

# Stratified activity: Vertical partitioning of the diel cycle by rainforest mammals in Borneo

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## Abstract

Animal activity is driven by the environmental conditions and physical structure of a habitat, and the need to interact with, or avoid, other animals. Knowledge of the proportion of the 24-hour cycle spent active (activity level), and the time/s of day in which activity is concentrated (activity pattern), informs our understanding of species' ecology and community dynamics. In multidimensional habitats such as tropical rainforests, arboreal (canopy-dwelling) taxa comprise up to three-quarters of vertebrate assemblages; yet, wildlife surveys are typically limited to ground level. Terrestrial-only sampling can result in activity metrics that do not take account of species' full use of horizontal and vertical habitat space. We paired ground- and canopy-level camera traps to characterize mammal activity across vertical strata in Borneo. Additionally, we sampled unlogged and recovering-logged rainforest to evaluate whether this activity was impacted by logging. Activity across vertical strata varied substantially among 37 species. Arboreal mammals were predominantly nocturnal or diurnal but never cathemeral, terrestrial mammals were mostly nocturnal or cathemeral, and semi-arboreal mammals appeared to fill the temporal niches under-utilized by other groups. Differences in activity between unlogged and recovering-logged forest were minimal, with 92% of species found in both forest types retaining the same activity pattern. Our study demonstrates that the inclusion of canopy-based sampling provides much greater insights into overall rainforest mammal activity than terrestrial sampling alone. Our results suggest that the varying opportunities and constraints of each stratum act in concert to influence the diel patterns of tropical mammals.

## KEYWORDS

activity level, activity pattern, arboreal, camera trap, community ecology, Southeast Asia, temporal niche partitioning, terrestrial

## Bahasa Melayu

Aktivi haiwan didorong oleh keadaan persekitaran dan struktur habitat, dan keperluan untuk berinteraksi dengan, atau mengelakkan, haiwan lain. Pengetahuan tentang bahagian kitaran 24-jam bahawa haiwan itu aktif (tahap aktiviti) dan masa sehari di mana aktiviti itu adalah tertumpu (corak aktiviti), memaklumkan pemahaman kita tentang

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ekologi spesies dan dinamik komuniti. Dalam habitat pelbagai dimensi seperti hutan hujan tropika, haiwan arboreal (yang tinggal di aras kanopi) merangkumi sehingga tiga perempat daripada semua himpunan vertebrata; tetapi, tinjauan hidupan liar biasanya terhad kepada aras tanah. Tinjauan di aras tanah sahaja boleh menghasilkan metrik aktiviti yang tidak mengambil kira penggunaan penuh spesies ruang habitat mendatar dan menegak. Kami memasang perangkap kamera di aras tanah dan kanopi untuk mencirikan aktiviti mamalia merentas strata menegak di Borneo. Di samping itu, kami meninjau di hutan hujan yang tidak pernah dibalok, dan hutan hujan yang dibalok di masa dahulu tapi sekarang sudah mula memulihkan, untuk menilai kalau metrik aktiviti ini telah terjejas oleh pembalakan. Aktiviti merentas strata menegak berbeza-beza dalam kalangan 37 spesies. Mamalia arboreal kebanyakannya aktif pada waktu malam atau waktu siang tetapi tidak pernah cathemeral (aktif sepanjang siang dan malam), mamalia darat (yang tinggal di aras tanah) kebanyakannya aktif pada waktu malam atau cathemeral, dan mamalia semi-arboreal (yang menggunakan aras tanah dan kanopi) mengisi ceruk masa yang kurang digunakan oleh spesies arboreal dan darat. Perbezaan dalam aktiviti antara hutan yang tidak dibalok dan hutan yang dibalok adalah kecil, dengan 92% spesies ditemui dalam kedua-dua jenis hutan mengekalkan corak aktiviti yang sama. Kajian kami menunjukkan bahawa kemasukan tinjauan berasaskan kanopi memberikan gambaran yang lebih besar tentang keseluruhan aktiviti mamalia hutan hujan berbanding tinjauan darat sahaja. Keputusan kami menunjukkan bahawa peluang dan kekangan yang berbeza bagi strata tanah dan kanopi bertindak bersama untuk mempengaruhi aktiviti harian mamalia tropika.

Abstract in Malay is available with online material.

## 1 | INTRODUCTION

For all mobile animals, activity—that is, movement from one place to another in order to forage, seek shelter, or engage in social behavior—is essential for survival. However, all activity incurs an energetic cost and risks exposure to predators, competitors, and environmental stresses (Rowcliffe et al., 2014). Knowledge of activity is therefore fundamental to understanding animal ecology and informing conservation actions (Lashley et al., 2018). How and when animals acquire food, encounter mates, and avoid predation or competition are questions that can be informed by examining diel cycles of activity and how they overlap with, or are mediated by, those of other species occupying the same habitat (Bridges & Noss, 2011).

Activity can be influenced by many variables including environmental conditions (such as temperature, moon-phase, and season), the presence or absence of other species, and human disturbances such as logging. For example, Japanese flying squirrels exhibit seasonal fluctuations in activity related to temperature changes (Suzuki & Ando, 2017); nocturnal Malay civets increase daytime activity in the absence of other diurnal competitors (Cheyne et al., 2010); and some terrestrial ungulates shift toward greater night-time activity in logged forests (Chapman, 2018; Davison et al., 2019), while some birds become more diurnal with increased human disturbance (Negret et al., 2023). Interactions between these extrinsic factors

and intrinsic biological traits, such as body size, taxonomy, and feeding strategy, can have a further impact. For example, small-bodied mammals may maintain lower activity levels to conserve energy more easily lost due to high metabolic rates (Hazlerigg & Tyler, 2019), while conversely, large mammals may spend more time foraging to meet the energetic demands of a bigger body (Cid et al., 2020); Anthropoid primates are the only mammalian group with specific eye adaptations for diurnal vision and most species within this group are active during daylight hours (Heesy & Hall, 2010; Tan et al., 2013); and frugivorous civets may utilize the nocturnal niche to avoid direct competition with large, day-active frugivores such as hornbills (Jayasekara et al., 2007; Nakabayashi et al., 2016).

Characterizing activity in the context of these multiple influences can thus help shed light on the drivers and constraints a species or population may be subject to, while showing how sympatric species may use temporal partitioning to facilitate co-existence (Azcarra et al., 2020). Yet, for most wild animals, patterns of activity are poorly documented due to the difficulties of accurate quantification in non-captive settings (Bridges & Noss, 2011; Rowcliffe et al., 2014). In these situations, animals are often not readily observed (Jayasekara et al., 2007), almost never observable across the 24-h cycle, and the presence of human observers is likely to influence the activity itself (Van Schaik & Griffiths, 1996; Whitworth et al., 2016). A further limitation is that most activity research focusses on a restricted set of

taxa, rather than considering the community as a whole. In the reality of wild ecosystems, every animal is potentially subject to multiple influences from multiple other species, as well as from members of its own species. Although this adds complexity, studies that consider these varied influences may present a more complete view of community dynamics.

