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ECOLOGY

When the wild things are: Defining mammalian diel activity and plasticity

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Circadian rhythms are a mechanism by which species adapt to environmental variability and fundamental to understanding species behavior. However, we lack data and a standardized framework to accurately assess and compare temporal activity for species during rapid ecological change. Through a global network representing 38 countries, we leveraged 8.9 million mammalian observations to create a library of 14,587 standardized diel activity estimates for 445 species. We found that less than half the species' estimates were in agreement with diel classifications from the reference literature and that species commonly used more than one diel classification. Species diel activity was highly plastic when exposed to anthropogenic change. Furthermore, body size and distributional extent were strongly associated with whether a species is diurnal or nocturnal. Our findings provide essential knowledge of species behavior in an era of rapid global change and suggest the need for a new, quantitative framework that defines diel activity logically and consistently while capturing species plasticity.

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INTRODUCTION

Modern eco-evolutionary science classifies animal temporal activity into four distinct diel phenotypes that reflect how species activity is distributed across a 24-hour period, based on light availability (*1*–*3*): nocturnal (darkness), crepuscular (low light), diurnal (full light), or cathemeral [multiple phases; (*3*–*8*)]. A species' diel phenotype is shaped by their trait combinations (i.e., morphology, physiology, phylogeny, and behavior), making it a core part of their fundamental niche (*2*, *3*, *5*–*9*). Diurnal mammals have evolved trait combinations that differ from nocturnal mammals (*7*). For example, mammalian eye shape is linked to the length of an animal's daylight activity (*10*), and the timing of daily rhythms of metabolic and hormonal processes are opposite for nocturnal and diurnal mammals (*11*). As such, species have evolved traits that likely optimize an individual's fitness when they constrain their activity to certain times of the day (*2*).

Yet, many species are believed to be flexible in their diel activity patterns (*7*, *8*). Such capacity for variation, hereafter plasticity, in an animal's diel behavior allows individuals to reduce the likelihood of risky environmental conditions or species interactions while accessing resources, thus adapting to interspecific competition, predation, food availability, or anthropogenic activity (*2*, *6*, *12*–*17*). For instance, meso- and large carnivores increase their nocturnal activity in more urbanized areas (*18*)—likely to avoid hours in which humans are most active (*16*, *17*)—while subdominant carnivores may switch from nocturnal to diurnal to avoid diel-shifting dominants (*19*). Whether such plasticity has positive fitness outcomes depends on whether diel shifts provide more benefits than costs. Diel plasticity could benefit a species or population to better cope with climate change (*20*, *21*), avoid predation (*2*, *6*, *14*, *17*, *22*), or access anthropogenic resources (*23*), but at the same time, circadian disruption can lead to negative demographic and health outcomes at the individual and population levels (*15*, *24*).

Scientists have increasingly recognized that to conserve species, we must not only know where they live and what they do but also the time of day they are active (*3*, *6*–*9*, *12*–*14*, *16*, *20*, *25*). Without this knowledge, we cannot understand a species' habitat (*26*, *27*), a cornerstone of biodiversity conservation (*28*–*30*). For example, a protected area that safeguards resources a species needs to persist may be less effective without considering a species diel activity. If human activity or other disturbances limit a species' ability to access these resources during the time of day they are active (*31*, *32*), then the protected area is not protecting the species, only the resources. Diel plasticity may be a fundamental mechanism by which species adapt to such a disturbance, and thus changes in species diel activity across space or time could serve as an indicator of anthropogenic impact and be a tool for conservation action (*33*, *34*).

In understanding diel activity and plasticity, it is fundamental to define diel phenotypes logically and consistently to evaluate change. Since there has yet to be the technology, methodology, and research network focused on understanding diel behavior, the conceptual and inferential frameworks to evaluate species diel phenotypes and characterize plasticity have varied among taxa, geography, and disciplines. This has inhibited cross-species and system assessments, potentially leading to misleading inference, and thus limited our understanding of the adaptability of species and usefulness of diel activity as an indicator of anthropogenic impact worldwide. By globally sampling wild animal activity and using a novel conceptual and statistical framework to classify a species diel phenotype with uncertainty (*35*), we can gain a holistic understanding of species' diel activity and plasticity. Doing so provides standardized empirical inference that we have yet to have, so that we better understand this fundamental niche dimension and learn how animal behavior is driven by species traits and environmental change, such as anthropogenic activity (*16*).

As the Global Animal Diel Activity Project (https://diel-project.github.io/; a consortium of 217 collaborators), we curated a camera trap dataset (Fig. 1) that combined 200 camera trap projects and included 20,080 camera sites across 38 countries and six continents. This dataset contains more than 8.9 million images that represent 1.7 million independent records of 445 small-to-large nonvolant mammal species from 67 families. This is one of the largest camera trap datasets in existence, with a combined sampling effort of 10 thousand years of camera-trap days. With this dataset, we addressed two critical questions. First, do conceptually framed empirical diel activity estimates agree with literature-informed classifications of species diel phenotypes? Second, how common is mammalian diel plasticity, and do species traits and anthropogenic factors affect interspecies variation and intraspecies diel plasticity? Our first question aims to evaluate the utility of the literature-informed reference

