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RESEARCH METHODS GUIDE

A model-based hypothesis framework to define and estimate the diel niche via the '`Diel.Niche`' R package

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Abstract

1. How animals use the diel period (24-h light–dark cycle) is of fundamental importance to understand their niche. While ecological and evolutionary literature abound with discussion of diel phenotypes (e.g. diurnal, nocturnal, crepuscular, cathemeral), they lack clear and explicit quantitative definitions. As such, inference can be confounded when evaluating hypotheses of animal diel niche switching or plasticity across studies because researchers may be operating under different definitions of diel phenotypes.
2. We propose quantitative definitions of diel phenotypes using four alternative hypothesis sets (maximizing, traditional, general and selection) aimed at achieving different objectives. Each hypothesis set is composed of mutually exclusive hypotheses defined based on the activity probabilities in the three fundamental periods of light availability (twilight, daytime and night-time).
3. We develop a Bayesian modelling framework that compares diel phenotype hypotheses using Bayes factors and estimates model parameters using a multinomial model with linear inequality constraints. Model comparison, parameter estimation and visualizing results can be done in the `Diel.Niche` R package. A simplified R Shiny web application is also available.
4. We provide extensive simulation results to guide researchers on the power to discriminate among hypotheses for a range of sample sizes (10–1280). We also work through several examples of using data to make inferences on diel activity, and include online vignettes on how to use the `Diel.Niche` package. We demonstrate how our modelling framework complements other analyses, such as circular kernel density estimators and animal movement modelling.
5. Our aim is to encourage standardization of the language of diel activity and bridge conceptual frameworks and hypotheses in diel research with data and models. Lastly, we hope more research focuses on the ecological and conservation importance of understanding how animals use diel time.

KEYWORDS
cathemeral, crepuscular, diel, `Diel.Niche`, diurnal, nocturnal, temporal activity, temporal niche

1 | INTRODUCTION

The rise and setting of the sun causes shifts in environmental conditions (e.g. temperature, humidity) and ecosystem processes (e.g. pollination, dispersal) that affects nearly all species on Earth (Cox & Gaston, 2023a; Gaston, 2019; Gaston et al., 2023). Animal groups, including insects, amphibians, birds, fish, molluscs and mammals, are well known to be influenced by the changes associated with the light–dark cycle (Anderson & Wiens, 2017; Flury & Levri, 1999; Hut et al., 2012; Kronfeld-Schor & Dayan, 2003; Saunders, 2012). An animal's diel activity has long been considered a component of an animal's niche (Carothers & Jaksić, 1984; Hutchinson, 1957; Kronfeld-Schor & Dayan, 2003; Levy et al., 2019; Pianka, 1973; Wiens et al., 2010). Yet, research on how animals use time within the diel period (24-h light–dark cycle) has until recently been an underappreciated focus of study (Anderson & Wiens, 2017; Carothers & Jaksić, 1984; Gaston, 2019; Kronfeld-Schor & Dayan, 2003; Wiens et al., 2010).

Among mammals, a species' diel activity or main time of day at which individuals display locomotor activity (Hut et al., 2012) has been viewed as a fixed behavioural trait (Levy et al., 2019) constrained by evolution, morphology and physiology (Anderson & Wiens, 2017; Hall et al., 2012). Major shifts in a species' diel niche (e.g. nocturnal → diurnal) have been predicted from ecological theory (Schoener, 1974a, 1974b) and observed (Kronfeld-Schor & Dayan, 2003) to be rare. Partly for these reasons, mammals are often attributed a single diel niche (e.g. diurnal; Mittermeier & Wilson, 2009; Nowak & Walker, 1999). Such a categorization makes the implicit assumption that all individuals—across populations and regardless of environmental conditions—would maintain this diel niche to optimize fitness (e.g. via foraging, predation risk and reproduction) based on their morphological and physiological traits.

However, recent studies have shown flexibility in mammals' circadian regulation of their physiology (Riede et al., 2017; van der Veen et al., 2017) which allows for more adaptability in diel activity than previously thought (Gaston, 2019; Rivera et al., 2022). Furthermore, there is growing empirical evidence that many mammal species alter their diel activity in response to environmental context (abiotic and biotic), including temperature (Gallo et al., 2022; Hut et al., 2012), season (Farris et al., 2015; Hut et al., 2012), anthropogenic activity (Gaynor et al., 2018; Moll et al., 2018), landscape features (Gallo et al., 2022; Rivera et al., 2022) and intra- and inter-specific competition (Cunningham et al., 2019). Translating whether these changes in activity can be characterized as a shift in an animal's diel niche (e.g. nocturnal → diurnal) depends on how we define the possible phenotypes.

The traditional diel phenotypes for tetrapods are diurnal, nocturnal and crepuscular (Anderson & Wiens, 2017). A species is commonly described as such based on the majority of their activity occurring in a single distinct period of light availability (daytime, night-time or dawn dusk respectively). Less often considered, but an important complementing diel phenotype, is cathemerality ('through the day'; Cox & Gaston, 2023b; Cox et al., 2023), which is an even amount of activity across the entire diel period, or a large amount of activity across multiple time periods (e.g. day and night; Tattersall, 2008). For many studies, there is little consideration for what constitutes a species being assigned one of these diel phenotypes.

Commonly, researchers plot activity curves and assign a species a diel phenotype based on visual interpretation (e.g. Ridout & Linkie, 2009). Studies that consider how species change their probability of activity through the day (Gallo et al., 2022; Gaynor et al., 2018) often do not assess switching among theoretically motivated diel phenotypes (e.g. diurnal, nocturnal etc.; Hut et al., 2012). We see three issues with these approaches. Foremost, without explicit definitions, we cannot propose hypotheses about diel phenotypes that are directly evaluated with empirical observations. Second, the lack of explicit quantitative definitions of diel phenotypes means that comparisons across studies may be inappropriate, because researchers may be operating under different definitions. This clearly complicates the evaluation of diel niche switching across studies. Third, qualitative interpretations of diel phenotypes are without measures of uncertainty describing how confident we are that a species is using a given diel phenotype. Our work aims to overcome these three concerns.

Research on the diel activity of wild animals is becoming increasingly prevalent (Supporting Information S1, Figure S1). This is partly due to the growing use of camera traps (Gilbert et al., 2022), which can continuously sample the spatio-temporal activity of small to large non-volant animals throughout the 24-h period (Frey et al., 2017). Recently, several thoughtful conceptual frameworks have proposed multiple lines of inquiry focused on diel niche hypotheses (Gaston, 2019; Gilbert et al., 2022). To help move animal diel research in the direction of advancing our understanding related to these conceptual frameworks, we need to connect diel terminology in ecology and evolution with hypotheses that can be tested using empirical data.

We propose a quantitative framework for defining diel phenotypes and probabilistic models that can be evaluated with empirical data and provide a measure of model hypothesis uncertainty. Importantly, we propose a framework that is appropriate even at relatively small sample sizes. This is critical for being able to evaluate the diel niche of rare and difficult to detect species. Furthermore, we offer multiple hypotheses sets that accomplish alternative objectives.

We implement our framework in the new `Diel.Niche` R package (R Core Team, 2023) available on Github at https://github.com/diel-project/Diel-Niche-Modeling. The fundamental elements of the package are (1) defining diel phenotypes, (2) model comparison among diel hypotheses using Bayes factors and (3) estimating probabilities of twilight (dawn and dusk), daytime (daylight hours) and night-time (night hours) activity. Users may use all three elements, or choose to estimate probabilities outside of this framework and only use the package to define their results according to preset diel phenotypes. Furthermore, users can modify existing hypotheses and also define completely new hypotheses. For non-R users, a visual online Shiny application is available for simple analyses (https://shiny.celsrs.uri.edu/bgerber/DielNiche/). We hope this work will encourage consistency in definitions for appropriate comparisons across studies.

2 | EXPLANATION OF THE METHOD

2.1 | Defining diel phenotypes

We define diel phenotypes based on the activity probabilities of the three fundamental light availability periods: twilight (tw), daytime (d) and night-time (n). We refer to these time periods as 'diel periods' throughout. The sample data are thus a vector of observed independent detection frequencies in each period, as $\mathbf{y} = \begin{bmatrix} y_{\text{tw}} & y_{\text{d}} & y_{\text{n}} \end{bmatrix}$ respectively. These frequencies depend on the respective probabilities of p_{tw}, p_{d} and p_{n}.

