

Consistent daily activity patterns across tropical forest mammal communities

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Abstract

Most animals follow distinct daily activity patterns reflecting their adaptations¹, requirements, and interactions²⁻⁴. Specific communities provide specific opportunities and constraints to their members that further shape these patterns^{3,4}. Here, we ask whether community-level diel activity patterns among long-separated biogeographic regions differ or converge and whether the resulting patterns indicate top-down (predation risk) or bottom-up processes (prey availability)? We estimated the diel activity of ground-dwelling and scansorial mammals in 16 protected areas across the tropics, using an extensive network of camera traps, and examined the relationship to body mass and trophic guild. We found that mammalian guilds exhibited consistent diel activity patterns across regions, indicating similar responses to similar evolutionary and ecological opportunities and constraints. Larger herbivores tended to be more nocturnal than smaller herbivores, whereas carnivores and omnivores showed the opposite pattern. Insectivores were exceptions, revealing regional differences in which larger insectivorous species were more nocturnal than smaller ones in the Afrotropical and Indo-Malayan regions, while the pattern reversed in the Neotropics. The consistent contrast between predators and prey suggests that diel activity within these communities is primarily determined by large predators and associated risk of predation.

Introduction

Diel activity patterns—the distribution of activity throughout the daily cycle—are fundamental in animal ecology⁵. These patterns reflect when organisms seek food, socialize, and perform other necessary tasks while also accounting for risks^{1,2}. Activity patterns vary among species. Some organisms may maintain activity over extended periods while others exhibit brief peaks⁶. They may be predominantly active during the night (nocturnal), day (diurnal), twilight (crepuscular), or may lack pronounced peaks with relation to day and night (catemeral). Furthermore, there can be substantial variation within species and between populations⁶. Mammals illustrate a broad range of such behaviours.

While mammals today occupy all temporal niches (day, night, twilight), early mammal species are thought to have been primarily nocturnal to avoid the predation risk imposed by diurnal dinosaurs—an idea known as the “nocturnal bottleneck” hypothesis⁷. Following the extinction of the non-avian dinosaurs (66 Ma)⁸, mammals diversified and adapted to fill the available temporal niches^{7,9}. Physiologic, morphological, and behavioural adaptations⁹ including endothermy, eye forms¹⁰, and enhanced sensorial systems allowed mammals to thrive under the different illumination and temperatures associated with day and night.

Endothermy permits mammals to exploit multiple temporal niches^{11,12}. Nonetheless, species-specific physiological characteristics, in interaction with morphology (e.g., body size), may still favour activity schedules that moderate thermal stress¹³. For instance, in the absence of other factors, large species in warm regions may be forced to avoid overheating by avoiding activity in the hottest periods¹⁴. By contrast, small species that can lose heat rapidly may avoid cold and focus activity in warmer

periods^{15,16}. Small mammals such as mice and rats avoid diurnal predation by favouring nocturnal activity but may nonetheless be active during the daytime due to food scarcity, low nighttime temperatures, or low risks from diurnal predation^{1,17}.

Species interactions may influence and control diel activity patterns within communities^{3,4}. For instance, predators may favour periods where their prey are active, whereas prey species may avoid periods when their predators are active^{5,18}. Potentially, this can involve both top-down or bottom-up processes^{19–21}. Bottom-up and top-down are key classifiers for the regulation of food web dynamics^{19–21} and have the potential to influence how species within an assemblage may behave²². In a top-down process, the temporal activities of certain species (e.g., prey) seek to avoid the time use of others (e.g., predators)²³. For example, small carnivores may avoid activity in periods when they are more likely to encounter larger predators, with similar avoidance expected for prey species to avoid their predators^{18,23}. Alternatively, this can be a bottom-up process in which predator species match their activities to that of their prey or competitors²². For instance, mesopredators in south-western Europe were found to match their activity to that of their prey²⁴. There is evidence for both bottom-up and top-down determination of activity patterns in a few sympatric species^{22–24}. Yet, we do not know the degree to which bottom-up and top-down processes operate in nature and whether the resulting patterns are consistent across regions.