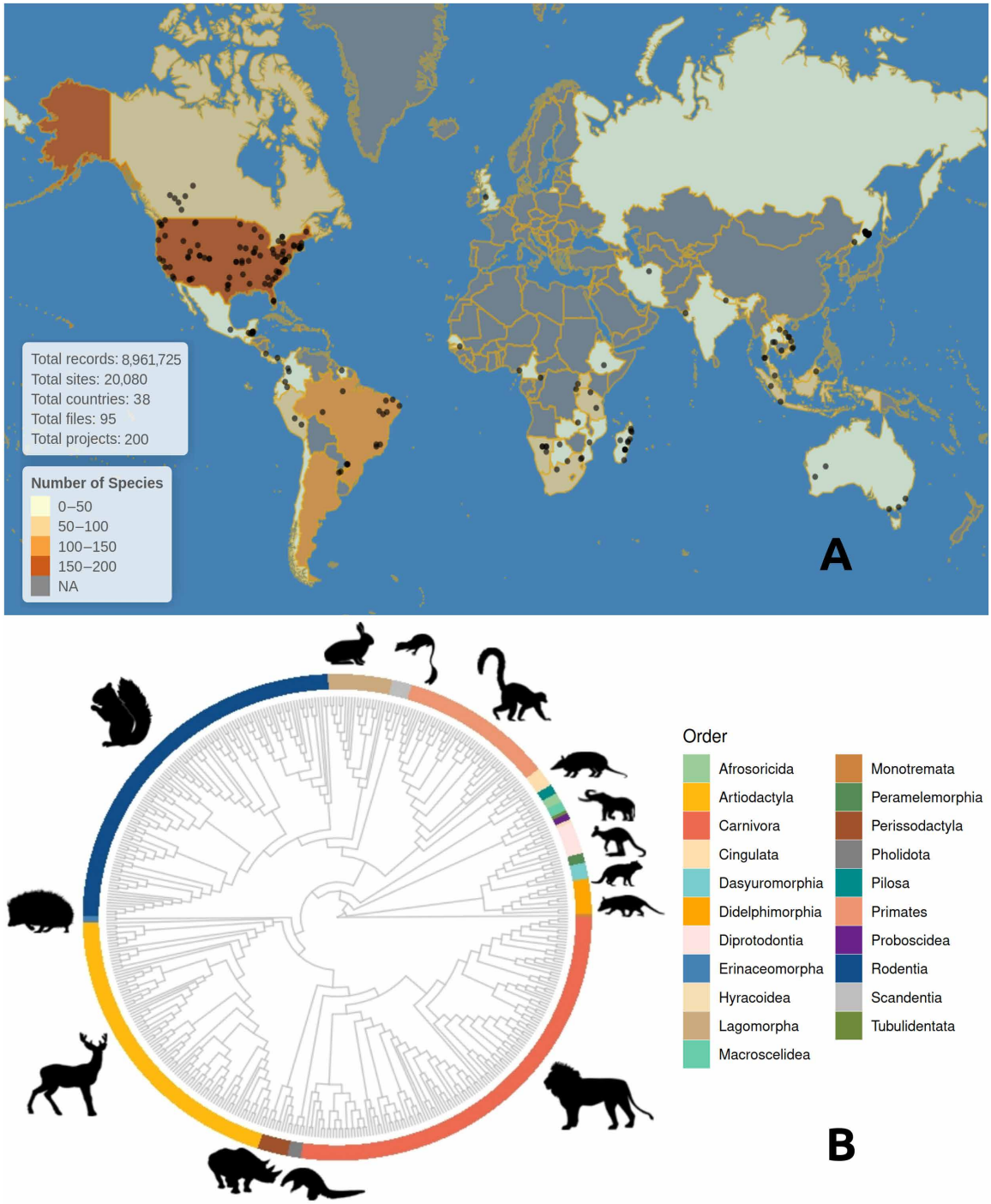

Fig. 1. Visual summary of the consolidated dataset with project countries color-coded by taxonomic richness along with a phylogeny of species in the dataset. (**A**) Summary of terrestrial coverage of the dataset we have compiled based on more than 8.9 million trail camera photo records spanning 38 countries color-coded by country-specific species richness. The semitransparent black dots on the map represent the average location of each camera trap project, which was summarized from the spatial coordinates of each project's camera trap locations. (**B**) Phylogeny of 445 nonvolant mammal species from 67 families and 21 orders, with major clades denoted by silhouettes of representative taxa. A subset of this dataset was used for subsequent analysis after data checks. NA, not applicable.

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classifications in capturing logical and consistent descriptions of species' diel activity. This is especially important because reference diel classifications are commonly used as data in ecological niche modeling, implicitly assuming that they are meaningfully and consistently defined and thus comparable. Our second question aims to understand the scope and drivers of diel plasticity in a changing world.

Specifically, we (i) provide comparable empirical diel activity estimates for a global distribution of mammals; (ii) contrast these estimates against literature-informed (hereafter reference) definitions; and (iii) quantify patterns and plasticity in diel phenotypes based on species traits (i.e., body size and extent of a species global distribution) as well as environmental (i.e., distance from the equator or hours of daylight) and anthropogenic factors (i.e., global human footprint). For species traits, we tested the predictions that smaller body mass species would most likely be nocturnal (*7*) and that species with a larger geographic extent would be more plastic because they have greater potential to experience a wide range of environmental conditions. For environmental and anthropogenic factors, we predicted that global human footprint would have the strongest influence on diel phenotypic plasticity (*6*, *8*, *9*, *12*, *16*, *19*). Furthermore, on the basis of a global biogeographical analysis (*3*, *7*) and the circadian thermoenergetic hypothesis that posits endotherms are more likely to be resting during colder parts of the day and active during the warmer parts of a day (*36*–*37*), we predicted that species further from the equator would be more diurnal or cathemeral. In an era of global human activity and disruption of ecological community dynamics, the biogeography of how animals adapt to environmental conditions through traits and behavioral change is critical to inform conservation actions (*3*, *6*–*9*, *12*–*14*, *16*, *19*–*22*, *25*, *31*–*34*).

RESULTS

Species diel activity

Using a standardized process, we binned the 1.7 million species detections into 14,587 analysis units, which represent subsets of a camera project's data that contain the frequency of species detections that occurred during the twilight, daytime, and nighttime (see Materials and Methods for details). The median number of analysis units per country was 169 (minimum = 4, maximum = 5985). The median number of analysis units per species was 10 (minimum = 1, maximum = 693). The median number of independent species detections per analysis unit was 32 (minimum = 10, maximum = 4559).

We estimated the diel phenotype of 445 mammal species across our analysis units. We present findings on supported diel hypotheses for each analysis unit in the Supplementary Materials and full details graphically as an online Shiny application [https://shiny.celsrs.uri.edu/bgerber/GlobalDiel/; code can be downloaded at (*38*)]. Our results can be used as a resource library of empirical findings involving species diel activity where users can examine and download country, project, and species specific results. Summarizing the results for all species with multiple analysis units provides evidence that mammals living in the modern environment commonly alter the diel behavior, using multiple diel phenotypes. Specifically, we found that of the species with two or more analysis units, 60% and 73% of species had more than one diel phenotype as their most supported model using the traditional and general hypothesis sets, respectively. Increasing to five or more analysis units, the proportions of species that used multiple diel phenotypes increased to 72% and 84%, respectively, for the traditional and general hypothesis sets.

