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The moon's influence on the activity of tropical forest mammals

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Changes in lunar illumination alter the balance of risks and opportunities for animals, influencing activity patterns and species interactions. We examined if and how terrestrial mammals respond to the lunar cycle in some of the darkest places: the floors of tropical forests. We analysed long-term camera trapping data on 86 mammal species from 17 protected forests on three continents. Conservative categorization of activity during the night revealed pronounced avoidance of moonlight (lunar phobia) in 12 species, compared with pronounced attraction to moonlight (lunar philia) in only three species. However, half of all species in our study responded to lunar phases, either changing how nocturnal they were, altering their overall level of activity, or both. Avoidance of full moon was more common, exhibited by 30% of all species compared with 20% of species that exhibited

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attraction. Nocturnal species, especially rodents, were over-represented among species that avoided full moon. Artiodactyla were more prominent among species attracted to full moon. Our findings indicate that lunar phases influence animal behaviour even beneath the forest canopy. Such impacts may be exacerbated in degraded and fragmented forests. Our study offers a baseline representing relatively intact and well-protected contexts together with an intuitive approach for detecting activity shifts in response to environmental change.

1. Introduction

The moon brightens the night and the 29-day lunar cycle alters the conditions faced by wildlife [1]. For some mammal species, especially those with limited night-vision or few nocturnal threats, the extra illumination provides periodic access to the night and associated foraging [2,3] or travel opportunities [4]. Other species are robbed of the cloak of darkness and become exposed to predators [3] or visible to prey [5]. Determining whether and how species react to changing lunar phase and related illumination can improve our understanding of the temporal dimension of the ecological niche. It can also inform efforts to predict behavioural responses to modified light conditions in an increasingly human-altered environment.

The daily activity pattern or 'diel activity' of an individual, a population or a species constitutes a fundamental part of its ecological niche, and has been studied extensively [6]. Despite intuitive expectations for attraction to or avoidance of moonlight (i.e. lunar philia and lunar phobia) and accumulating evidence for each, we still know little about the prevalence of these behaviours in nature. While some species seem to respond strongly to lunar illumination [1], others apparently do not respond at all [7,8]. The most comprehensive assessment of species responses to moonlight is a meta-analysis of 58 species that found that moonlight reduced the activity of species in open habitats yet increased the activity of species in forested environments [3]. However, this meta-analysis included only 20 species that were studied in tropical forests. Moreover, 10 of these species were arboreal primates which consistently responded positively to moonlight. Thus, it remains unknown whether the results from that study apply to the broad spectrum of tropical forest-dwelling species, particularly those living on the forest floor, the darkest part of tropical forests. Despite the fact that the diel activity of species is a fundamental part of their niche, and moonlight may influence diel activity patterns, there has yet to be an assessment of the relationship between lunar phase and animal activity patterns based on community-level data collected across multiple locations and regions using standardized data collection and analytical methods.

There are both fundamental and applied reasons why we should identify diel activity responses to lunar phases and associated changes in illumination. First, the recurrent change in potential risks and opportunities faced by entire communities provides a testing ground for ecological theory about species adaptations [6], interactions [9] and the temporal dimension of the ecological niche [10,11]. Studies have tested for, and in some cases found, evidence that lunar illumination triggers niche shifting, with animals modifying when and where they are active dependent on the moon's phase [11]. Second, a species' response (or lack thereof) to moonlight may be indicative of whether and how it may respond to artificial light. This is crucial as light pollution already impacts a substantial part of Earth [12,13], with consequences for wildlife behaviour [14–16] and community dynamics [17,18]. Finally, knowledge about the relationship between illumination and animal behaviour in densely canopied and less-impacted systems offers a baseline for detecting changes in human-modified habitats. Even apparently 'natural' light regimes change because of human-driven habitat alteration. For example, tropical forests, which harbour a substantial portion of earth's biological diversity, are cleared, fragmented and degraded at an alarming rate [19,20]. Not only does this result in direct habitat loss and modification, but also in reduced canopy cover which exposes forest-dwelling species to increased solar and lunar illumination.

What is the prevalence and direction of responses to lunar phases in wildlife communities in some of the darkest places on earth, the floors of tropical forests? Camera trapping offers an opportunity to answer this question. Camera traps can be deployed and record animal activity 24/7 for months (one or more complete lunar cycles) and may thus capture wildlife responses to changing levels of moonlight. In fact, camera traps are now widely used for monitoring and studying terrestrial biodiversity [21–23] and several studies have relied on time-stamped camera trap images to quantify and study animal diel activity [24–26]. We used images from a pantropical camera trap study in tropical forests on three continents. Standardized survey methods allowed us to simultaneously examine diel and nocturnal activity of 86 mammal species from 16 orders and 35 families.

We analysed photographic detection data using a novel framework—multinomial regression combined with ternary classification—for consistent categorization and quantification of the temporal niche and shifts therein (see also [27]). The flexible framework allowed us to not only compare activity associated with different lunar phases, but also test hypotheses about how lunar illumination impacts activity beyond the night. Previous studies have shown that lunar illumination can trigger shifts in overall diel activity [1]. These changes may arise in various ways. At one extreme (fully additive), animals can reduce or increase their nocturnal activity during full moon, without a change in activity during day or twilight. This strategy will result in a corresponding decrease or increase in overall net activity. On the other extreme (fully compensatory), animals may shift activity into or out of the illuminated period, for example by moving their activity from the twilight period into the night, without a change in overall net activity.

The aim of this study was to better understand impacts of moonlight on animal activity in tropical forests. We investigated whether and how tropical forest mammals alter their activity with lunar phases. First, we investigated which species exhibited conspicuous lunar philia or phobia, manifested as selection for moonless or moonlit periods during the night. Second, we tested for a link between a species' degree of nocturnality and the response to lunar phases. We predicted that species that were more nocturnal would be more likely to avoid full moon. Third, we quantified the extent to which mammals altered their diel activity with lunar phases. Specifically, we tested whether, during moonlit periods, animals shifted activity into or out of the night (compensatory), changed their overall level of activity (additive) or both. Becoming less nocturnal and/or reducing activity during periods of full moon would constitute evidence of avoidance. Conversely, increased nocturnality and/or increasing activity during periods of full moon would constitute evidence of attraction to the full moon phase or the conditions it creates.