We translate each diel phenotype as a probabilistic multinomial model with linear inequality constraints on the probabilities (Heck & Davis-Stober, 2019) following the implied relationship under the given phenotype. The inequalities specify which probability combinations for the diel period are defined as a certain phenotype. Specifically, we define inequality constraints by matrix **A** and vector **b**, such that $\mathbf{A}\theta \leq \mathbf{b}$, where $\theta = \begin{bmatrix} p_{\text{tw}} & p_{\text{d}} \end{bmatrix}$. The sum of the three probabilities is always one, such that there are two free model parameters, where p_{n} is derived as $1 - p_{\text{tw}} - p_{\text{d}}$.

As an example of how constraints are used within this modelling framework, let us define a phenotype where we are interested in whether an animal is primarily diurnal, such that the majority of its activity occurs during the daytime. This phenotype is general without any specific constraints on how much activity occurs during the twilight or night-time. Simply, the probability of activity in the daytime is greater than the activity probability during twilight or night-time. We can define this phenotype as a set of two inequalities,

$$p_{\text{tw}} \leq p_{\text{d}}, \tag{1a}$$

$$p_{\text{n}} \leq p_{\text{d}}. \tag{1b}$$

To translate these into the above inequality setup, we redefine Equation (1a) as,

$$\begin{gathered} p_{\text{tw}} \leq p_{\text{d}} \\ p_{\text{tw}} - p_{\text{d}} \leq 0, \text{ such that} \\ (1) \times p_{\text{tw}} + (-1) \times p_{\text{d}} \leq 0, \end{gathered} \tag{2}$$

and, given that $p_{\text{n}} = 1 - p_{\text{tw}} - p_{\text{d}}$ according to our earlier definition, Equation (1b) is,

$$\begin{gathered} p_{\text{n}} \leq p_{\text{d}} \\ 1 - p_{\text{tw}} - p_{\text{d}} \leq p_{\text{d}} \\ 1 - p_{\text{tw}} - p_{\text{d}} - p_{\text{d}} \leq 0 \\ (-1) \times p_{\text{tw}} + (-2) \times p_{\text{d}} \leq -1. \end{gathered} \tag{3}$$

The constants within the parentheses on the left of the inequality sign are packaged into matrix **A** and the constants on the right are packaged into vector **b**, such that

$$\mathbf{A} = \begin{bmatrix} 1 & -1 \\ -1 & -2 \end{bmatrix}, \mathbf{b} = \begin{bmatrix} 0 \\ -1 \end{bmatrix}. \tag{4}$$

Altogether, the full inequality phenotype statement is,

$$\begin{gathered} \mathbf{A}\theta \leq \mathbf{b} \\ \begin{bmatrix} (1) \times p_{\text{tw}} + (-1) \times p_{\text{d}} \\ (-1) \times p_{\text{tw}} + (-2) \times p_{\text{d}} \end{bmatrix} \leq \begin{bmatrix} 0 \\ -1 \end{bmatrix} \\ \begin{bmatrix} p_{\text{tw}} - p_{\text{d}} \\ -p_{\text{tw}} - 2p_{\text{d}} \end{bmatrix} \leq \begin{bmatrix} 0 \\ -1 \end{bmatrix}. \end{gathered} \tag{5}$$

We use the same procedure to specify a number of phenotypes that together represent four complete hypothesis sets with mutually exclusive diel phenotype hypotheses: *Maximizing*, *Traditional*, *General* and *Selection* (Figures 1 and 2). The first three hypothesis sets are strictly on how much an animal uses each diel period, while the fourth (*Selection*) is based on the selection of a diel period, where the probability of use is greater than the proportional amount of time available in a diel period (Gallo et al., 2022; Northrup et al., 2022). The file Supporting Information S2 describes and mathematically defines the set of inequalities for each phenotype.

2.2 | Diel hypothesis sets

We propose three hypothesis sets aimed at characterizing the probability of activity or use in the three diel periods (*Maximizing*, *Traditional*, *General*; Table 1). To discriminate among the hypotheses of diurnal, nocturnal and crepuscular in regard to how much activity is distributed among their respective diel periods, we believe it is logical to define the hypotheses with equivalent thresholds or constraints. This equivalence means that the hypotheses are standardized in regard to how much activity is required in the respective diel periods to be called diurnal, nocturnal or crepuscular. Since the focus is on estimating the amount of activity, these hypotheses sets do not account for the different available amount of time in the three periods. We are estimating the use of the three diel periods within the context of the study design and sampling period. This has important consequences, especially for being defined as crepuscular as the twilight period is relatively short, which we discuss in the Caveats section. To move beyond use and to quantify use relative to availability, we also propose a fourth hypothesis set (*Selection*) that accounts for the available amount of time in the diel periods to evaluate selection (i.e. disproportional use, given availability; Table 1).

The *Maximizing* hypothesis set includes three diel phenotype hypotheses (Figure 1; Crepuscular Max, Diurnal Max and Nocturnal Max) with the objective of evaluating which diel period is used most.

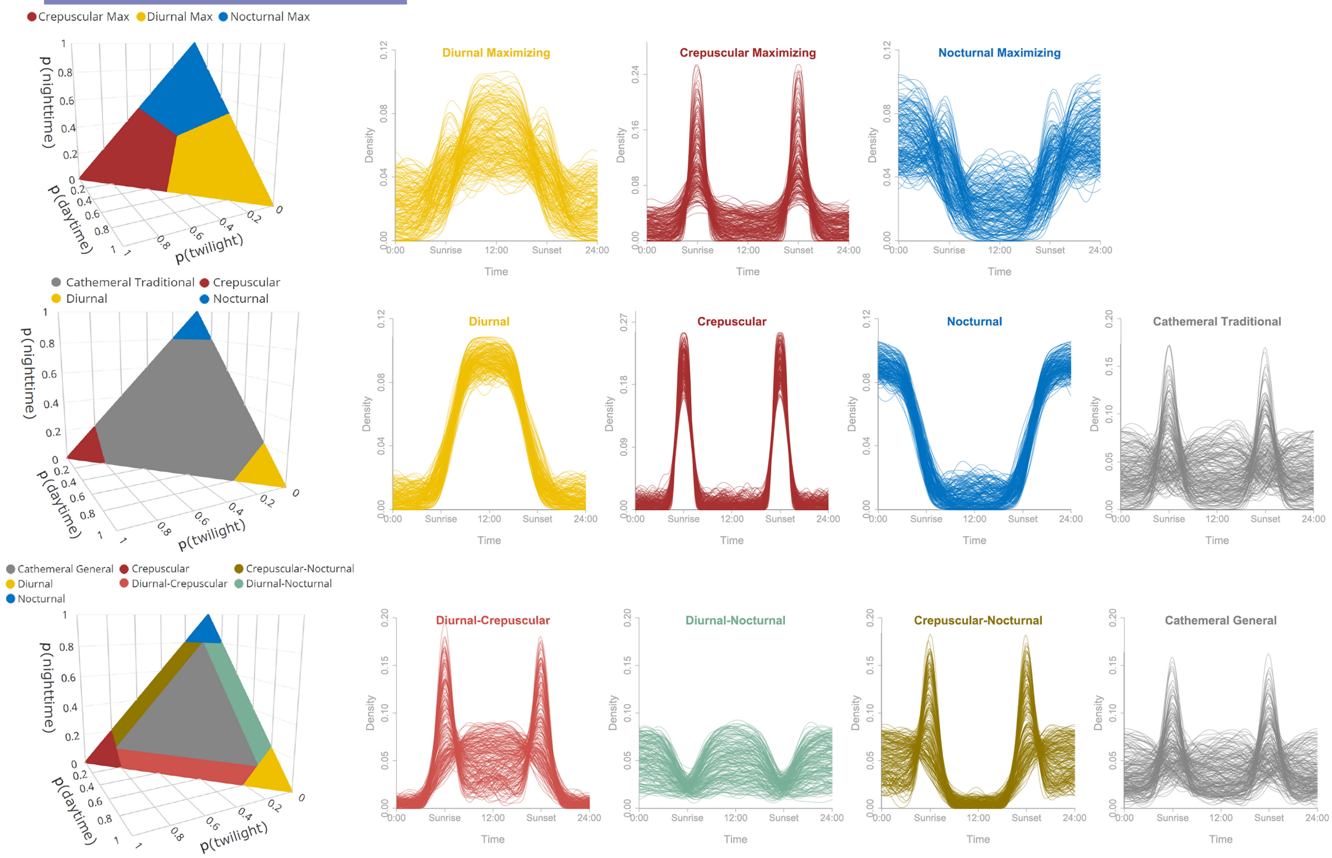

FIGURE 1 Diel niche hypothesis sets (first column, from top to bottom: maximizing, traditional, general) as defined by the probability of activity during daytime, night-time and twilight. For each hypothesis in a set, examples of circular kernel density estimates are plotted over the 24-h period. Note that the general hypothesis set (third row) includes the diel hypotheses of diurnal, nocturnal and crepuscular, which are plotted with the traditional hypothesis set (second row).

