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ARTICLE

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Abstract: Fifteen extant species of cats inhabit India, and the northeastern region of the country is among the richest with nine species. Among these are the "standard four", an assemblage of Clouded Leopard *Neofelis nebulosa*, Asiatic Golden Cat *Catopuma temminckii*, Marbled Cat *Pardofelis marmorata*, and Leopard Cat *Prionailurus bengalensis*, which also occur across southeastern Asia. Within India, despite several surveys in this region, very little information exists on the ecology of this assemblage to explain their co-occurrence. In this paper, we put together data from several independent camera trapping studies over 10 sites across northeastern India to examine and interpret diel activity patterns of this group. While we present results for all the four species, we focus on two species, the Marbled Cat and Leopard Cat, which are of very similar body size and are potential competitors. We used kernel density estimates to measure diel activity patterns of all four species and overlap in activity between Marbled Cat and Leopard Cat at the regional scale as well as the point scale. We obtained 783 captures of the standard four from >27,500 trap nights. The Asiatic Golden Cat and Marbled Cat were strongly diurnal, Clouded Leopard largely crepuscular and nocturnal, and Leopard Cat largely nocturnal. The degree of overlap between Marbled Cat and Leopard Cat activity was low and in consensus with other studies across southeastern Asia. We interpret this as the differing niche spaces of the two cats due to their specific pre-existing adaptations, not restricted to the effects of competition. The point scale analysis when both cats are captured at the same location and separately show no shift in activity pattern, supporting our hypothesis of pre-existing differences in resources, such as food, playing a major role in facilitating co-existence. Our study, however, is preliminary and additional information with robust analysis is required to test this finding.

Keywords: Asiatic Golden Cat, camera trap, *Catopuma temminckii*, Clouded Leopard, competitive exclusion, Leopard Cat, Marbled Cat, *Neofelis nebulosa*, *Pardofelis marmorata*, *Prionailurus bengalensis*, standard four.

Abbreviations: CF - community forest, CL - Clouded Leopard, GC - Golden Cat, IUCN - International Union for Conservation of Nature, LC - Leopard Cat, MC - Marbled Cat, NP - national park, TR - tiger reserve, VCR - village community reserve, WS - wildlife sanctuary.

INTRODUCTION

India's geographic location at the confluence of major biogeographic realms has contributed towards its extraordinary biodiversity (Mani 1974). The family Felidae is particularly well-represented in India with 15 extant species, constituting around 37% of the global felid diversity (Kitchener et al. 2017). While speciation seems to have played a major role in structuring the felid assemblage of South America, the Indian felid assemblage resulted from a series of colonization events (Johnson et al. 2006). Consequently, of the 14 felid genera recognized by Kitchener et al. (2017), nine occur in India.

Due to different environment conditions and species adaptations, felids are not homogenously distributed throughout the country. The highest species richness (nine species) is observed in the semi-arid and arid region to the west due to colonization from Middle-Eastern species, and in the northeastern forests due to the colonization of species from southeastern Asia (Johnson et al. 2006). Obligate carnivory in cats along with very similar physiologies and overall morphologies shared across the family raise interesting questions related to sympatry. Several studies throughout the globe addressed co-occurrence patterns in the Felidae and in most studies inferences are drawn around possible competitive interactions and avoidance thereof. Segregation over body size, diet, space, and time are recognized as the major facilitators of co-existence in carnivores, including wild cats (Caro & Stoner 2003; Morales & Giannini 2010; Sunarto et al. 2015; Cruz et al. 2018; Hearn et al. 2018).

In northeastern India, felid body mass spans almost two orders of magnitude. The smallest are Marbled Cat and Leopard Cat with body mass ranging from 2.4–3.7 kg and 2.7–3.6 kg, respectively (Pocock 1939; Sunquist & Sunquist 2002), while the largest, the Tiger *Panthera tigris,* weighs up to 260kg in the Indian subcontinent (all of these were Chitwan tigers immobilised by Smith et al. 1983). The other species include the Leopard *P. pardus* (31–63 kg), Snow Leopard *P. uncia* (30–50 kg), Clouded Leopard (18–20 kg), Asiatic Golden Cat (9–16 kg), Fishing Cat *Prionailurus viverrinus* (5–16 kg), and Jungle Cat *Felis chaus* (2.3–8.6 kg) (Pocock 1939; Sunquist & Sunquist 2002; Athreya & Belsare 2006; Hunter 2015). The larger species such as the Tiger tend to prey on large or medium-sized ungulates (Andheria et al. 2007; Lyngdoh et al. 2014), while the Clouded Leopard and Asiatic Golden Cat are likely to focus on small ungulates, primates, larger rodent species, and pheasants (Ross et al. 2013; Xiong et al. 2017). On the other hand, small wild cats like Leopard Cat and Jungle Cat are largely dependent on murid rodents, and to a smaller extent on birds, amphibians, and reptiles to meet their energy requirements (Mukherjee et al. 2004; Shehzad et al. 2012; Xiong et al. 2017).

Though similar body sizes and diet could impose potential inter-species competition, some species are mainly found in specific habitats. For instance, the Fishing Cat inhabits mainly the lowland swamps and wetlands, the Jungle Cat occurs in open habitat and shrubland areas, and the Snow Leopard is restricted to higher elevations (Nowell & Jackson 1996). The remaining six wild cat species tend to co-occur in the northeastern forests. In similar habitats across southeastern Asia, the assemblage of Leopard Cat, Marbled Cat, Asiatic Golden Cat, and Clouded Leopard is common and was named as the standard four by Duckworth et al. (2014).

The similar body size of Leopard Cat and Marbled Cat raises interesting questions related to co-occurrence. Asynchronous activity patterns can potentially explain co-occurrence, and Marbled Cat and Leopard Cat were found to have low activity overlap (Lynam et al. 2013; Singh & Macdonald 2017; Hearn et al. 2018), thereby supporting this argument. Apart from competition, predation from a larger cat could also determine temporal patterns of activity and it would be expected for specific pairs of cats, Clouded Leopard-Golden Cat, Golden Cat-Marbled Cat, and Golden Cat-Leopard Cat, to have low temporal activity overlaps. Clouded Leopard-Golden Cat and Golden Cat-Marbled Cat, however, were found to have similar activity periods (Azlan & Sharma 2006; Lynam et al. 2013; Singh & Macdonald 2017). Activity patterns can also vary regionally, but current information on the activity of the standard four comes mainly from southeastern Asia with very few studies from India (e.g., Singh & Macdonald 2017).