2. Methods

(a) Data collection

(i) Camera trapping

We derived observations of mammal activity in protected tropical forests from camera trap data collected as part of the Tropical Ecology Assessment and Monitoring (TEAM) Network [28]. Following a common protocol [29], cameras were deployed between 2008 and 2017 throughout 17 protected areas in Indomalaya, the Neotropics and the Afrotropics. The number of years of deployment varied between protected areas (2–10 years; mean = 6.8 years), as did the number of locations sampled (60–90 camera trap locations; total: 1062). Spatial configuration and deployment were standardized, with cameras configured in either a 1 × 1 km or 2 × 2 km regular grid, at a height of approximately 30–50 cm off the ground. On average cameras were active for 33.2 days (s.d. = 7.5). However, cameras were rotated sequentially until all sites were sampled within the wider sampling season. As a result, multiple lunar cycles are recorded at each protected area within a sampling season. For additional information about camera trapping protocols and species identification, see [28]. In this analysis, we included more than 2.1M photographs of 86 mammal species with ≥25 detection events (number of 15 min intervals with at least one detection at a camera trap) during night (total across all protected areas; electronic supplementary material, tables S1–S3). Observations associated with species identifications that were flagged as uncertain were excluded from the analysis. Due to concerns about identification, species in the genus *Tragulus* were considered jointly (*Tragulus* sp.).

(b) Analysis 1: prevalence of lunar phobia and philia

(i) Multinomial logistic regression

We use a Bayesian multinomial logistic regression model to simultaneously assess diel (entire 24 h period; figure 1*c*) and nocturnal (lunar) activity patterns (figure 1*d*). We distinguished three diel periods (day, night and twilight) and three lunar periods (full moon, transitional, new moon). We chose discrete diel and lunar periods (see definitions below) instead of continuous values based on illumination [30], as it enabled the multinomial analysis and an intuitive categorization of activity (figures 1 and 2).

This model contained two submodels, one for diel activity and one for lunar activity. The submodel for diel activity consisted of a multinomial logistic regression model to estimate species-specific probability of photographic capture in one of the three major diel periods (day, night, twilight; see also [31]):

$$\boldsymbol{y}\,.\,\boldsymbol{diel_i} \;\sim\; \text{Multinomial}(\boldsymbol{p}\,.\,\boldsymbol{diel_i},\; N\,.\,diel_i) \tag{2.1}$$

Here, $\boldsymbol{y}\,.\,\boldsymbol{diel_i}$ is the length-3 vector of the number of independent photographic capture events of species i in each diel period, $N\,.\,diel_i$ the total number of detections ($N\,.\,diel_i = \sum \boldsymbol{y}\,.\,\boldsymbol{diel_i}$) of that species across all diel periods, and $\boldsymbol{p}\,.\,\boldsymbol{diel_i}$ the length-3 vector of detection probabilities in each diel period.

The constituent probabilities $p\,.\,diel_{ik}$ of the multinomial probability vector $\boldsymbol{p}\,.\,\boldsymbol{diel_i}$ can be defined using logistic regression:

$$\log\left(\frac{p\,.\,diel_{ik}}{p\,.\,diel_{iK}}\right) = \beta\,.\,diel_{0ik} + \sum_{j}^{J} \beta\,.\,diel_{kj}x_{ij}, \qquad \text{for k} = 1, \ldots, \text{K} - 1 \tag{2.2}$$

where $\beta\,.\,diel_{0ik}$ is the species-specific intercept term associated with categorical outcome k (diel period) out of the total possible number of outcomes K (i.e. 3: day, night, twilight), and $\beta\,.\,diel_{kj}$ the j'-th (out of J) coefficient associated with predictor x_{ij}. The quotient on the left side of equation (2.2) signifies that the last outcome ($p\,.\,diel_{iK}$) serves as a reference value for the other $K - 1$ outcomes.

Predictor variables and associated coefficients shown in equation (2.2) were omitted in our multinomial logistic regression model for diel activity as we were primarily interested in estimating species-specific intercepts and corresponding probabilities:

$$\log\left(\frac{p\,.\,diel_{ik}}{p\,.\,diel_{iK}}\right) = \beta\,.\,diel_{0ik} + s\,.\,diel_{ik} \tag{2.3}$$

In addition to species-specific intercepts, we incorporated an offset variable $s\,.\,diel_{ik}$ defined as the log-transformed proportion of time (rounded to number of 15 min intervals in our analysis) during which cameras were active (available for making photographic captures) within each diel period k, relative to the reference period K. The offset variable accounts for differences in 'availability' (see also [31]) and has the effect of calibrating the intercept term in accordance with the amount of camera trap

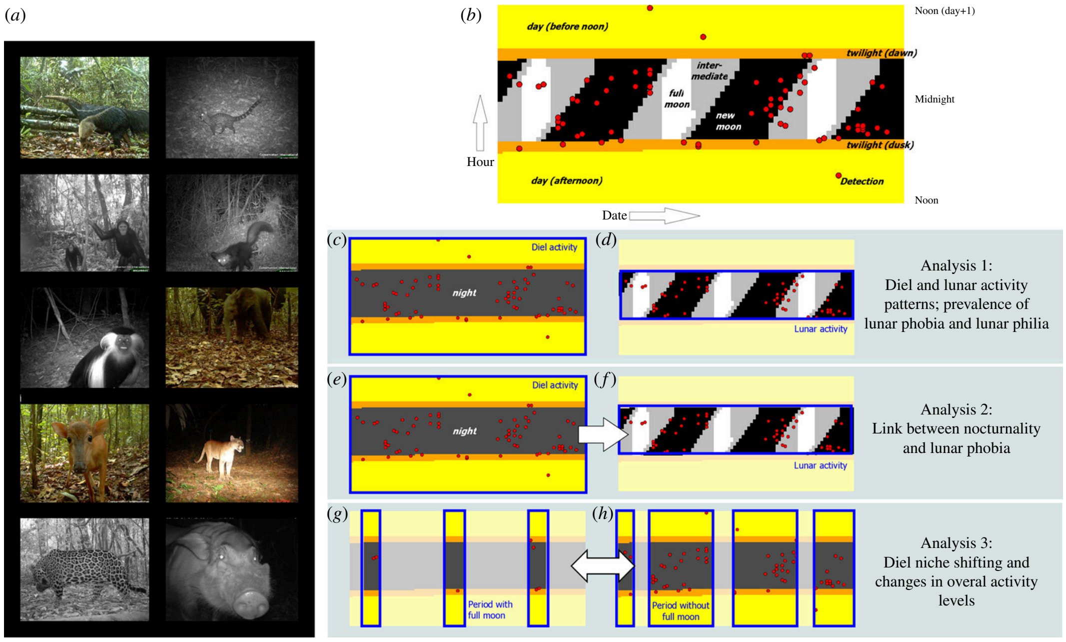

Figure 1. Illustration of the study design. (*a*) Time-stamped camera trap images are aggregated into 15 min intervals and mapped onto available site-specific diel and lunar periods. (*b*) Red dots in the example belong to the nine-banded armadillo (*Dasypus novemcinctus*), an apparently lunar phobic species. Multinomial logistic regression models are used to quantify the probability of a species using a given diel or lunar period. (*c–h*) Three analyses explore (1) diel activity patterns (*c*) and the prevalence of lunar phobia and lunar philia during nocturnal activity (*d*), (2) the effect that the level of nocturnality of a species (*e*) has on its propensity to exhibit lunar phobia (*f*), and (3) changes in diel activity patterns and total activity levels during periods with full moon (*g*) versus other lunar phases (***h***). The blue boxes delineate the part of the diel region involved in each assessment or comparison. Photos: TEAM Network.