Empirical and literature diel comparison

Scientists' past diel categorizations of mammals differed from our standardized empirical diel phenotypes. Agreement between reference diel phenotypes and our results was only well supported (>0.80 probability of reference diel phenotype) for 39% of all species (175 of 445) and moderately to well supported (>0.50 probability of reference diel phenotype) for 65% of all species (291 of 445). This high level of disagreement does not inherently indicate that past diel categorizations are, for the most part, incorrect. We expected disagreement for four primary reasons, most of which are related to possible differences in methodology. First, our quantitatively defined diel phenotypes may not match the qualitatively defined phenotypes historical studies used, which suggests that historical definitions are, at a minimum, inconsistent. Second, data may have been collected in different parts of a species range or under different environmental conditions, both of which could result in differences in a species diel behavior. Third, a species diel phenotype could have shifted since their historical diel phenotype classification due to landscape change or anthropogenic activity. Because both types of differences are related to intraspecies variability in diel behavior, they suggest that species may be more plastic in their diel phenotypes than historically suggested. Our results reinforce this notion. Fourth, diel phenotype classifications could vary because historical studies may have used a variety of sampling methodologies, whereas we only used camera traps. Together, this result suggests that there is a lack of logical clarity or consistency in reference diel phenotypes, which could be corrected by recognizing that many species are plastic in their diel activity and giving diel phenotypes clear, quantitative definitions.

While reference diel categorizations only had 39% agreement with our empirical estimates overall, the amount of agreement varied by reference diel phenotype (Fig. 2). Even when assigning higher prior probabilities to the reference phenotype, there was strong evidence that our quantitatively defined phenotypes differed from those in the reference literature (fig. S1). Furthermore, these

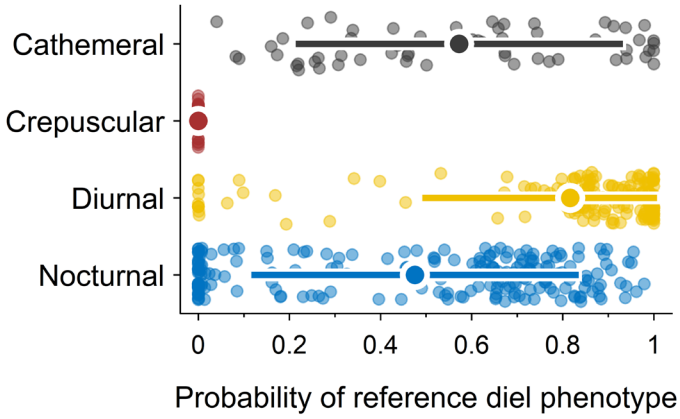

Fig. 2. A comparison of species reference phenotypes with empirical data. Large dots for each reference phenotype (*y* axis) represent the among-species average probability of support for a given diel phenotype (*x* axis), horizontal bars are ±1 SD of species-specific estimates, and smaller dots are species-specific estimates across all of their respective analysis units. For each species' analysis unit, the traditional hypothesis set was fitted with equal prior weight on each diel phenotype. Crepuscularity ($n = 24$) was least accurate at 0%, while nocturnality ($n = 202$) was found to be about 58% accurate. Diurnality ($n = 159$) had the best accuracy at 82%, followed by cathemerality at 57% ($n = 60$) when compared to empirical data.

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results did not change when we restricted our analyses by subsetting to species most readily detected by camera traps (ground dwelling and >500 g; fig. S2). Diurnal references were in highest agreement (mean = 82%, n = 159), followed by cathemeral references (mean = 57%, n = 60). Notably, in contrast to the reference literature, no species was defined as strictly crepuscular because mammals that were highly active during twilight also used other diel phases. This difference emphasizes the need for standardized definitions based on a consistent conceptual framework. When considering a hypothesis set with separation among biphasic and triphasic hypotheses (i.e., general; Fig. 3), we saw that 46% of cathemeral species were more accurately defined as "diurnal-nocturnal" and 11% "crepuscular-nocturnal" (fig. S3). This provides evidence that the standard phenotype descriptions used may be overly general, which could lead to misinterpretation and suggest a need for refinement.

How well a species' reference phenotype agreed with our estimated standardized phenotypes (Fig. 4) also varied among families. Overall, a few families (e.g., primates in *Cebidae* or *Cercopithecidae*) had many species whose reference phenotypes were in agreement with our categorization, which may be due to how well these species were studied. Of 26 families, only 35% (9 of 26) had a mean agreement probability of >0.80. The families with the lowest accuracy were dissimilar (e.g., deer, cats, rabbits and hares, and weasels; Fig. 4), which suggests that disagreement occurs across disparate families. Assigning higher prior probability support to the reference phenotype did not change our results (fig. S4) nor did subsetting to species most readily detected by camera traps (ground dwelling and >500 g; fig. S5).

Environmental and anthropogenic factors

We explored whether species traits, environmental factors, and anthropogenic factors were associated with plasticity in species diel phenotypes with a subset of our data. Specifically, we kept non-arboreal species ≥ 500 g that had at least 20 analysis units with 0.80 support for a diel phenotype (n = 126 species; see the Supplementary Materials for additional details). We linked the most supported diel phenotype from each analysis unit to environmental and anthropogenic factors using multinomial logistic regression where cathemeral was treated as the baseline category for comparison. Our model included analysis unit-level covariates (distance from the equator, number of daylight hours per day, and global human footprint; see fig. S6 for a graphical display of analysis-unit level variation in latitude and the number of daylight hours per day), species traits (log mass and distributional

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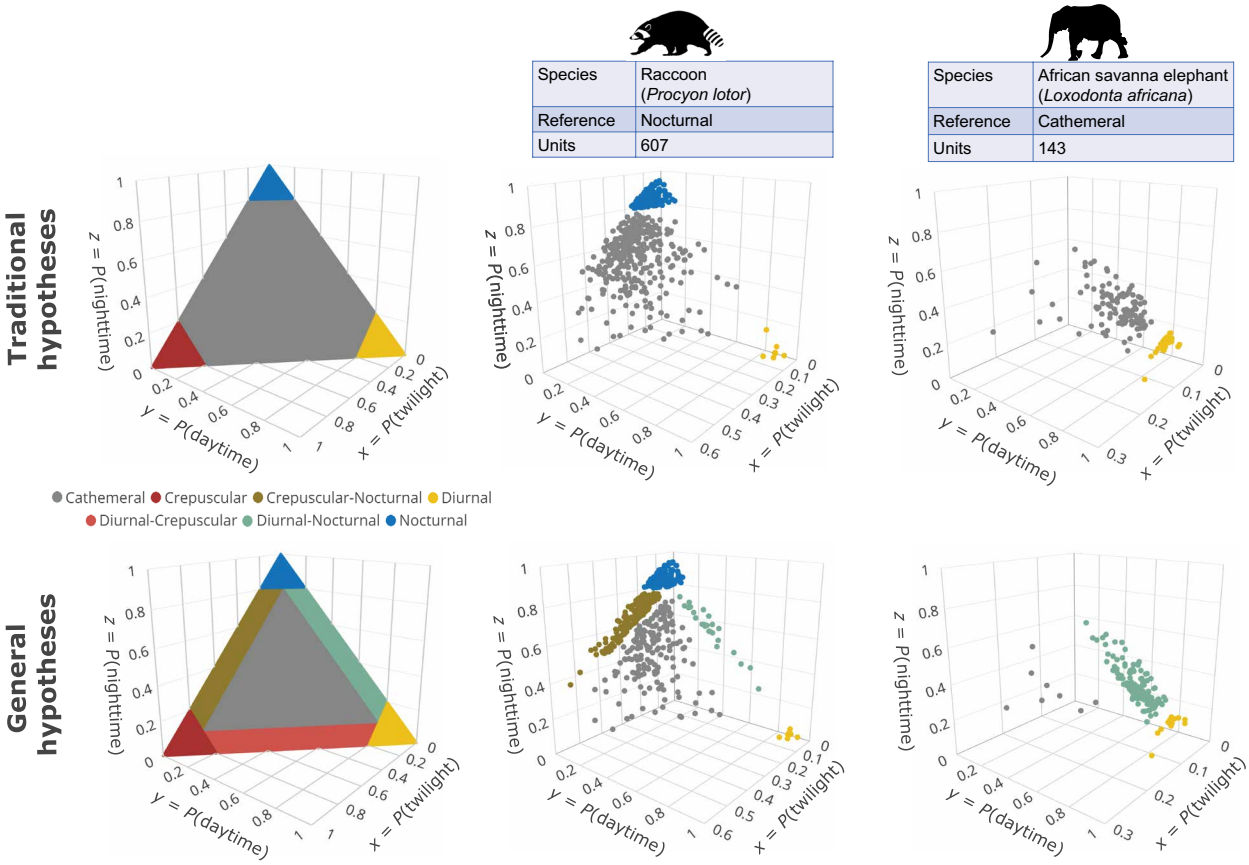

