

Rethinking Habitat Occupancy Modeling and the Role of Diel Activity in an Anthropogenic World

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ABSTRACT: Current methods to model species habitat use through space and diel time are limited. Development of such models is critical when considering rapidly changing habitats where species are forced to adapt to anthropogenic change, often by shifting their diel activity across space. We use an occupancy modeling framework to specify the multistate diel occupancy model (MSDOM), which can evaluate species diel activity against continuous response variables that may impact diel activity within and across seasons or years. We used two case studies, fosas in Madagascar and coyotes in Chicago, Illinois, to conceptualize the application of this model and to quantify the impacts of human activity on species spatial use in diel time. We found support that both species varied their habitat use by diel states—in and across years and by human disturbance. Our results exemplify the importance of understanding animal diel activity patterns and how human disturbance can lead to temporal habitat loss. The MSDOM will allow more focused attention in ecology and evolution studies on the importance of the short temporal scale of diel time in animal-habitat relationships and lead to improved habitat conservation and management.

Keywords: camera traps, diel, habitat, multistate, occupancy, spatial-temporal activity.

No description of where an animal lives and what it does can be complete without considering when the activity takes place. (Enright 1970)

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Introduction

Understanding a species' or community's habitat is one of the most fundamental aims of ecology (Mitchell 2005) and conservation (Campomizzi et al. 2008). Historically, habitat was defined by Odum et al. (1975, p. 76) as “the place where an organism lives, or place where one would go to find it.” This fundamental definition has evolved in recent years to address both space and time, such as “a description of a physical place, at a particular scale of space and time, where an organism either actually or potentially lives” (Kearney 2006, p. 187). Redefining habitat to encompass both spatial and temporal scales has allowed studies to improve hypotheses of how organisms interact with their environment (Kearney 2006; Morano et al. 2019), which better recognizes how space and time are two fundamental axes of a species' niche (Pianka 1973).

Empirical knowledge of species' habitat has grown with the development of spatial modeling, including species distribution (Segurado and Araújo 2004), occupancy (MacKenzie et al. 2017), and resource selection (Northrup et al. 2022) models. Inferences from these models have helped identify critical habitats of threatened species (Guisan et al. 2013), manage invasive species (Guisan et al. 2013), and understand how landscape structure (e.g., landcover) impacts species habitat use (Hirzel et al. 2006; Angelieri et al. 2016). However, while the application of these models can identify fine-scale spatial information of a species' habitat, they focus on larger temporal patterns, such as seasonal or yearly scales (MacKenzie et al. 2003; Fidino and Magle 2017). Species activity over diel time, typically described via defined modalities like diurnal or nocturnal (Anderson and Wiens 2017), also has a fundamental role in their space use

(Pianka 1973). These studies ignore this critical temporal period, making it difficult to understand how rapidly changing conditions and landscapes impact a species' daily activity (Ellis et al. 2010; Helm et al. 2017; Gaston 2019). The limited studies that do consider space use and diel activity predominantly treat them separately (i.e., not modeled in a single framework), such as making spatial inferences via occupancy modeling (Long et al. 2011) and diel temporal inference via circular kernel density methods (Ridout and Linkie 2009). Furthermore, diel temporal changes are often limited to evaluating binary categorical predictor variables, such as presence or absence of artificial light, via P values (Martin et al. 2021). Thus, these models provide only descriptive inferences rather than an explicit estimation of hypothesized effects from categorical or continuous predictor variables, such as distance to forest (James et al. 2013). Studies that ignore diel activity when making spatial inferences have largely focused on the "average daily conditions rather than those prevailing at the time of day when individuals would tend to be most active" (Gaston 2019, p. 484).

Evaluating space use in diel time is especially urgent given increasing anthropogenic pressures across landscapes globally (Ellis et al. 2010). If species can adjust their diel activity, then it could be a mechanism by which they adapt to changing landscapes, climate, or ecological communities. For instance, mesocarnivores and large carnivores have been found to increase their nocturnal activity in urbanized areas (Gehrt 2007; Carter et al. 2012), likely to avoid time periods when humans are most active (Gaynor et al. 2018). During hunting seasons, harvested species such as deer can become more nocturnal to avoid hunters (Kilgo et al. 1998). Animals may also change their diel activity in the presence of introduced species, as is the case with many mammals (ungulates, carnivores, and small mammals) that temporally avoid domestic dogs (Lenth et al. 2008; Farris et al. 2015a, 2015b). By modifying behavior across the 24-h light-dark cycle, species can access space that would otherwise be inaccessible. This flexibility, however, may have physiological, morphological, or even ecological constraints, such as limited diel periods in which food is available for hunting or foraging (Kronfeld-Schor et al. 2017). Understanding a species' spatial activity across diel time use can therefore provide insight into these constraints, leading to a more complete understanding of where species live and how pressures impact their daily habitat. For example, a species may lose spatial resources altogether or lose spatial resources during a specific diel time period, such as hours when humans are most active (Ellington et al. 2020). Pumas (*Felis concolor*), for instance, exhibit diminished daily access to food resources in response to simulated human disturbance via playback (Smith et al. 2017). By considering spatial and temporal habitat jointly in a single modeling framework, we can explicitly evaluate hypotheses regarding how an animal's relation-

ship with the landscape changes as humans alter resources and the risk of obtaining those resources.