Community perspectives of animal activity are perhaps most challenging in tropical rainforests, due to their high biodiversity and the partitioning of resources over vertical as well as horizontal space. Mammals are one of the most diverse vertebrate taxa within rainforests, comprising species of wide-ranging body sizes and ecological roles (Nakabayashi et al., 2019), utilizing the entire three-dimensional habitat space from forest floor to tree crowns (Kays & Allison, 2001). Indeed, arboreal (canopy-dwelling) taxa comprise a substantial portion of rainforest mammal communities (Emmons et al., 1983; Haysom et al., 2021; Moore et al., 2020), but most of our knowledge of these communities comes from studies of terrestrial (ground-dwelling) species, or observations of arboreal species from ground level (Whitworth et al., 2016). Consequently, the activity of many arboreal mammals, and the canopy element of semi-arboreal mammal activity, is poorly characterized (see as examples Van Schaik & Griffiths, 1996; Oliveira-Santos et al., 2008), with community-wide investigations of arboreal mammal activity particularly lacking; we could find only two such studies (Azcarra et al., 2020; Gracanic & Mikac, 2022).

Furthermore, human actions are changing forests globally, with selective logging for timber being one of the most pervasive influences (Watson et al., 2018). Forest structure affects the vertical distributions and activity of canopy-dwelling wildlife (Basham et al., 2023; Nakamura et al., 2017). Tree height influences the amount of available habitat space while tree architecture, such as the interconnectedness of branches and presence of tree holes, determines how animals are able to use that space by providing movement pathways and environmental niches (Cockle et al., 2011; McLean et al., 2016). In tropical forests, microhabitat conditions vary considerably between the ground and uppermost canopy (Nakamura et al., 2017). Vertical stratification—that is, spatial partitioning of the canopy layers—has been noted among many vertebrate and invertebrate taxa (Basham et al., 2023) and plays a key role in facilitating the co-existence of such a high diversity of species (Oliveira & Scheffers, 2018). Selective logging alters a forest's structure and biotic conditions by removing the largest trees, resulting in a lower height profile (Deere, Guillera-Aroita, Swinfield, et al., 2020), increased light penetration (Fauset et al., 2017), and warmer temperatures (Hardwick et al., 2015). These effects are likely to be most noticeable in the canopy, where they cause a substantial reduction in three-dimensional niche space, and thus may disproportionately affect arboreal species that co-exist by vertically partitioning this space (e.g., Hanya et al., 2020; Nakagawa et al., 2007; Sushma & Singh, 2006). This raises the question of whether a reduced ability to spatially separate activity in logged forests may lead to a more pronounced temporal partitioning of activity by canopy-dwelling

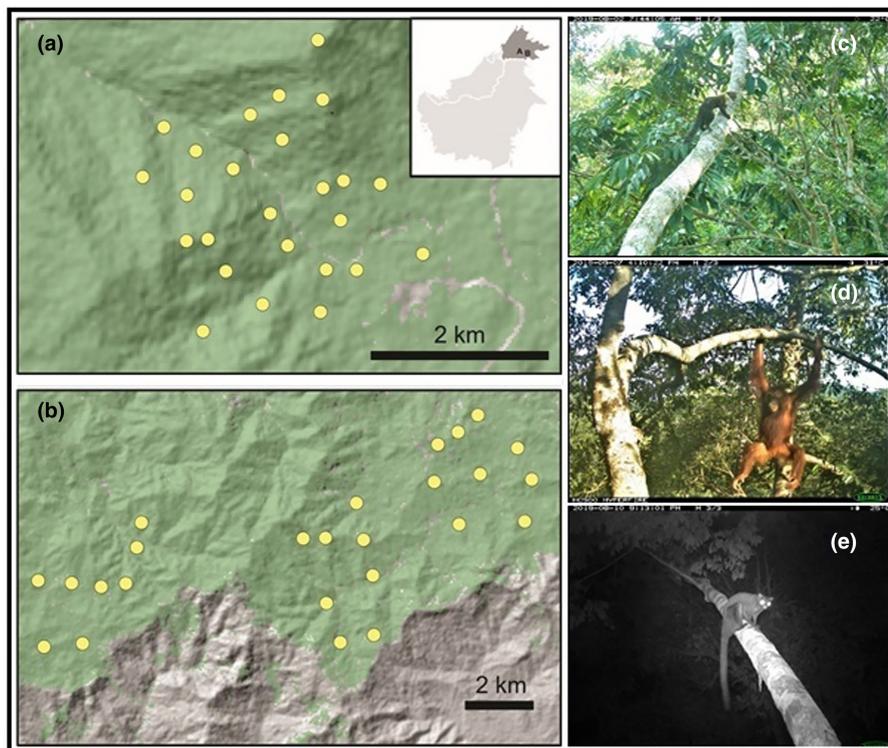
species. Yet, while one study in Chile showed the arboreal marsupial *Dromiciops gliroides* to be significantly less active in more degraded forests (Rodríguez-Gomez & Fonturbel, 2020), and certain bat species show reduced activity in logged and fragmented habitats (Appel et al., 2021; Medinas et al., 2019), we could find no further research investigating the impact of logging on arboreal mammal activity at either the species or community level. The widespread influence of logging and consistently high arboreal mammal diversity of tropical regions (Kays & Allison, 2001) underlines the importance of understanding activity for canopy-dwelling wildlife in undisturbed forests, as well as how this may change in response to human disturbances.

Here, we conducted the first community-wide investigation of non-volant mammal activity across both canopy and terrestrial strata and in both unlogged and recovering-logged tropical rainforest. We undertook our assessment in Borneo, where almost half of remaining rainforests have undergone at least one round of selective logging (Gaveau et al., 2016). Borneo is renowned for its high mammal diversity, with 135 non-volant species, over 50% of which are arboreal or semi-arboreal (Payne & Francis, 2007). The island's distinct arboreal and terrestrial mammal assemblages make sampling only at ground level insufficient to reliably characterize the entire community (Haysom et al., 2021). Recent advances in camera trapping technology and canopy access techniques provide a means to study animal activity patterns in the upper forest strata. We therefore deployed camera traps on the ground and in the canopy of unlogged and recovering-logged forest, and used detection data to quantify activity metrics for 37 mammal species. We further investigated whether, and to what extent, activity varied between (i) canopy and terrestrial strata (for six semi-arboreal species), (ii) unlogged and recovering-logged forest (for 25 species present in both), and (iii) biological traits (body size, taxonomy, and feeding strategy).

## 2 | METHODS

### 2.1 | Study site

Research was undertaken in and around the Stability of Altered Forest Ecosystems Project (Ewers et al., 2011) in Sabah, Malaysian Borneo. We sampled mammals in unlogged forest at Maliau Basin Conservation Area, and in recovering-logged forest at the Mt. Louisa Forest Reserve, approximately 60 km away (Figure 1). These areas form part of an extensive block of lowland-hill tropical rainforest covering approximately one million hectares in south-central Sabah and are dominated by trees of the commercially-valuable *Dipterocarpaceae* family (Reynolds et al., 2011). Mt. Louisa experienced multiple rounds of selective logging between 1978–2008, but has since been formally protected from further timber extraction. Both areas have low levels of human hunting within the regional context (Deere, Guillera-Aroita, Platts, et al., 2020).



**FIGURE 1** Camera-trap locations in (a) unlogged and (b) recovering-logged forest, with the location of sampling areas in relation to Borneo shown on the inset map. Examples of species detected by canopy camera traps in this study include (c) yellow-throated marten *Martes flavigula*, a predominantly crepuscular semi-arboreal member of the Carnivora, (d) orangutan *Pongo pygmaeus*, a diurnal semi-arboreal primate, (e) black flying squirrel *Aeromys tephromelas*, a nocturnal arboreal rodent.