Fig. 3. Diel phenotype hypotheses and their associated probability space for the traditional and general hypothesis sets, as well as empirical support under each hypothesis set for two sample species (raccoon and African savanna elephant). The Traditional hypotheses are composed of diurnal, nocturnal, crepuscular, and cathemeral phenotypes while the General hypotheses encapsulates more phenotypes (crepuscular-nocturnal, diurnal-crepuscular, and diurnal-nocturnal). Subplot axes indicate the probability of activity in twilight (x), daytime (y), and nighttime (z).For the species results, each circle represents an analysis unit's posterior median probabilities of activity, colored by the supported diel phenotype. For both species we see the loss in information when the Traditional hypotheses are considered while the General provides more specific insights, making a clear separation of biphasic activity (e.g., diurnal-nocturnal) from triphasic activity (e.g., General cathemeral). Note that "Reference" refers to the literature reference classification and "Units" is the number of unique analysis units.

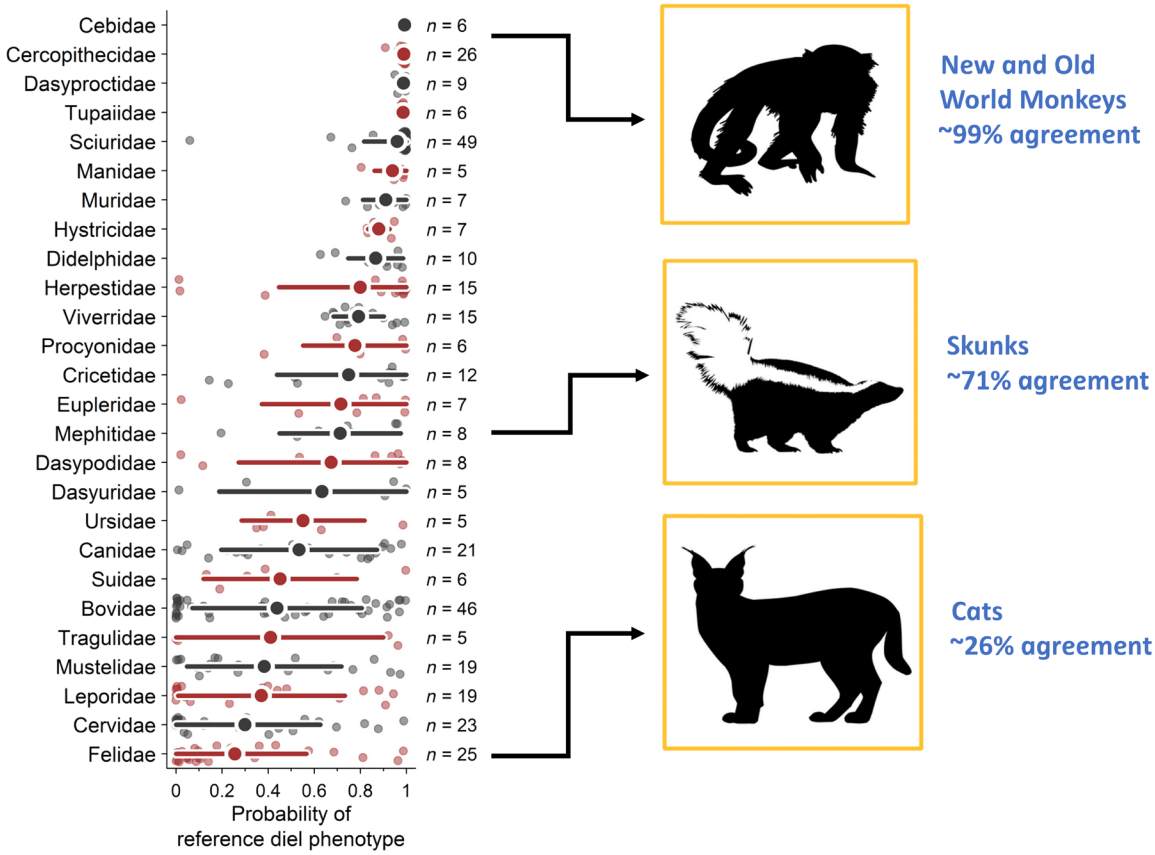

Fig. 4. Probability of agreement for each species with reference phenotype category mapped to phylogeny. Only families with five or more species are plotted (n = the number of species per family that were included in our analysis). Lower probability values mean that, for the corresponding species, there are many analysis units that do not agree with their reference classification. Large dots for each reference phenotype represent the among-species average, horizontal bars are ±1 SD of species-specific estimates within a family, and smaller dots are species-specific estimates across their respective analysis units. For each species' analysis unit, the traditional hypothesis set was fit with equal prior weight on each diel phenotype.

extent), and the statistical interaction between these covariate classes. Median pairwise correlation ($|r|$) among variables was minimal (mean = 0.05, range = 0.00, 0.43). In addition to these covariates, we included three different kinds of random effects in our model. This included random species-level intercept and slope terms to allow for species-specific responses to analysis unit covariates, random family-level intercepts to account for non-independence among species, and random project-level intercepts to account for non-independence within a camera trap project's analysis units.