With increasing availability of camera traps, which allow for passive and continuous sampling of wild animal populations (Rovero et al. 2013), we also have increasing access to fine-scale spatial-temporal data required for joint analyses of space use and diel activity. To advance theories of ecology and their application, we require a single modeling framework that can incorporate continuous covariates on diel behavior and account for variation in detectability and in sampling methodology. Developing a flexible model such as this will help bridge gaps in the capabilities of the few existing diel habitat models (Distiller et al. 2020; Gallo et al. 2021). As such, we specify static and dynamic occupancy models (MacKenzie et al. 2017) in a Bayesian framework to incorporate diel activity information and variation in detection and sampling methodology through the incorporation of random effects (multistate diel occupancy models [MSDOMs]). We exemplify these models by investigating how anthropogenic development and activity may alter simultaneously where and when species occur. We do so by presenting a case study on Madagascar's largest endemic carnivore, the fosa (*Cryptoprocta ferox*), to demonstrate the static MSDOM, and a case study on the urban ecology of coyotes (*Canis latrans*) to demonstrate the dynamic MSDOM. With this adapted model and the growing availability of spatial and temporal data, it is possible to evaluate hypotheses on wildlife diel activity across space and through time, which represents a major advancement over current methods (Distiller et al. 2020; Azzou et al. 2021; Gallo et al. 2021).

Material and Methods

Multistate Diel Occupancy Models

Static Model: A Single-Season Occupancy Analysis. The MSDOM is a form of the multistate occupancy model with state uncertainty (Nichols et al. 2007; MacKenzie et al. 2009) and is defined below with four states equivalent to the original co-occurrence model (MacKenzie et al. 2004) with two species; the static model can also be understood as a special case of the species co-occurrence model by Rota et al. (2016) and the dynamic model as a special case of Fidino et al. (2019). However, the MSDOM considers biologically important diel time periods for state segregation; this segregation can be based on any set of time periods of interest. In our case, sites are defined in one of four ($M = 4$) mutually exclusive states: (1) no use, (2) day use, (3) night use, and (4) night and day use. While these are coarse categorizations for diel behavior, these states provide us the ability to quantify the strength of drivers to diel shifts across continuous space and therefore identify biologically informed

thresholds for species diel habitat use. Surveys are conducted over spatial locations, or camera trap sites ($i = 1, \dots, N$), which are independently sampled on $j = 1, \dots, K$ occasions (e.g., days or weeks). Our state definitions do not follow a hierarchical ordering, as commonly applied in multistate occupancy models (Nichols et al. 2007) and implemented in R packages (unmarked; Fiske and Chandler 2011). For example, if site i was observed in state 2, it precludes the site from ever being in state 3, as these states do not co-occur over a given survey period.

Full model (no covariates). Let ψ^m be the probability that a site is in occupancy state m , where $\psi = [\psi^1 \psi^2 \psi^3 \psi^4]$ is the state probability vector, $\psi^1 = 1 - \psi^2 - \psi^3 - \psi^4$, and $\mathbf{1} \times \psi = 1$ (see the parameter descriptions in app. S). The marginal occupancy probability (regardless of state) is $\psi = \psi^2 + \psi^3 + \psi^4$. Then, let $p_j^{m,l}$ be the probability of observing the occupancy state l given that the true state is m in survey j . The detection probability matrix for survey j (assuming no site or survey variation) is $M \times M$ with the observed (columns) and true states (row) with rows summing to 1:

$$\mathbf{P} = \begin{bmatrix} 1 & 0 & 0 & 0 \\ 1 - p^{2,2} & p^{2,2} & 0 & 0 \\ 1 - p^{3,3} & 0 & p^{3,3} & 0 \\ p^{1,4} & p^{2,4} & p^{3,4} & p^{4,4} \end{bmatrix}. \quad (1)$$

Together, the true occupancy state for site i is defined by the latent variable, $z_i \sim \text{Categorical}(\psi)$, and the observed state in survey j is defined as $y_{ij} \sim \text{Categorical}(\mathbf{P}_{z_i,1:M})$. Taking a Bayesian modeling framework, we can assume diffuse prior distributions for model parameters as $\psi, \mathbf{P}_{4,1:M} \sim \text{Dirichlet}(1, 1, 1, 1)$ and $p^{2,2}, p^{3,3} \sim \text{Beta}(1, 1)$. Note that in this full model, there is no relationship among state-specific detection probabilities (i.e., $p^{2,2}, p^{3,3}, \mathbf{P}_{4,1:M}$) and occupancy probabilities (i.e., ψ^2, ψ^3, ψ^4) across associated M states. Specifically, state 4 (night and day use) occupancy and detection is not defined by state 2 (day use) and state 3 (night use). This suggests that there is a fundamental difference between sites or species activity that occupy state 4. Species present during the night-and-day-use state may be cathemeral, indicating that they have intermediate adaptations allowing them behavioral flexibility to manage disturbance (Bennie et al. 2014). We can also estimate a species' temporal use on the landscape by conditioning on species presence to examine how species navigate anthropogenic features via time partitioning. We do this by investigating an occupied state of interest over the sum of all occupied states. For example, the likelihood a species will use the night-use state given it is present is ψ^3 / ψ .

Reduced model (no covariates). The reduced model is a simpler parameterization that defines the occupancy and detection probabilities of state 4 (night and day use) as the product of states 2 and 3. Therefore, we assume that the diel time periods of night and day are independent random events, allowing their probability products (detection and occupancy) to result in the probability of occurring or being detected during the night and day. Here, we can redefine our model in terms of the probability of using a site during the day, regardless of use at night (marginal probability; $\psi^{\text{Day.M}}$), and the probability of using a site at night, regardless of use during the day ($\psi^{\text{Night.M}}$). Our state occupancy probabilities are then

$$\begin{aligned} \psi^1 &= (1 - \psi^{\text{Day.M}})(1 - \psi^{\text{Night.M}}), \\ \psi^2 &= \psi^{\text{Day.M}}(1 - \psi^{\text{Night.M}}), \\ \psi^3 &= (1 - \psi^{\text{Day.M}})\psi^{\text{Night.M}}, \\ \psi^4 &= \psi^{\text{Day.M}}\psi^{\text{Night.M}}. \end{aligned} \quad (2)$$

Similarly, we can define \mathbf{P} using the probability of detection during the day ($p^{\text{Day.M}}$) and night ($p^{\text{Night.M}}$) as

$$\mathbf{P} = \begin{bmatrix} 1 & 0 & 0 & 0 \\ 1 - p^{\text{Day.M}} & p^{\text{Day.M}} & 0 & 0 \\ 1 - p^{\text{Night.M}} & 0 & p^{\text{Night.M}} & 0 \\ (1 - p^{\text{Day.M}})(1 - p^{\text{Night.M}}) & p^{\text{Day.M}}(1 - p^{\text{Night.M}}) & (1 - p^{\text{Day.M}})p^{\text{Night.M}} & p^{\text{Day.M}}p^{\text{Night.M}} \end{bmatrix}. \quad (3)$$

We can assume diffuse prior distributions for our reduced model parameters: $\psi^{\text{Day.M}}, \psi^{\text{Night.M}}, p^{\text{Day.M}}, p^{\text{Night.M}} \sim \text{Beta}(1, 1)$.