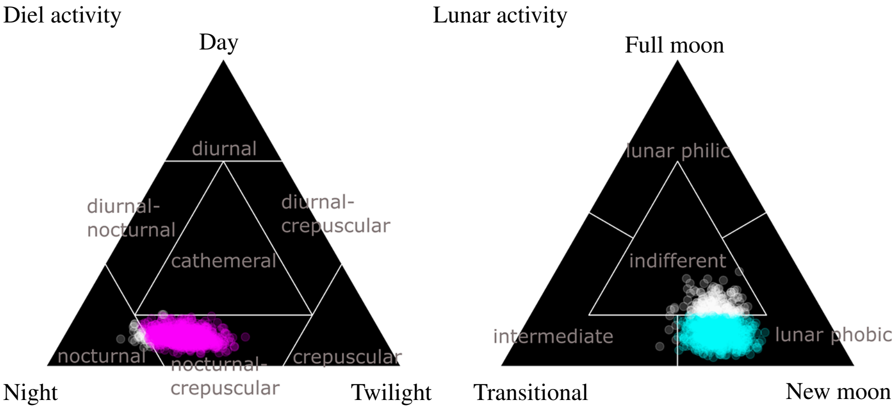

Figure 2. Posterior samples (dots) of multinomial probabilities mapped onto ternary diagrams. Shown are example posterior samples for diel activity (left; activity during day, night and twilight periods) and lunar activity (right; nocturnal activity during full moon, new moon and transitional phases). The ternary diagrams are divided into seven and four regions for diel and lunar activity delineation, respectively. Designation to activity categories (grey text) is made according to the region into which the majority (coloured dots) of posterior samples are mapped. The examples show a diurnal-crepuscular (left) and a lunar phobic species (right).

effort in each record. For example, the crepuscular period is significantly shorter than periods of daylight and night (figure 1*c*). Similarly, the period of full moon only makes up a small proportion of total nighttime (figure 1*d*). The relative 'availability' of different diel periods also changes over the course of seasons, particularly at latitudes farther from the equator. The model thus produces comparable estimates of selection for or against a given period, reflecting activity 'density' (15 min intervals with photographic captures per number of 15 min intervals of camera operation during a period).

The probabilities of interest are

$$\log\left(\frac{\dot{p}\,.\,diel_{ik}}{\dot{p}\,.\,diel_{iK}}\right) = \beta\,.\,diel_{0ik}, \tag{2.4}$$

where both $\dot{p}\,.\,diel_{ik}$ and $p\,.\,diel_{ik}$ are normalized across the K multinomial outcomes.

Detection data ($\boldsymbol{y}\,.\,\boldsymbol{diel_i}$) used in the analysis constituted the number of 15 min intervals with at least one detection of a given species in each diel period (daylight, twilight and night) at each camera trap site, summed across all sites. The sum of activity of a species across all diel periods makes up its total activity $N\,.\,diel_i$. Availability (to calculate the offset $s\,.\,diel_{ik}$) was derived as the number of 15 min intervals that fell into a given diel period at each camera trap site, summed across all camera trap sites. Diel periods were delineated using local (study area specific) astronomical sunrise, sunset and twilight times, assuming a flat landscape, and obtained using R package 'suncalc' version 0.5.1 [32]. Dawn was delineated by the beginning of astronomical twilight (sun 18° below the theoretical horizon) and sunrise (when the bottom edge of the sun touches the theoretical horizon). Dusk was delineated by the beginning of sunset and astronomical sunset (sun 18° below the horizon). Night was delineated as the period between astronomical dusk and dawn and day as the period between sunrise and sunset.

The submodel for lunar activity was structurally identical to the diel activity model described above. In the lunar submodel, the multinomial probability vector $\boldsymbol{p}\,.\,\boldsymbol{lunar_i}$ represents species-specific estimates of the probabilities of photographic capture in the three major lunar periods l during the night (figure 1*d*), roughly corresponding to full moon, new moon and the combined intermediate phases (waxing, waning).

$$\boldsymbol{y}\,.\,\boldsymbol{lunar_i} \sim \text{Multinomial}(\boldsymbol{p}\,.\,\boldsymbol{lunar_i},\ N\,.\,lunar_i)\,. \tag{2.5}$$

The sum of detected activity of a species during the night across all lunar periods makes up its total detected lunar activity $N\,.\,lunar_i$.

As in the diel activity submodel, the elements of the multinomial probability vector associated with lunar activity are defined as

$$\log\left(\frac{p\,.\,lunar_{il}}{p\,.\,lunar_{iL}}\right) = \beta\,.\,lunar_{0il} + s\,.\,lunar_{il}, \tag{2.6}$$

including the offset variable $s\,.\,lunar_{il}$ defined as the log-transformed proportion of time (rounded to number of 15 min intervals in our analysis) during which cameras were active in each lunar period l, relative to the reference period L.

The probabilities of interest are thus

$$\log\left(\frac{\dot{p}\,.\,lunar_{il}}{\dot{p}\,.\,lunar_{iL}}\right) = \beta\,.\,lunar_{0il}, \tag{2.7}$$

where both $\dot{p}\,.\,lunar_{il}$ and $p\,.\,lunar_{il}$ are normalized across the L multinomial outcomes.

Moon phases were delineated for the night (as defined above) using moon altitude (angular elevation) and illumination, again with R package 'suncalc'. Full moon was defined as the period when the moon had an altitude ≥18° above the theoretical horizon and was ≥90% illuminated. New moon was defined as the period when the moon had an altitude <18° above the theoretical horizon or was <10% illuminated. All other lunar periods were designated as transitional phases.

(ii) Model fitting

We fitted each models using Markov chain Monte Carlo (MCMC) using NIMBLE version 1.0.0 [33] in R version 4.3.0 [34]. We executed 4 MCMC chains with 40 000 iterations each, then discarding a 20 000-iteration burn-in period. Chains were thinned by a factor of 5. We considered models as converged when the Gelman–Rubin diagnostic [35] was ≤1.1 for all parameters and after visually inspecting trace plots.