In this collaborative study that collates activity information from ten independent camera trapping studies in northeastern India, we address a knowledge gap pertaining to the activity of the standard four in India. Northeastern India comprises of the northwestern edge of Clouded Leopard, Asiatic Golden Cat, and Marbled Cat distribution, and hence is of geographic significance to these species (Grassman et al. 2016; McCarthy et al. 2016; Ross et al. 2016). We estimated activity patterns of small to medium felids (<20kg average body mass) and compared them to patterns found throughout southeastern Asia. In addition, we explored potential activity pattern variation at different elevations, where larger cats tend to be absent or less abundant, and

under different management regimes associated with different levels of human disturbance.

STUDY AREAS

The northeastern region of India encompasses a vast gradient of elevations (<50–>8,000 m), climate conditions, and vegetation associations. As a result, the region provides a wide range of habitats and species adapted to each of these habitats.

This study incorporates camera trap data obtained from 10 study sites spread over five states of northeastern India, which include Assam, Arunachal Pradesh, Nagaland, Meghalaya, and Mizoram (Table 1; Fig. 1). The predominant vegetation across most of these sites is tropical evergreen, subtropical evergreen, tropical semi-evergreen, or moist deciduous forest (Champion & Seth 1968). Temperate broad-leaved and temperate conifers occur in the higher elevations (2,000–4,000 m) in Arunachal Pradesh, within the study sites included in this paper (Kaul & Haridasan 1987).

Management regimes range from legally delineated NPs and WSs to locally-managed CFs and VCRs. While Arunachal Pradesh and part of Assam constitute a part of the eastern Himalayan biodiversity hotspot, the study locations in Nagaland, Meghalaya, part of Assam, and Mizoram fall within the Indo-Burma biodiversity hotspot (Mittermeier et al. 2004).

Arunachal Pradesh: This study incorporates data collected between May 2013 and March 2017 from Pakke-Eaglenest landscape and Talle Valley WS. The Pakke-Eaglenest landscape comprises of Pakke TR, which covers an area of 862km², Eaglenest WS spread over 217km², and the recently proposed Singchung-Bugun VCR. While Pakke TR has an elevation gradient of ≥100m to 1,500m, Eaglenest WS is located at a higher elevation, between 500m and 3,250m. Talle Valley covers an area of 337km² in the Lower Subansiri Valley, northeast of the Pakke-Eaglenest landscape. The elevation gradient of the reserve is between 1,500m and 2,825m. Though all study sites within this landscape support most mammalian species typical of this landscape, the larger cats, Tiger and Leopard, are found largely in Pakke TR.
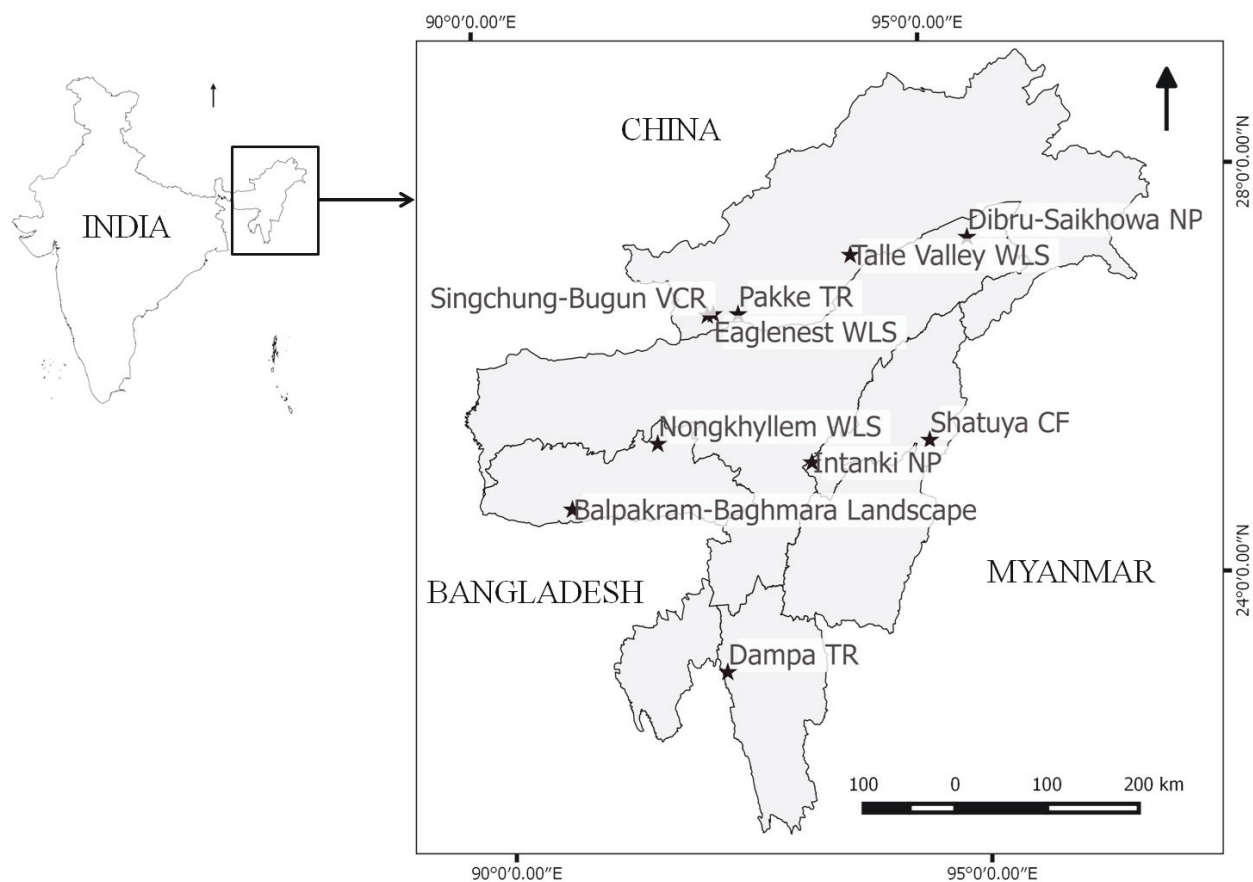

Figure 1. Sampling sites in northeastern India.

Table 1. Sampling areas and results of camera trapping used in this study.