Null model. It is important to compare more complex models with one that does not consider diel time partitioning. This null model would thus be a single-season occupancy model (MacKenzie et al. 2002), cast in a multistate framework for model comparison purposes. Our state occupancy probabilities are then

$$\begin{aligned} \psi^1 &= 1 - \psi, \\ \psi^2 &= \psi/3, \\ \psi^3 &= \psi/3, \\ \psi^4 &= \psi/3, \end{aligned} \quad (4)$$

with the following detection matrix:

$$\mathbf{P} = \begin{bmatrix} 1 & 0 & 0 & 0 \\ 1 - p^* & p^* & 0 & 0 \\ 1 - p^* & 0 & p^* & 0 \\ 1 - p^* & p^*/3 & p^*/3 & p^*/3 \end{bmatrix}. \quad (5)$$

We can assume the following diffuse prior distributions for the null model parameters: $\psi, p \sim \text{Beta}(1, 1)$.

Models with covariates. All versions of the MSDOM (full, reduced, null) allow for the incorporation of site-level covariates as explanatory variables of ψ and \mathbf{P} and survey-level covariates for \mathbf{P} . We use separate design matrices for modeling each state ($\mathbf{x}_i^{\text{Day}}, \mathbf{x}_i^{\text{Night}}, \mathbf{x}_i^{\text{ND}}$) that for each site i are $1 \times Q_m$ (the number of columns) and associated vectors of coefficients ($\alpha^{\text{Day}}, \alpha^{\text{Night}}, \alpha^{\text{ND}}$) that are $Q_m \times 1$. We link state-specific linear models with occupancy probabilities using the multinomial logit link. The full model with covariates is specified as

$$\begin{aligned} \psi_i^1 &= \phi_i^1 / (\phi_i^1 + \phi_i^2 + \phi_i^3 + \phi_i^4), \\ \psi_i^2 &= \phi_i^2 / (\phi_i^1 + \phi_i^2 + \phi_i^3 + \phi_i^4), \\ \psi_i^3 &= \phi_i^3 / (\phi_i^1 + \phi_i^2 + \phi_i^3 + \phi_i^4), \\ \psi_i^4 &= \phi_i^4 / (\phi_i^1 + \phi_i^2 + \phi_i^3 + \phi_i^4), \\ \phi_i^1 &= 1, \\ \phi_i^2 &= e^{x_i^{\text{Day}} \alpha^{\text{Day}}}, \\ \phi_i^3 &= e^{x_i^{\text{Night}} \alpha^{\text{Night}}}, \\ \phi_i^4 &= e^{x_i^{\text{Day}} \alpha^{\text{Day}} + x_i^{\text{Night}} \alpha^{\text{Night}} + x_i^{\text{ND}} \alpha^{\text{ND}}}. \end{aligned} \quad (6)$$

Here, ϕ_i^2 and ϕ_i^3 contain only first-order parameters, which respectively represent the log odds that a species occupies site i in either state 2 or state 3 (i.e., they are associated with a single state). The parameter ϕ_i^4 , however, also contains second-order parameters ($x_i^{\text{ND}} \alpha^{\text{ND}}$), which represent the log odds difference a species occupies site i in the night-and-day-use state relative to the aforementioned first-order parameters (see Dai et al. 2013). Thus, the second-order parameters for the night-and-day-use state allow us to evaluate whether this state is different from the day-use and night-use states combined. To specify the reduced model, we remove $x_i^{\text{ND}} \alpha^{\text{ND}}$ from the linear model on ϕ_i^4 . The null model with covariates is recast to leverage the unoccupied state equally to the combination of the identical but multiple occupied states as

$$\begin{aligned} \phi_i^1 &= 3, \\ \phi_i^2 &= e^{x_i \alpha}, \\ \phi_i^3 &= e^{x_i \alpha}, \\ \phi_i^4 &= e^{x_i \alpha}. \end{aligned} \quad (7)$$

We can assume diffuse prior distributions for all coefficients as $\alpha_m \sim \text{Logistic}(0, 1)$ (Northrup and Gerber 2018). Including covariates on the detection matrix similarly uses the multinomial logit link (see Gerber et al. 2022).

Dynamic Model: Across-Season Occupancy Analysis. The dynamic MSDOM considers how site use at the diel scale

changes over longer timescales, such as seasons or years. The sampling protocol is identical to that of a static MSDOM, except that sites are sampled over $t = 1, \dots, T$ primary sampling periods. Furthermore, we assume the occupancy state, $z_{i,t}$, depends on the state in the previous primary period, $z_{i,t-1}$, which allows transitions to be estimated in terms of state-specific local colonization (γ) and extinction (ε) for all sampling periods except the first. Instead, we estimate initial occupancy for the first sampling period as we did for the static MSDOM. For all dynamic MSDOM, let τ be an $M \times M$ transition matrix whose rows sum to 1 and contains the rates that describe the probability a site either stays in the same occupancy state or transitions to a new state from one primary sampling period to the next.