Interspecies variation in the size of a mammal's distributional extent, their mass, and their average distance from the equator were all strongly associated with their expected diel phenotype (Fig. 5). The size of a species distributional extent had the strongest association such that mammals with a larger distributional extent were, on average, less likely to be diurnal [$\beta_{\text{diurnal, extent}} = -1.09$, 95% confidence interval (CI) = −1.92, −0.30]. Holding other covariates in the model at their mean, a species with a distributional extent of 90,000 km^2 had a 0.88 probability of diurnality (95% CI = 0.51, 0.98) while a species with a 1 SD increase in extent (450,000 km^2) had a 0.70 probability (95% CI = 0.45, 0.87). Making the same comparison for nocturnality, an average species with a 450,000 km^2 extent was 3.35 times more likely to be nocturnal than a species with a 90,000 km^2 extent (95% CI = 1.24, 10.46). This relationship did, however, interact with variation in the number of daylight hours per day. Specifically, we found that species with a small distributional extent were more likely to be nocturnal in areas with less than average daylight hours per day but be diurnal in areas with more than average daylight hours per day ($\beta_{\text{nocturnal, extent} \times \text{daylight}} = 0.16$, 95% CI = 0.02, 0.29; figs. S7 and S8). Conversely, species with a large distributional extent were more likely to be cathemeral across the entire gradient of daylight hours per day (fig. S9). Log body mass was negatively associated with nocturnality ($\beta_{\text{nocturnal, mass}} = -0.80$, 95% CI = −1.60, −0.02). Holding other covariates in the model at their mean, a 0.5-kg mammal was 4.5 times more likely to be nocturnal than a 50-kg mammal, which respectively had 0.41 (95% CI = 0.08, 0.83) and 0.09 (95% CI = 0.03, 0.27) probabilities of nocturnality. In agreement with our prediction and the circadian thermoenergetic hypothesis, species who were, on average, further from the equator were less likely to be nocturnal ($\beta_{\text{nocturnal, mean |latitude|}} = -0.77$, 95% CI = −1.47, −0.09) and, as a result of this, more likely to be diurnal or crepuscular. For example, a species that was most commonly sampled along the equator was 1.9 times more likely to be nocturnal (0.41, 95% CI = 0.12, 0.76) than a species most commonly sampled at 20° latitude (0.21, 95% CI = 0.07, 0.45). Last, we also found evidence of a statistical interaction between an analysis unit's distance from the equator and a species

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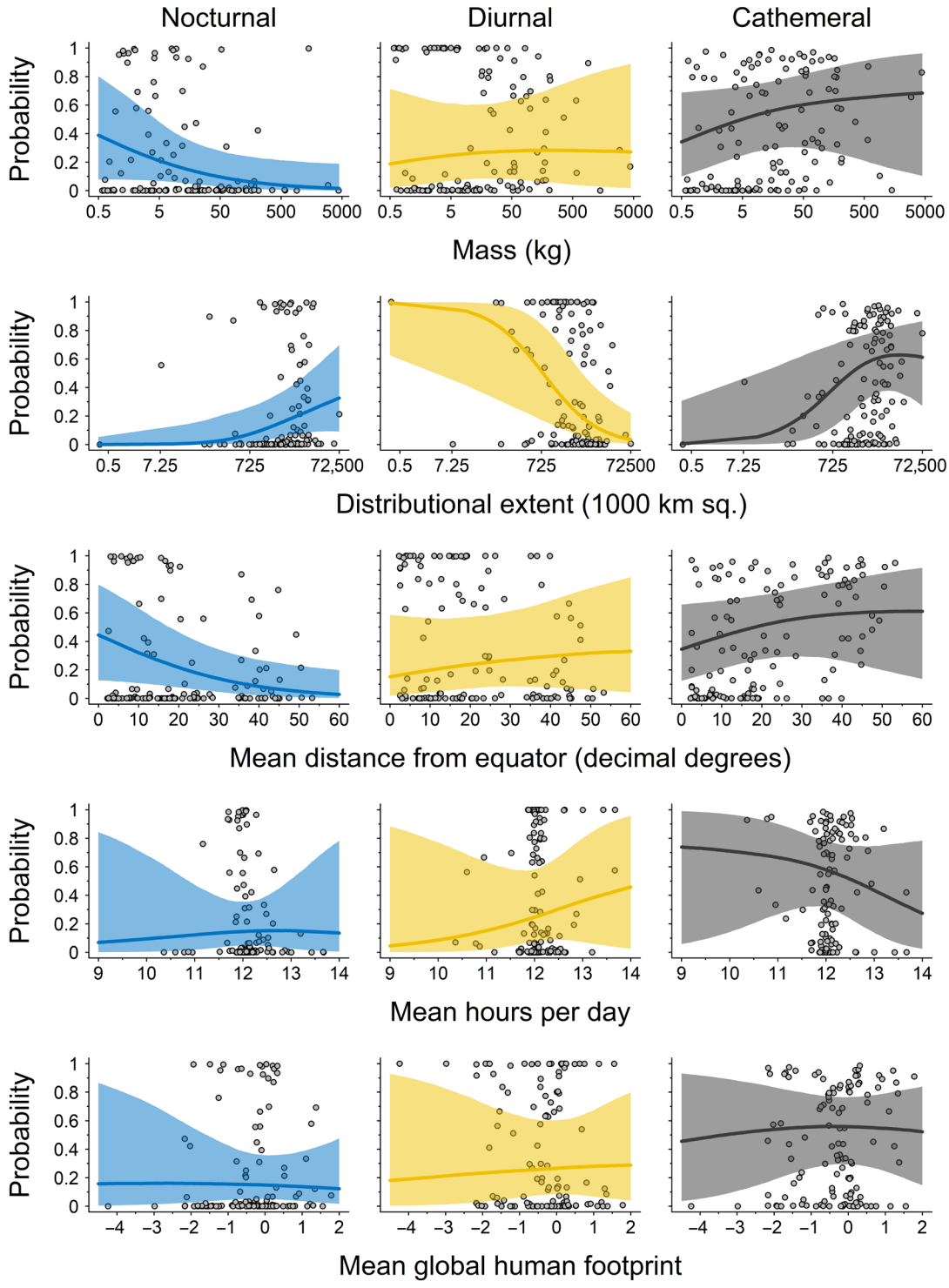

Fig. 5. The predicted probability of a species being nocturnal, diurnal, or cathemeral depending on a species' level trait value, average environmental, or anthropogenic gradient. The solid line and shaded ribbon for each plot respectively represent the median estimate across species and its associated 95% credible interval. Points are species-specific probabilities of nocturnality, diurnality, or cathemerality that were either estimated at their trait value (e.g., mass or distributional extent) or their among analysis-unit average for a given environmental or anthropogenic gradient (e.g., mean distance from the equator, mean hours per day, and mean global human footprint).