Humid tropical forests provide a useful context for exploring these questions as the influence of seasonality is low and similar environmental conditions are found in biogeographically distinct regions¹³. These forests encompass many of the most diverse and rich terrestrial biomes on earth and the maintenance of such diversity likely involves biotic interactions²⁵. Trophic composition of tropical forest mammal communities appears relatively consistent across tropical regions²⁶ and has been attributed to convergent evolution, likely due to similarities in environment and adaptations across distant forests²⁷. We expect that the processes that shape trophic interactions and composition may also influence diel activity patterns.

We studied the daily activity patterns of ground-dwelling and scansorial mammals inhabiting protected tropical forests across the Neotropics, Afrotropics, and Indo-Malayan tropics (Fig. 1). We used time-stamped images from standardized large-scale camera-trap surveys implemented by the Tropical Ecology Assessment and Monitoring (TEAM) Network in 16 protected areas (Table S1)²⁸. Using multinomial analysis, we investigated how diurnal, nocturnal, and crepuscular activity was related to trophic guild and body size and whether any such patterns were consistent among regions.

We tested three hypotheses (Fig. 2). First, if top-down processes regulate the diel activity of animals in a community (H1), we predicted (1a) that prey species (e.g., herbivores) should exhibit diel activity patterns that avoid those of predators (e.g., carnivores and omnivores) of a similar size (interguild avoidance), and (1b) smaller members of a trophic guild (especially carnivores and omnivores) should exhibit diel activity patterns that avoid that of larger members of the same guild (intraguild avoidance). If bottom-up processes regulate the diel activity of animals in a community (H2), then (2) diel activity patterns of

predators should match that of prey species (herbivores, insectivores, and small omnivores). Finally, if the energetic cost of thermoregulation constrains diel activity of tropical mammals (H3), then (3) large mammals should be more active during the night when it is colder and small mammals more active during the day when it is warmer.

We extracted the probability for the activity (0–1) during day, night, and twilight, and the correspondent upper (UCI) and lower (LCI) 95% confidence intervals for the given range of body mass and trophic guild derived from the multinomial model in every region with the lowest AIC. Diel activity was best modelled when including body mass, trophic guild, and their interaction for the three regions (Fig. 3, Table S2).

Fig. 3. Distribution of daily activity in relation to body size and trophic guilds of tropical ground-dwelling and scansorial mammals in three regions. Estimates correspond to the probability of activity during the day, night, and twilight extracted from the model fitted to TEAM camera-trap data. Tick marks above the x-axis indicate the typical body mass of species analysed. Colour hue indicates where the model interpolates among observations of the sizes presented (darker) versus extrapolates beyond values in the data for that trophic guild and region (lighter).

Consistent Patterns

We found consistent patterns of diel activity in relation to trophic guild and body mass across regions (Fig. 3, Fig. S1, Table S2) indicative of top-down processes playing a dominant role in shaping community activity patterns (H1). Following our prediction 1a, the interguild relationships between nocturnality and body mass showed contrasting patterns for predators (i.e., carnivores, omnivores) and prey (i.e., herbivores, and perhaps insectivores) indicating avoidance of predators by prey across regions. In general, larger prey species were nocturnal whereas larger predators were diurnal (Fig. 3). For example, in the Neotropics, the highest diurnal probability for large predators was 0.64 (LCI:0.63, UCI:0.74, body mass = 96 kg). Herbivores (i.e., prey) were more likely to exhibit a high nocturnal activity as the body mass increased to a maximum probability of 0.60 (LCI:0.48, UCI:0.71, body mass = 210 kg).

Among carnivores, we found a negative relationship between body mass and nocturnality supporting prediction 1b. Thus, small carnivores, which risk predation by larger carnivores²⁹, were more likely to be nocturnal than larger carnivores. For example, carnivores in the Afrotropics decreased nocturnality probability from 0.81 (LCI: 0.74, UCI:0.87, body mass = 1 kg) to 0.21 (LCI: 0.14, UCI: 0.28, body mass = 61 kg) as size increased. Such temporal partitioning has previously been identified as a strategy for mitigating intraguild predation among carnivores, thus aiding their coexistence^{3,4,18,22,29-31}. Finally, our analyses indicate that among both herbivores and insectivores, smaller species were more likely to be diurnal than larger species which we suggest is likely a consequence of avoiding small and medium-sized predators.

