap in Diel Activity Patterns Potentially Intensifies Interspecific Competition Among Sympatric Large Carnivores in the Sanjiangyuan Region of China. *Animals*, *15*(14), p.2059.

Watabe, R., Tsunoda, H. and Saito, M.U., 2022. Evaluating the temporal and spatio-temporal niche partitioning between carnivores by different analytical method in northeastern Japan. *Scientific Reports*, *12*(1), p.11987.

Weber, M.G. and Strauss, S.Y., 2016. Coexistence in close relatives: beyond competition and reproductive isolation in sister taxa. *Annual Review of Ecology, Evolution, and Systematics*, *47*(1), pp.359-381.

Wooster, E.I., Lundgren, E.J., Nimmo, D.G., Cowan, M.A., Fricke, E.C., Frank, A.S., Carthey, A.J., Grabowski, K.L., Green, J.R., Linley, G.D. and McEvoy, T.J., 2026. Predator-prey temporal niche partitioning under human disturbance: a meta-analysis. *Nature Communications*. Article in press

Zanni, M., Brivio, F., Grignolio, S. and Apollonio, M., 2021. Estimation of spatial and temporal overlap in three ungulate species in a Mediterranean environment. *Mammal Research*, *66*(1), pp.149-162.

Zhao, G., Yang, H., Xie, B., Gong, Y., Ge, J. and Feng, L., 2020. Spatio-temporal coexistence of sympatric mesocarnivores with a single apex carnivore in a fine-scale landscape. *Global Ecology and Conservation*, *21*, p.e00897.

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