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average distance from the equator, such that species were more likely to be diurnal if they were located further from the equator than their average distance ($\beta_{\text{diurnal, unit}|\text{latitude}| \times \text{mean}|\text{latitude}|} = 0.91$, 95% CI = 0.06, 1.79). Together, these results demonstrate how both species traits and geography are intricately tied to the diel activity patterns of mammals.

For the 126 species for which we could quantitatively assess intraspecies plasticity across analysis units, 74% of all species (93 species; >0.90 probability) switched diel phenotypes due to variation in distance from the equator (15 species), daylight hours per day (71 species), and global human footprint (38 species; see figs. S10 and S11 for species-specific slope terms). While mammals change their diel phenotype with increasing anthropogenic pressure (*16*), we found that they do not solely change from diurnal to nocturnal (*19*). In our analysis, 17 species were more likely to be nocturnal with increasing global human footprint, whereas 2 species were less likely to be nocturnal. Likewise, 5 species were more likely to be diurnal with increasing global human footprint, and 14 species were less likely to be diurnal. Species that became more nocturnal with increasing global human footprint included urban adapted mammals like the striped skunk (*Mephitis mephitis*) as well as other species like snowshoe hare (*Lepus americanus*), gray fox (*Urocyon cinereoargenteus*), North American porcupine (*Erethizon dorsatum*), and crab eating fox (*Cerdocyon thous*; Fig. 6). Overall, the number of daylight hours available per day was the strongest supported covariate of diel phenotype change, but anthropogenic factors and latitudinal differences also resulted in shifts for many species (figs. S10 and S11). As most species switched their diel phenotype along at least one environmental gradient, these changes demonstrate large shifts in when species are active over the 24-hour light-dark cycle.

Last, we quantified species-level diel plasticity as the likelihood that species would switch their diel phenotype along gradients of latitude, daylight hours per day, and global human footprint. For each species, we predicted the probability of diurnality, nocturnality, and cathemerality along these three gradients and then calculated the maximum expected SD across diel phenotypes for each gradient. We then used this plasticity metric to identify which species were most variable along each gradient and plotted these patterns for the most (figs. S12 to S14) and least (figs. S15 to S17) plastic species.

Together, our results indicate that mammals commonly switch diel phenotypes in the modern global environment. While other studies have demonstrated variability in how much time species are active throughout the 24-hour period (*12*, *16*), we find that these changes can be marked shifts from one phenotype to another (i.e., spending >80% of their time active during one diel phase to >80% in another diel phase). Our results empirically support the hypothesis (*7*) that the mammalian diel phenotype is plastic.

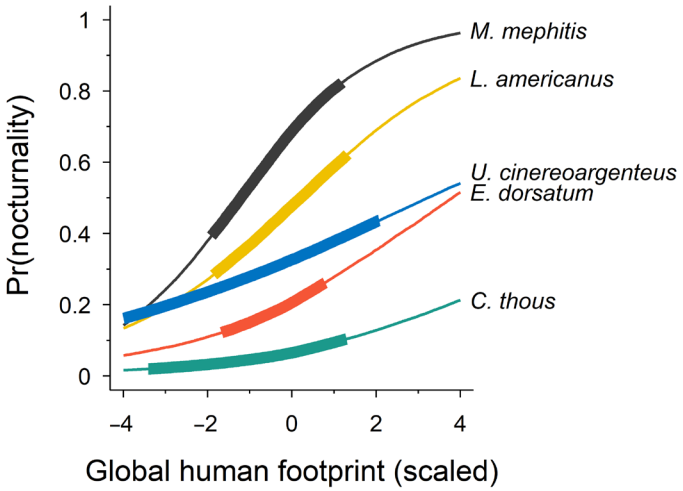

Fig. 6. Roughly a third of the species analyzed demonstrated plasticity in their diel phenotypes along gradients of global human footprint. This plot is a representative example of species that became more nocturnal (*y* axis) with increasing global human footprint (*x* axis), which includes the striped skunk (*Mephitis mephitis*), snowshoe hare (*Lepus americanus*), gray fox (*Urocyon cinereoargenteus*), North American porcupine (*Erethizon dorsatum*), and the crab-eating fox (*Cerdocyon thous*). Lines represent median species-specific estimates. The thinner line represents nocturnality predictions for global human footprint values that fall either above or below the range observed across a species' analysis units, whereas the thicker line represents predictions that fall within that range.

DISCUSSION

We found that reference diel phenotypes were inconsistent with findings from our conceptually motivated empirical diel estimates for many species and families. Notably, mammals traditionally categorized as crepuscular (active at twilight) are active during other times of the day (e.g., at the hours surrounding twilight), such that the crepuscular phenotype does not describe mammal activity well. This is not to say that mammals do not use the twilight phase but simply do not or cannot concentrate enough of their activity within this limited period of time. What makes our definition of crepuscular unique is that we mathematically define it by the amount of activity within twilight (which it is regularly descriptively defined as) and use the equivalent logical threshold that defines the other two traditional uniphasic phenotypes (diurnal, nocturnal; i.e., one diel phase predominantly used), thus enforcing comparability among phenotypes. Of the species that were classified as crepuscular by the reference literature, we found that under the traditional hypothesis set, they were mostly supported as cathemeral (secondly, diurnal) and, under the general hypothesis set, as a mix of cathemeral, diurnal, and diurnal-nocturnal. Given these results, we conclude that traditional categorizations of mammal diel phenotypes should be reevaluated.

Among the other reference diel categorizations (diurnal, nocturnal, and cathemeral), we found considerable variability in species agreement between reference diel phenotypes and our empirically estimated diel phenotypes. These differences are likely due to a mixture of inconsistencies in definitions, meanings of activity, plasticity, and sampling methodologies. Overall, we found only 39% agreement between our results and reference classifications, which further suggests that we need to reevaluate species diel behavior to fully understand their niche and how to conserve them in an anthropogenic world (*6*, *7*, *16*, *25*). To do this, we need to standardize the definitions of diel phenotypes using quantitative approaches and explicitly recognize that mammal species have multiple diel phenotypes. Furthermore, we should consider whether commonly used diel phenotypes (diurnal, nocturnal, crepuscular, and cathemeral) appropriately capture distinctive diel activity outcomes. We found that more specific diel phenotype designations led to more accurate descriptions of biphasic and triphasic diel activity for many species (e.g., general hypothesis set; Fig. 2). This suggests that the 11.8% of mammals classified as cathemeral (*24*) could be described more accurately. Thus, our framework can help unify research on this topic, which is sorely needed to better understand how species use diel time in a changing world (*6*, *9*, *16*, *25*, *39*).