State	Sampling areas	Approximate number of camera trap locations	Trap nights	Trapping period	Min-Max elevation (m) of records	Small felid species (<25kg average body mass) detected
Arunachal Pradesh	Pakke TR	213	~10,260	Nov 2015 to Mar 2017	123–732	Clouded Leopard (n=40), Asiatic Golden Cat (n=3), Marbled Cat (n=40), Leopard Cat (n=394), Jungle Cat (n=4), Tiger, Leopard
Arunachal Pradesh	Eaglenest WS	250	8,044	May 2013 to Apr 2016	1,640–3,220	Clouded Leopard (n=4), Asiatic Golden Cat (n=28), Marbled Cat (n=27), Leopard Cat (n=59)
Arunachal Pradesh	Singchung-Bugun VCR	100	1,155+	May 2013 to Mar 2018	1,459–3,217	Clouded Leopard (n=3), Asiatic Golden Cat (n=22), Marbled Cat (n=1), Leopard Cat (n=43)
Arunachal Pradesh	Talle-Valley WS	22	1,063	Mar 2016 to May 2016	2,352–2,446	Asiatic Golden Cat (n=8), Leopard Cat (n=14), Tiger
Nagaland	Intanki NP	23	826	May 2015 to Jul 2015	304–532	Leopard Cat (n=14)
Nagaland	Shatuya CF	5	≤50	Jun 2011	~1,300	Leopard Cat (n=1)
Meghalaya	Nongkhyllem NP	31	1,094	Mar 2015 to May 2015	378–863	Clouded Leopard (n=4), Asiatic Golden Cat (n=2), Leopard Cat (n=12)
Meghalaya	Balpakram-Baghmara landscape	425	3,857	Jan 2013 to Jun 2015	104–856	Clouded Leopard (n=4), Marbled Cat (n=2), Leopard Cat (n=40), Jungle Cat (n=1), Leopard
Mizoram	Dampa TR	9	~150	Nov 2017 to Dec 2017	567–826	Clouded Leopard (n=6), Marbled Cat (n=1), Leopard Cat (n=2)
Assam	Dibru-Saikhowa NP	27	1,065	May 2016 to Jul 2016	119–123	Leopard Cat (n=9), Leopard
Total	**10 sites**	**~1105**	**~27,567**			**(n=788)**

Tiger presence was recorded in Talle Valley (André P. Silva unpublished data), while there are no recent reports of the big cats from Eaglenest WS or Singchung-Bugun VCR.

Assam: Located in Upper Assam, Dibru-Saikhowa NP along with the adjoining reserved forest cover an area of 340km² in Tinsukia District. To its north, Brahmaputra and Lohit rivers form the park boundary, while to the south Dibru River demarcates the reserve. Elevation of the area is generally below 150m. Data were collected in this study site between May and July 2016. The park faces threats from illegal logging and poaching, erosion by the Brahmaputra River, and military activities (Sekhsaria 2012). Among big cats, only Leopard was detected at this site.

Nagaland: Data used in this study were derived mainly from a single study conducted in Intanki NP between May and July 2015. A single data point was also incorporated from a survey conducted in 2011 in Shatuya CF in Phek District of eastern Nagaland (Grewal et al. 2012), along the international border with Myanmar. Intanki NP covers an area of ~200km², located in Peren District along the Dhansiri River, and is contiguous with the Dhansiri Reserve Forest in Assam. It is a low-lying protected area with elevation ranging between 200m and 682m. The reserve faces high hunting pressure and

is impacted by insurgency and encroachment (Longchar 2013). Leopard was the only big cat detected in the area.

Meghalaya: We used data collected between 2013 and 2015 in the Balpakram-Baghmara landscape. This site is in the South Garo Hills District of Meghalaya, in proximity to the border with Bangladesh to the south, covering ~600km². While Balpakram NP covers an area of 220km², Baghmara Reserve Forest covers ~45km². The two protected areas are disjunct, with community-owned land called 'Aking' separating them. Data collected in Nongkhyllem WS between March and May 2015 was also used in this study. Nongkhyllem is located in Ri Bhoi District, close to the border with Assam. It covers an area of 29km² with an elevation ranging from 200m to 965m. Among big cats, Leopard was detected in the Baghmara-Balpakram landscape.

Mizoram: Data collected in November–December 2017 from a limited area, covering ~20km² in Dampa TR was used in this study. Located in western Mizoram, Dampa TR is contiguous to the west with the Chittagong Hill tract region of Bangladesh. The protected area is highly undulating with elevation ranging between 150m and 1,100m. A recent study by Singh & Macdonald (2017) reports the presence of the standard four felid species in the region, although no Leopard or Tiger was

recorded during the same period.

MATERIALS AND METHODS

Camera trapping

We used data on small and medium-sized sympatric felids found in northeastern India, obtained via camera traps. This data was assembled from multiple studies (Table 1) that used camera traps as a tool to assess the distribution and population status of the mammalian fauna of the region. The general study design followed by all contributors to this study involved placement of camera traps 20–50 cm above ground level, along animal trails, river beds, or ridge-lines, which are expected to support the highest animal movement in forested landscapes. We chose this height above ground to increase the detectability of small mammals by the camera traps. Camera traps used in all studies were equipped with in-built wide lenses and placed with the aim of capturing all felid species found in the landscape. Camera traps were regularly checked to ensure uninterrupted functioning and continuous data-collection in 24-hour cycles. All images obtained the contained date and timestamps.

Activity patterns

To ensure the independence of camera trap images, we considered consecutive records of the same species at the same camera trap location within an interval of ≤30min as a single capture event (Linkie & Ridout 2011; Sunarto et al. 2015; Singh & Macdonald 2017). If two consecutive images, however, were triggered by the same species within the 30min-period, but by differently marked individuals, we recognized each photographed individual as a separate event. Similarly, if a single image captured multiple individuals of a single or different cat species, we treated each individual as a separate event.

To visualize activity patterns for each species and to estimate activity overlaps, we used a method designed by Ridout & Linkie (2009), which accounts for the circular nature of time by using a non-parametric kernel density estimation approach. We used package Overlap (Meredith & Ridout 2018) available in R (R Core Team 2014), to analyse species-specific activity patterns and overlaps after pooling data from all sites. We used a smoothing parameter of 1.2 for sample sizes >75, and a smoothing parameter of 0.8 for sample sizes <50, to smoothen spikes in the graphs as recommended by Meredith & Ridout (2018) to generate the coefficient of overlap ($\hat{\Delta}_1$). $\hat{\Delta}_1$ was defined following Ridout & Linkie

(2009) as $\hat{\Delta}_1 = \int_0^1 \min \{\hat{f}(t), \hat{g}(t)\}dt$. To calculate 95% CI, we generated 10,000 bootstraps of our samples and present bootstrap bias-corrected percentiles.