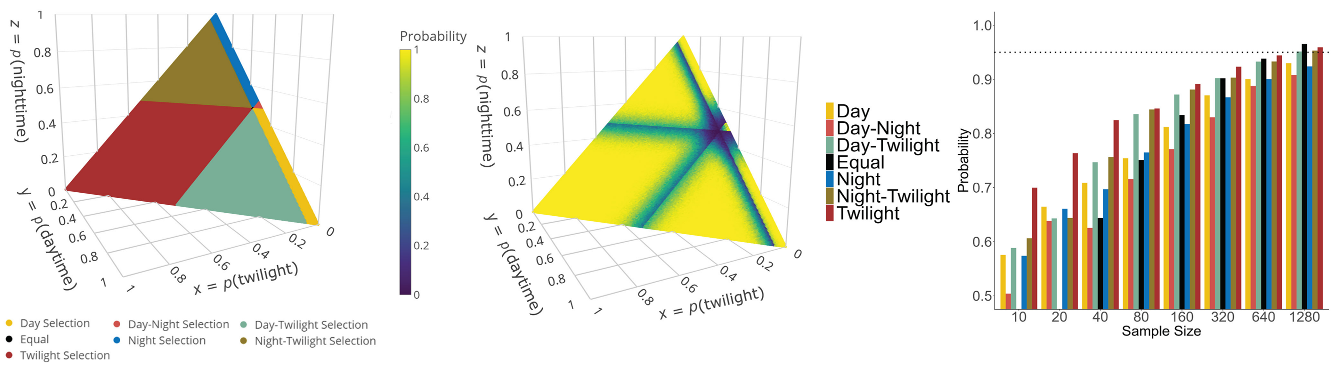

FIGURE 2 The selection hypotheses (left) as defined by the disproportional amount of activity during twilight, daytime and night-time, given their respective available amount of time in each period (availability defined as 0.04, 0.48 and 0.48 for the respective diel periods). The middle plot depicts the probability that the generating model is most supported by parameter combinations when the sample size is 100 total observations. The right plot comprises results of the probability the generating model was most supported across varying sample sizes. Complementary simulation results are found in Supporting Information S1, Figure S4.

As such, there is no hypothesis about activity across multiple diel periods (i.e. cathemeral). The *Traditional* hypothesis set includes four diel phenotype hypotheses (Figure 1; crepuscular, diurnal, nocturnal, traditional cathemeral) that aim to capture the general interpretation of these hypotheses from the literature. Crepuscular, diurnal and nocturnal are defined based on having at least 0.80 probability (threshold probability, $\xi_1 = 0.80$) in their respective diel periods. If an animal is not mostly active in one period than it is defined as traditional cathemeral; this occurs when either two or three diel periods are used more than $1 - \xi_1$. The logic behind the threshold of 0.80 is that an animal is predominately active in one diel period, but is not so strict that there can be some moderate amount of activity outside

TABLE 1 Hypothesis sets and their objectives.

Hypothesis set	Objective
Maximizing	Evaluate which diel period (daytime, night-time, twilight) is used the most. No consideration of bimodal or trimodal phenotypes, or the available time in each diel period
Traditional	Evaluate the support of standard diel phenotypes in the literature based on use of each diel period. No consideration of bimodal phenotypes or consideration of available time in each diel period
General	Evaluate support of the standard diel phenotypes based on use of each diel period with separation between bimodal and trimodal phenotypes. No consideration of available time in each diel period
Selection	Evaluate the disproportional use or selection of diel periods by incorporating the available time in each diel period while considering bimodal phenotypes

of this period. While $\xi_1 = 0.80$ is the default value in `Diel.Niche`, it can easily be modified by a user when fitting these hypotheses to their data.

The *General* hypothesis set includes seven diel phenotype hypotheses (Figure 1). The diurnal, crepuscular and nocturnal hypotheses are defined the same as in *Traditional*. The main difference is the separation of the probability space of traditional cathemeral into four more specific hypotheses: general cathemeral, crepuscular–nocturnal, diurnal–nocturnal and diurnal–crepuscular. The general cathemeral hypothesis—which represents a subset of the parameter space taken by the previously mentioned traditional cathemeral—aims to define when an animal uses all three diel periods at equal to or more than a minimum amount (i.e. $\xi_2 \leq p_{\text{tw}},\ p_d,\ p_n \leq \xi_1$). We defined the lower threshold probability as $\xi_2 = 0.10$, such that we consider it important to differentiate animal activity when a diel period is used at least this much (Figure 1). However, if only two diel periods are used above ξ_2, then we classify this activity using one of the binomial hypotheses (crepuscular–nocturnal, diurnal–nocturnal and diurnal–crepuscular). For example, suppose a species is active mainly during the day ($p_d = 0.78$), but is also relatively active during twilight ($p_{\text{tw}} = 0.16$), and not very active at night ($p_n = 0.06$). We would define this activity as diurnal–crepuscular because $p_{\text{tw}},\ p_d \geq \xi_2$, while $p_n < \xi_2$. However, if night activity was also higher than ξ_2, such that $p_d = 0.70$ and $p_{\text{tw}},\ p_n = 0.15$ then we classify this activity as general cathemeral because a moderate to large amount of activity is occurring in all three diel periods. In summary, the *Traditional* hypothesis set distinguishes between unimodal and multimodal diel activity, while the *General* set distinguishes among unimodal, bimodal and trimodal activity. The *General* hypothesis provides a more clear definition of cathemerality compared to the original description (Tattersall, 2008) by separating bimodal and trimodal activity periods.

The *Selection* hypothesis set includes seven diel phenotype hypotheses (Figure 2; day, day–night, day–twilight, equal, night, night–twilight and twilight selection). Each are defined based on an inputted (i.e. not estimated) amount of proportional time available to an animal in each diel period ($\mathbf{p}_{\text{avail}} = [\,p_{\text{av.tw}},\ p_{\text{av.d}}\,]$; the available time in the night period is derived as, $1 - p_{\text{av.tw}} - p_{\text{av.d}}$). As such, the combination of parameter values defined as a certain phenotype and the parameter space area of each phenotype will change based on $\mathbf{p}_{\text{avail}}$. The values of $\mathbf{p}_{\text{avail}}$ will depend on the day of the year and location of sampling. Each phenotype is defined based on a single diel period or multiple diel periods being used greater than available. For example, diurnal selection occurs when $\frac{p_d}{p_{\text{av.d}}} > 1$ and $\frac{p_{\text{tw}}}{p_{\text{av.tw}}}, \frac{p_n}{p_{\text{av.n}}} \leq 1$. The equal selection hypothesis is different in that it tests the equality among the probabilities and $\mathbf{p}_{\text{avail}}$.

We offer these definitions as a means to standardize the diel activity hypothesis language. Each hypothesis set is preset and available for use in `Diel.Niche`. The function 'hyp.sets' can be used to list the code names for each hypothesis and can be used to pass to the 'triplot' function to provide a 3D plot of the parameter space (Figure 1; first column) as,

```
hyps <- hyp.sets('General')
triplot(hyp=hyps)
```

This is known as a ternary plot that describes three variables that sum to a constant value and has been long used to characterize soil ratios (Shepard, 1954). The package also allows the specification of new hypotheses (see 'Section 6'). Researchers interested in changing the probability threshold values (ξ_1 and ξ_2) or defining novel hypotheses should report these in their research.

2.3 | Modelling and estimation

Applying inequality constraints on the parameters of multinomial models is a well-known modelling and estimation issue in statistics (Silvapulle & Sen, 2011). Implementing these models is often challenging in general purpose software. We used a Bayesian approach and take advantage of a general Gibbs Markov-Chain Monte Carlo (MCMC) sampler developed and implemented in the R package `multinomineq` (Heck & Davis-Stober, 2019). The sampler is highly efficient and implemented in C++, making the MCMC sampler relatively fast compared to general purpose software implementations. Generalized model specification and the likelihood function are fully detailed in Heck and Davis-Stober (2019). The core modelling and estimation in the `Diel.Niche` package are done using wrapper functions that implement more general functions of the `multinomineq` package. In terms of model parameter (θ) prior specification, probabilities are given a Dirichlet prior distribution with a truncated support that is defined by the constrained parameter space (Heck & Davis-Stober, 2019). The default hyperparameters used in `Diel.Niche` for the prior are shape parameters of 1 for each free model parameter. This is equivalent to a multiparameter uniform prior for each parameter, which is thus a very uninformative prior.