(iii) Designation of diel and lunar activity categories

For visual inspection, categorization and presentation, species-specific posterior samples of multinomial probabilities produced by the MCMC analysis were plotted onto ternary diagrams [36] using package 'ternary' [37] in R. The diel and lunar activity pattern of each species was delineated with the help of the ternary diagrams. We considered several alternative ternary configurations for categorization [36,38–40], but ultimately chose a subdivision into seven regions for diel activity and four regions for nocturnal activity as it relates to the lunar cycle. The lower number of categories for nocturnal activity was motivated by the smaller sample size (only observations made during the night are considered for categorizing lunar activity) and ease of interpretation. For categorizing diel activity, we divided the ternary diagram into seven regions (figure 2): three corner triangles (each capturing cases that contain >2/6 of all activity) for the 'pure' diel activity categories (e.g. diurnal), three transitional regions between pairs of corner regions for intermediate categories (e.g. diurnal-crepuscular) and one central triangle that indicates cathemerality (activity during all diel periods). This classification follows Shepard's [36] approach for delineating soil categories, but without the additional splitting of the intermediate regions along the sides of the ternary. We divided the ternary diagram for lunar activity categorization into only four regions (figure 2): one central triangle (identical to the cathemeral region in the ternary diagram for diel activity) representing indifference (referred to as 'lunar neutrality' by Gursky [4]) to the phase of the moon and three main lunar categories (activity during full moon, new moon and intermediate lunar phases).

Species activity was categorized based on the position of the posterior distribution of multinomial probabilities ($\dot{p}\,.\,diel$, $\dot{p}\,.\,lunar$) within the ternary space. Species-level designation (diel and lunar activity category/strategy/niche) was made based on the region that contained the largest proportion of the posterior samples of the multinomial probability vector (figure 2).

(c) Analysis 2: link between nocturnality and lunar phobia

To estimate the relationship between diel and lunar activity, we used the model from analysis 1 as a starting point, but now linking the lunar activity submodel (equations (2.5) and (2.6)) with the diel activity submodel (equations (2.1), (2.3) and (2.4), figure 1*e*,*f*):

$$\log\left(\frac{\bar{p}\,.\,lunar_{il}}{\bar{p}\,.\,lunar_{iL}}\right) = \bar{\beta}\,.\,lunar_{0l} + \bar{\beta}\,.\,lunar_{night,\,l}\,\dot{p}\,.\,diel_{i,\ night} + \varepsilon_{il} + \bar{s}_{il}\,, \tag{2.8}$$

where $\dot{p}\,.\,diel_{i,\,night}$ is the strength of selection for nocturnal activity estimated in the diel submodel and $\bar{\beta}\,.\,lunar_{night,\,l}$ is its effect on the multinomial probability associated with lunar period l out of a total of L lunar periods. Whereas $\dot{p}\,.\,diel_{i,\,night}$ is species-specific, we estimate one coefficient $\bar{\beta}\,.\,lunar_{night,\,l}$ in this analysis across the entire species data set. In other words, the calibrated probability of nocturnal activity $\dot{p}\,.\,diel_{i,\,night}$ estimated in the diel submodel becomes a covariate whose effect $\bar{\beta}\,.\,lunar_{night,\,l}$ on the strength of selection for each of the three lunar periods is then estimated in the lunar submodel. The intercept $\bar{\beta}\,.\,lunar_{0l}$ is not species specific. Instead, variation between species in the baseline multinomial probabilities associated with lunar activity is modelled by the addition of the normally distributed random error ε_{il} centered on 0 and with standard deviation σ.

Model fitting proceeded as in analysis 1. We used the posterior distribution of $\bar{\beta}\,.\,lunar_{night,\,l}$ and $\bar{\beta}\,.\,lunar_{0l}$ to derive fitted values (means) and associated 95% Bayesian credible intervals (BCI) of the link between nocturnality and the probability of association with new moon and full moon periods.

(d) Analysis 3: diel activity shifting and changes in overall activity levels

We used a third Bayesian model to assess whether and how animals altered their diel activity in response to changes in lunar illumination. Specifically, we tested whether species (i) reduced or increased their overall activity (number of photographic capture events) during the periods that contained nights with full moon and/or (ii) shifted their diel activity to become more or less nocturnal (figure 1*g*,*h*). We used two submodels, one for modelling the number of photographic detection events during 24 h periods with and without at least one 15 min interval with full moon at night and a multinomial logistic model for overall diel activity during the same time periods.

The model for the total number of photographic detection events $\ddot{N}\,.\,diel_{im}$ for species i during a given period m (days with versus without full moon at night) was formulated as a generalized linear model with a log-link (Poisson regression):

$$\log(\lambda_{im}) = \ddot{\beta}_{0im} + \ddot{s}_{im}, \tag{2.9}$$

$$\ddot{N}\,.\,diel_{im}\ \sim\ \mathrm{Poisson}(\lambda_{im}), \tag{2.10}$$

where λ_{im} is the parameter of the Poisson distribution (expected number of events) and $\ddot{\beta}_{0im}$ the species-specific intercept. As in the multinomial models in analyses 1 and 2, we included an offset term $\ddot{s}_{im}$ to account for differences in availability, provided as the log-transformed proportion of of 15 min intervals of camera trap operation during periods with or without full moon over all camera trap sites and sampling seasons in protected areas where species i was detected at least once. This allowed direct comparison of periods with and without moonlit nights via $\dot{\lambda}_{im}$, derived as

$$\dot{\lambda}_{im} = e^{\ddot{\beta}_{0im}}\,. \tag{2.11}$$

The multinomial model for diel activity in analysis 3 was structurally identical to the diel activity submodels in analyses 1 and 2:

$$\ddot{\boldsymbol{y}}\,.\,\boldsymbol{diel_{im}}\ \sim\ \mathrm{Multinomial}\left(\ddot{\boldsymbol{p}}\,.\,\boldsymbol{diel_{im}},\ \ddot{N}\,.\,diel_{im}\right), \tag{2.12}$$

$$\log\left(\frac{\ddot{p}\,.\,diel_{ikm}}{\ddot{p}\,.\,diel_{iKm}}\right) = \ddot{\beta}\,.\,diel_{0ikm} + \ddot{s}\,.\,diel_{ikm}, \tag{2.13}$$

$$\log\left(\frac{\hat{p}\,.\,diel_{ikm}}{\hat{p}\,.\,diel_{iKm}}\right) = \ddot{\beta}\,.\,diel_{0ikm}\,. \tag{2.14}$$

The main difference between the diel activity submodel in analyses 1, 2 and 3 was in the design: whereas in analyses 1 and 2, we estimated the multinomial probabilities of being active during the three diel periods (day, night, twilight) at any point during monitoring, in analysis 3 we estimated separate multinomial probabilities for a given type of period m (multiple days) out of two possible types, periods with full moon during at least one 15 min interval at night and periods without full moon at night (figure 1*g*,*h*).