To explore the variation of activity patterns, we compared the extent of overlap in the same species reported in other studies across southeastern Asia that also used the kernel density analysis. In addition, we analysed activity patterns across an elevation gradient and management regimes for all species, depending on data availability. For elevation comparisons, we divided our samples into two categories, ≤1,500m and ≥1,500m, given variations in habitat and vegetation types across these categories and availability of data. We had ≥20 samples for Leopard Cat from several different sites (n=4); hence, we compared activity cycles for the same species across different study sites.

Since Marbled Cat and Leopard Cat are very similar in body size, we attempted to examine if competition influences their activity patterns. To determine this, we analysed activity patterns for the two cats at the point location at every camera trap location, a) where both species were recorded, b) where only one of the species was recorded, and c) overlap of the activity results for each of the two species, i.e., Marbled Cat captured with Leopard Cat at the same location and Marbled Cat captured individually, and the same for Leopard Cat.

RESULTS

We obtained 788 records of five felid species, namely, Clouded Leopard (n=61), Asiatic Golden Cat (n=63), Marbled Cat (n=71), Leopard Cat (n=588), and Jungle Cat (n=5) from >27,500 trap nights in 10 sampling areas across northeastern India (Images 1–4). Details about results from the different study areas are provided in Table 1.

Of these, the highest records (61%) were from Pakke TR, since annual camera trapping is conducted in the reserve, primarily to assess the Tiger population as part of the All India Tiger Monitoring exercise followed by Eaglenest WS and the contiguous Singchung-Bugun VCR (24%). Clouded Leopard showed weak activity during the day and was most active during dawn and dusk (Fig. 2a). Marbled Cat (Fig. 2b) and Asiatic Golden Cat (Fig. 2c) were almost entirely diurnal, while Leopard Cat (Fig. 2d) was predominantly nocturnal. The highest overlap in diel activity patterns was seen between Marbled Cat and Asiatic Golden Cat with $\hat{\Delta}_1$ of 0.82 (0.71–0.92), and Clouded Leopard and Leopard Cat with of 0.79 (0.71–0.87; Fig. 3). The lowest $\hat{\Delta}_1$ was observed between

a) Clouded Leopard (n = 61)

b) Marbled Cat (n = 71)

c) Golden Cat (n = 63)
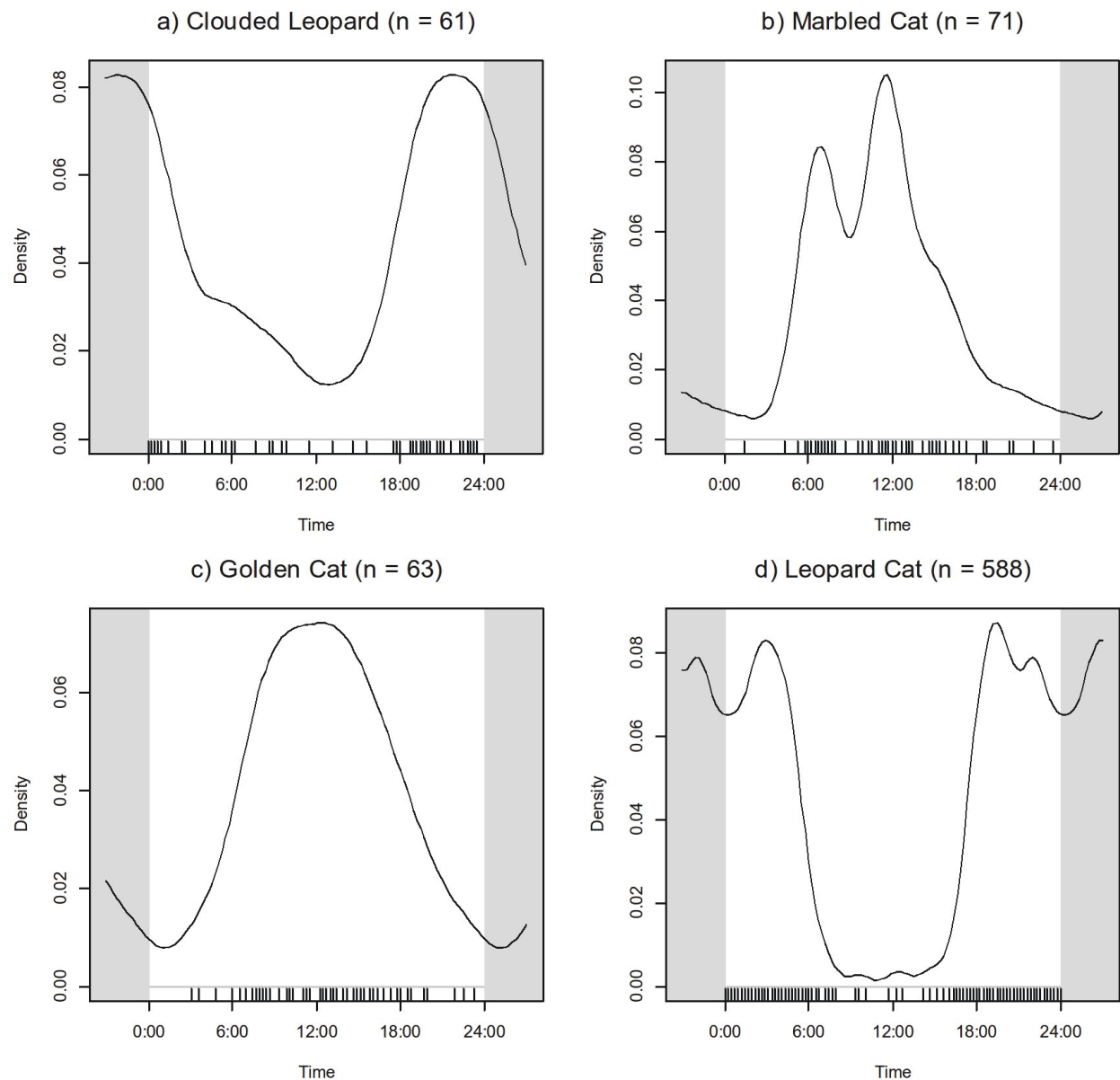
d) Leopard Cat (n = 588)

Figure 2. Kernel density plots of activity patterns of four felids in northeastern India.

Leopard Cat and Marbled Cat (0.32; 0.19–0.35), and Leopard Cat and Asiatic Golden Cat (0.38; 0.24–0.43; Fig. 3).