Model comparison is done via Bayes factors (Berger, 2013) for models with inequality constraints (Klugkist & Hoijtink, 2007), which implicitly provides a trade-off between model fit and complexity. Each model within a hypothesis set requires a prior to compute posterior model probabilities from the Bayes factors. `Diel.Niche` uses a default of equal weight among the set, but this can be changed. For example, if the literature attributes a species as nocturnal, a researcher may want to increase the prior of the nocturnal hypothesis. The prior will therefore depend on the goal of the study.

3 | THINGS TO CONSIDER BEFORE USING THIS METHOD

3.1 | The data

The study of diel activity describes when behavioural actions occur within the 24-h light–dark cycle. However, capturing all animal behaviours is generally impossible without direct and continuous behavioural sampling. This is often not possible for many species that cannot be followed to record behavioural observations without changes in animal behaviour occurring due to human presence. Even when individual animals can be followed, tracking continuously over many 24-h periods is logistically infeasible. Here, we focus on the traditional definition of diel activity in terms of animal movement (Hut et al., 2012) as it is a fundamental behaviour to ecosystem functioning and species survival (Tucker et al., 2018). Increasingly, high-frequency GPS telemetry is used to sample the location and movement of many species. These data sets could be very useful to estimate diel activity, especially as behavioural state modelling may help separate when and where specific behaviours are occurring (Michelot & Blackwell, 2019). This would allow diel activity to be separated by movement and behaviour types, rather than movement alone. Limitations of these data include the (1) expense in tracking many individuals in a population to gain a population-level inference, (2) difficulty in trapping many rare or small species, which are not readily or legally able to be trapped and (3) morphology of some species which poses challenges for external attachment (e.g. neck collars) thereby necessitating possibly risky surgery for a transmitter to be implanted.

The type of data that primarily motivated this work was species detections from camera traps. However, any spatially fixed technology that samples species activity throughout the 24-h period continuously is applicable. This could include autonomous audio recording units, where species can be identified and calling conveys an important activity. The fundamental data unit we are considering is a set of detection frequencies (**y**). Considering common camera trap sampling designs, where a set of *n* cameras are deployed at unique spatial locations over a period of interest (e.g. a climatic season), **y** may be an aggregation of detections across all cameras for this specified period of time. Thus, inference is at the study area and sampling period level. However, if enough data are available, inference could be made either at the camera trap level or among a subset of cameras within a study area (e.g. cameras placed in different habitat types).

We assume that dependencies in the data have been removed, such as temporal autocorrelation among a species' detections at a sampling location. Thus, frequencies of detections during twilight, daytime and night-time are independent. For camera trap sampling, it is common to have several to many sequential photographs of the same individual at the same location. Commonly, correlation is removed by subsetting data to exclude detections within a specified period of time (e.g. 10, 15, 30 min; Farris et al., 2015). A more quantitative approach would be to test this correlation using lorelograms (Iannarilli et al., 2019).

Of fundamental importance is the classification of each independent detection into the appropriate diel period. Fortunately, this can be determined if you know the date, time and spatial location of a given sample. This information can be used to calculate the start and end of various sunlight phases (e.g. sunrise, sunset, dusk) and are implemented in R with the `suncalc` package (Thieurmel & Elmarhraoui, 2019). We suggest samples be assigned to the three diel periods following astronomical definitions, as shown below.

- *Twilight*: The sample occurred during either dawn or dusk. Dawn is the time between the start of morning astronomical twilight (i.e. the sun is 18 below the horizon) and sunrise (i.e. the top of the sun is at the horizon). Dusk is the time between sunset and the end of evening astronomical twilight. These definitions represent the entire twilight period, which separates day from night.
- *Daytime*: The sample occurred during the day, which is the time between sunrise and sunset.
- *Night-time*: The sample occurred during the night, which is either between midnight of that day and the start of morning astronomical twilight or between the end of evening astronomical twilight and midnight of the following day.

Using this classification scheme makes it possible to generate a frequency table of detections that can then be used within the `Diel.Niche` package.

3.2 | Hypothesis discrimination

Prior to implementing this framework, it is important to understand how sample size affects the ability to discriminate among hypotheses within a set. For each of our four hypothesis sets, we simulated 4000 data sets under each hypothesis within a set at a wide range of total samples sizes (10, 20, 40, 80, 160, 320, 640, 1280; $\sum_{i=1}^{3} y_i$). We fitted each data set and estimated the posterior model probability of the hypothesis generating the data; each model was given equal prior weight. Since each hypothesis is mutually exclusive (i.e. non-overlapping defined parameter space), model uncertainty will be highest when the true probability parameters are near the boundary of a hypotheses parameter space and adjacent to another hypotheses parameter space. This will occur more often with hypotheses with small parameter spaces (e.g. *General* hypotheses). We considered how this would alter model selection and certainty by only simulating data such that hypotheses parameter spaces are separated by at least 0.1 and 0.2 (Supporting Information S1, Figure S2).

Lastly, we explicitly demonstrate how the arrangement of hypotheses' parameter space affects the ability to identify the hypothesis generating the data. To do so, we use the *Selection* hypothesis set to simulate 200 data sets with a sample size of 100 for each combination of parameter values (θ) at increments of 0.05 and estimate the probability the generating hypothesis is most supported within the set. We set $p_{avail} = [0.04\ 0.48]$.

We found the ability to identify the generating model with the most support (i.e. highest posterior model probability) to vary by hypothesis set (Figures 2 and 3; Supporting Information S3 and S4).