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We found clear patterns of inter- and intraspecies variation in mammalian diel phenotypes. Among species, mammal's use of day and night varied with their body size, distributional extent, and environmental conditions (Fig. 5). Smaller species were more likely to be nocturnal globally, which agrees with other global research (*7*), but not in the context of the forested tropics (*40*). We also found that our results provided support for the thermoenergetic hypothesis in that mammals were more likely to be diurnal or cathemeral in colder environments farther from the equator. Prior research has also associated increased light availability with the distribution of diurnal and crepuscular species (*3*). While we only found minimal associations between interspecies variation in light availability and diel phenotypes, intraspecies diel plasticity was most strongly associated to light availability. As such, our results provide nuance in that light availability increased plasticity in many species; increasing light availability allowed species with small distributional extents to become more diurnal while species with larger extents become more cathemeral.

While light availability played a substantial role in diel plasticity, we also found that increasing anthropogenic pressure prompted some mammals, primarily North American mammals, to shift to a nocturnal phenotype. This may have occurred for two reasons. First, more than 48% of analysis units came from North America. Thus, North American mammals were well represented and therefore likely candidates to find this relationship. Second, our quantitative delineations for diel phenotypes required a species to spend 80% or more of their activity at night to be quantified as nocturnal. It may be that species increased nocturnality with greater anthropogenic pressure (*16*) but not to the extent that they would be classified as nocturnal. Regardless, even with our strict diel phenotype definitions, 74% of species expressed plasticity in their diel phenotypes along environmental gradients, which showcases the extent to which species express large-scale behavioral shifts in their diel activity.

The scale and methodology used in our study led to certain limitations that should be recognized. First, camera traps provide a Eulerian or population-based view of the animal community, as most species cannot be reliably individually identified. As such, we could not evaluate inter- or intraindividual variation in diel activity. Both are important sources of variation when considering behavioral plasticity (*41*). Second, all camera traps in this study were ground based and thus unable to detect burrowing and strictly arboreal species. Species that use multiple strata may have different diel activity patterns across strata levels (*42*). We investigated whether our results comparing empirical and reference diel classification were sensitive to the inclusion of small mammals < 500 g or arboreal species but found no differences (fig. S2). We might expect high disagreement in certain families that include arboreal species, such as Cercopithecidae, but found there to be high agreement. Third, in comparing our results with reference diel classifications, we were unable to control for differences due to the sampling technique; different techniques (e.g., camera traps versus animal follows) may be measuring different aspects of activity. Whereas the literature classifications potentially combine multiple sampling techniques, which likely leads to amalgamations of meanings of diel activity, we consider data from a single sampling approach (i.e., camera traps) that maintains a consistent definition. Last, animal diel activity is known to change across climatic seasons (*43*). However, we could not directly model this source of variation in our multinomial logistic regression analysis due to the scale of our study. More specifically, it was difficult to reliably categorize time periods into distinctive seasons due to variation in the number of climatic seasons at different locations on Earth, variation in elevation across camera trap projects, and interannual variation in the timing of meteorological conditions. We did, however, include the number of daylight hours per day in our model which covaries with seasonality. Despite these limitations, we contend that this analysis sets a solid foundation for researchers to further investigate and define diel phenotypes which will, in turn, make it easier to evaluate how species are or are not modifying their diel behavior in a rapidly changing world.

Diel activity is a fundamental animal behavior that intersects evolution and ecology (*1*, *2*). Despite morphological and physiological adaptations that have been traditionally believed to constrain animal activity (*8*, *10*, *11*, *21*), our results provide empirical evidence that mammals change their diel activity to adapt to environmental conditions worldwide. By leveraging a global network of scientists and a novel methodological framework that allows logical and comparable inference on diel activity, we have updated our understanding of a fundamental species behavior based on empirical observations. These 14,587 diel estimates, as well as the software used to make them (*35*), are available to eco-evolutionary researchers to further expand our understanding of how animal morphology and physiology are shaped through evolutionary and ecological processes. As the world is experiencing a time of rapid environmental change, many species are shifting their diel phenotypes with unknown fitness consequences. Furthermore, species that are not shifting diel phenotypes may be incurring worse fitness outcomes by being inflexible in this behavior. Recognizing the fitness consequences of species' diel phenotype plasticity and lack thereof is an important next step to understand the impacts of environmental change and can help direct conservation actions.

MATERIALS AND METHODS

We used a novel model-based hypothesis framework to define and estimate species' diel phenotype with the "Diel.Niche" R package (https://github.com/diel-project/Diel-Niche-Modeling) (*35*). This framework uses logical and consistent definitions of diel phenotypes and probability theory to evaluate the evidence of support using empirical observations. To use this framework, we discretized the sampling effort from camera trap projects to calculate the frequency of species detections that occurred during the twilight, daytime, and nighttime ($\boldsymbol{y} = [y_{tw}, y_d, y_n]$). To do so, we identified periods of continuous sampling within each camera trapping project, split these periods of continuous sampling into smaller pieces if they were sufficiently large following a standardized set of rules, and then calculated the frequency of species detections within each temporal subset of a camera project's data (Fig. 7 and see the Supplementary Materials for additional details). For brevity, we refer to these species-specific temporal subsets as analysis units.

To identify periods of continuous sampling for our analysis units, we first calculated the number of operational cameras per day for each camera trap project. Following this, we identified periods where at least one camera was sampling within each camera trap project (see the Supplementary Materials for more information). For example, some projects deployed cameras on specific months of a year and so had multiple deployments punctuated by periods without sampling, while other projects had cameras operational for

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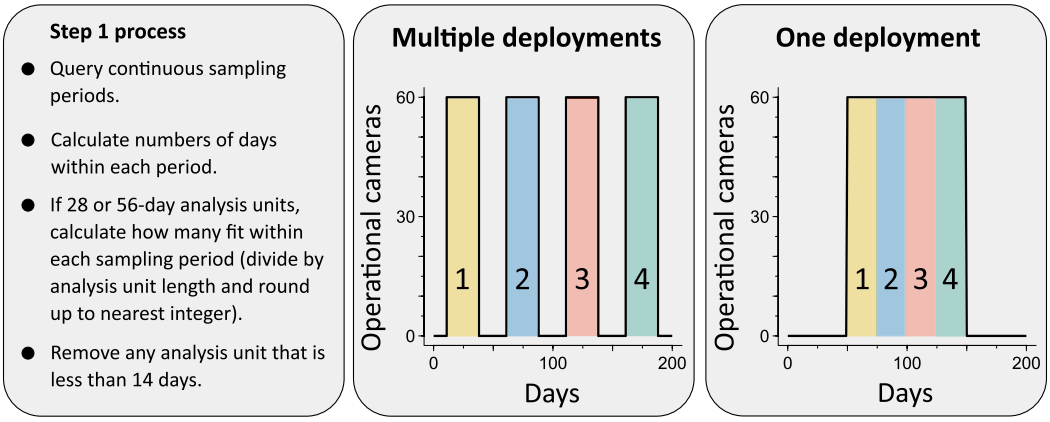
Step 1:
Identify possible analysis units based on days cameras were active for a project, starting with 28-day analysis units.