Full Model (No Covariates). While the most general full model would independently estimate all $M \times M$ transitions among states, such a model may be difficult to fit with typical sample sizes from real-world data. Thus, we imposed a few biologically reasonable constraints to reduce the number of model parameters and allow for more sparse but realistic data sets to be used. For the full model, let τ be

$$\tau = \begin{bmatrix} (1 - \gamma^{\text{D}})(1 - \gamma^{\text{N}}) & \gamma^{\text{D}}(1 - \gamma^{\text{N}}) & (1 - \gamma^{\text{D}})\gamma^{\text{N}} & \gamma^{\text{D}}\gamma^{\text{N}} \\ \varepsilon^{\text{D}}(1 - \gamma^{\text{ND}}) & (1 - \varepsilon^{\text{D}})(1 - \gamma^{\text{ND}}) & \varepsilon^{\text{D}}\gamma^{\text{ND}} & (1 - \varepsilon^{\text{D}})\gamma^{\text{ND}} \\ (1 - \gamma^{\text{DN}})\varepsilon^{\text{N}} & \gamma^{\text{DN}}\varepsilon^{\text{N}} & (1 - \gamma^{\text{DN}})(1 - \varepsilon^{\text{N}}) & \gamma^{\text{DN}}(1 - \varepsilon^{\text{N}}) \\ \varepsilon^{\text{DN}}\varepsilon^{\text{ND}} & (1 - \varepsilon^{\text{DN}})\varepsilon^{\text{ND}} & \varepsilon^{\text{DN}}(1 - \varepsilon^{\text{ND}}) & (1 - \varepsilon^{\text{DN}})(1 - \varepsilon^{\text{ND}}) \end{bmatrix}, \quad (8)$$

where the rows respectively describe state transitions from the four occupancy states. For example, the probability a site changes from state 2 (day use) to state 3 (night use) is $\tau^{2,3} = \varepsilon^{\text{D}}\gamma^{\text{ND}}$, where ε^{D} is the site extinction probability in the day-use state and γ^{ND} is the probability of colonization of the night-use state given the day-use state in the previous primary period. We assume that transitions depend on the state in the previous primary period and that transitions from occupied states (i.e., 2, 3, or 4) may not be equivalent to transitions from the unoccupied state (i.e., state 1).

As with the full static MSDOM, the initial occupancy probability of the four states at $t = 1$ is $\psi_i = [\psi_i^1 \psi_i^2 \psi_i^3 \psi_i^4]$. The latent state of the model is then $z_{i,1} \sim \text{Categorical}(\psi_i)$ for $t = 1$ and $z_{i,t} \sim \text{Categorical}(\tau_{z_{i,t-1}, 1:M})$ for $t > 1$, where $z_{i,t-1}$ indexes the appropriate row of τ . The observed state is specified like the full static MSDOM except we indexed the observed data and latent state through time such that $y_{ijt} \sim \text{Categorical}(\mathbf{P}_{z_{i,t}, 1:M})$, where \mathbf{P} is equation (1) and $z_{i,t}$ indexes the appropriate row of \mathbf{P} . Finally, we assume the same diffuse prior distributions as the full static

MSDOM for ψ and \mathbf{P} , while all colonization (γ) and extinction (ϵ) parameters have their own respective Beta(1, 1) distributions.

Reduced model (no covariates). The reduced dynamic model is similar to the full dynamic model except initial occupancy becomes equation (2), τ lacks conditional parameters, and \mathbf{P} becomes equation (3). Therefore, τ simplifies to

$$\tau = \begin{bmatrix} (1 - \gamma^D)(1 - \gamma^N) & \gamma^D(1 - \gamma^N) & (1 - \gamma^D)\gamma^N & \gamma^D\gamma^N \\ \epsilon^D(1 - \gamma^N) & (1 - \epsilon^D)(1 - \gamma^N) & \epsilon^D\gamma^N & (1 - \epsilon^D)\gamma^N \\ (1 - \gamma^D)\epsilon^N & \gamma^D\epsilon^N & (1 - \gamma^D)(1 - \epsilon^N) & \gamma^D(1 - \epsilon^N) \\ \epsilon^D\epsilon^N & (1 - \epsilon^D)\epsilon^N & \epsilon^D(1 - \epsilon^N) & (1 - \epsilon^D)(1 - \epsilon^N) \end{bmatrix}. \quad (9)$$

With the exclusion of conditional parameters, this model assumes that transitions between day and night are independent random events.

Null model (no covariates). Casting the dynamic MSDOM as a standard multiseason occupancy model requires splitting the associated colonization and extinction probabilities across each respective row of τ to ensure each row still sums to 1, such that

$$\tau = \begin{bmatrix} 1 - \gamma & \gamma/3 & \gamma/3 & \gamma/3 \\ \epsilon & (1 - \epsilon)/3 & (1 - \epsilon)/3 & (1 - \epsilon)/3 \\ \epsilon & (1 - \epsilon)/3 & (1 - \epsilon)/3 & (1 - \epsilon)/3 \\ \epsilon & (1 - \epsilon)/3 & (1 - \epsilon)/3 & (1 - \epsilon)/3 \end{bmatrix}. \quad (10)$$

As with the static null MSDOM, initial occupancy becomes equation (4) and \mathbf{P} becomes equation (5).