## 2.2 | Camera trapping

Camera traps (Hyperfire HC500, Reconyx, USA) were deployed across 50 locations between October 2017 and September 2019. Locations were divided equally between unlogged and recovering-logged forest (mean distance between locations 1.26 km; range 0.5–4.0 km) and covered similar elevations in both forest types (mean 482 m, range 225–933 m). Each location comprised one terrestrial camera trap set 0.3 m above the ground, paired with one or two canopy camera-traps set in the mid- or upper-canopy (9.8–52.3 m height, in trees located within 10 m horizontal distance of the ground placement). The average height of cameras in unlogged (36.0 m) and recovering-logged forest (19.3 m) reflects the differences in canopy height between these forest types. After accounting for malfunction, sampling comprised 17,226 camera-trap nights (CTN): 6661 on the ground (3995 in unlogged, 2666 in logged forest) and 10,565 in the canopy (6944 in unlogged, 3621 in logged forest). Further details on camera-trap deployment are provided in Data S1.

## 2.3 | Characterizing mammal activity

Prior to analysis, we expressed site-specific camera-trap encounters as independent mammal detections, with independence defined as photographic captures of different species, or of the same species separated by  $\geq 30$  min (Ridout & Linkie, 2009). Where focal trees contained two canopy camera traps, these were treated as one sampling unit, so that detections of a species on one camera were excluded if the same species had been detected on the second within 30 min.

As we were interested in the entire non-volant community, there was no size cutoff for mammals in either stratum. Species detected represent a range of body size, taxonomic, and functional groups (Table S1). Rarefaction analyses of the same dataset showed both arboreal and terrestrial communities approaching asymptote within our sampling period, indicating that most species able to be detected by this method had been (Haysom et al., 2021).

We used all independent detections of each species to characterize two core features of activity for mammals with sufficient sample sizes ( $\geq 10$  detections, Ridout & Linkie, 2009). “Activity level” quantifies the proportion of the 24-h cycle spent active (Rowcliffe et al., 2014), and “activity pattern” describes the time or times of activity across the 24-h cycle (Vazquez et al., 2019). We used the R package “activity” to calculate an average activity level per species, given as a figure between 0 and 1 that represents the proportion of time spent active. Uncertainty was expressed using 95% confidence intervals. Activity pattern is typically assessed by building a visual profile of independent detections across the diel cycle and is commonly divided into four main categories: diurnal (predominantly/exclusively active during daylight); nocturnal (predominantly/exclusively active during darkness); crepuscular (most activity occurs during twilight, i.e., 1 h before and after dawn and dusk); and cathemeral (substantial activity during daylight and darkness with no clear majority in either, Tattersall, 2006).

For each species, activity patterns were categorized by calculating the proportion of detections during daylight, darkness, and twilight, following Gomez et al. (2005) (Table 1, Table S2). We aligned species detections with solar time (the deviation of clock time from sunrise and sunset) specific to geographic location, as failing to account for solar time can create inaccuracies in how activity patterns

TABLE 1 Activity pattern definitions.

Category	Definition	Time period in our study region
Nocturnal	Strictly $\geq 90\%$ detections in darkness Mostly $\geq 70\%$ detections in darkness	19.26–04.59 h
Diurnal	Strictly $\geq 90\%$ detections in daylight Mostly $\geq 70\%$ detections in daylight	07.31–16.49 h
Crepuscular	$\geq 50\%$ detections during twilight	05.00–07.30 h 16.50–19.25 h
Cathemeral	$>10\%$ but $<70\%$ detections in both daylight and darkness	n/a

Note: As sunrise and sunset times in Sabah varied across the year by 30 and 45 min, respectively, we defined the crepuscular period to encompass 1 h before and 1 h after the maximum variation (05:00–07:30 h and 16:50–19:25 h); with diurnal and nocturnal periods between these times.

are categorized (Vazquez et al., 2019). Kernel density functions were fitted to detection data using the R packages “activity” and “overlap” (Ridout & Linkie, 2009; Rowcliffe, 2016), and we produced activity pattern plots for each species from all detections of that species across all camera traps. Once primary activity patterns had been defined, we assessed the significance of the deviation from expected proportions using a binomial test (following Van Schaik & Griffiths, 1996). Any secondary patterns were noted where, after the primary pattern had been determined, the proportion of remaining detections showed a clear tendency toward activity during another period. For example, a species with the majority of detections during twilight and the remainder during daylight would be categorized as “crepuscular with diurnal tendencies.”

## 2.4 | Activity comparisons among strata, forest types and mammal groups

Activity metrics were compared between (i) strata, for six species with sufficient detections on both canopy and terrestrial camera traps, and (ii) unlogged and recovering-logged forest, for 25 species with sufficient detections in both, using the R package “overlap” (Ridout & Linkie, 2009) (Table S2). To achieve this, we first produced average activity levels, and quantified activity patterns, split by stratum and by forest type for each species (i.e., using detections from only canopy camera traps, only terrestrial camera traps, only unlogged forest camera traps, and only recovering-logged forest camera traps). To compare activity levels between strata and between unlogged/recovering-logged forest, we used a Wald test to evaluate statistical differences between two estimates. For activity patterns, we calculated the coefficient of overlap ( $\Delta$ ) with 95% bootstrapped confidence intervals, corrected to account for small sample sizes where necessary (Ridout & Linkie, 2009). The degree of overlap of two activity patterns is measured on a scale from 0 to 1, where 0 indicates no overlap, and 1 indicates identical patterns. We produced overlap plots for each comparison. As activity can be influenced by species' traits, further comparisons were made between body size, taxonomic, and functional groups as defined in Table S1.

## 3 | RESULTS

Fifty-seven species were recorded across 17,226 CTN, and 37 species with  $\geq 10$  total independent detections were retained for analyses (Tables S1 and S2). Community composition between strata was largely distinct, with 10 species detected only by canopy camera traps (hereafter, “arboreal species”), 21 only by terrestrial camera traps (“terrestrial species”), and six by camera traps in both strata (“semi-arboreal species”), all with sufficient canopy and terrestrial detections to allow comparative analyses across strata. Between unlogged and recovering-logged forest, community composition was very similar, with five species detected only in unlogged forest, two only in recovering-logged, and 30 in both (25 of which had sufficient detections in both to allow comparative analyses) (Table S2).

### 3.1 | Activity level

On average across all species, mammals were active for approximately 35% of the 24-h cycle (range 0.14–0.59) (Table 2, Table S1). Arboreal mammals were consistently less active than terrestrial species (difference between mean arboreal and terrestrial activity levels: overall  $-8\%$ , unlogged forest  $-8\%$ , recovering-logged forest  $-14\%$ ), although the canopy and terrestrial activity levels of semi-arboreal mammals were very similar (difference  $-1\%$ ) (Table 2). While the greatest differences in activity levels between arboreal and terrestrial mammals were observed in recovering-logged forest, logging itself did not appear to have a large effect on mammal activity (difference between mean activity levels in unlogged and recovering-logged forest: all species  $+1\%$ , arboreal species  $-4\%$ , terrestrial species  $+2\%$ , semi-arboreal species  $+4\%$ ).