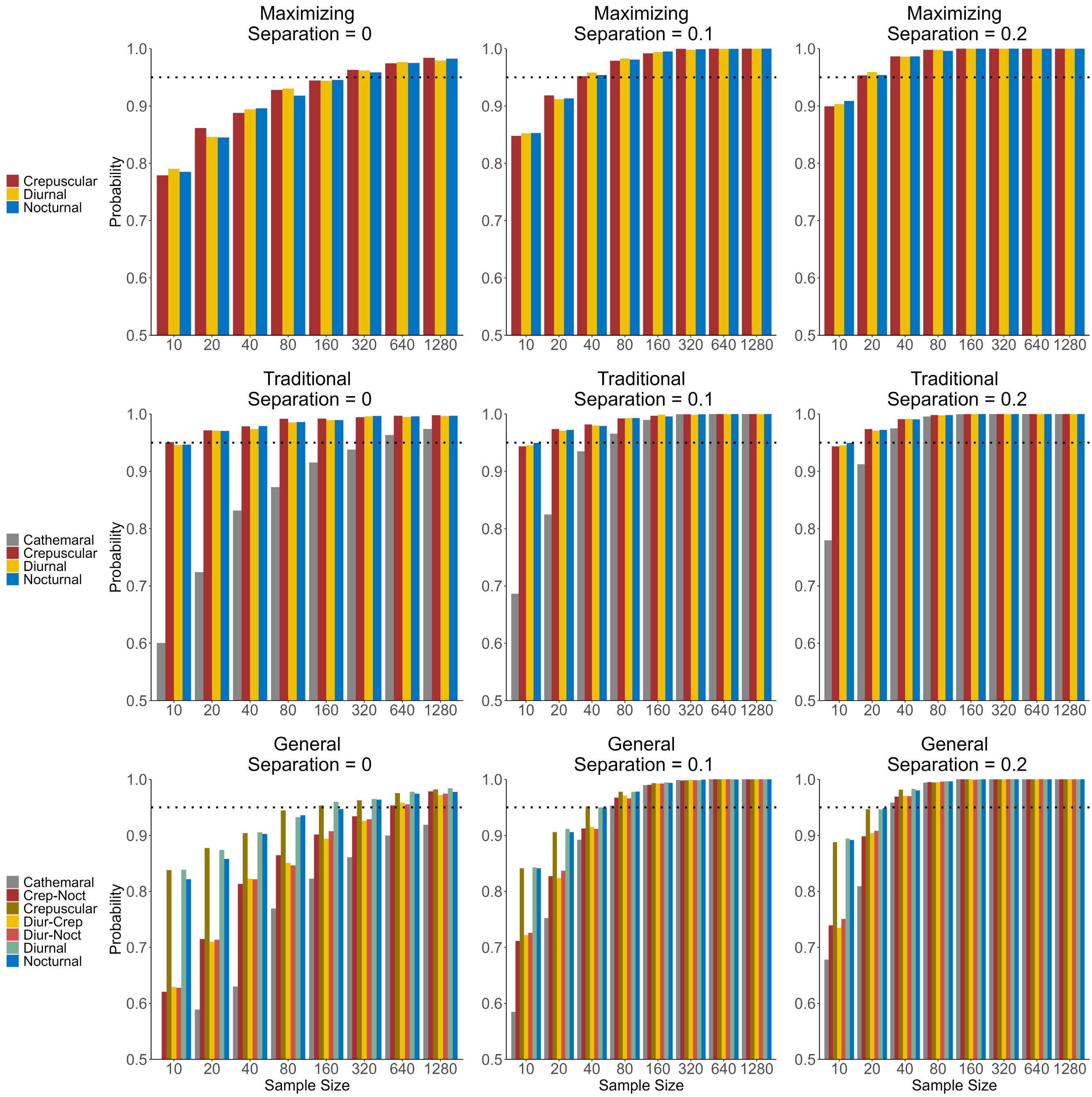

FIGURE 3 Simulation results of the probability the generating model was most supported across varying sample sizes and the extent of separation in probability space between hypotheses within a hypothesis set. Increasing separation values indicate more difference in probability values between hypotheses used to simulate data. Complementary simulation results are found in Supporing Information S1, Figure S3.

Considering the *Maximizing* hypothesis set, 320 independent samples were required to obtain a 95% probability that the most supported model in the set was the generating model. There was little variation by hypothesis because all hypotheses had the same area of parameter space and length of parameter space adjacent to another hypothesis. We also found that when separating hypotheses by a probability of 0.1 and 0.2, only 40 and 20 samples, respectively, were needed to obtain a 95% probability. Thus, as probabilities are further from equal ($p_{\text{tw}} = p_d = p_n = 0.333$), the easier it is to discriminate among the hypotheses in the *Maximizing* set with high probability.

Considering the *Traditional* hypothesis set, 10 independent samples were needed to obtain a 95% probability that the most supported model in the set was the generating model for the crepuscular, diurnal and nocturnal hypotheses (Figure 3; Supporting Information S1, Figure S3). There was considerably more model uncertainty for the traditional cathemeral hypothesis. This hypothesis required 640 samples to achieve the same probability. However, when separating hypotheses by a probability of 0.1 and 0.2, only 80 and 40 samples were required respectively. Thus, in cases where traditional cathemeral hypothesis probabilities are more equal, less data are needed to identify the data generating hypothesis with high probability.

Considering the *General* hypothesis set, 160 independent samples were required to obtain a 95% probability that the most supported model in the set was the generating model for the crepuscular, diurnal and nocturnal hypotheses (Figure 3; Supporting Information S1, Figure S3). The bimodal hypotheses required 640 samples, while 1280 samples were still not enough for the cathemeral general hypothesis to obtain a 95% probability of support. Again, separating the hypotheses increases the ability to discriminate among them. Since these hypotheses have less parameter space and more adjacency to other hypotheses parameter space, discriminating among them will require larger sample sizes compared to hypotheses of the other sets. For the cathemeral general hypothesis, there is also higher implicit variance in the probabilities as they get closer to 0.5, which also makes it harder to discriminate against the other hypotheses.

Considering the *Selection* hypothesis set, 1280 independent samples or more were required to obtain a 95% probability that the most supported model in the set was the generating model (Figure 2; Supporting Information S1, Figure S4). The twilight selection hypothesis was more easily identified as the generating model for smaller sample sizes because it has the largest parameter space area. These results would suggest this hypothesis set to be only moderately useful to many realistic sample sizes. However, looking at how the probability of the generating model being most supported varies throughout the parameter space, we see a large set of parameter values where it is easy to identify the generating model (probability near 1) at a sample size of 100 (Figure 2). The ability to identify the generating model in this hypothesis set and all others depends strongly on how close the true probabilities are to one or more other hypotheses, which depends on the area of parameter space for the hypothesis (Supporting Information S1, Figure S5).

3.3 | The unconstrained model

What is the benefit of constraining model parameters? In other words, why not fit an unconstrained multinomial model, which can more easily be specified hierarchically to link probabilities of activity to spatial temporal covariates (see Gallo et al., 2022)? The main reason is that our aim is to focus on a priori definitions of diel phenotypes, so that we can offer them as hypotheses to be evaluated using empirical data. By constraining parameters, we can focus on the hypothesis and not simply a change in probabilities. Considering inference across data analysis units (multiple **y** values pertaining to different study areas or sampling periods) or studies allows an accurate interpretation of diel niche switching. Second, for a given hypothesis, model parameters will be more precise because of the constraints. Thus, even with small sample sizes, parameter estimates will be more precise compared to a model with unconstrained parameters. Lastly, we do not need to ignore the unconstrained model and can actually incorporate it into our hypotheses sets in the `Diel.Niche` package (see Section 6).

For researchers who take an alternative procedure to model diel activity, we encourage them to consider post hoc classification of their inference using the diel phenotypes defined here. If results can be summarized into the three probabilities (p_{tw}, p_d, p_n), then this framework could be of use (see Section 4). Specifically, it may help differentiate between changes in activity within a diel phenotype and the switching to a new diel phenotype (e.g. nocturnal →diurnal).

4 | WORKED EXAMPLES

The fundamental data analysis unit (**y**) should be considered as a set of observations of a species of interest that was continuously sampled throughout the 24-h period in a place and time of interest. In the following, we consider five worked examples with varying goals that demonstrate the use of the `Diel.Niche` package. The first three examples are based on camera trap data collected at 131 spatial locations deployed through urban greenspace in Chicago (Illinois, USA) to better understand the spatio-temporal dynamics of urban mammals (Magle et al., 2019). The fourth example highlights the issue of visually translating results from circular kernel density analyses into diel phenotypes and how using the `Diel.Niche` package can overcome this issue. Lastly, the fifth example demonstrates how the `Diel.Niche` package can be used to complement an animal movement analysis using telemetry data. Vignette's describing the full set of code and results for each worked example can be found on GitHub and as part of the package.

4.1 | Single data unit analysis

Here, we are interested in classifying the traditional diel niche of the Virginia opossum (*Didelphis virginiana*) in an urban environment during the winter of 2018–2019. Specifically, sampling occurred for a total of 27 days from 29th December to 24th January. These data are available in the package using the 'diel.data' object. After removing sequential photos at the same site within a 15-min period, we aggregated these observations across all camera locations, such that $\mathbf{y} = [5\ 20\ 30]$.

Using the 'diel.fit' function to estimate model probabilities assuming equal weights on each model,

```
out <- diel.fit(
y = as.matrix(y),
hyp.set = hyp.sets(Traditional),
post.fit=TRUE,
n.chains=3,
n.mcmc=5000,
burnin=1000
)
```

We find that the cathemeral hypothesis is supported with a posterior model probability of 1.0. Using base R plotting and the 'triplot' function as triplot(out), we can visualize the posterior distributions of the activity probabilities (Figure 4).

We see the opossum is most active at night in the winter, but also has a relatively high amount of activity during the daytime. The 3D figure allows us to consider where in the *Traditional* hypothesis set, these probabilities fall. Given the low amount of activity at twilight, we find using the *General* hypothesis set that the diurnal–nocturnal hypothesis would be a more accurate description of the opossum's winter diel niche.

4.2 | Multiple species with one data analysis unit

Commonly with passive sampling techniques, such as camera traps, the focus of a study is on a community rather than a single species. Here, our objective is to evaluate the diel niche of a community of urban mammals in the winter by considering support for hypotheses from the *General* hypothesis set. Again, we use the 'diel.data' object to obtain the aggregated data from cameras deployed in Chicago (Illinois, USA) for 25 days between 25 January 2018 and 20 February 2019. We estimated and compared the diel niche of each observed species following the same procedure as in the first example.

A total of seven native terrestrial mammal species were observed with total species detections ranging from 25 to 284 (Table 2). We found a high-level of evidence (model probability >0.9) that white-tailed deer (*Odocoileus virginianus*) are diurnal–nocturnal, northern raccoon (*Procyon lotor*) and eastern cottontail (*Sylvilagus floridanus*) are nocturnal and the grey squirrel (*Sciurus carolinensis*) and fox squirrel (*Sciurus niger*) are diurnal. We are moderately confident (model probability near 0.75) that coyote (*Canis latrans*) and Virginia opossum (*Didelphis virginiana*) are diurnal–nocturnal. Comparing these results to the literature (Cox et al., 2021), we see agreement with only the northern raccoon and both squirrel species. There is disagreement with all other species, where the literature considered the diel niche of the Virginia opossum to be nocturnal, and the white-tailed deer and the eastern cottontail to be crepuscular. The coyote diel niche difference is more subtle, where they are considered as cathemeral in the literature, we estimated their activity to be a specific form of cathemerality (i.e. diurnal–nocturnal).