The high degree of diurnality among large carnivores evident in our study sites contrasts with reports from other forests, as in Madagascar and North America where carnivores were largely active at

night^{32,33}. These previous studies focused on more anthropogenic landscapes, where carnivores appear to avoid interacting with humans by becoming more nocturnal³²⁻³⁴. Our sites are within protected areas and therefore suffer lower human impacts than elsewhere and may permit greater diurnality.

Explanations

While top-down processes appear to shape overall activity patterns within each community, notable variation among species persists, even within the same trophic guild and for comparable body sizes (Fig. S4). Species-specific diel activity patterns likely arise from a combination of bottom-up and top-down processes, and other influences (e.g., habitat features, environmental conditions, intra-specific dynamics, etc.). Furthermore, some patterns cannot be attributed unambiguously to one process or factor, for example, the nocturnal activity of small omnivores may reflect avoidance to top predators (top-down) and/or following of omnivore prey (bottom-up, Prediction 2, Fig. 2, Fig. 3). Both explanations have merits when we consider better-known species such as the ocelot (*Leopardus pardalis*), a neotropical felid, which is known to prey on various species including nocturnal omnivores such as opossums and racoons³⁵, and is also known to avoid jaguars. Although bottom-up regulation can influence the abundance of species³⁶, we did not find further evidence for this process in the activity of other trophic groups.

Larger-bodied herbivores and insectivores tended to be more nocturnal consistent with the thermoregulatory constraint hypothesis (H3). For example, for Afrotropical herbivores, nocturnality probability increased from 0.09 (LCI: 0.06, UCI: 0.11, body mass = 0.70 kg) to 0.60 (LCI: 0.51, UCI: 0.69, body mass = 4334 kg) as the body mass increased (Fig. 3). Similarly, the probability of being nocturnal among insectivores in the Indo-Malayan increased with body mass from 0.01 to 0.98 (Fig. 3). While daily temperature is more stable in tropical rainforests than in many other ecosystems, it does vary³⁷. Most tropical mammals are adapted to survive in a narrow thermal tolerance range^{38,39}, thus both high and low temperatures can increase energy expenditure⁴⁰. Small-bodied species can reduce energy loss by being active during warmer periods of the day¹⁵, while large-bodied animals (e.g., tapirs⁴¹, aardvark⁴²) can reduce thermal stress by focusing activity during cooler periods of the day^{14,41,43}. For example, in the Neotropics the probability of being active during the night was two times higher for a 290 kg herbivore (e.g., *Tapirus bairdii*) than for one of 1 kg (e.g., *Myoprapta acouchy*). In contrast, we found a positive relationship between size and diurnality for carnivores, omnivores and neotropical insectivores. If thermoregulatory constraints were sufficiently powerful, we might anticipate it to manifest across all trophic guilds. Perhaps this was not apparent because interactions may be more influential than other factors (eg., physiology) in tropical forests compared to other biomes²⁵ due to more stable climatic conditions. Megafaunal species were also scarce among non-herbivores and thus thermal stress may be less influential.

Although all our study areas are relatively well-protected none are completely free of human impacts²⁸ raising the question of how this may influence the observed patterns. Clearly, human presence influences

animal activity patterns too; for example, some species have become more nocturnal to avoid hunters⁴⁴. This was recognised in one of our study sites, where ungulates became more nocturnal as hunting increased⁴⁵. In this context, it is remarkable that the general patterns were so robust and remained consistent across sites despite variation in hunting pressure. We acknowledge the inability of our study to clarify the role of large carnivores and hunters in determining the specific details of the patterns reported. However, simple approaches using human activity may be misleading as evasive responses among mammals are not universal and can change over time (for example, the gorillas in Bwindi have been habituated to humans), and in some locations, animals favour human settlements to access certain foods or avoid predation. At some of our sites, certain large predators (e.g., leopards in Bwindi⁴⁶) are now absent due to earlier extinctions and more recent losses^{47,48}. This, however, does not necessarily mean release from diurnal risks and disturbance from omnivorous mammals (e.g., chimpanzees), birds of prey, reptiles (e.g., pythons, anacondas), and humans (tourists and hunters). Furthermore, current activity patterns may reflect the anachronistic top-down regulation by “ghosts of predators past”. Further work is needed to explore these nuances. To ensure we are not misunderstood, we underline that the robust and consistent patterns we observed in these comparatively well protected forest communities do not contradict past work indicating that widespread species decline and loss can have a devastating impact on ecosystems^{49–51}.