### 3.2 | Activity pattern

Across all species, nocturnality was the most common activity pattern, (15 of 37 species, 41%), and diurnality the second (9 species, 24%). Eight species (22%) were cathemeral, and five (13%) crepuscular (Figure 2, Tables S1 and S2). Activity patterns are often not

clear-cut (Van Schaik & Griffiths, 1996), and indeed, almost half of mammals detected (17 species, 46%) exhibited secondary patterns (Table S1). Arboreal mammals were nocturnal (4 of 10 species, 40%), diurnal (4 species, 40%), or crepuscular (2 species, 20%) (Figure 2, Table 2, Table S1), but not cathemeral. Terrestrial mammals showed all activity patterns, but were predominantly nocturnal (11 of 21 species, 52%) or cathemeral (7 species, 33%); few were diurnal (2 species, 10%) or crepuscular (1 species, 5%). When detection data were pooled across strata and forest types, semi-arboreal mammals were mainly diurnal (50%, 3 species) or crepuscular (33%, 2 species), with one species (17%) cathemeral, and none nocturnal.

### 3.3 | Effect of forest stratum and logging on mammal activity

#### 3.3.1 | Activity level

A third of semi-arboreal species (2 of 6, 33%) had significantly lower activity levels in the canopy (horse-tailed squirrel *Sundasciurus hippurus*, pig-tailed macaque *Macaca nemestrina*), and none were significantly higher (Table S3). Activity levels were significantly lower in

recovering-logged forest for four of 25 (16%) species (two arboreal: Prevost's squirrel *Callosciurus prevostii*, black flying squirrel *Aeromys tephromelas*; and two terrestrial: Malay porcupine *Hystrix brachyura*, and Malay civet *Viverra zangalunga*), while 3 (12%) were significantly more active in recovering-logged forest (one arboreal: giant squirrel *Ratufa affinis*; and two terrestrial: red muntjac *Muntiacus muntjak*, greater mousedeer *Tragulus napu*).

#### 3.3.2 | Activity pattern

Activity patterns of individual species typically differed between strata but were consistent between unlogged and recovering-logged forest, with statistical comparisons corroborating these findings (Table S3). Semi-arboreal species (N=6) showed an overall trend toward dissimilarity in activity patterns between strata (average coefficient of overlap 0.47, range 0.16–0.68), and four (67%) had a different activity pattern in the canopy than on the ground. Species detected in both forest types (N=25) showed strong similarity in activity patterns (average coefficient of overlap 0.74, range 0.52–0.90), and only 2 (8%) had different patterns in unlogged versus recovering-logged forest (Figure 3, Table S3).

TABLE 2 Mean activity levels for arboreal, terrestrial, and semi-arboreal mammals, compared across strata, and unlogged and recovering-logged forest, and the proportion of species in each grouping that were nocturnal, diurnal, crepuscular, and cathemeral, given as a percentage of the total number of species in that grouping.

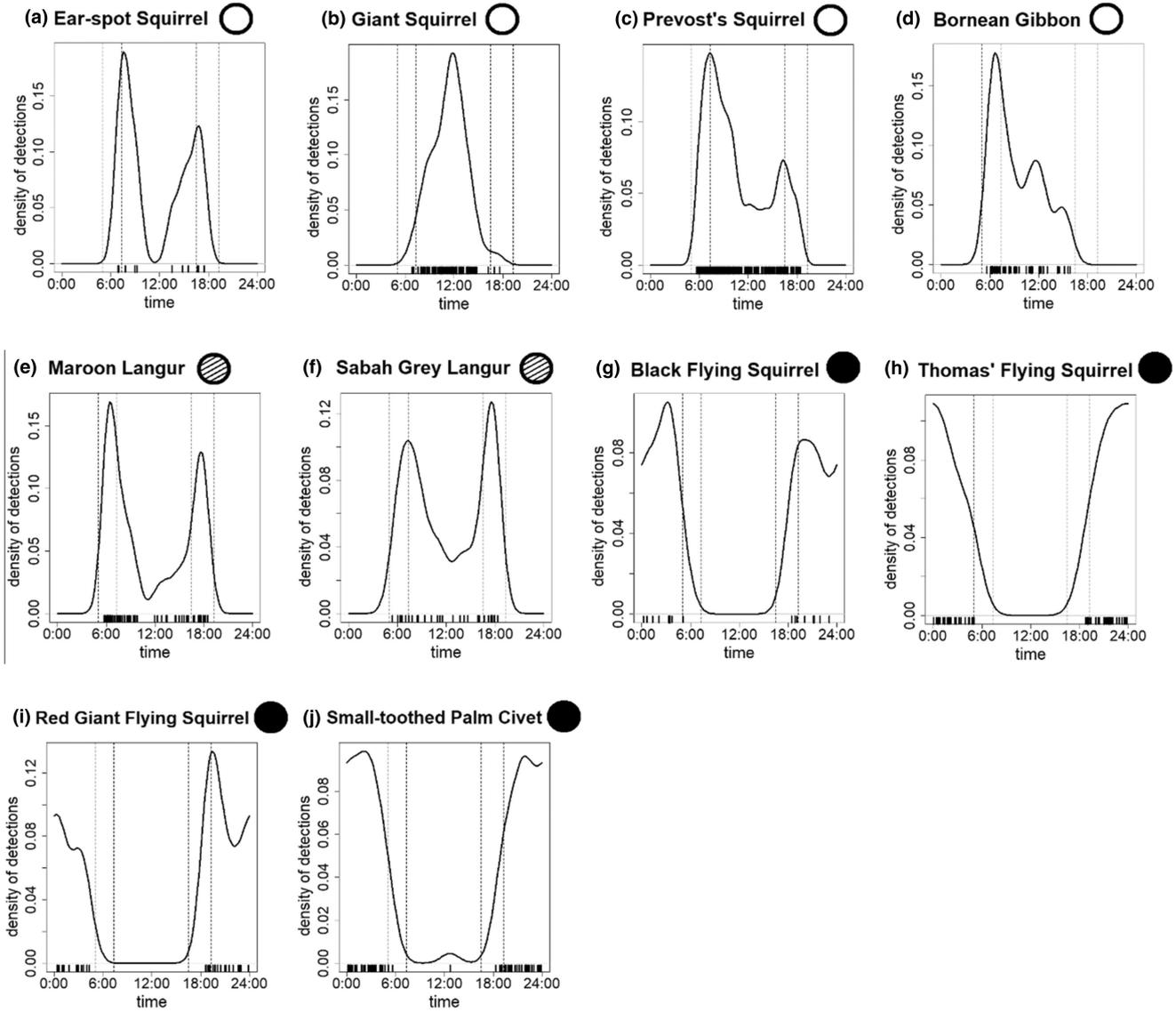
Dataset	Activity level		Activity pattern (% species)			
	Mean	Range	Nocturnal	Diurnal	Crepuscular	Cathemeral
All data, all species (N=37)	0.35	0.14–0.59	41	24	13	22
All arboreal species (N=10)	0.30	0.22–0.42	40	40	20	0
All terrestrial species (N=21)	0.38	0.19–0.59	52	10	5	33
All semi-arboreal species (N=6)	0.37	0.14–0.52	0	50	33	17
All species UL (N=25)	0.36	0.09–0.50	32	32	20	16
All species RL (N=25)	0.37	0.17–0.61	32	28	16	24
Arboreal species UL (N=6)	0.30	0.18–0.44	33	50	17	0
Terrestrial species UL (N=15)	0.38	0.29–0.50	40	27	13	20
Semi-arboreal species UL (N=4)	0.35	0.09–0.48	0	25	50	25
Arboreal species RL (N=6)	0.26	0.17–0.37	33	50	17	0
Terrestrial species RL (N=15)	0.40	0.30–0.61	40	20	7	33
Semi-arboreal species RL (N=4)	0.39	0.19–0.58	0	25	50	25
Semi-arboreal species C (N=6)	0.29	0.04–0.45	0	50	33	17
Semi-arboreal species T (N=6)	0.30	0.19–0.42	17	66	17	0

Note: Mean values and percentages were calculated from information in Table S2.