Model fitting and assessment of convergence/mixing was performed as in analyses 1 and 2. Diel activity was categorized using the ternary approach described earlier. We used the difference $logit\left(\hat{p}\,.\,diel_{night,\,fullmoon}\right) - logit\left(\hat{p}\,.\,diel_{night,\,nofullmoon}\right)$ between periods with and without full moon nights to derive species-specific estimates of the effect of full moon on the selection for nocturnal activity. Significant change in $\hat{p}\,.\,diel_{night}$ (95% BCI of the difference did not include zero) without a change in activity category were considered activity timing shift, a term also used by Gilbert [16]. A significant change in $\hat{p}\,.\,diel_{night}$ together with a change of activity category (ternary region) was considered evidence of temporal niche switching. We used the difference $log\left(\dot{\lambda}_{i,\,fullmoon}\right) - \log\left(\dot{\lambda}_{i,\,nofullmoon}\right)$ between periods with and without full moon nights to derive species-specific estimates of the effect of full moon on overall activity levels. We considered a species to show evidence of altered overall activity levels in response to lunar illumination when the 95% BCI of this derived quantity did not include zero. We interpreted a significant shift towards nocturnality and/or an increase in overall activity during periods with full moon as evidence for attraction to moonlit periods. Conversely, we interpreted a significant shift away from nocturnality and/or decrease in overall activity during periods with full moon as evidence for avoidance.

3. Results

(a) Diel activity

Of the 86 species included in the analysis, we categorized 19 species as predominantly nocturnal and nine as diurnal, following the multinomial regression analysis controlling for temporal availability and the ternary classification scheme (figure 2; electronic supplementary material, tables S4–S6). Only one species (common tapeti, *Sylvilagus brasiliensis*) was categorized as predominantly crepuscular. Most species ($n = 41$) fell into one of the two categories bordering crepuscularity (figure 3; electronic supplementary material, tables S4–S6). All remaining species ($n = 16$) were categorized as cathemeral (electronic supplementary material, tables S4–S6). The cathemeral designation, by nature of its position within the ternary, is associated with greater uncertainty [41]. In data-sparse situations, it may be difficult to distinguish between a species being truly cathemeral and the model not having enough information to assign the species to another category. However, all species categorized as cathemeral in this analysis had more than 100 observations (15 min intervals with at least one detection; mean = 769, range = 136–3250; electronic supplementary material, tables S1–S3).

(b) Prevalence of lunar phobia and philia

Of the 86 species included in the analysis, 12 were categorized as lunar phobic and three as lunar philic using the strict classification defined in the ternary diagram (figure 3; electronic supplementary material, tables S4–S6). Only the chimpanzee (*Pan troglodytes*) was categorized as selecting for intermediate lunar phases ('transitional'). Rodents were the most common lunar phobic taxa ($n = 9$), followed by armadillos ($n = 2$) and one opossum (grey four-eyed opossum, *Philander opossum*). The representation of rodents among lunar phobic species was disproportionate to their prevalence among the species in our sample (75% versus 23%). The three mammal species exhibiting lunar philia were the white-lipped peccary (*Tayassu pecari*, order Artiodactyla) and the common tapeti (*Sylvilagus brasiliensis*, order Lagomorpha) in the Neotropics, and the four-toed elephant shrew (*Petrodromus tetradactylus*, order Macroscelidea) in the Afrotropics. The remaining 70 species were categorized as indifferent towards lunar phases, either because their nocturnal activity was not associated with lunar illumination or because their data had such a high noise-to-signal ratio that it prevented designation to one of the peripheral ternary regions (electronic supplementary material, tables S4–S6). In our dataset, 14 (20%) of the species categorized as indifferent towards lunar phases had less than 50 observations during the night and we consider these species as data-sparse. Nonetheless the sample size was relatively high with an average of 462 nocturnal observations (range: 25–4189; electronic supplementary material, tables S1–S3) of species categorized as indifferent towards lunar phases.

(c) Link between nocturnality and lunar phobia

Species with a greater probability of being active at night were more likely to be more active also at new moon ($\beta_{night,\,newmoon} = 1.01$, 95% CrI: 0.58 to 1.46) and, conversely, less likely to be active at full moon ($\beta_{night,\,fullmoon} = -0.7$, 95% CrI: −1.07 to −0.29, electronic supplementary material, figure S3).

(d) Temporal niche shifting and changes in overall activity

Twenty-five species shifted their diel activity during periods of full moon (figure 3; electronic supplementary material, figure S4); 12 of these shifts constituted a niche switch; i.e. a change in diel category (e.g. *Dasypus novemcintus*, figure 4). Overall, 14 species shifted towards more nocturnal activity whereas 11 species became less nocturnal.

Thirty-three species changed their overall activity during periods with full moon, with 9 species increasing and 14 species decreasing activity. Sixteen species changed both their overall level activity and degree of nocturnality during periods with full moon; species that became more nocturnal during full moon periods consistently showed a reduction in overall activity level whereas species that became less nocturnal consistently showed an increase in overall activity level (electronic supplementary material, figure S4). No species became less nocturnal and also increased overall activity during full moon periods (figure 3; electronic supplementary material, figure S4). Of the 15 species categorized as either lunar phobic or lunar philic ('strict' categories, analysis 1), 14 also responded significantly to full moon periods (analysis 3) by changing their level of nocturnality, reducing their overall activity or both (electronic supplementary material, figure S4).