The odd-one-out: Neotropical insectivores

Insectivores were an exception to the consistent patterns across regions: while Afrotropical and Indo-Malayan species revealed a positive relationship between greater body mass and the likelihood of nocturnal activity (e.g., Afrotropical increased from 0.01 to 0.91), a negative relation was found in the Neotropics with a decrease of nocturnality with greater body mass, from a probability of 0.99 (LCI: 0.99, UCI: 0.99, body mass = 0.12 kg) to 0.32 (LCI: 0.22, UCI: 0.44, body mass = 43.30 kg). We do not know the cause for this exception but can speculate. The pattern reported for insectivores in Afrotropical and Indo-Malaya regions is consistent with the thermoregulatory constraints hypothesis (H3). However, the higher diurnality of large insectivore species than small ones in the Neotropics, was mostly driven by three species (*Myrmecophaga tridactyla*, *Tamandua tetradactyla*, and *Tamandua mexicana*) which may derive from the distinct biogeographic history of the Neotropics, where insectivores are among the few native lineages that persisted after the great interchange⁵². In any case, the difference may reflect different characteristic requirements (e.g., African aardvarks dig burrows, whereas neotropical anteaters live above ground).

Conclusion

Despite their distinct origins, biogeographic histories, and taxonomic compositions, community level diel activity patterns for tropical forest mammals, examined by trophic guild and body size, are remarkably consistent across 16 sites and three tropical regions. As shown previously for trophic structures⁴⁷, diel activity patterns appear shaped by common processes regardless of biogeography. Convergent evolution

across regions appears manifested in many ways including, as we see here for the first time, diel activity strategies. These community-level activity patterns appear shaped primarily by larger predators through top-down processes

Methods

1) Study areas and camera trapping

We used camera-trap data from the Tropical Ecology Assessment and Monitoring (TEAM) Network⁴⁷. TEAM data comprise data from three tropical biogeographic regions (Neotropics, Afrotropics and Indo-Malayan tropics) and 16 protected areas (TEAM Network, 2011) (Fig. 1). Camera-traps were deployed following a standardized protocol through all protected areas during the dry season between 2008 and 2017. At each protected area the monitoring run from two to ten years with the deployment of 60 to 90 cameras. Camera-traps were placed at a density of 0.5 - 1 camera/km² (1 camera every km² or 1 camera every 2 km²) and remained active for ~30 consecutive days^{28,47}. We excluded data from camera-trap sites with inconsistent date-time stamps, yielding a total of 60-89 cameras per protected area (Fig. 1, Table S1).

2) Data

A total of 2 312 635 camera-trap pictures corresponded to mammals. We further filtered the dataset to delimitate our study for species with a body mass greater than 75 g (smaller species have high uncertainty of identification and are difficult to detect) and species strictly terrestrial or scansorial (i.e., we excluded all arboreal and aquatic species)^{26,53}. A total of 166 species, 38 families, and 15 orders of ground-dwelling and scansorial species were detected (Table S1). Since camera-traps usually take consecutive pictures, we avoided pseudo-replication of individuals by establishing independent events (time interval between pictures > 1-hour per camera for a given species). This resulted in a total of 126 382 independent events (Supplementary Material 2). To analyse diel activity, we used the time-stamp recorded in each independent event⁵⁴ and summarized the number of events for each of the following three categories 1) day, 2) twilight, or 3) night. Each event was classified by protected area, location, time, and date to specify the sunrise, sunset, nautical dawn, and dusk using the R library 'mapprojtools'⁵⁵. Twilight was defined as the interval between dawn and sunrise and between sunset and "nautical dusk"⁵⁶. Day was defined as the interval between sunrise and sunset. Night was the interval between nautical dusk and nautical dawn.