Comparison of activity overlap between pairs of cats from several studies (Lynam et al. 2013; Sunarto et al. 2015; Singh & Macdonald 2017; Fig. 3) reveals similar overall patterns, with the highest $\hat{\Delta}_1$ between Clouded Leopard and Leopard Cat (0.73–0.90) and lowest between Leopard Cat and Marbled Cat (0.26–0.54). In the current study, however, Clouded Leopard and Asiatic Golden Cat were spatially separated and hence could not be compared for overlap. The detected $\hat{\Delta}_1$ in the current

study between Leopard Cat and Marbled Cat (0.32; 0.19–0.35) is within that observed in other studies.

At the point scale, Marbled Cat showed a slight variation in activity when captured on locations with (n=34) and without (n=37) Leopard Cat captures, with $\hat{\Delta}_1$ of 0.81 (0.79–0.91), while Leopard Cat activity did not change in the presence (n=85) or absence (n=503) of Marbled Cat (Fig. 4). With respect to management regimes, 90% of our image-captures were obtained from protected areas and the remaining 10% from community forests. We could not compare differences in activity patterns for Clouded Leopard (n=3, OPA)
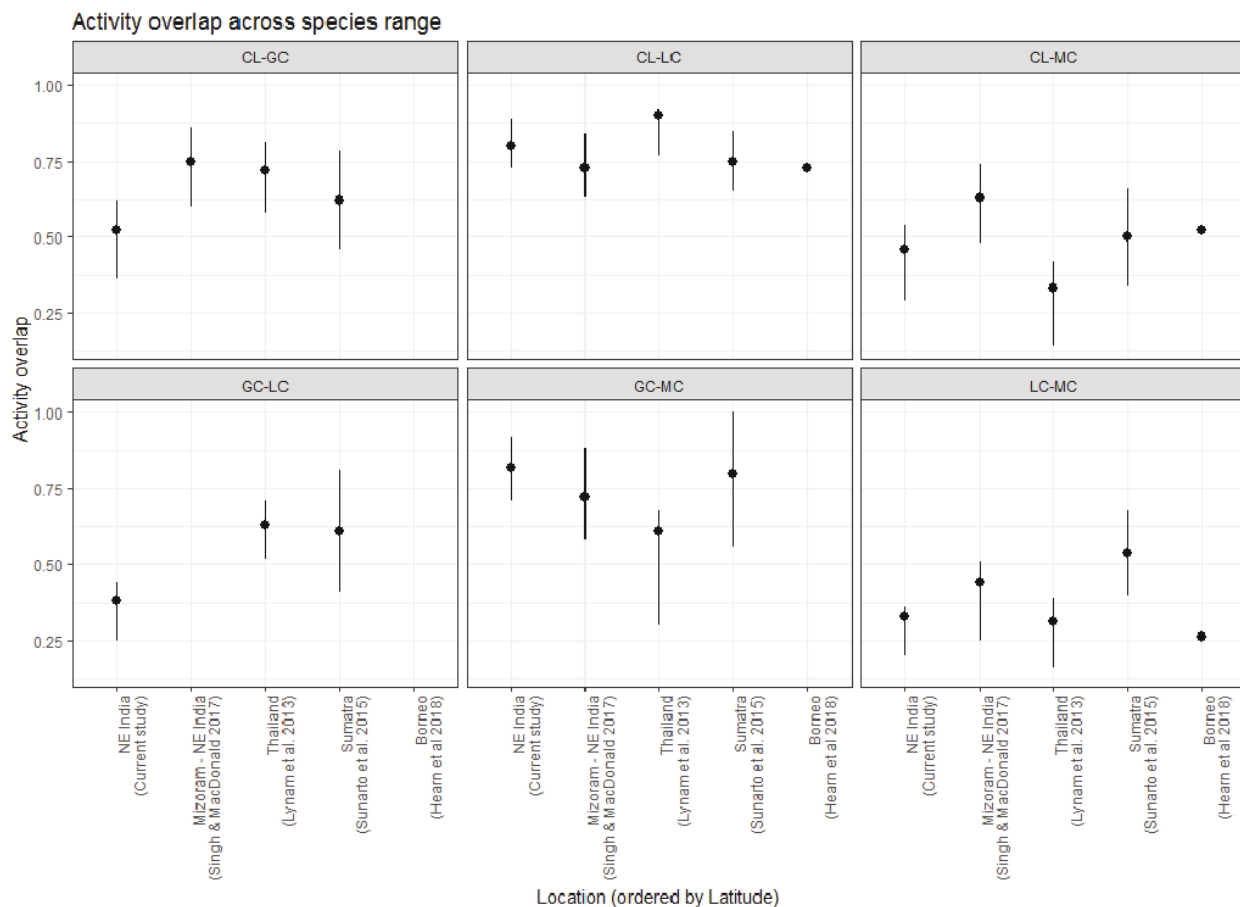
Figure 3. Comparison of activity overlaps for the standard four felids across their geographic range, based on information obtained from other comparable studies (Lynam et al. 2013; Sunarto et al. 2015; Singh & Macdonald 2017; Hearn et al. 2018). Asiatic Golden Cat does not occur in Borneo and, therefore, activity estimates for the species are not present in Hearn et al. (2018). Estimates for overlaps of Asiatic Golden Cat and Leopard Cat are not provided in Singh & Macdonald (2017).

and Marbled Cat (n=1, OPA) across protected and non-protected landscapes due to limited data, while Asiatic Golden Cat showed the same activity pattern across differing management regimes (Fig. SD1.3). In the case of altitude, we had two categories, ≥1,500m (25% samples) and ≤1,500m (75% samples). Leopard Cat was the only felid captured across all sites and accounted for 75% of total captures. Leopard Cat activity remained mostly unchanged irrespective of altitude category (Fig. SD1.1), study site (Fig. SD1.2), or management regime (Fig. SD1.3). The $\hat{\Delta}_1$ of 0.76 for Marbled Cat across the two elevation categories, however, indicates a slight variation in its activity pattern (Fig. SD1.1). Above 1,500m, Marbled Cat showed a decline in activity post a pre-noon peak.