Step 2:
For each species, calculate the number of independent events within each possible analysis unit. Retain analysis units for each species that have at least 10 independent events.

Step 3:
Retain names of species where analysis units were created for each project.

Step 4:
For species within a project where analysis units could not be created, repeat steps 1–3 with 56-day analysis units.

Step 5:
For species within a project where 28 or 56-day analysis units could not be created, treat all data within a project as a possible analysis unit and follow steps 2 and 3. These are the "all data" analysis units.

Fig. 7. Examples of how analysis units—which represent a subset of a camera trap project's data—could be generated under different camera trap deployment scenarios and the steps we followed to create them. We created these analysis units to discretize a camera trap project's sampling effort, calculate the frequency of species detections that occurred during the twilight, daytime, and nighttime, and connect a species detection data to spatiotemporal covariates (e.g., global human footprint and mean hours of daylight per day).

the entire length of their study (Fig. 7). Analysis units were first generated from these periods of continuous sampling using a 28-day sampling period, which was chosen because it falls within the minimum suggested sampling effort for camera trap studies (*44*). To determine the number of analysis units that would fit within a period of continuous sampling for a project, we divided the number of sampled days by the analysis unit length and rounded up to the nearest integer. For example, if a camera trap project had one continuous sampling period of 100 days, we would generate four 25-day analysis units from it (i.e., 100 days of sampling divided by 28 days and then rounded up to the nearest integer). Following this, we tabulated the frequency of detections for each species within each proposed analysis unit per camera trap project.

We first attempted to use 28-day analysis units for all camera trap projects and species but found that this protocol resulted in some species with analysis units that had fewer than 10 species detections, which was insufficient for estimating a species diel phenotype (*35*). Therefore, for species with an insufficient sample size, we increased the analysis unit sampling window to either 56 days or to use all the data within a project if a 56-day analysis unit was also insufficient. For example, after generating 28-day analysis units for a camera trap project, if a species did not have any analysis units with at least 10 detections, then we would generate 56-day analysis units for the project instead for that species. Likewise, if a species did not have a 56-day analysis unit with at least 10 detections assigned to it within a camera trap project, then we used all the data within the project to generate one analysis unit for that species within that project. We used this scheme so that we could make inference on both common and rare species. For example, while nearly 95% of our analysis units came from 28-day periods, using the 56-day and all data analysis units added an additional 78 species to our analysis.

Overall, our creation of these analysis units, $\boldsymbol{y} = [y_{tw}, y_d, y_n]$, leads to using a multinomial distribution to estimate the probability of use within each category ($\boldsymbol{p} = [p_{tw}, p_d, p_n]$). We added constraints to our

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models to represent alternative hypotheses about diel phenotypes (Fig. 2). We fitted models to each analysis unit using two hypothesis sets (traditional and general; Fig. 2 and the Supplementary Materials) that differed in the number of diel phenotypes and their definitions. The traditional hypothesis set aims to capture the general interpretation of the fundamental phenotypes used in the literature (diurnal, nocturnal, crepuscular, and cathemeral). Crepuscular, diurnal, and nocturnal are defined on the basis of having at least 0.80 probability in their respective diel phases. The general hypothesis set defines these phenotypes the same as in the traditional set; the main difference being the definition of cathemerality, where the general hypothesis set aims to differentiate phenotypes in terms of uniphasic, biphasic (i.e., two diel phases predominately used; e.g., nocturnal-diurnal), and triphasic activity (i.e., three diel phases predominately used; e.g., cathemeral), while the traditional set only differentiates between uniphasic and multiphasic (i.e., more than one diel phase predominantly used) diel activity. As such, the general hypothesis is more specific and clear regarding activity types (*35*) (for additional details, see the Supplementary Materials). Within each hypothesis set, we used Bayes factors to estimate and compare empirical support via modal probabilities for each diel phenotype hypothesis.

We used the model probabilities for each diel phenotype hypothesis in two subsequent analyses to address our fundamental questions. First, we evaluated whether diel reference categorizations provide fully accurate, logical, and consistent species descriptions by comparing these with our standardized empirical results from the traditional hypothesis set using the model probability of the reference phenotype. This helps frame our results in the context of the current summarized knowledge about species diel activity. Specifically, we made species-level inference on the empirical support of the reference phenotype by modeling the model probabilities of each analysis unit by fitting Bayesian ordered beta regression models (*45*). These models accommodate the support of the model probabilities (i.e., values from 0 to 1) while allowing us to weight model probabilities by sample size and include nested random effects of camera project within species within family, thus accounting for the nested structure of these data and the dependence within group (see the Supplementary Materials for additional details). There is no standardized framework for how species' reference categorizations were made. Yet, reference categorizations are regularly used to describe species' baseline or preferred activity times and are used as data in ecological niche modeling; the implicit assumptions being that historical species activity categorizations are meaningfully and consistently defined and thus comparable and that species have a single diel phenotype. Our empirical results provide an unprecedented opportunity to determine how much support such assumptions have so that we can refine and enhance the accuracy of species activity categorizations in ecological studies.

The second analysis explored how species traits and analysis unit-level environmental variables were associated with inter- and intraspecies variation in diel phenotypes using a subset of our data. Specifically, we kept non-arboreal species $\geq$ 500 g that had at least 20 analysis units with 0.80 support for a diel phenotype (n = 126 species). We modeled the probability of an analysis unit being supported in a given diel phenotype using a Bayesian multinomial logistic regression model; similar to the previous analysis type, we incorporated a three-way nested random effect of camera project within species within family (see the Supplementary Materials for a full model description).

Supplementary Materials

The PDF file includes:

Supplementary Text
Figs. S1 to S17
Table S1
Legends for data S1 to S8
References

Other Supplementary Material for this manuscript includes the following:

Data S1 to S8

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