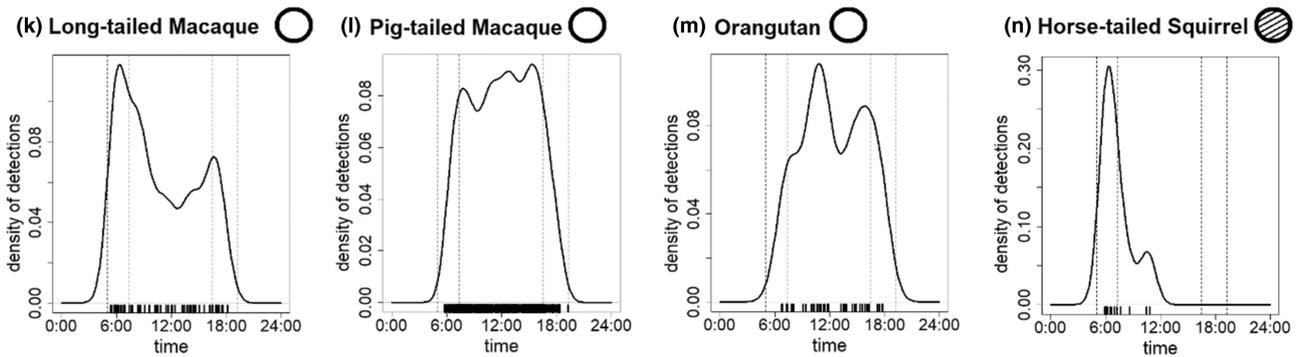
Abbreviations: C, canopy camera traps only; RL, recovering-logged forest only; T, terrestrial camera traps only; UL, unlogged forest only.

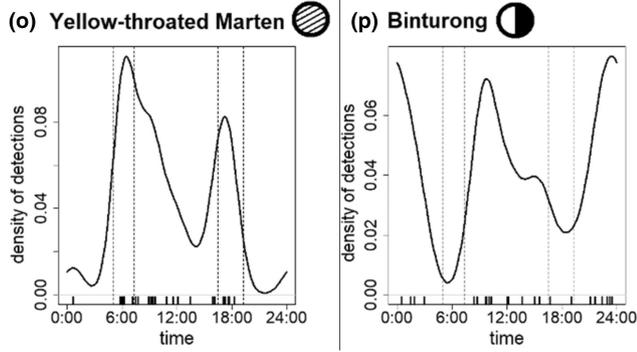
FIGURE 2 Activity plots for 37 mammal species showing times of activity across the 24-h cycle, using data pooled from all detections of each species across all camera-trap locations. Dashed vertical lines indicate the crepuscular period around dawn and dusk. Symbols denote primary activity pattern (see Key, and see Table S2 for calculations). Total number of independent detections is indicated by the density of black vertical bars along x-axes and is also noted in Table S2. Plots (a–j) denote arboreal species (those detected exclusively by canopy camera traps), (k–p) semi-arboreal species (those detected by cameras in both strata), and (q–k2) terrestrial species (those detected exclusively by cameras on the ground).

**Arboreal Species**



**Semi-Arboreal Species**





### Terrestrial Species

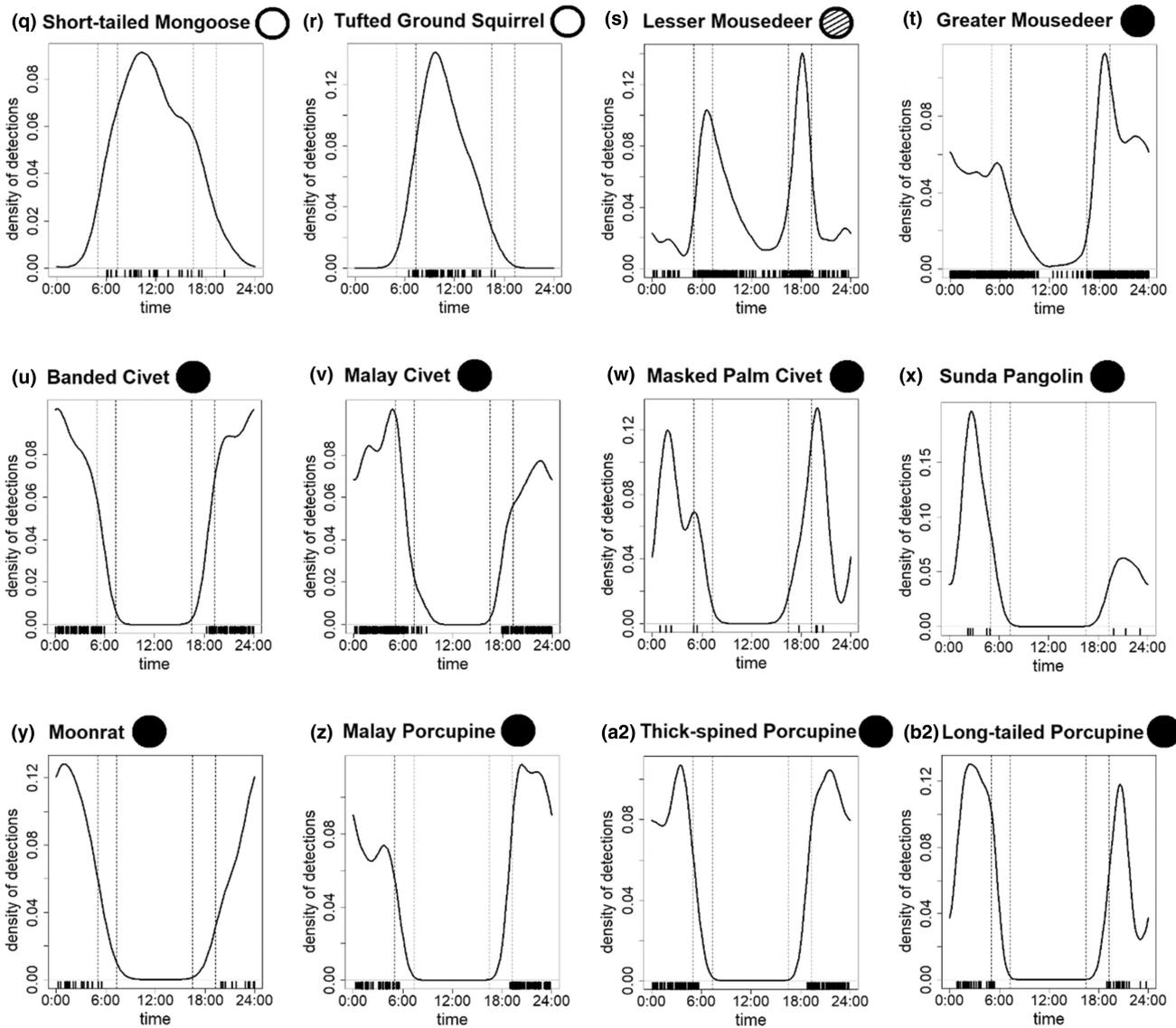


FIGURE 2 (Continued)