DISCUSSION

For the first time, we estimated activity patterns of small wild cats across northeastern India complementing the existing studies in southeastern Asia, allowing future analyses on the variation of activity patterns across the species range. Interestingly, we simultaneously unveiled new information on the species distribution across the northeastern Indian landscape. Based on information used in this study, an assemblage of the four felids Clouded Leopard, Asiatic Golden Cat, Leopard Cat, and Marbled Cat occurred in three of the 10 study sites, namely, Pakke TR, Eaglenest WS, and Singchung-Vugun VCR. Marbled Cat had very low captures (≤2; Singchung-Bugun VCR, Baghmara-Balpakram landscape, Dampa) or was not captured at several sites (n=5), except for Pakke TR and Eaglenest WS, while the Clouded Leopard had very low captures in all but Pakke TR. This could be an indication of the sensitivity of these species to habitat
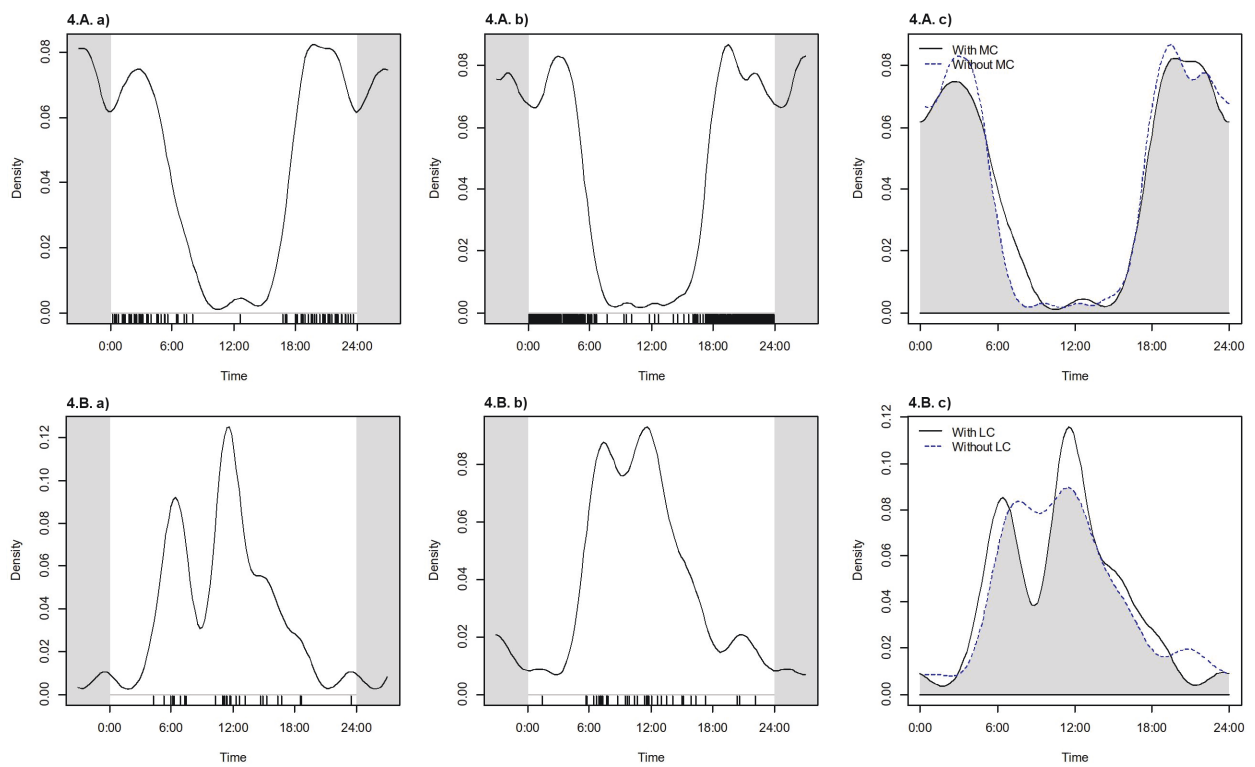
Figure 4. Point scale analyses of activity patterns of Leopard Cat (A) and Marbled Cat (B): a - when both were photographed at the same location (Marbled Cat, n=34; Leopard Cat, n=85); b - when only one species was photographed at a location (Leopard Cat, n=503; Marbled Cat, n=37); c - overlap of activity of each species with and without the presence of the other.

Image 1. Asiatic Golden Cat *Catopuma temminckii* (Eaglenest Wildlife Sanctuary 25 March 2015). © SACON Eaglenest Small Cat Team.

change and forest loss, both being species largely associated with primary closed-canopy forests or, more likely, of unequal capture efforts. The effort in Dampa TR and Shatuya CF may not have been adequate in terms of camera placements as well as the number of trap nights at each location to record Marbled Cat and Clouded Leopard, which are intrinsically rare and arboreal.

Our data capture one aspect of the ecology of an assemblage of felids, and despite the relatively large dataset for a group of little known, rare, and elusive species, our analysis remains preliminary. Although the results of our work are not very different from other studies on the same assemblage of cats, we suggested an alternative explanation for the temporal segregation between Marbled Cat and Leopard Cat. This needs to be tested through further information on diet and spatial use of habitats of these two cats. Several camera trapping studies by various groups were conducted in India, mostly focusing on the large cat, and by-catch data on the smaller cats often remains unanalyzed (e.g., Borah et al. 2014). Moreover, studies at individual sites are often limited in time and areas covered and hence are data-poor. Joint analysis of data through collaborative ventures such as ours could provide important information on basic ecological aspects such as activity patterns and habitat use of this poorly studied group.

Given the range and overlap of body sizes between pairs of cats, we expected temporal segregation in activity patterns between Asiatic Golden Cat and Clouded Leopard, and Leopard Cat and Marbled Cat. Consistent with our expectations, Leopard Cat and Marbled Cat were mainly nocturnal and diurnal, respectively. In our study, the Clouded Leopard and Asiatic Golden Cat captures were spatially separated. Most Clouded Leopard captures were in Pakke TR and Asiatic Golden Cat captures in the Eaglenest landscape, and hence were not compared for their activity overlaps. Individual species activity patterns of the standard four over several studies, however, are in consensus with some exceptions. For example, Gumal et al. (2014) report crepuscular activity of Asiatic Golden Cat and nocturnal activity of Clouded Leopard in peninsular Malaysia. In contrast, Zaw et al. (2014) report diurnal and nocturnal activity of Clouded Leopard and cathemeral activity of Asiatic Golden Cat in Myanmar. In northeastern India, we found Clouded Leopard to be largely crepuscular and Asiatic Golden Cat diurnal, in accordance with results from Dampa TR reported by Singh & Macdonald (2017).