Models with covariates. As with the static MSDOM, transition probabilities for each dynamic model can be made a function of covariates. To do so, we use separate design matrices for each model parameter, which are $1 \times Q_m$ (e.g., \mathbf{x}_i^D , \mathbf{x}_i^N , $\mathbf{x}_i^{D|N}$, and $\mathbf{x}_i^{N|D}$) and associated vectors of coefficients that are $Q_m \times 1$ (e.g., \mathbf{b}^D , \mathbf{b}^N , \mathbf{d}^D , \mathbf{d}^N , $\mathbf{g}^{D|N}$, $\mathbf{g}^{N|D}$, $\mathbf{h}^{D|N}$, and $\mathbf{h}^{N|D}$). Temporal or spatiotemporal covariates may also be included in dynamic MSDOM, resulting in $T \times Q_m$ design matrices for colonization, extinction, or detection parameters. Following Fidino et al. (2019), the linear predictors for the parameters of the full model are

$$\begin{aligned} \beta_i^{\gamma^D} &= \mathbf{x}_i^D \mathbf{b}^D, & \beta_i^{\gamma^{D|N}} &= \mathbf{x}_i^{D|N} \mathbf{g}^{D|N}, \\ \beta_i^{\gamma^N} &= \mathbf{x}_i^N \mathbf{b}^N, & \beta_i^{\gamma^{N|D}} &= \mathbf{x}_i^{N|D} \mathbf{g}^{N|D}, \\ \beta_i^{\epsilon^D} &= \mathbf{x}_i^D \mathbf{d}^D, & \beta_i^{\epsilon^{D|N}} &= \mathbf{x}_i^{D|N} \mathbf{h}^{D|N}, \\ \beta_i^{\epsilon^N} &= \mathbf{x}_i^N \mathbf{d}^N, & \beta_i^{\epsilon^{N|D}} &= \mathbf{x}_i^{N|D} \mathbf{h}^{N|D}, \end{aligned} \quad (11)$$

for the dynamic model; $\beta_i^{\gamma^D}$, $\beta_i^{\gamma^N}$, $\beta_i^{\epsilon^D}$, $\beta_i^{\epsilon^N}$ are first-order parameters, while $\beta_i^{\gamma^{D|N}}$, $\beta_i^{\gamma^{N|D}}$, $\beta_i^{\epsilon^{D|N}}$, and $\beta_i^{\epsilon^{N|D}}$ are second-order parameters. In this case, the second-order parameters are the log odds difference given the presence of another state in either the current time step (t) for occupancy and detection or in the previous time step ($t - 1$) for colonization and extinction. Let ω be a matrix with the same dimensions as τ that contains the linear predictors of the dynamic model. We set the diagonal of the matrix as the reference category so that transitions are estimated relative to a site staying in the same state from one time step to the next:

$$\omega_i = \begin{bmatrix} \mathbf{1} & e^{\beta_i^{\gamma^D}} & e^{\beta_i^{\gamma^N}} & e^{\beta_i^{\gamma^D} + \beta_i^{\gamma^N}} \\ e^{\beta_i^{\epsilon^D}} + \beta_i^{\epsilon^{D|N}} + \beta_i^{\epsilon^N} + \beta_i^{\epsilon^{N|D}} & \mathbf{1} & e^{\beta_i^{\epsilon^D} + \beta_i^{\epsilon^{D|N}} + \beta_i^{\epsilon^N}} & e^{\beta_i^{\epsilon^D} + \beta_i^{\epsilon^{D|N}} + \beta_i^{\epsilon^N} + \beta_i^{\epsilon^{N|D}}} \\ e^{\beta_i^{\epsilon^D}} + \beta_i^{\epsilon^{D|N}} & e^{\beta_i^{\epsilon^D} + \beta_i^{\epsilon^{D|N}}} & \mathbf{1} & e^{\beta_i^{\epsilon^D} + \beta_i^{\epsilon^{D|N}}} \\ e^{\beta_i^{\epsilon^N}} + \beta_i^{\epsilon^{N|D}} & e^{\beta_i^{\epsilon^N} + \beta_i^{\epsilon^{N|D}}} & e^{\beta_i^{\epsilon^N} + \beta_i^{\epsilon^{N|D}}} & \mathbf{1} \end{bmatrix}. \quad (12)$$

Dividing each element of a row by its respective row sum (i.e., applying the multinomial logit link) converts ω_i to τ_i (Fidino et al. 2019). The reduced model removes all second-order parameters from ω_i and becomes

$$\omega_i = \begin{bmatrix} \mathbf{1} & e^{\beta_i^{\gamma^D}} & e^{\beta_i^{\gamma^N}} & e^{\beta_i^{\gamma^D} + \beta_i^{\gamma^N}} \\ e^{\beta_i^{\epsilon^D}} + \beta_i^{\epsilon^N} & \mathbf{1} & e^{\beta_i^{\epsilon^D} + \beta_i^{\epsilon^N}} & e^{\beta_i^{\epsilon^D} + \beta_i^{\epsilon^N}} \\ e^{\beta_i^{\epsilon^D}} + \beta_i^{\epsilon^N} & e^{\beta_i^{\epsilon^D} + \beta_i^{\epsilon^N}} & \mathbf{1} & e^{\beta_i^{\epsilon^D} + \beta_i^{\epsilon^N}} \\ e^{\beta_i^{\epsilon^N}} + \beta_i^{\epsilon^D} & e^{\beta_i^{\epsilon^N} + \beta_i^{\epsilon^D}} & e^{\beta_i^{\epsilon^N} + \beta_i^{\epsilon^D}} & \mathbf{1} \end{bmatrix}. \quad (13)$$

The null model, which is a multiseason occupancy model with covariates, ω_i , becomes

$$\omega_i = \begin{bmatrix} 3 & e^{\beta_i^{\gamma^D}} & e^{\beta_i^{\gamma^N}} & e^{\beta_i^{\gamma^D} + \beta_i^{\gamma^N}} \\ 3 \times e^{\beta_i^{\epsilon^D}} & 1 & 1 & 1 \\ 3 \times e^{\beta_i^{\epsilon^N}} & 1 & 1 & 1 \\ 3 \times e^{\beta_i^{\epsilon^D}} & 1 & 1 & 1 \end{bmatrix}, \quad (14)$$

where $\beta_i^{\gamma^D}$ and $\beta_i^{\epsilon^D}$ are respectively logit linear predictors for colonization and extinction. The dynamic MSDOM with covariates uses the same process to incorporate detection-level covariates, save for the fact that the detection matrix and data vary across the secondary sampling periods.