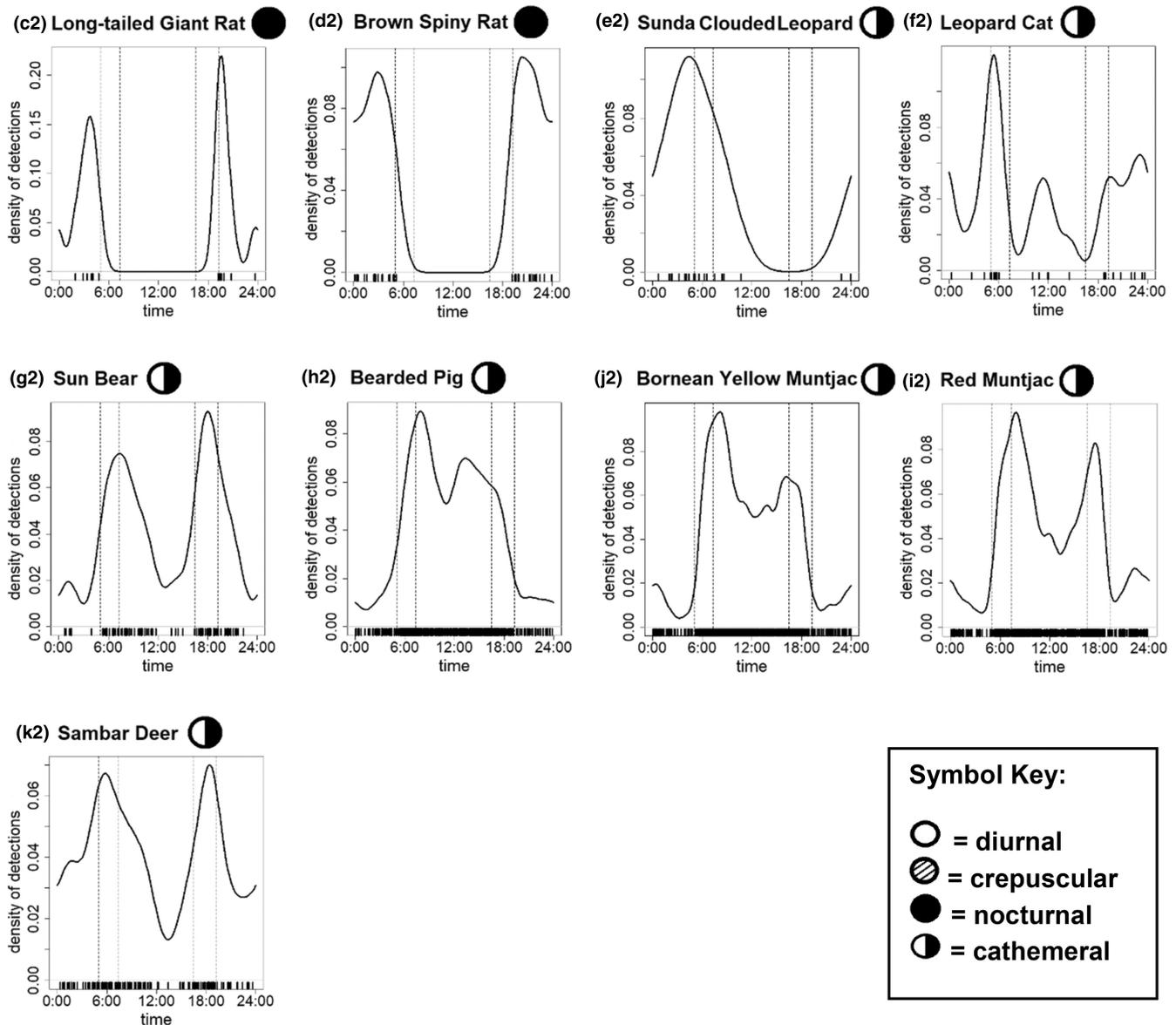


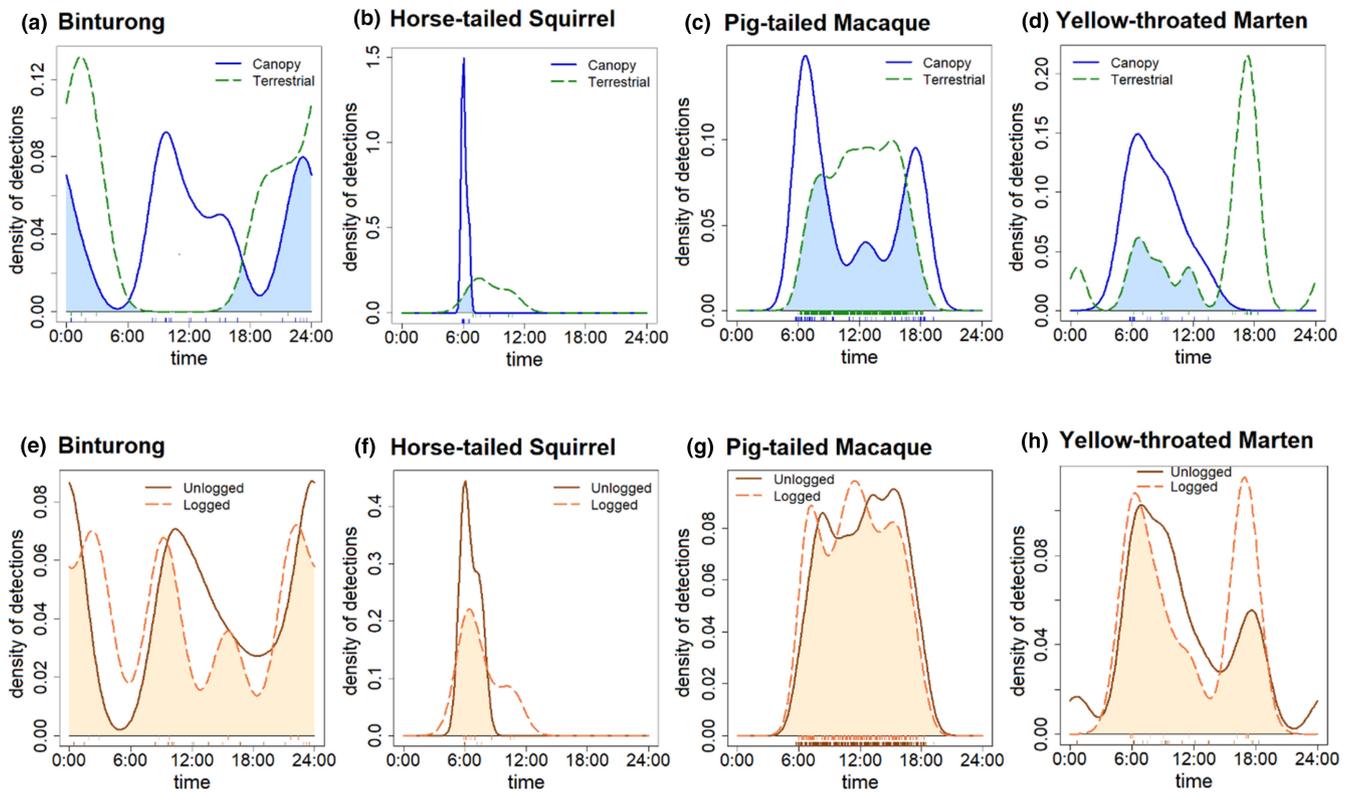
FIGURE 2 (Continued)

### 3.4 | Activity within groups

Small-bodied rodents and Insectivora had the lowest activity levels, spending on average 11%–20% less of the 24-h cycle active than large-bodied ungulates and Carnivora (Table 3). Activity levels within functional groups were less variable, although differences between herbivore sub-groups were more defined, with folivores 11% more active than granivores. For activity patterns, the clearest trends were also observed across size groups, with small- and medium-bodied mammals predominantly nocturnal and large-bodied mammals predominantly cathemeral. Most ungulates were cathemeral, as were both carnivore species. Primates were exclusively diurnal or crepuscular, omnivores and insectivores predominantly nocturnal, and herbivores were equally likely to be diurnal or nocturnal.