Using the most supported model by species, we plotted the estimated probability of diel activity for the three diel periods (Figure 5). Interestingly, the coyote is active in all three diel periods, but is most active during the night, which is also when their prey species, the eastern cottontail, is active. White-tailed deer were found to be most active during the daytime, which is surprising given that they are not avoiding periods of high human activity in an urban environment. We also found that the eastern cottontail has the most amount of activity during the twilight from this mammal community.

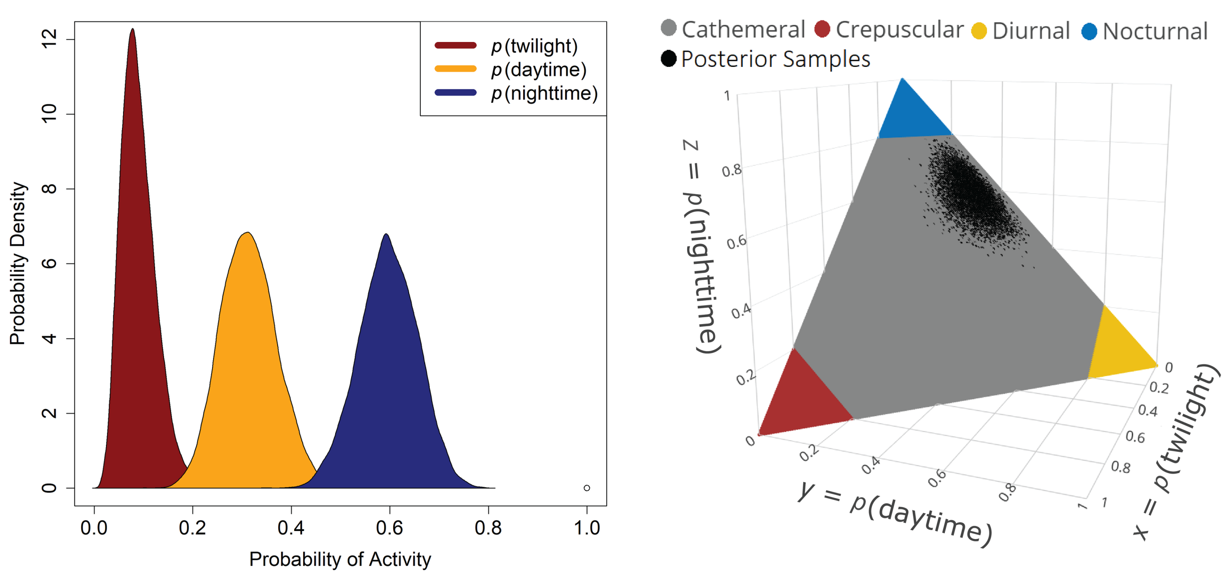

FIGURE 4 Posterior distributions of the probability of activity (left) and the same in three-dimensional form (right) overlaying the traditional hypothesis set for the Virginia opossum sampled in Chicago, IL, United States, in the winter of 2018.

TABLE 2 Detection frequencies of urban mammals in Chicago, Illinois, United States, during the winter of 2019 and posterior model probabilities of support from the General hypothesis set. Crep, Crepuscular; Diur, Diurnal; Noct, Nocturnal.

Species	Twilight	Day	Night	Diurnal	Nocturnal	Crepuscular	Cathemeral	Diur-Crep	Diur-Noct	Crep-Noct
Coyote	3	8	23	0.00	0.07	0.00	0.17	0.00	0.75	0.00
Virginia opossum	0	7	18	0.00	0.21	0.00	0.02	0.00	0.77	0.00
White-tailed deer	4	39	20	0.00	0.00	0.00	0.07	0.00	0.93	0.00
Northern raccoon	6	8	133	0.00	1.00	0.00	0.00	0.00	0.00	0.00
Eastern grey squirrel	0	284	0	1.00	0.00	0.00	0.00	0.00	0.00	0.00
Eastern fox squirrel	0	49	0	1.00	0.00	0.00	0.00	0.00	0.00	0.00
Eastern Cottontail	13	5	123	0.00	0.99	0.00	0.00	0.00	0.00	0.01

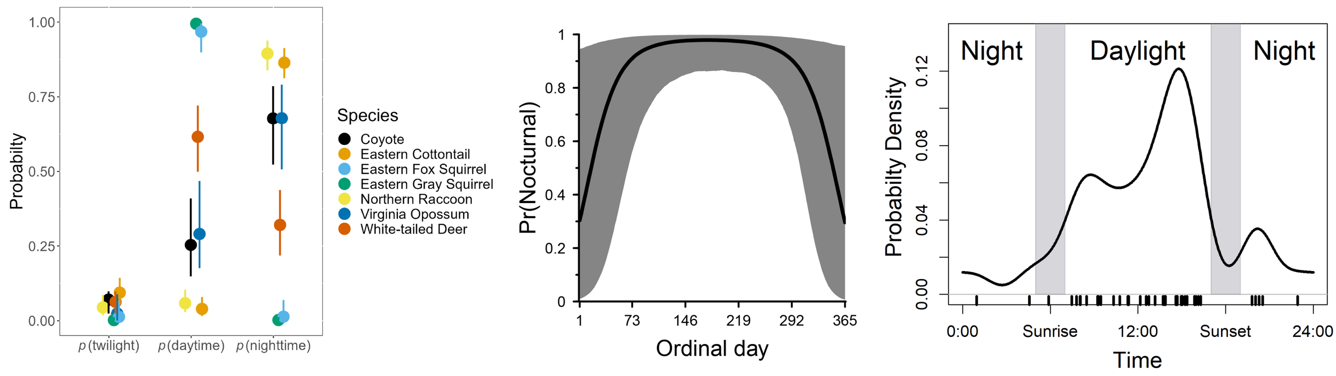

FIGURE 5 Results from worked examples 2 (left), 3 (middle) and 4 (right). Left: the posterior median (circles) and 95% credible intervals of the probability of activity for the Chicago, IL mammal community in the winter of 2019; parameters are from the most supported model for each species using the General hypothesis set. Middle: the posterior predicted probability of the nocturnal hypothesis for the Virginia opossum in Chicago, IL, United States. Right: an example circular kernel density plot. The shaded area indicates periods of twilight and the x-axis tick marks represent each observation. Using the hypothesis sets of Maximizing, Traditional and General leads to classifying this activity pattern as diurnal max, cathemeral traditional and diurnal–nocturnal respectively.

4.3 | One or more species with multiple data units

Our framework has outlined a process for making inference on the diel niche of species for a given spatial area and sampling period. A natural question is how to link hypotheses about how the diel niche of a species may change over time or over space. Simply, how do we link spatial or temporal covariates to findings of diel niche classification? Ideally, a fully hierarchical model that synthetically connects the diel niche classification to covariates would be specified, such that parameter estimation is done jointly and all parametric uncertainties are fully recognized. However, the constrained optimization of the multinomial model makes this challenging at this time.

We offer a two-staged modelling process that accomplishes the goal. First, estimate the diel niche for a species at each spatial or temporal period of interest to identify the most supported hypothesis. Second, use the hypotheses as data in a subsequent categorical regression model that links the hypotheses to covariates of interest. It should be understood that if there is uncertainty in the most supported model, then this does not get acknowledged in the regression model. To remediate this concern, researchers may want to only consider using hypotheses with a given high level of probability of support (e.g. model probability ≥ 0.80) or propagate this uncertainty into the subsequent analysis.

As one example, Virginia opossum are a predominately nocturnal species that become more active during the day in the winter in temperate environments (Gallo et al., 2022). As a result, we might expect this species to switch between diel phenotypes over the course of a year. As the previous Chicago data are from a long-term biodiversity monitoring survey, we compiled 27 different sampling periods, each of which represented roughly 28 days of sampling across 131 sites in Chicago, Illinois. To capture seasonal variation, cameras were deployed in January, April, July and October, and data come from between 2013 and 2019 (all of which is available in the 'diel.data' object).