As species characteristics we used 1) trophic guild and 2) body mass(g) which we extracted from the PHYLACINE database⁵⁷ (Fig. S2). We classified each mammal species into four trophic guilds: carnivore, herbivore, insectivore, or omnivore. Categories were based on diet reported in the PHYLACINE database and we classified as carnivore species feeding on $\geq 80\%$ vertebrates, herbivore species feeding on $\geq 80\%$ plant materials, insectivore feeding on $\geq 80\%$ insects, the remaining species were categorized as omnivores (e.g., feeding on vertebrates and fruits)^{57,58}.

3) Analysis

To test how trophic guild (carnivores, herbivorous, insectivores, and omnivores) and body mass (log-transformed) is associated with the number of independent events of each diel activity (day, night, twilight) of tropical ground-dwelling and scansorial mammals we fitted a multinomial logit model⁵⁹ using package 'mclgit'⁶⁰. Multinomial modelling allowed us to assess three instead of two response classes (day, night, and twilight). We built a set of candidate models for each tropical region using maximum likelihood (ML) and with a convergence tolerance (ϵ) of 1e-6 (Table S1). To account for the variability between the activity of species in different protected areas we include protected areas as a random effect within all models. We selected the best model for each tropical region using Akaike information criterion (AIC). We ranked models using Δ AIC and considered models with a Δ AIC <2 to equally be supported. Once we selected the best models, we run the models with a restricted maximum likelihood (REML) to arrive at final estimates for each tropical region. We predicted relative activity with the package 'mpred'⁶⁰. This allowed us to extract the predicted probability of activity in each diel category for the range of body mass in each trophic guild and region.

To show the diversity of activity patterns we characterized species-specific activity patterns when the number of independent events was 25 or more⁶¹. We gathered the data of all protected areas in each biogeographic region to display species activity patterns (Fig. 1, Fig. S3). To correct for diel differences on the delimitation of day, night and twilights between protected areas and distinct dates of the year of sampling we anchored activity patterns to sunrise and sunset⁶² using the 'activity' package⁶³ (Fig. S3). Then we plotted species activity with the package 'overlap', which employs kernel density estimation that circumvents the conflation of data required for histograms⁶¹.

Declarations

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Author contribution statements

DS and RB proposed the study and accessed funding. A.F.V-V., R.B. and D.S. developed the approach and hypotheses presented here. A.F.V-V. developed and performed the analyses. R.B. verified the analysis. A.F.V-V. wrote the manuscript with support from R.B., D.S., A.S-P., and L.B. The authors D.S. J.A., R.Bitariho., S.E., V.E., P.A.J., C.K., E.H.M., M.G.M.L, B.M., F.R., J.S., F.S., W.R.S., and E.U. were responsible of

the camera trap data collection in the TEAM sites. A.F.V-V. R.B and D.S. finalized the manuscript with input and approval from all authors.

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Supplementary Material

1. Table S1. Additional information about the protected areas included in the study.
2. Table S2. Candidate models by biogeographic region.
3. Figure S1. Multinomial models' coefficients estimates by each region with carnivores as the reference group
4. Figure S2. a) Distribution of body mass for the three different biogeographic regions. b) Number of species in each trophic guild and each biogeographic region.
5. Figure S3. Density plot of activity by biogeographic region and trophic guild
6. Figure S4. Predicted probability of diurnal, crepuscular, and nocturnal activity for a sequence of body mass values and raw proportions of all species included in the study.