## 4 | DISCUSSION

Overall, our findings indicate that the vertical dimension of rainforests greatly influences mammal activity—including for semi-arboreal species that regularly move between strata—underlining the stark differences in environmental conditions between canopy and terrestrial habitats. Previous work in Borneo (Haysom et al., 2021) and elsewhere (Peru, Whitworth et al., 2019; Cameroon, Hongo et al., 2020; Rwanda, Moore et al., 2020; Brazil, Scabin & Peres, 2021; Argentina, Agostini et al., 2022) has shown that tropical arboreal mammal communities are largely distinct from their terrestrial counterparts, and can be effectively inventoried by canopy camera-trap surveys. Our findings further demonstrate the ability of canopy camera traps to define mammal activity metrics in much the same way as cameras deployed for this purpose on the ground. We draw attention



**FIGURE 3** Overlap plots showing comparisons of activity patterns for four mammal species detected in both: canopy vs. terrestrial strata (top panel [a–d]), and unlogged vs. recovering-logged forest (bottom panel [e–h]). The degree of overlap between patterns is represented by shaded areas, and bars on the x axes show the independent detections from which the patterns derive. These plots illustrate the trend toward similarity in patterns in unlogged and recovering-logged forest, but dissimilarity between strata (quantified by coefficient of overlap statistics, [Table S3](#)). See also [Figure S1](#) for overlap plots of a further 23 species with comparisons only between strata ( $N=2$ ) or between unlogged and recovering-logged forest ( $N=21$ ).

to the added value of detection data that incorporates the three-dimensionality of rainforest ecosystems, and recommend that future activity studies consider a paired terrestrial-and-canopy design (although sampling protocols should take into account the longer deployment periods needed in the canopy, see Haysom et al., 2021).

#### 4.1 | Effect of logging

To our knowledge, this is the first study to investigate the activity of multiple species within an arboreal mammal community and to compare this to equivalent species on the ground. As such, it is not yet clear whether the consistently lower activity levels of arboreal mammals ([Table 2](#), [Table S1](#)) is a trend common to tropical regions. Although logging appeared to have a negligible effect on overall activity levels, when split by stratum, the greatest differences between arboreal and terrestrial species were observed in recovering-logged forest, with arboreal mammals 14% less active than their terrestrial counterparts. Disruption of the canopy architecture caused by logging reduces lateral movement pathways for arboreal species, and navigating within logged forest canopies likely requires greater energy expenditure than within the more uniform and connected canopies of unlogged forest (Davies et al., 2017). Thus, arboreal

species in recovering-logged forest may reduce the overall amount of time they spend active in order to balance the increased energetic cost of movement in this habitat. However, there was no consistent effect of logging on the activity levels of individual species in our study in either stratum, nor on the type of species affected ([Table 2](#), [Tables S1](#) and [S3](#)), corroborating previous research on terrestrial mammals in Borneo (Wearn et al., 2022). Furthermore, 92% of all species retained the same activity pattern in unlogged and recovering-logged forest, again consistent with findings for terrestrial mammals (Maiwald et al., 2021). These results are encouraging in the conservation context, suggesting that the structural changes caused by logging do not have a clear or predictable impact on the diel patterns of animal activity in either stratum, at least not in previously logged forests that are now recovering.

#### 4.2 | Diel cycles across strata

Across all species, nocturnality was the dominant activity pattern. Evidence suggests that all extant mammals are descended from nocturnal ancestors (Maor et al., 2017), and it may be that the environmental conditions of rainforests today (e.g., high daytime temperatures, Curtis & Rasmussen, 2006), together with biotic factors

**TABLE 3** Mean activity levels and predominance of activity patterns for species grouped according to body size, taxonomic order, and functional group (i.e., feeding strategy).

Group (N = no. species)	Activity level		Activity pattern (% species)			
	Mean	Range	Nocturnal	Diurnal	Crepuscular	Cathemeral
<b>Body size</b>						
Large (N = 13)	0.46	0.23–0.59	0	31	15	54
Medium (N = 18)	0.35	0.21–0.50	67	17	11	5
Small (N = 6)	0.26	0.14–0.40	50	33	17	0
<b>Taxonomic order</b>						
Ungulates (N = 6)	0.43	0.30–0.59	17	0	17	66
Carnivora (N = 10)	0.41	0.31–0.52	40	10	10	40
Primates (N = 6)	0.33	0.23–0.45	0	67	33	0
Rodents (N = 13)	0.30	0.14–0.40	61	31	8	0
Insectivora (N = 2)	0.27	0.21–0.32	100	0	0	0
<b>Functional group</b>						
Omnivores (N = 12)	0.40	0.31–0.52	50	17	8	25
Carnivores (N = 2)	0.36	0.34–0.37	0	0	0	100
Insectivores (N = 4)	0.35	0.21–0.46	75	25	0	0
Herbivores (N = 19)	0.32	0.14–0.59	32	32	21	15
Folivores (N = 7)	0.37	0.23–0.59	14	14	29	43
Frugivores (N = 6)	0.32	0.19–0.39	50	33	17	0
Granivores (N = 4)	0.26	0.14–0.40	25	50	25	0

Note: Results here derive from metrics for individual species, presented in Table S2. Species groupings are defined in Table S1. Feeding preferences of two herbivores are unknown, so the total number of folivores, frugivores, and granivores does not equal that of herbivores.

such as eye morphology (Heesy & Hall, 2010) and avoidance of diurnal competitors (e.g., Nakabayashi et al., 2016), mean that nocturnality remains advantageous for many species in both strata.

Diurnality was rare among terrestrial mammals but the most common pattern for arboreal and semi-arboreal species, especially primates and non-gliding squirrels, in line with global trends (Thorington Jr. et al., 2012; Tan et al., 2013, Table S1). These taxa were among the first to evolve the ability to be active during daylight (Maor et al., 2017), so may be better-placed to take advantage of brighter light conditions, particularly in the canopy, which stays illuminated for longer than the more shaded forest floor (Wong et al., 2004). Differing light levels between strata may also explain why four of five crepuscular species were arboreal or semi-arboreal (Figure 2, Table S1), as the canopy presents extended foraging opportunities around dawn and dusk compared to the ground. Although twilight represents the shortest time-period in which to be active, for species with adaptations to daylight or darkness that do not translate well to the opposite light conditions, the transition between the two may offer an advantageous compromise. Movement during twilight may afford some protection from visually-hunting predators such as raptors due to lower light levels (Becker et al., 1985), as well as from predators with acute hearing such as felids due to background noise from the insect chorus, which is loudest around dawn and dusk (Gogala & Riede, 1995).

Cathemerality appears by its prevalence to have advantages for terrestrial mammals. The ability to be active across the 24-h cycle affords increased foraging opportunities (Van Schaik & Griffiths, 1996) and the flexibility to concentrate activity during times that minimize predation or competition, and/or maximize the likelihood of encountering prey (Curtis & Rasmussen, 2006). Notably, no arboreal species displayed cathemeral activity (Table 2, Figure 2), a finding consistent with studies in Indonesia (Van Schaik & Griffiths, 1996), Brazil (Oliveira-Santos et al., 2008), and Mexico (Azcarra et al., 2020). Visual acuity in mammals has evolved to be optimum in either bright or dark conditions (Heesy & Hall, 2010; Veilleux & Kirk, 2014). Consequently, while terrestrial animals moving on a flat plane may be able to contend with sub-optimal vision and spread activity across a wide temporal niche, for those traveling along branches at height, the risk of a fall associated with poor vision may lead to behavioral adaptations that favor activity during a defined light period.