We fitted a *Traditional* hypothesis set to each analysis unit with equal prior weights on each model, and retained each analysis unit that had a probability of model support ≥ 0.80. This resulted in a total of 23 analysis units. We then fitted a categorical regression model to these data. More specifically, we let m_i be a numeric representation of the diel phenotype for the ith analysis unit, such that 1 = cathemeral, 2 = diurnal and 3 = nocturnal. While there is the possibility of there being four diel categories, in this specific case opossum were either classified as nocturnal or cathemeral. As a result, we dropped out the crepuscular category, but retained the diurnal category to demonstrate the use of this model across more than two diel phenotypes. Furthermore, let $\boldsymbol{p}$ be a vector of probabilities that sum to 1 and represent the probability a given diel phenotype is used. The most basic model without covariates is then

$$\begin{aligned} m_i & \sim \text{Categorical}\,(\mathbf{p}) \\ \mathbf{p} & \sim \text{Dirichlet}\,(1,1,1). \end{aligned} \tag{6}$$

To expand the model, we connect **p** with a vector of covariates that varies across sampling units by using the softmax function, treating cathemeral as the reference category. For this analysis, we consider whether the time of year affects the opossums diel niche. Specifically, we used the average ordinal date of an analysis unit as well as the square of that ordinal date (to allow for a non-linear relationship) as covariates, such that

$$\begin{aligned} p_i^1 & = \theta_i^1/(\theta_i^1+\theta_i^2+\theta_i^3) \\ p_i^2 & = \theta_i^2/(\theta_i^1+\theta_i^2+\theta_i^3) \\ p_i^3 & = \theta_i^3/(\theta_i^1+\theta_i^2+\theta_i^3) \\ \theta_i^1 & = 1 \\ \theta_i^2 & = e^{\mathbf{a}^D\mathbf{x}_i} \\ \theta_i^3 & = e^{\mathbf{a}^N\mathbf{x}_i}, \end{aligned} \tag{7}$$

where $\mathbf{a}^D$ and $\mathbf{a}^N$ are a vector of conformable regression coefficients for diurnal and nocturnal categories while $\mathbf{x}_i$ is a vector of covariates with the first element being a 1 for the intercept. Weakly informative priors were used for all regression coefficients as $\text{Normal}\,(0,2)$.

We fitted this model in v0.12.2 of Nimble (de Valpine et al., 2017) and used slice samplers for all parameters. Following a 10,000 step burn-in, we sampled parameter posterior distributions for a total of 80,000 iterations across four chains. Overall, we found evidence that the probability Virginia opossum were nocturnal greatly decreased at the start and end of the year, when it is coldest in Chicago (Figure 5). This pattern was largely determined by the squared ordinal day term, which was strongly negative ($a_3^N = -1.36$, 95% CI = −2.61, −0.27). This switch in diel phenotypes was quite dramatic, with the probability of nocturnality ranging from a high of 0.98 (95% CI = 0.86, 1.00) on 6th June to a low of 0.30 (95% CI = 0.01, 0.96) on 31st December.

4.4 | Diel classification with a circular kernel density analysis

A common statistical approach used in the diel ecology literature is that of the non-parametric circular kernel density estimators (Ridout & Linkie, 2009; Figure 5). Researchers can complement this analysis type by using the `Diel.Niche` package to define their findings in terms of diel phenotypes. After using the `overlap` R package's 'densityPlot' function to fit the kernel density estimator, the outputted object (kernel.out) can be passed to the `Diel.Niche` function 'prob.overlap' to integrate under the curve at the intervals along the x-axis that correspond to the diel periods (twilight, daytime, night-time) to estimate these probabilities as,

```
probs <- prob.overlap(
kernel.out, dawn = c(6,7), dusk = c(17,18)
)
```

The other input required are the numeric values defining the beginning and end periods of dawn and dusk. Using example data from Figure 5, the probabilities of twilight, daytime and night-time were estimated as 0.055, 0.748 and 0.194 respectively. From here, the probabilities can be passed to the function 'posthoc.niche' that will match the diel phenotype within a hypothesis set that includes these probabilities as,

```
posthoc.niche (probs, hyp = hyp.sets ('Traditional')).
```

Using the *Traditional* hypothesis set, the results depicted in Figure 5 would be defined as the cathemeral traditional hypothesis. This may be unintuitive simply by looking at the plot. While there is a large amount of activity during the daytime, the probability of night-time use is also quite high at a probability of 0.194, thus supporting the cathemeral designation. If we use the *Maximizing* hypothesis set, we find that the diurnal max hypothesis is most supported, while using the *General* hypothesis set, the most supported hypothesis is more specifically the diurnal–nocturnal hypothesis.

By defining the diel hypotheses a priori and explicitly, we can more accurately make inference based on a given objective. Visually, the kernel density plot shows this animal is most active during the daytime, which is confirmed with the diurnal max hypothesis being most supported in the *Maximizing* hypothesis set. However, considering more traditional definitions of diel activity, we should define this animal as cathemeral, given its support under the cathemeral traditional hypothesis. More so, if we want to make a clear delineation between activity at two diel periods (bimodal) vs three diel periods (trimodel), the *General* hypothesis set makes it evident the species is mostly active during only two diel periods, as supported by the diurnal–nocturnal hypothesis.

4.5 | State-dependent movement with diel activity

Animal movement ecology and modelling are rich fields of study with much variation and complexity (Hooten et al., 2017). We offer one approach of how to complement a movement modelling analysis using the `Diel.Niche` package. Specifically, we modified an example of fitting a hidden Markov model in the `momentuHMM` package (McClintock & Michelot, 2018) to continuous telemetry data on an African elephant (*Loxodonta africana*) available from Wall et al. (2014). We considered two movement states (encamped and exploratory) and allowed model parameters to be constant or to vary by daily cycles caused by temperature variation. Using the most supported movement model, we predicted the movement state at each hourly location between March 2008 and September 2010 (Figure 6).

We found step lengths to vary by movement states on average (encamped: 186 m ± 5.4, exploratory: 866 m ± 29.3) and vary cyclically depending on the time of day (Figure 6). We predicted that the diel phenotype of this individual would vary between movement states and change throughout the year. We evaluated this by summarizing the