Figures

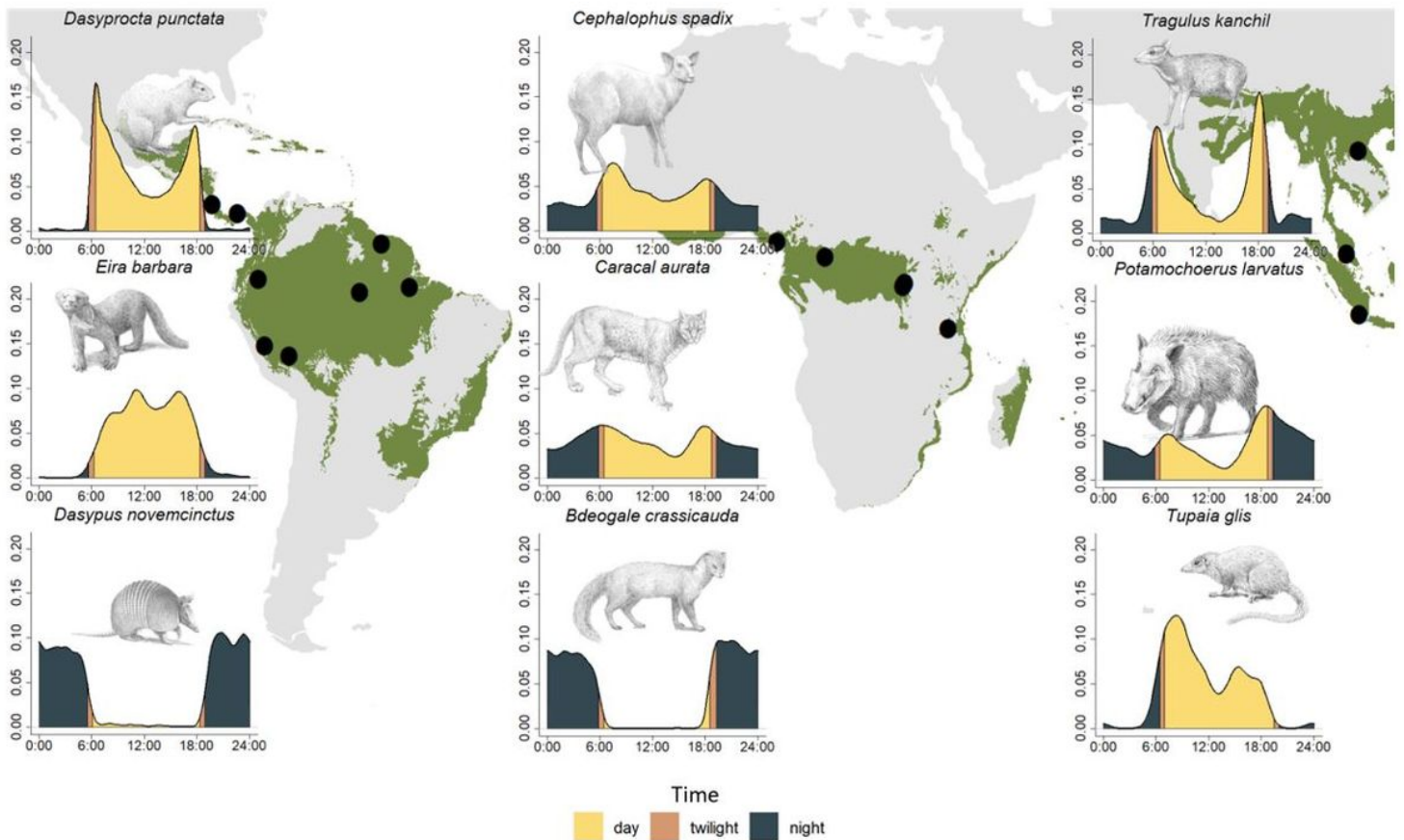


Figure 1

Map of the study sites and activity density examples. 16 protected areas within 14 countries and three biogeographic regions at which mammal activity data were collected using the standardized TEAM camera-trapping protocol. Activity density plots represent examples of species in each region. Green areas denote tropical forests.