4. Overall pattern

Overall (analyses 1 and 3), the activity of 43 species appeared associated with lunar phases: responses of 26 species indicated selection against full moon (i.e. lunar avoidance) and 17 species exhibited responses indicating selection for full moon (i.e. lunar

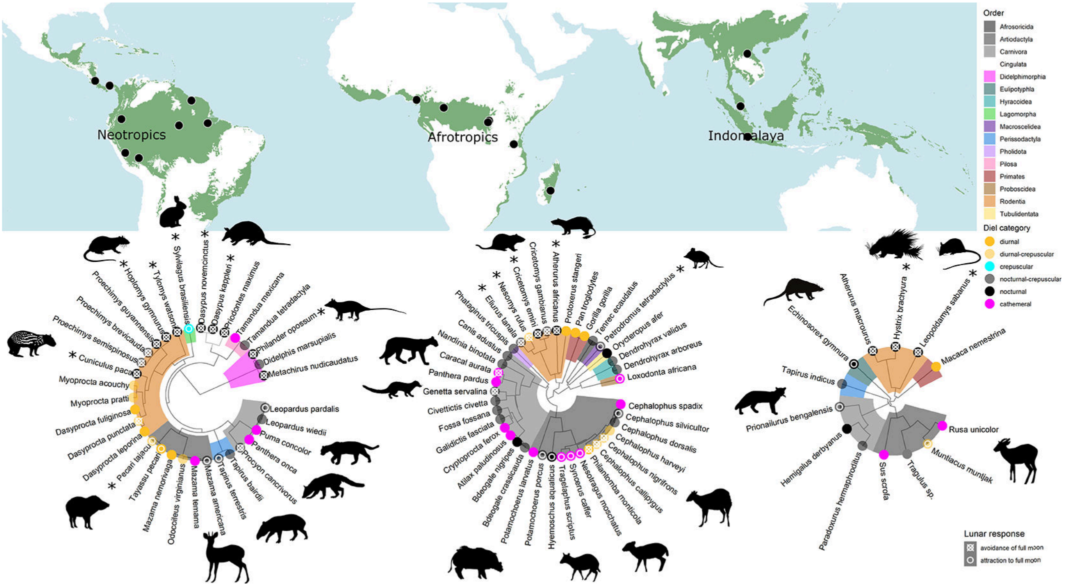

Figure 3. Diel and lunar categorization charted across phylogenetic trees of tropical forest mammals in three realms. The distribution of tropical moist broadleaf forest (green regions) and location of study areas (black dots) included in this analysis are shown on the map. Lunar responses are shown for species that exhibited altered activity patterns suggesting avoidance of or attraction to the moon. Species exhibiting lunar phobia or lunar philia based on strict categorization of nocturnal activity are marked with an asterisk. Lunar phobia, manifested as reduced activity during moonlit nights, was more common than lunar philia, manifested as increased activity during moonlit nights. Rodents, particularly nocturnal species, were overrepresented among lunar phobic species, followed by members of the Cingulata (including armadillos) and Didelphimorphia (opossums). Phylopic silhouettes credits: *Cuniculus paca, Dasypus novemcinctus, Silvilagus brasiliensis* and *Tayassu pecari* by Gabriela Palomo-Munoz; *Philander opossum* by Milena Cavalcanti, Patricia Pilatti and Diego Astúa; *Hoplomys gymurus, Atherurus africanus, Cricetomys emini, Hystrix brachyura* and *Leopoldamys sabanus* provided by Anonymous; *Petrodromus tetradactylus* under universal public domain license.

attraction, analyses 1 and 3 combined). The representation of rodents among species exhibiting lunar avoidance was disproportional to the prevalence of rodents in our sample (56% versus 23%; figure 3). By comparison, none of the 17 species exhibiting positive responses to full moon were rodents. Artiodactyla were overrepresented among species that responded positively to full moon compared with their prevalence in the sample (59% versus 27%). Conversely, Artiodactyla were underrepresented (12%) among species that responded negatively to full moon. See electronic supplementary material, figures S1 and S2, tables S4–S6, for detailed results for all species included the analysis.

(a) Discussion

How wildlife responds to phases of the moon remains poorly known and not well understood. We applied a novel analysis of activity patterns to data from standardized camera trapping in 17 tropical forests across the globe. We found that even in the understory of protected tropical forests, characterized by densely shaded habitats, the moon's phases appear linked to the activity of many mammal species. While few species were categorized as lunar phobic and lunar philic based on a strict classification of activity during the night, half of all species responded to the moon. Species did so by either adjusting their degree of nocturnality during periods with full moon, changing their overall activity level or both. Avoidance of the moon was more common than attraction to it, with rodents most prominent among species avoiding full moon and Artiodactyla most common among species exhibiting attraction to full moon. Additionally, we detected a pronounced negative association between nocturnality and selection for full moon. These findings raise further questions including how changes in illumination (e.g. through changes in canopy vegetation or artificial illumination) may affect species activity, and ultimately interactions in tropical forest communities.

(b) Lunar philia and lunar phobia in tropical forest mammal communities

Our conservative categorization based strictly on activity during the night, suggests that lunar philia, as defined here, is rare among terrestrial tropical forest mammals. Only three among the 86 species studied here significantly increased their exposure to camera traps during moonlit nights. Lunar philia has previously been reported as comparatively rare and has been associated with species, such as arboreal primates, relying on visual cues for foraging and predator avoidance [3]. The three species classified as lunar philic in our study were a peccary (white-lipped peccary, *Tayassu pecari*), a rabbit (common tapeti, *Silvilagus brasiliensis*) and an elephant shrew (four-toed elephant shrew, *Petrodromus tetradactylus*). Apparent lunar philia in the common tapeti has previously been reported in Argentina [42], and contrasts lunar phobic behaviour reported in another lagomorph, the snowshoe hare (*Lepus americanus* [43]). Lunar philia in elephant shrews is consistent with descriptive studies on the order [44]. Similarly, white-lipped peccaries, large group-living mammals (40 kg) which may make them less vulnerable to predators, have been reported to change routes and increase movement in the forest during full moon [45,46].