Fosa Case Study

Fosas are a medium-sized carnivore (5.5–9.9 kg; Goodman 2012) in the monophyletic Eupleridae family, which is endemic to Madagascar. Fosas face increasing anthropogenic pressure from deforestation (Morelli et al. 2020), unsustainable hunting (Golden 2009), and exotic species (Farris et al. 2017). As a generalist species with a diverse diet, activity of fosas near human settlements and their consumption of livestock has caused conflict with humans (Kotschwar Logan et al. 2014; Borgerson 2016). Previous studies show that their diel activity is largely cathemeral (Gerber et al. 2012a; Farris et al. 2015a). Their ubiquitous occurrence across forests and use of the entire 24-h period (Gerber et al., forthcoming) make them an exemplar species to investigate the utility of MSDOM in the context of human disturbance. We analyzed data from Makira Natural Park (Farris et al. 2015b) and Ranomafana National Park (Gerber et al. 2012a; see table S5) regions.

These two parks have unique histories that have shaped differing human activity in each region (changes in forest cover, agriculture, invasive species introduction, etc.) and subsequent impact on native wildlife species (Goodman et al. 2019). As such, we have formed unique hypotheses about anthropogenic factors that impact fosas in these regions. Given high human activity within forests of Makira (Farris et al. 2015b) compared with Ranomafana (Gerber et al. 2012b; Farris et al. 2017), we used human activity at camera locations to quantify human disturbance. Human activity was calculated as the number of human detection events (photos taken within 30-min intervals) per diel period (i.e., day and night) for each camera site divided by the number of sampling days the site was active. At Ranomafana, human activity within the protected boundaries was low, in contrast to Makira. The riskiest areas for fosas at Ranomafana were found outside the park boundaries or along forest edges, where villages are located and there is high human activity. Therefore, we used the distance to the nearest village and distance to the nearest matrix (non-forest) from each camera trap to quantify human disturbance (for details, see Gerber et al. 2012a).

We fitted static MSDOMs to the Makira and Ranomafana data separately. For both regions, we hypothesized that occupancy would vary in diel time by the level of disturbance. We also hypothesized that the day-use state would be occupied least by fosas because of diurnal human activity near areas of high disturbance. Specifically, we predicted that fosa occupancy during the day would decrease with increasing human disturbance and that fosa occupancy at night would be higher than day occupancy, regardless of human disturbance. We also expected increasing night occupancy with increasing human disturbance. Day was defined by hours after civil sunrise and before civil sun-

set, while night was defined by hours following civil sunset and before civil sunrise, calculated using the package `sunCalc` (Thieurmel and Elmarhraoui 2019) in R version 4.0.2. To determine detected diel states of fosas, we used 6-day occasions. All models were coded and fitted in JAGS version 4.0.2 (Plummer 2003) with the `runjags` package (Denwood 2016) in R version 4.0.2. We assessed convergence using the Gelman-Rubin diagnostic (Gelman and Rubin 1992) to ensure that all values were <1.1 and by visually examining trace plots of the posterior distributions. We compared models using the conditional predictive ordinate (CPO; Hooten and Hobbs 2015) and evaluated evidence of an effect with the most supported model by investigating whether 95% credible intervals (CIs) of parameter estimates included zero and deriving the probability of an effect being less than or greater than zero.

We fitted 18 candidate models to two years (one season per year) of Ranomafana data (table S6): full, reduced, and null model, each with state occupancy modeled with and without individual covariates (distance to village and matrix were modeled separately) and a categorical variable for survey. Over the two years, 111 camera traps were deployed 420–670 m apart across four primary, selectively logged, and fragmented forests sites totaling in an area roughly 33.5 km² (Gerber et al. 2012b). Detection parameters were not modeled with covariates. The most supported model was the full model with the covariate distance to village influencing state occupancy. We found strong support for (1) variation in state occurrence (fig. 1) and detection (see fig. S1; table S7) and (2) multistate occurrence varying with human disturbance (fig. 2A). We found little support that day occurrence varied by distance to village based on the mode and 95% CI ($\alpha^{\text{Day,Dist.Vill}} = -0.002$, 95% CI = -1.31 to 1.37), with only a 0.50 probability that the distribution was above zero (fig. 1). This did not support our hypothesis. However, we found moderate to strong support that night-day occurrence increased with distance to village ($\alpha^{\text{ND,Dist.Vill}} = 1.45$, 95% CI = -0.17 to 2.95 , $\Pr(\alpha^{\text{ND,Dist.Vill}} > 0) = 0.97$), supporting our hypothesis. These results suggest that if fosas use sites during day hours, it is in conjunction with night hours, and the probability of using sites during the day is greater farther away from human disturbance. We also found moderate to strong support that night-use state occurrence declined with increasing distance to village ($\alpha^{\text{Night,Dist.Vill}} = -1.16$, 95% CI = -2.38 to -0.02 , $\Pr(\alpha^{\text{Night,Dist.Vill}} < 0) = 0.98$). Results from conditional probabilities of use (given that fosas are present) revealed similar probabilities (fig. 2B) to those of occurrence. This was due to the widespread distribution of fosas within the study area. We found that the probability of detecting a fosa at night, given that it was present during the day and night ($p^{4,3}$), to be the highest detection probability (see fig. S1; table S7). Detection of a fosa