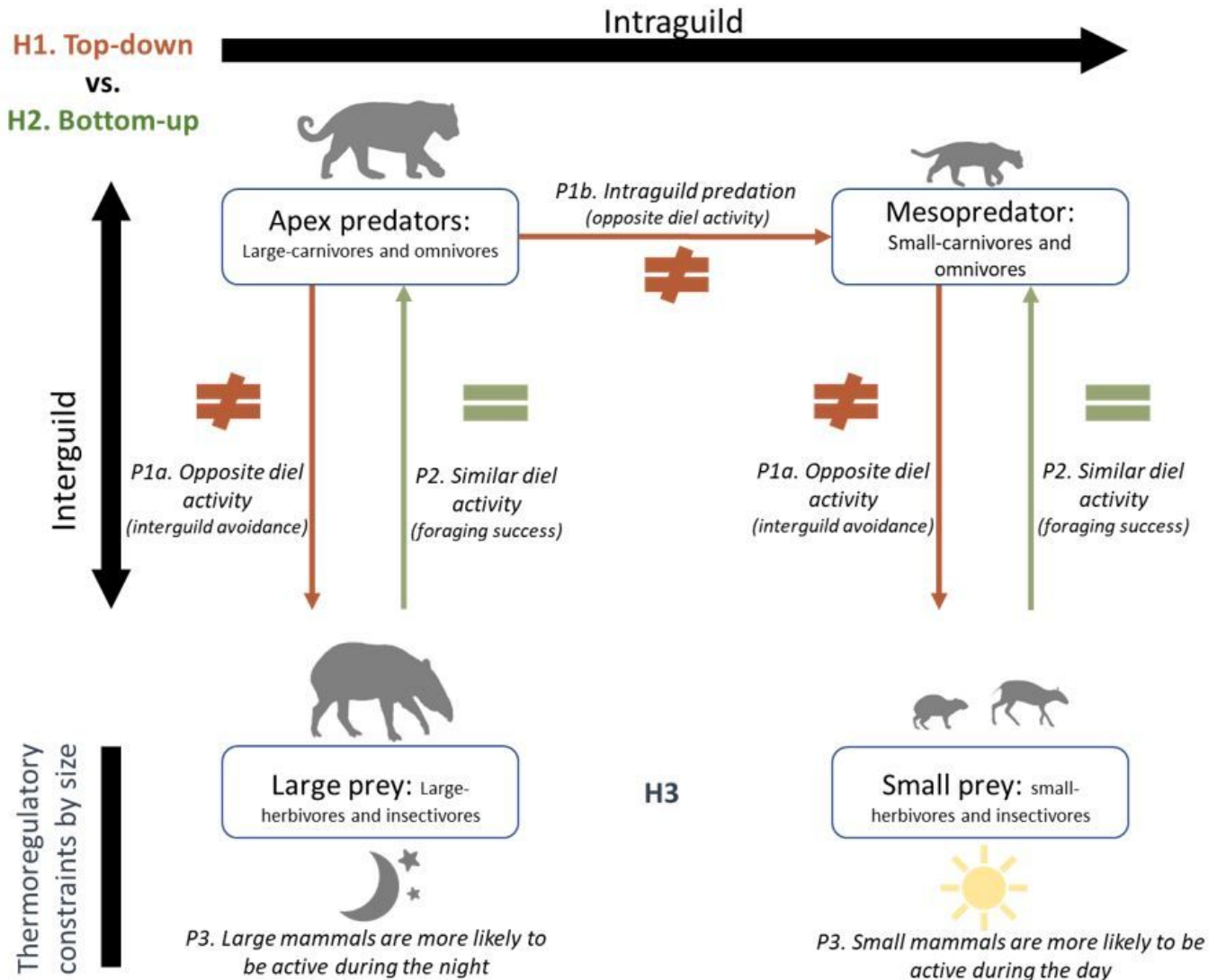


Figure 2

Hypotheses on the determination of diel activity patterns in tropical forest mammal communities, with associated predictions (P1-3). If top-down regulation dominates (H1), then at the intraguild level we predict that small predators will avoid top-predators (1a) while at the interguild level, potential prey species will avoid their predators (1b). If bottom-up regulation dominates (H2), predators will follow the diel activity of their prey (2). If the energetic cost of thermoregulation dominates (H3), we expect a positive relationship between body mass and nocturnality (3), regardless of trophic guild. Silhouette images were downloaded from phylopic.org.