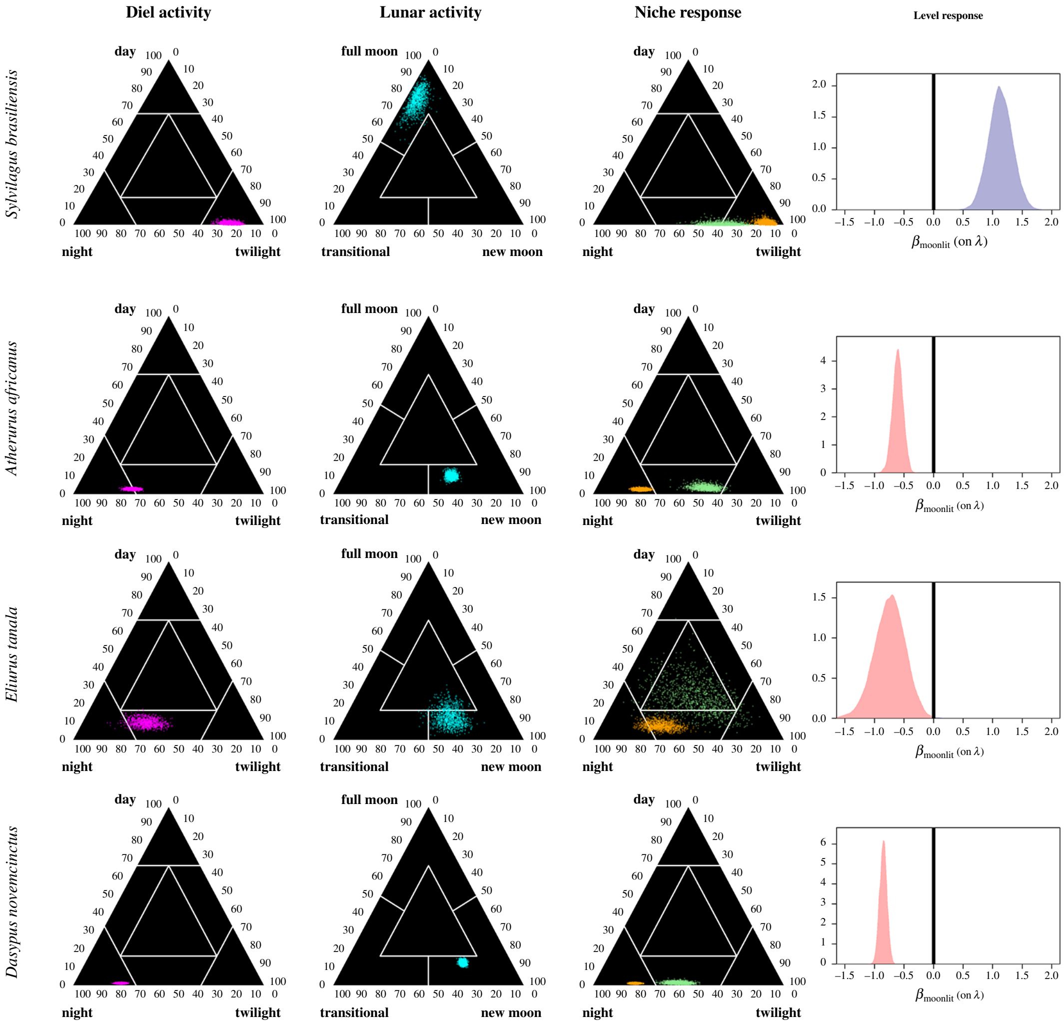

Figure 4. Overview of ternary classifications for diel and lunar activity (columns 1 and 2) and responses to lunar phases (columns 3 and 4) for four example species (rows). The species shown in the top row (common tapeti or forest cottontail) was classified as lunar philic, whereas the bottom three rows show lunar phobic species. Column 1: ternary plots of diel activity posteriors. Column 2: ternary plot of lunar activity posteriors. Column 3: ternary plots showing difference of diel activity (potential temporal niche shifting) between periods with full moon (green) and without moonlit nights (orange). Column 4: posterior distribution of the difference between overall activity (related to the number of photographic detection events) during periods with versus without full moon. Negative (red) and positive (blue) values indicate a reduction or an increase, respectively, in overall activity during periods (multiple 24 h periods; figure 1) with full moon. See electronic supplementary material, figures S1–S3, for results for all species classified as either lunar phobic or philic.

Lunar phobia, in contrast, was more common. It was exhibited primarily by small-to-medium sized mammals that are prey of carnivores like ocelots (*Leopardus pardalis* [5]) and jaguars (*Panthera onca* [47]). Nevertheless, the fact that pronounced lunar phobia was disproportionately found in rodents, raises questions about evolutionary differences among prey groups that influence responses to moonlight above and beyond ecological responses to predators as prey, potentially related to their sensory ecology. The paca, one of the largest lunar phobic rodents in our study (8000 g), has been classified as lunar phobic also in other study areas (but see [48]), as were armadillos [49,50]. Lunar phobia may allow pacas and armadillos to avoid predators, as well as avoiding hunting by rural and indigenous communities [51,52]. Although another study detected no changes in the activity of the common opossum (*Didelphis marsupialis*) in response to moonlight [49], evidence on lunar phobia in the grey four-eyed opossum (*Philander opossum*) in our analysis matches reports for other members of the Didelphimorphia (e.g. *Didelphis aurita*, *Caluromys philander* [53,54]).

We simultaneously analysed and categorized activity data from many species using one standardized approach (analysis 1). While the approach is intuitive and repeatable, the outcome depends on an arbitrary choice of categories (in our case quite conservative). There is also an increased risk of misclassification as sample size decreases. Furthermore, lunar illumination can change environmental conditions and community dynamics and may thus have both direct and indirect effects on animal behaviour [1]. In other words, species might change their activity with the phases of the moon, even if they are not active at night or if they did not emerge as clearly lunar phobic or philic using our conservative and arbitrary categorization. Our additional analyses revealed how extensively tropical forest mammals responded to the lunar cycle (analysis 2 and, more so, analysis 3).

(c) The link between lunar phobia and nocturnality

The more nocturnal species are, the more likely they are to exhibit lunar phobic behaviour (electronic supplementary material, figure S3). Lunar phobia has been explained as a strategy to avoid the elevated predation risk during periods with higher illumination [1,55]. The large number of species included in our study and a standardized classification approach support this explanation. The avoidance of moonlight could reduce vulnerability to detection by visually hunting predators or, in the case of lunar phobic predators, detection by prey. Rodents, for example, generally seem to reduce foraging activity during bright nights [3,56,57]. Conversely, we found that lower nocturnality was associated with higher activity during full moon periods. These effects were also reflected in the diel activity of species that responded to lunar phases (analyses 1 and 3): 54% of species exhibiting avoidance of full moon were categorized as nocturnal, compared with only 12% of species that responded positively to full moon (figure 3; electronic supplementary material, tables S4–S6). Thus, moonlight appears to give species adapted to daylight and twilight better visual access to the night even in the understory of tropical forests.

(d) Temporal niche shifting in response to moon phases

Lunar illumination can trigger changes in diel activity and our results showed evidence of temporal niche shifting and switching among tropical forest mammals in all three tropical realms (figure 3; electronic supplementary material, tables S4–S6). We found that 16 species both changed their overall activity level and their probability of nocturnal activity during periods with full moon (electronic supplementary material, figure S4). These results are in line with observations on snowshoe hares (*Lepus americanus* [58]), and Marriam's kangaroo rats (*Dipodomys merriani* [55]), which reduce their activity during moonlit nights and increase their diurnal and crepuscular activity, respectively. Potentially indicative of compensatory response to lunar illumination (i.e. shift in diel activity), nine species adjusted their nocturnal activity without an apparent change in overall activity during periods with full moon. Conversely, 17 species changed their overall activity without a clear shift in nocturnality, suggesting a more additive response. We speculate that this is caused by behavioural inflexibility (i.e. strict nocturnality); although it may be purely a result of insufficient statistical power or animals shifting to habitat strata less well-covered by camera traps (e.g. open areas, or tree canopies).