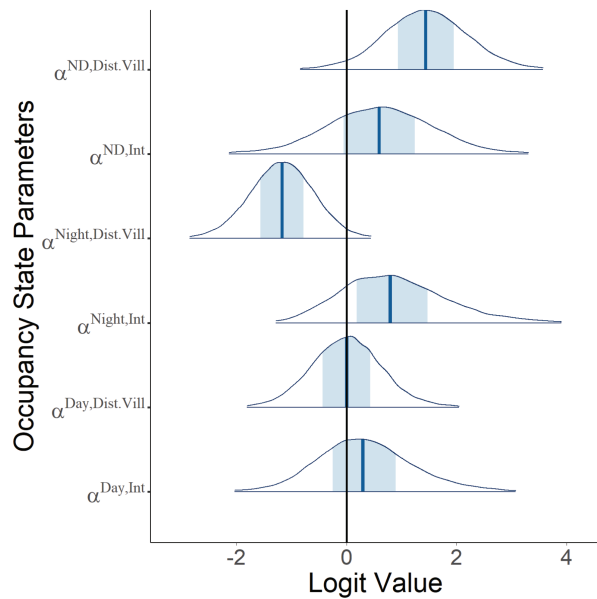


Figure 1: Posterior distributions of fosa (*Cryptoprocta ferox*) state occupancy model parameters for the most supported model using the Ranomafana National Park data. Shaded areas represent the 50% probability density, and dark lines indicate the posterior mode. Y-axis labels with “Int” indicate an intercept for the states (day use, night use, and night and day use [ND]), and “Dist.Vill” indicates the slope parameter associated with the variable distance to village.

during the day-night state (p^{44}) was the lowest. This suggests that this low density and wide-ranging species does use sites during the day and night, but not regularly.

We fit six candidate models to 7 years (one season per year) of Makira data (table S8): full, reduced, and null model, each with and without the human activity covariate. Detection parameters were not modeled with covariates. From 2008 to 2015, 18–26 camera trap stations (with two cameras per station) were deployed roughly 500 m apart across seven sites with varying levels of forest degradation (Farris et al. 2015a, 2015b). We found all models to fit the data ($.1 > \text{Bayesian goodness-of-fit } P \text{ value} < .9$). We found the most supported model to be the full model without an effect of human activity. These results support that there is variation in multistate occurrence and detection, but not regarding our hypothesis that human disturbance influenced occurrence. We found that fosa occupancy was highest during the night-use state ($\psi^3 = 0.33$, 95% CI = 0.11 to 0.60), followed by the day-use state ($\psi^2 = 0.20$, 95% CI = 0.06 to 0.44) and the night-and-day-use state ($\psi^4 = 0.18$, 95% CI = 0.05 to 0.41; fig. 3). The large parametric uncertainty of the detection parameters made drawing conclusions difficult, although results indicate that fosas

are most detectable at night when present during the night-and-day-use state (fig. S2; table S9).

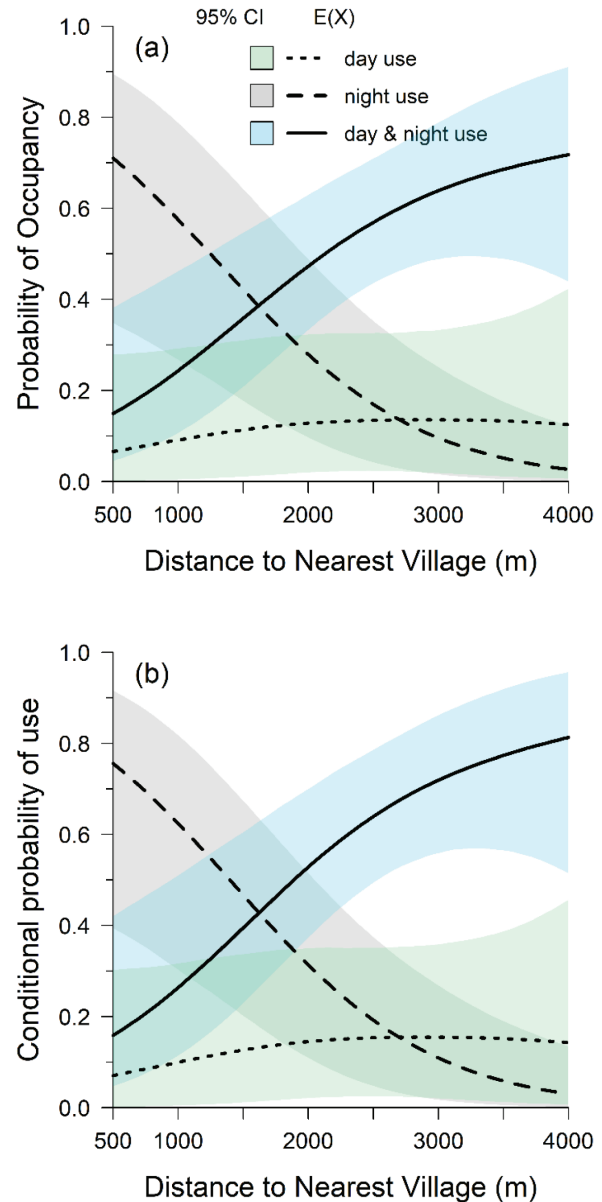


Figure 2: A, Probability of use for fosas (*Cryptoprocta ferox*) for each diel category with the expected value, $E(X)$; the median of the posterior of a given parameter; and the 95% credible interval (CI). B, Probability of use for fosas for each diel category given that fosas are present with $E(X)$ and 95% CI (note that state 1 [no use] is not included here). Both are estimated from the most supported model using the Ranomafana National Park data, which incorporated the covariate distance to village.