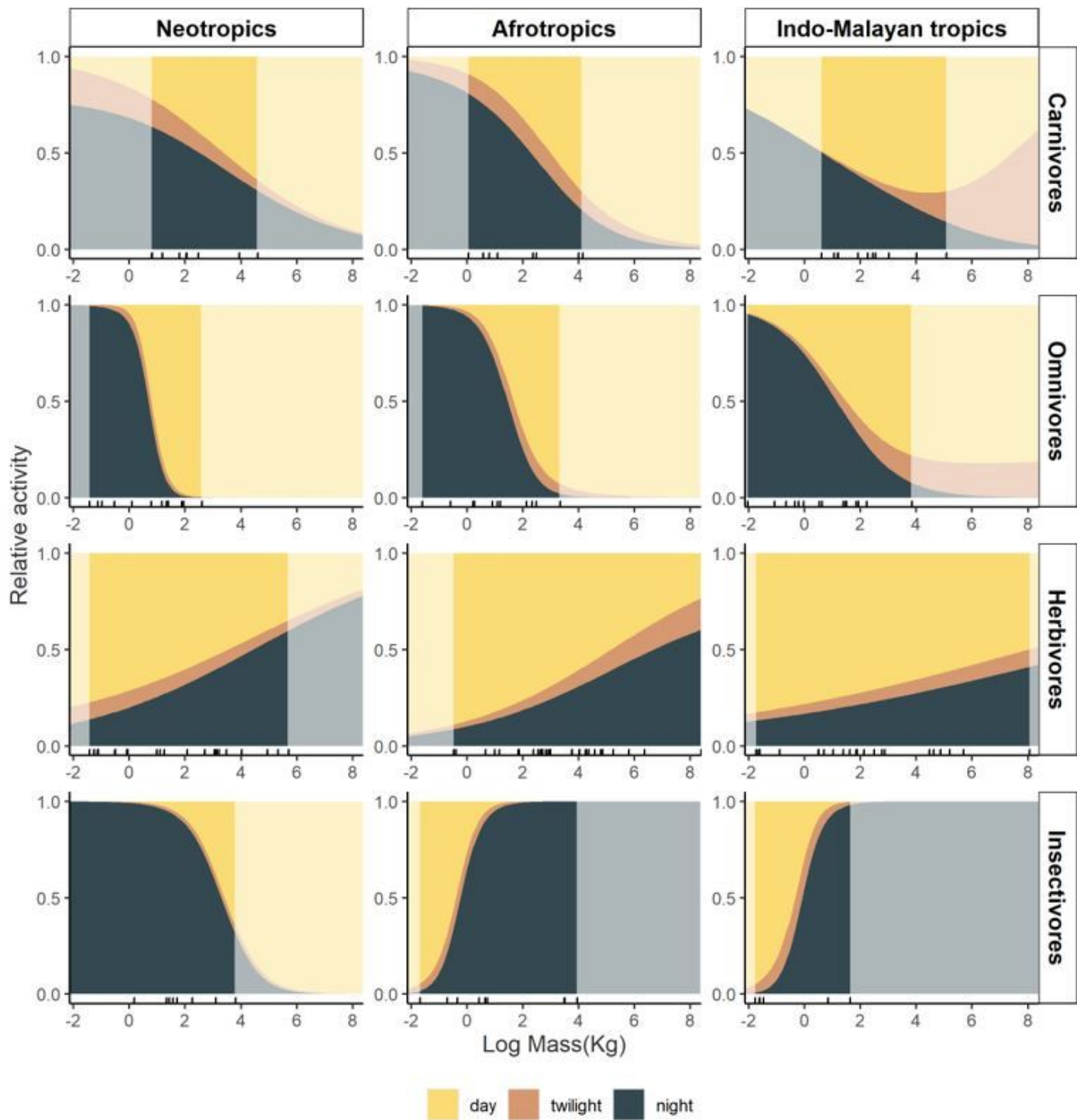


Figure 3

Distribution of daily activity in relation to body size and trophic guilds of tropical ground-dwelling and scansorial mammals in three regions. Estimates correspond to the probability of activity during the day, night, and twilight extracted from the model fitted to TEAM camera-trap data. Tick marks above the x-axis indicate the typical body mass of species analysed. Colour hue indicates where the model interpolates among observations of the sizes presented (darker) versus extrapolates beyond values in the data for that trophic guild and region (lighter).

Supplementary Files

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