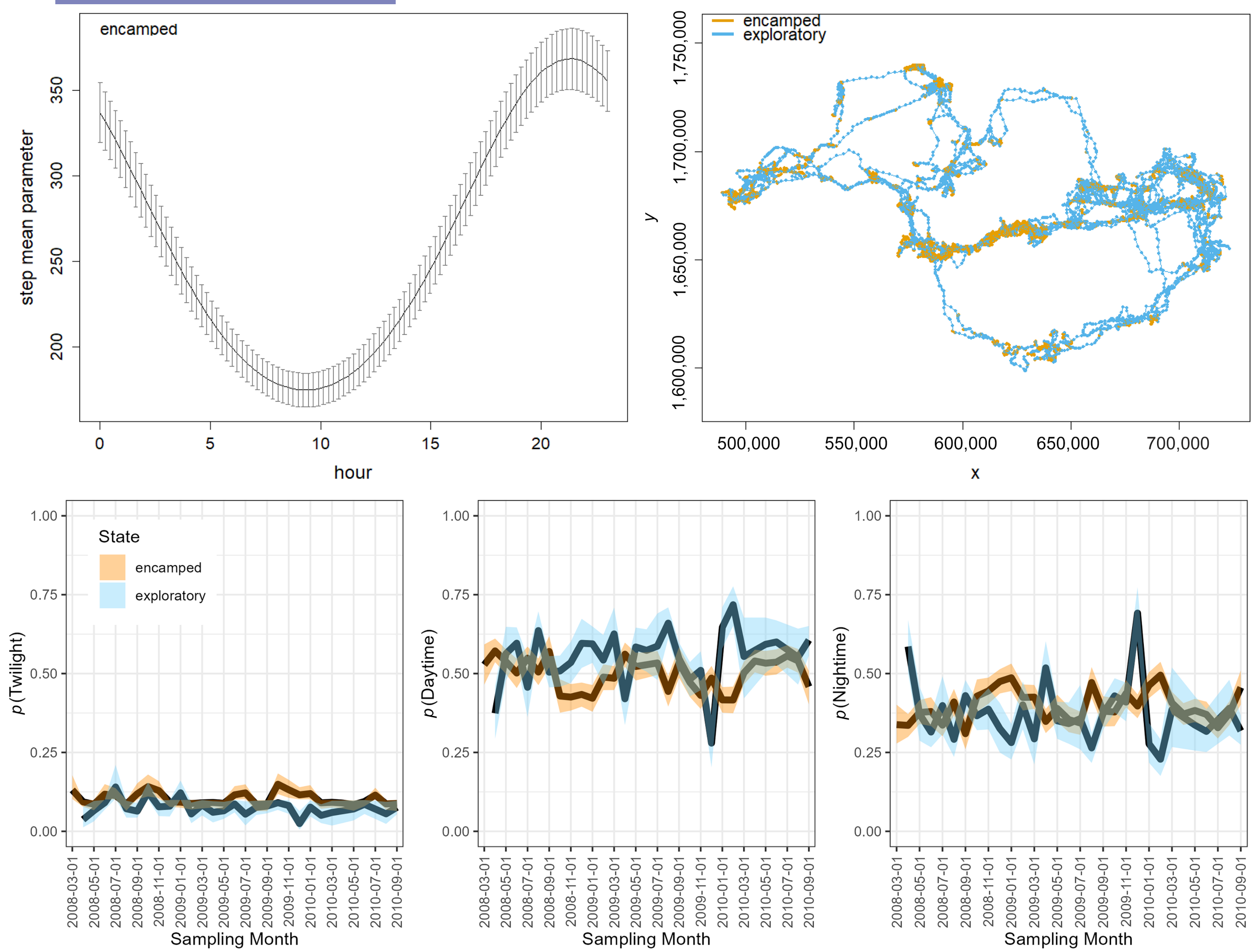

FIGURE 6 Results from worked example 5 on Africa elephant movement and diel activity: The top row is the predicted mean step length in the encamped movement step over the diel period and the predicted state (encamped or exploratory) for the entire track. The bottom row is the predicted diel activity by movement state and diel period.

number of observations at each hourly location into the three diel periods by sampling month and movement state. For each month and state, we estimated the most supported phenotype from the *General* hypothesis set and predicted the probability of activity in each diel period.

When this individual elephant was in the encamped movement state, roughly 60% of the time they used the diurnal–nocturnal phenotype ($n=18$) while 40% of the type they used the general cathemeral phenotype ($n=13$). Conversely, when the elephant was exploratory, they were almost always classified as diurnal–nocturnal (25 of 28 samples). The difference between phenotypes was only a small increase in activity during twilight (Figure 6). Largely, this individual was almost always moving, regardless of state behaviour, during the daytime and night-time.

5 | CAVEATS

Our goal was to focus on defining, estimating and modelling hypotheses of diel phenotypes motivated by the animal ecology and evolution literature. It is important to recognize the probability of activity in the three diel periods is a simplification of a complex process (e.g. see kernel density plots in Figure 1; Gaston, 2019; Gilbert et al., 2022). More detailed inference, how animals use time from minute to minute or hour to hour are warranted and needed. However, we hope that researchers will consider how they translate their findings into standardized diel language and hope that the `Diel.Niche` package will be of use in doing so.

The *Maximizing*, *Traditional* and *General* hypothesis sets focus on characterizing an animal's diel phenotype based on the amount of activity or use in a diel period. Since the focus is on use within the context of the study design and sampling period, these hypothesis sets do not account for the amount of available time in each diel period. We defined diurnal, nocturnal and crepuscular phenotypes with the same thresholds to make fair comparisons. This has especially important implications for identifying an animal as crepuscular in these hypotheses sets. We contend that terrestrial vertebrate species may have been poorly defined as crepuscular in the literature due to a lack of clear distinction between use and selection, lack of standardized definitions of phenotypes (e.g. non-equivalence of thresholds in regard to use) and non-standardized sampling throughout the entire diel period.

Given our definition for the twilight period, there will only ever be a small amount of time available for the animal (e.g. <0.10), such that it may be unusual to find an animal using the twilight with a probability of 0.80 or greater (the lower constraint for defining crepuscular in the *Traditional* and *General* hypothesis sets). One option would be to modify our definitions of twilight and increase the amount of time defined as twilight when classifying observations. Rather than strictly defining twilight around sunlight times, which leaves only a small portion of the day available for a species to be crepuscular, some studies have added a buffer period (30 min or 60 min) around dusk/dawn (Farris et al., 2015; Haysom et al., 2023). This change assumes that astronomical twilight does not represent biological twilight to a species, which seems intuitive, but does introduce subjectivity as one must decide how much to widen the twilight period. Defining twilight is an open question, but regardless, how and why it is defined should be clear in future diel studies.

Furthermore, if there are other logical definitions that lead to unequal constraints being used to define diurnal, nocturnal and crepuscular, then researchers can implement them in the `Diel.Niche`. However, each is defined, this should be explained and documented when reporting results.

It is also important to consider extremes in the amount of time available in each diel period, which can occur with data collected during the summer and winter months further from the equator. As such, there may be times of year where certain diel periods are not available to a species, and care should be taken when classifying a species diel phenotype when this occurs. This is partly why we constructed the *Selection* hypothesis set, as it could compliment the other hypothesis sets during diel 'extremes'.

Finally, our framework currently does not differentiate between morning and evening twilight. This may be warranted for certain species and ecosystems or times of the year. Notably, ectotherms, such as insects or amphibians, may be more likely to be active during evening twilight when temperatures are warmer relative to morning twilight, which is often the coldest portion of the diel cycle. Predators may also be more active during morning or evening twilight depending on the vulnerability of their prey species. Our current framework is built around constraints of only three diel periods. However, this could be expanded to any number of diel periods defined by the user in future developments.

6 | ADDITIONAL RESOURCES

The main vignette for the package `Diel.Niche` is provided on the GitHub repository demonstrating key functions. This includes simulating data under a hypothesis, model fitting and estimation, plotting and example data. This vignette can also be accessed in the package (assuming vignettes have been built during package installation) as vignette ('Diel-Niche-Vignette'). A secondary vignette ('Diel-Niche-Additional') is also available that describes additional hypotheses (defined and described in Supporting Information S2), as well as how a user may change default values (e.g. ξ_1 and ξ_2) and even specify novel hypotheses. Furthermore, each worked example is provided as a vignette in the package or on Github, as well as a sixth worked example demonstrating how to make inference from the *Selection* hypothesis set.

Users who prefer a graphical interface can use `Diel.Niche` through the R Shiny web application (https://shiny.celsrs.uri.edu/bgerber/DielNiche/). The current implementation allows users to specify a single data analysis unit ($\mathbf{y}$) and to choose among the four hypotheses sets. The application will automatically generate a table of model probabilities and posterior quantities of model parameters. Both 2D and 3D plots of model parameters are generated and can be downloaded.

7 | CONCLUSION

Studies of animal diel ecology and evolution provide inference to how animal activity is shaped within the 24-h light–dark cycle. This leads to a more complete understanding of an animal's niche (Cox et al., 2021), as well as having implications for how to conserve wild animal populations (Cox et al., 2023; Rivera et al., 2022). As non-invasive sampling and animal-borne sensors continue to evolve and make it easier to continuously collect data on wild animals throughout the diel cycle, we expect increasing studies focused on how animals use diel time.

We offer the `Diel.Niche` R package as a framework to quantitatively define and thus standardize diel ecology language regarding diel phenotypes. We hope this will lead to more accurate comparisons across studies and reduce potential confounding from qualitative and visual interpretations of diel phenotypes. We offer several complete diel phenotype hypotheses sets that aim to accomplish different study objectives. The `Diel.Niche` package can be used to compare models, estimate parameters and visualize results, or be used to complement other analyses by defining their inference into standardized terminology. We suggest researchers report their results following similar text as—'Using the <insert name> hypothesis set, we found that <species name> were <diel phenotype> (p = <insert model probability>), spending x (95% CI = low, hi) amount of time active during the night, y (95% CI = low, hi) amount during the day and z (95% CI = low, hi) amount during twilight'. Ultimately, we hope our framework and R package will assist resource managers and researchers to more clearly and effectively define and differentiate how animals use diel time to improve conservation approaches.

AUTHOR CONTRIBUTIONS

All authors developed the idea for this Research Methods Guide. Brian D. Gerber led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

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CONFLICT OF INTEREST STATEMENT

The authors have no conflicts of interest to declare.

DATA AVAILABILITY STATEMENT

All data are available in the R package on GitHub (https://github.com/diel-project/Diel-Niche-Modeling) and archived on Zenodo https://doi.org/10.5281/zenodo.10019122.

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SUPPORTING INFORMATION

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

Supporting Information S1: Additional figures on the numbers of publications related to diel activity, simulation setup, and simulation results.

Supporting Information S2: Explanations and mathematical descriptions of hypothesis sets and hypotheses implemented in `Diel.Niche`.

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