The pattern of species segregation over space, time, or diet can be a result of various processes including competition for resources and species sorting over a gradient of resources (Leibold et al. 2004). Competition occurs when species that require similar resources and function in an ecologically similar manner meet at range boundaries and overlap zones, the outcomes of which are either competitive exclusion or co-occurrence through adjustments in specific character traits. Co-occurrence in the face of stiff competition for limited resources is often attained through character displacement where species shift some characteristics of their niches to fit into sympatry (Brown & Wilson 1956; Schoener 1974; Dayan et al. 1990; Losos 2000). On the other hand, species sorting occurs over a gradient of resources where each species is adapted to procuring a specific set of resources (Leibold et al. 2004). In this scenario, species from an assemblage would not require shifting of their niche characters and would fit in due to pre-existing differences in their requirements and adaptations.

In the case of the similar-sized Marbled Cat and Leopard Cat, competition is expected, especially in prime habitats, and their diel activity patterns would lead to that conclusion since they are largely segregated over time. This contrasting pattern of the nocturnal Leopard Cat and diurnal Marbled Cat is consistent almost throughout their range and is often attributed to competition due to the significant overlap in body size (Gumal et al. 2014; Pusparini et al. 2014; McCarthy et al. 2015; Singh & Macdonald 2017; Hearn et al. 2018). The Marbled Cat, though sometimes detected by on-ground camera traps, is morphologically suited for an arboreal life, as indicated by its very long tail (longer than its body) and perhaps also largely restricted to prime, closed canopy forests (Pocock 1939; Sunquist & Sunquist 2002; Gumal et al. 2014; Hunter 2015, Mukherjee et al. 2016). Northeastern India has an impressive diversity of Sciuridae as well (Pocock 1939), and they are largely diurnal and arboreal. Therefore, the Marbled Cat's diurnal and arboreal activities could be a result of targeting arboreal prey (Hearn et al. 2018) and not necessarily related to the presence of the Leopard Cat. Unfortunately, there is limited and incidental data on Marbled Cat diet. Borries et al. (2014) account of one observation of a Marbled Cat attempting predation on a juvenile Phayre's Leaf Monkey *Trachypithecus phayrei.* It was not clear, however, whether the attempt was made on the ground or in the canopy. Davis (1962 as cited in Hearn et al. 2018) reported a species of *Rattus* in the stomach of a Marbled Cat. On the other hand, studies on Leopard Cat diet across its global range show a very strong dependence on murid rodents that are

Image 2. Clouded Leopard *Neofelis nebulosa* **(Pakke Tiger Reserve, 19 December 2015). © A.P. Silva, S. Nadig & R. Navya.**

Image 3. *Prionailurus bengalensis* **(Pakke Tiger Reserve, 9 December 2015). © A.P. Silva, S. Nadig & R. Navya.**

Image 4. Marbled Cat *Pardofelis marmorata* (Pakke Tiger Reserve, 18 December 2015). © A.P. Silva, S. Nadig & R. Navya.

largely nocturnal (Shehzad et al. 2012; Lorica & Heaney 2013; Mukherjee et al. 2016; Xiong et al. 2017). Future studies on Marbled Cat diet are therefore a priority to test our inference.

The spatial scale of focus also matters since sympatry could occur at regional or local scales (Palomares et al. 2016). One way to test for species-sorting over competition for explaining co-existence in these pairs would be to look at diel activity patterns and habitat use in areas where each of the species occurs in allopatry and to compare it to areas of co-occurrence to look for character displacement and release. This can be done at various spatial scales, e.g., the point scale of camera trap locations, the grid scale in studies that use grids within their sampling design, at the scale of estimated home ranges of focal species, within a protected area and at larger regional scales.

Our analyses at the point scale for Marbled Cat and Leopard Cat showed that the pattern of activity did not change significantly for either cat when both were recorded at the same location or separately. This lends support to our hypothesis that their activity patterns could be largely determined by factors other than competition. Additional data on diet, activity and the influence of climate factors on both species, however, is required to robustly address this hypothesis.

Predation from larger cats could also play a role in determining activity patterns and habitat use. The Leopard appears to be absent in Eaglenest WS and Singchung-Bugun VCR while the Clouded Leopard was recorded on rare occasions by Velho et al. (2015) and in the current study. This could be an explanation for the highest number of Golden Cat captures in this study being from Eaglenest WS and the adjacent Singchung-Bugun VCR.

This, however, is speculative and needs to be tested. The combined impact of several processes acting at different spatial scales is likely to be responsible for structuring assemblages (Leibold et al. 2004).

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Supplementary Figure 1.1. Marbled Cat and Leopard Cat activity across different elevation categories (Marbled Cat below 1,500m, n=43; Marbled Cat above 1,500m, n=28; Leopard Cat below 1,500m, n=482; Leopard Cat above 1,500m, n=106).
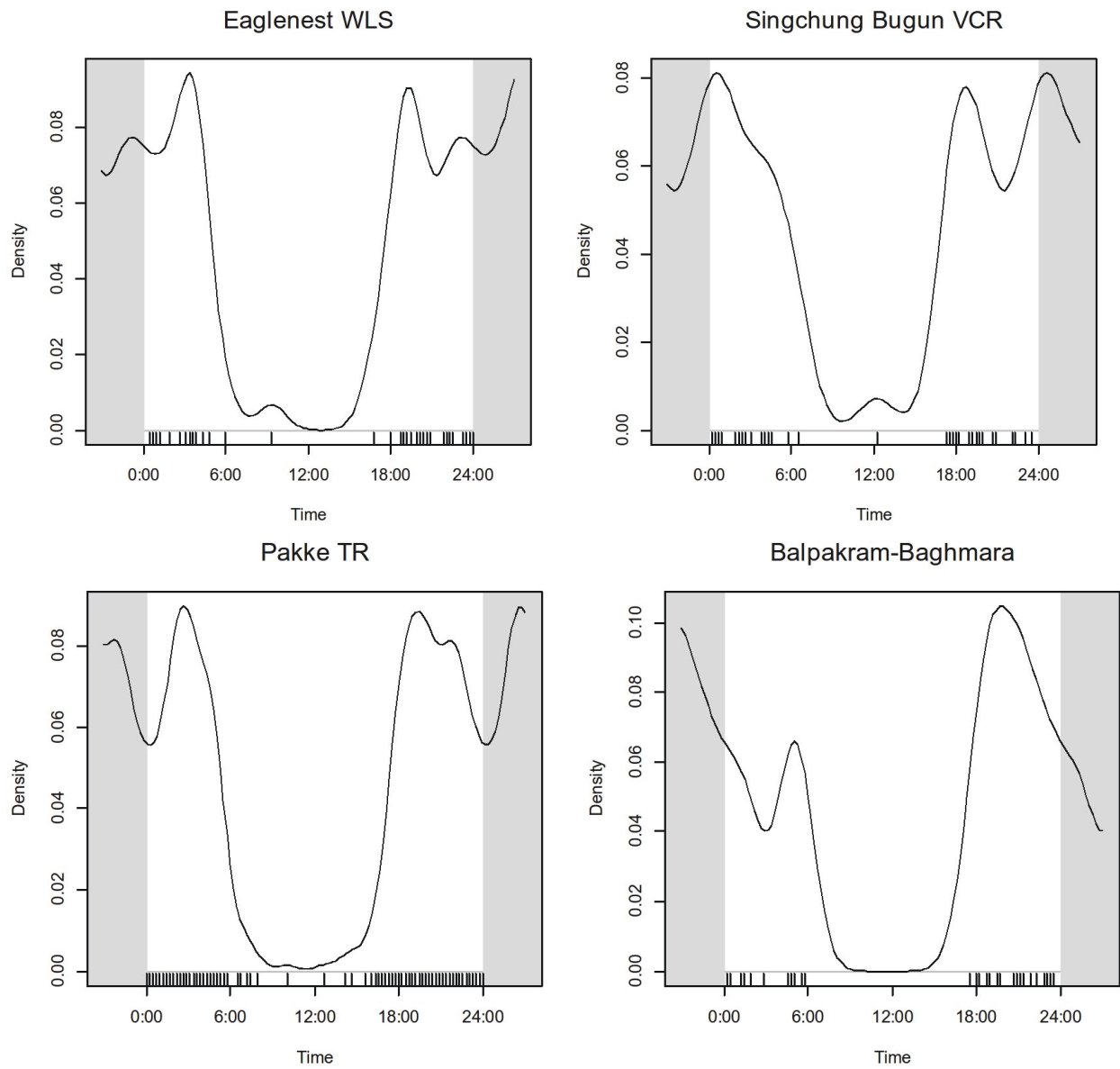
Supplementary Figure 1.2. Leopard Cat activity across different study sites (Eaglenest WS, n=59; Singchung-Bugun VCR, n=43; Pakke TR, n=394; Balpakram-Baghmara, n=40).