### 4.3 | Semi-arboreal mammals

Semi-arboreal mammals appeared to fill the niches least used in either stratum (Table 2, Table S1). In the canopy, binturong *Arctictis binturong* followed a cathemeral activity pattern not shown by any arboreal species, while on the ground, semi-arboreal primates

(long-tailed macaque *Macaca fascicularis*, pig-tailed macaque *M. nemestrina*, and orangutan *Pongo pygmaeus*) filled the diurnal niche under-utilized by terrestrial mammals. Horse-tailed squirrels *S. hippurus* were most active in the early morning at both ground- and canopy-level (Figure 3), which may be linked to competitor avoidance. This small-bodied rodent specializes in consuming hard-shelled nuts, and likely competes with the arboreal giant squirrel *R. affinis* and the predominantly terrestrial tufted ground squirrel *Rheithrosciurus macrotis*, both of which have similar diets (Marshall et al., 2020) but are larger and more strongly diurnal (Figure 2). As the latter two species mainly utilize different strata, they are unlikely to directly compete with each other, whereas the semi-arboreal horse-tailed squirrel could conceivably compete with both and, due to its smaller size, be at a disadvantage. Temporal avoidance of competitors has been noted in temperate squirrels (Di Cerbo & Biancardi, 2013), and Bornean felids (Hearn et al., 2018), while spatial partitioning along vertical gradients has been observed in tropical rodent assemblages (Nakagawa et al., 2007). Similarly, a crepuscular activity pattern may allow species such as horse-tailed squirrels to avoid potentially harmful interactions at both ground- and canopy-level, while maintaining the ability to optimize foraging across vertical niches.

Data pooled across forest types revealed two of six semi-arboreal species were significantly more active on the ground, while three were more active in the canopy, although not significantly so (Table S3). This may reflect species-specific preferences between strata and thus serve to inform researchers where to concentrate census surveys or monitoring. We did not detect any significant increase in terrestrial activity levels of semi-arboreal mammals in recovering-logged forest (Table S3), consistent with observations elsewhere in Borneo for orangutan (Ancrenaz et al., 2014), suggesting that these species are not descending to the ground more often because of structural changes post-logging (e.g., as proposed in Berry et al., 2010). The additional data collected on the canopy aspect of semi-arboreal mammals' lives (Tables S1 and S3) underline the importance of including canopy-based sampling for these species, even if they can be readily recorded at ground level. Studies utilizing only terrestrial camera traps may mischaracterise activity metrics for mammals that habitually use both strata, restricting our ability to understand their behavior, ecology, and interspecific interactions.

#### 4.4 | Activity within groups

Activity may vary predictably with species traits such as body size, taxonomic order, and feeding strategy (Cid et al., 2020; Heesy & Hall, 2010; Rowcliffe et al., 2014; Van Schaik & Griffiths, 1996), although some studies contradict this (e.g., Clauss et al., 2021). Small-bodied mammals were notably less active than larger species and were predominantly nocturnal (Table 3, Table S1), potentially supporting hypotheses that small mammals maintain lower activity

levels to conserve energy (Hazlerigg & Tyler, 2019), and are more active at night when thermoregulatory pressures are eased (Crompton et al., 1978). Large mammals, on the contrary, may spend more time foraging to meet increased energetic demands (Cid et al., 2020), particularly carnivores, whose prey is often patchily distributed (Azlan & Sharma, 2006), and herbivores, who may consume more in order to compensate for the lower nutritional quality of their diet (Shafique et al., 2006). Indeed, most cathemeral species in our study were large-bodied carnivores or herbivores (Table S1). When herbivores were further split into sub-groups, leaf-eaters spent 11% more time active than seed-eaters. This could be explained by the poor energetic value of leaves compared to seeds (Mitsuzuka & Oshida, 2018) and the durability of seeds, which allows caching for later consumption (e.g., Becker et al., 1985) thereby also reducing overall foraging time for granivores.

#### 4.5 | Caveats

Reduced canopy activity levels may reflect the different conditions of this stratum compared to the ground (including smaller effective sampling area per camera and lower density of species per cubic kilometer, see Haysom et al., 2021). Sampling duration and environment should therefore be considered when comparing the amount of time different communities spend active. Care should also be taken when interpreting changes in activity level, as a reduction is not necessarily negative. For example, animals that need to travel less to forage (e.g., due to new vegetation growth in canopy gaps) are arguably at an energetic advantage to those needing to travel further to fulfill daily requirements.

Although our results imply that the major ecosystem components driving mammal activity are not sufficiently altered by selective logging to cause significant changes, our recovering-logged forest site was of relatively high quality. Logging ceased a decade prior to sampling, and the area has low levels of hunting (Deere, Guillera-Aroita, Platts, et al., 2020). Both factors can affect activity patterns (e.g., for bearded pig *Sus barbatus* and sun bear *Helarctos malayanus*, Chapman, 2018; Davison et al., 2019; Meijaard et al., 2005), and sampling locations with higher levels of structural degradation and/or hunting may thus report greater shifts in the diel activity of resident wildlife.

Finally, activity analyses do not extend to examination of abundance changes. Our finding that past selective logging has a minimal effect on animal activity is encouraging, but should not be interpreted as a message that logging has no effect on mammals. Indeed, certain species were more noticeable by their absence, for example, our negligible records of two of the three large flying squirrels and our failure to record Sabah gray langur *Presbytis sabana* in recovering-logged forest (Tables S1 and S2). While logging may not greatly alter diel activity for species still present, there may be some that simply cannot persist in viable numbers in post-logging environments.

## 5 | CONCLUSION

Our study represents the first community-wide investigation of rain-forest mammal activity encompassing both arboreal and terrestrial communities in both unlogged and recovering-logged forest. We demonstrate clear differences in activity patterns between canopy and terrestrial strata, likely arising from species' adaptations to these structurally diverse habitats. We further show that within the rain-forest mammal community, all temporal niches across the 24-h cycle are filled, and that this is most evident when species utilizing the vertical dimension are taken into account. Our findings add to the growing body of evidence from across the tropics demonstrating the effectiveness of canopy camera traps for arboreal surveys. We show that the utility of this method extends beyond inventories to include ecological and behavior-focused research. In complex and biodiverse rainforest ecosystems, cross-strata sampling enables a much more complete understanding of mammal community dynamics, revealing how species interact and partition activity across temporal and spatial niches.

### AUTHOR CONTRIBUTIONS

Conceptualization: J.K. Haysom (JH), M.J. Struebig (MS), and N.J. Deere (ND). Investigation and data curation: JH. Formal analysis: JH, ND. Project administration: A. Mahyudin (AM). Writing—original draft: JH. Writing—review & editing: JH, MS, ND, AM.

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### CONFLICT OF INTEREST STATEMENT

The corresponding author confirms on behalf of all authors that there have been no involvements that might raise the question of bias in the work reported or in the conclusions, implications, or opinions stated.

### DATA AVAILABILITY STATEMENT

The data that support the findings of this study are openly available in Zenodo at <https://zenodo.org/record/5018280#YNM-pehKiUk>.

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## SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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