(e) Methodological insights and other considerations

In this study, we adjusted and deployed a novel framework to delineate diel and nocturnal activity categories using multinomial probability distributions, and ternary diagrams [31,41]. This approach is both visually intuitive and quantitative, facilitating detection of ecological patterns related to activity, such as temporal niche partitioning and niche shifting/switching in response to moonlight. Any analytical approach that can estimate the probability of designation and the associated uncertainty can be substituted for the Bayesian multinomial approach used here. The advantage of the latter is that it produces posterior samples of multinomial probabilities, which readily allow propagation of uncertainty to the ternary projection and subsequent classification. In addition, our approach allows direct integration of categorical and continuous predictor variables on the multinomial probabilities that describe selection for and against different diel and lunar periods. Future analyses could include spatial, temporal and species-specific covariates on the multinomial probabilities associated with diel and lunar periods, thereby helping boost our understanding of the sources of variation in activity patterns. Similarly, covariates are readily incorporated to model and examine their influence on temporal niche shifting and switching.

We considered activity patterns accessible to camera traps. Camera trap data lend themselves to comparative and comprehensive diel (and lunar) activity studies as they monitor entire communities [26,59] and are less invasive than traditional methods such as direct observation and telemetry. The rapidly expanding spatial and temporal scope of camera trapping in wildlife ecology offers opportunities for revising and filling gaps in our understanding of the temporal niche of wildlife and its dynamics. Nonetheless, camera trapping has limitations and inferences should be drawn with caution. For example, if arboreal or scansorial animals shift their activity to lower forest strata during moonlit periods or if species move into more densely vegetated areas from beyond forest edges, lunar phobia may increase terrestrial activity as detected through photographic captures by understory cameras. In our study, all but one of the species with lunar responses are classified as terrestrial [60]. Yet other sampling methods (or sampling in other strata [61,62]) may, in some situations and for certain species be more suitable to obtain reliable data on activity. Any sampling approach that does not influence activity itself and produces timestamped observations can be used.

Finally, the consistency of photographic capture and reliability of species identification from camera trap images can be affected by species size, movement speed, look-alikes and lighting conditions [63,64]. Particularly smaller species can in some cases be difficult to identify, and many camera trap studies therefore exclude species below a certain size threshold. In this analysis, we chose to include also smaller species (mostly small rodents and insectivores), as these (particularly small rodents) have been shown to respond to moonlight and artificial light in other studies [15]. We removed observations flagged as uncertain, and qualitative inferences about the prevalence of lunar phobia among nocturnal small mammals are not weakened by potential misidentification of species in this case. Nonetheless, studies focusing on small mammals may consider a customized camera trap set-up [65,66]. Alternatively, models can be expanded to estimate and account for added uncertainty because of imperfect species identification [67].

(f) Implications

The influence of natural and artificial light raises important questions and concerns in wildlife conservation and ecosystem functioning [68,69]. Yet we still know remarkably little about the implications of illumination on the activity of mammals [70]. The higher prevalence of avoidance of the moon in our study suggests there may be more losers than winners when illumination increases in tropical forests. Moreover, 96% species that respond negatively to moonlight in our study did so at least in part by reducing their overall activity during periods with full moon. If these results extend to artificial light, a loss of dark nights could curtail the amount of time some species invest into foraging and other important activities. Strong responses to artificial light have already been observed in nocturnal mammals [3]. For example, the common spiny mouse (*Acomys cahirinus*) shows a clear reduction in overall activity and foraging time when exposed to artificial light [15]. The sustained reduction of activity due to artificial light may impact individuals, populations and even communities but predicting the fitness consequences based on a species' responses to lunar phases remains speculative. Seemingly indifferent species without adaptations to changing nocturnal light conditions may not be impacted at all or could bear the brunt of brighter nights resulting from canopy loss and light pollution if they are made vulnerable by increased visibility. Species that change their overall activity level in response to nocturnal illumination may be more strongly impacted than species that can maintain their activity level by adjusting its timing. Along those lines, lunar phobic species could be expected to cope better with artificial light if they follow a cathemeral activity pattern as this is indicative of behavioural plasticity that may be advantageous in a changing world (temperature changes, artificial light [71]). However, in tropical regions, cathemeral activity patterns appear to be less common than at higher latitudes [6].

Our study sheds new light on the relationship between moonlight and animal behaviour. By using systematic camera trap data in conjunction with an intuitive and flexible analytical approach, we reveal a rich picture of how light and dark determine how animals use their time. Such knowledge opens new questions and avenues for research and application. We described responses to moonlight on the forest floor. It would be interesting for future studies to examine responses in the canopy of tropical forests, where lunar illumination likely has more pronounced effects on animal behaviour. It is also worthwhile to extend research into the effects of moonlight and artificial light to other vertebrate species (birds, reptiles and amphibians) and fauna more generally.

Ethics. This work did not require ethical approval from a human subject or animal welfare committee.

Data accessibility. The data and code for performing the analyses described in this article are available in the Dryad repository [72].

Supplementary material is available online [73].

Declaration of AI use. We have not used AI-assisted technologies in creating this article.

Authors' contributions. R.Bis.: conceptualization, formal analysis, funding acquisition, investigation, methodology, project administration, resources, validation, visualization, writing—original draft, writing—review and editing; A.F.V.-V.: investigation, writing—original draft, writing—review and editing; A.S.-P.: investigation, writing—review and editing; S.D.S.: investigation, writing—review and editing; L.B.: data curation, investigation, writing—review and editing; D.T.: investigation, methodology, software, validation, writing—review and editing; P.A.J.: data curation, investigation, writing—review and editing; F.R.: data curation, investigation, writing—review and editing; S.E.J.: data curation, investigation, writing—review and editing; M.G.M.L.: data curation, methodology, writing—review and editing; F.S.: data curation, investigation, writing—review and editing; E.U.: data curation, investigation, writing—review and editing; S.E.: data curation, investigation, writing—review and editing; J.A.A.: data curation, investigation, writing—review and editing; R.Bit.: data curation, investigation, writing—review and editing; J.S.: data curation, investigation, writing—review and editing; B.M.: data curation, investigation, writing—review and editing; M.N.S.: data curation, investigation, writing—review and editing; D.S.: conceptualization, data curation, funding acquisition, investigation, writing—original draft, writing—review and editing.

All authors gave final approval for publication and agreed to be held accountable for the work performed therein.

Conflict of interest declaration. We declare we have no competing interests.

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