Leopard Cat_IPA

Leopard Cat_OPA

Golden Cat_IPA
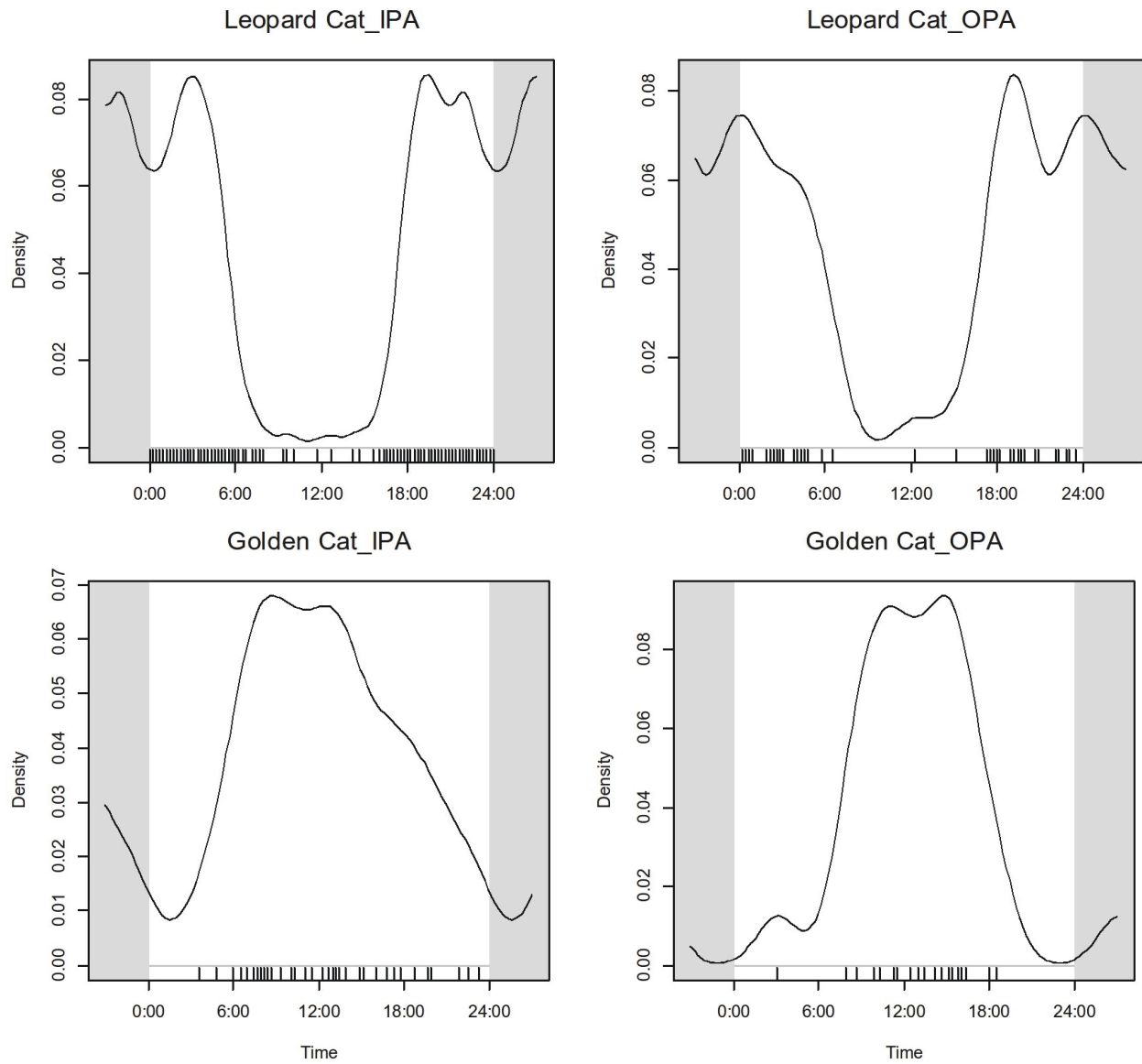
Golden Cat_OPA

Supplementary Figure 1.3. Leopard Cat and Asiatic Golden Cat activity across different protection regimes (Leopard Cat IPA, n=536; Leopard Cat OPA, n=52; Asiatic Golden Cat IPA, n=41; Asiatic Golden Cat OPA, n=22). IPA - inside protected area; OPA - outside protected area.

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