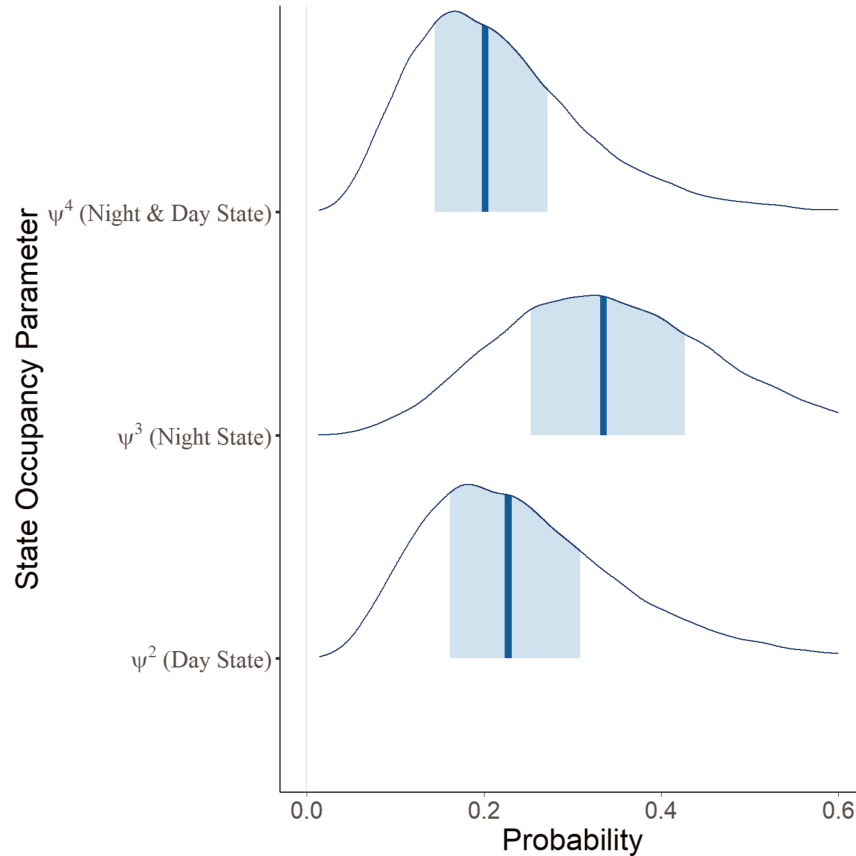


Figure 3: Posterior distributions of fosa (*Cryptoprocta ferox*) state occupancy model parameters (mean across all sites) for the most supported model using the Makira Natural Park data. Shaded areas represent the 50% probability density, and dark lines indicate the posterior mode. ψ^2 is the probability a species is present during the day only, ψ^3 is the probability a species is present during the night only, and ψ^4 is the probability a species is present during the night and day.

Coyote Case Study

Coyotes are a medium-sized carnivore (8–14 kg; Bekoff and Gese 2003) native to North America that have expanded their distribution across the United States, Canada, and South America in the last century (Hody and Kays 2018). As generalists, coyotes exploit an array of habitats from prairies to urban cities (Elliot et al. 2016). Coyote diel activity is quite plastic, specifically in the presence of anthropogenic disturbance (Way et al. 2004; Gehrt et al. 2007). Therefore, we quantified whether coyotes modify their diel activity along an urbanized gradient.

To do so, we fit dynamic MSDOMs to 13 sampling periods of camera trapping data collected between July 2016 and July 2019 in the greater Chicago metropolitan area. Camera deployments followed protocols outlined by the Urban Wildlife Information Network (see Magle et al. 2019). In brief, 105 cameras were placed along three 50-km transects radiating outward from downtown Chi-

cago, Illinois (table S10). Cameras were a minimum of 1 km apart and were located within a 2-km buffer of their respective transects. Data were summarized such that each 4-week deployment (July 2016, October 2016, etc.) was treated as a primary sampling period and each week was a secondary sampling period. To determine the detected diel state for a given week (occasion length), we used the `suncalc` package in R following the same diel categorization process as in the fosa study. While the static MSDOM (with four states) can potentially have three linear predictors for the latent state, the dynamic MSDOM potentially has 11, thereby exacerbating the number of different covariate combinations and parameters to be estimated. To simplify our model fitting strategy, we fitted three models that differed in their fundamental structure (i.e., the full, reduced, and null dynamic MSDOM) and included an urban intensity metric on all first-order parameters. We made two additional changes to the full model because daytime coyote detections were sparse ($n = 54$) relative to night ($n = 286$)

or night and day ($n = 183$). First, we excluded urban intensity on second-order colonization or extinction parameters because second-order slope terms failed to converge when included. Second, we used equation (3) as the detection matrix, which assumes that the probability of detecting night and day use (state 4) as the product of the probabilities of detecting day use (state 2) and night use (state 3). Models were compared with CPO, and we evaluated evidence of an effect with the best-fit model by investigating whether 95% CIs of parameter estimates included zero and deriving the probability of an effect being less than or greater than zero.

To derive the urban intensity metric, we used principal component analysis for tree cover (%; CMAP 2016), impervious cover (%; CMAP 2016), and housing density (units km^{-2} ; Hammer et al. 2004) within a 1-km buffer of each sampling location. Negative values represented increased forest cover coupled with decreased impervious cover and housing density, while positive values represented increased levels of impervious cover and housing density coupled with low canopy cover. Models were fit in JAGS version 4.3.0 in R version 4.0.3. We evaluated model convergence by inspecting trace plots to ensure proper mixing and using the Gelman-Rubin statistic.

Of the possible 1,365 deployments (105 sites across 13 sampling periods), we collected data for 1,172 deployments. The no-use state was the most observed ($n = 650$), followed by the night-use state ($n = 286$), the night-and-day-use state ($n = 183$), and the day-use state ($n = 53$). Overall, the full model (22 parameters, CPO = 3,131.46) had the most support, followed by the reduced model (16 parameters, CPO = 3,209.17) and then the null model (eight parameters, CPO = 3,334.52). With the most supported model, the average occupancy probability during the first season was 0.41 for the no-use state (95% CI = 0.26 to 0.56), 0.18 for the day-use state (95% CI = 0.06 to 0.33), 0.07 for the night-use state (95% CI = 0.01 to 0.19), and 0.32 for the night-and-day-use state (95% CI = 0.19 to 0.48). Thus, assuming a site was occupied by coyotes during the first primary period, coyotes were on average most likely to use sites during the day and night. Across the urbanization gradient, the day-use state was more negatively associated with urban intensity ($a_{\text{URB}}^{\text{D}} = -1.05$, 95% CI = -1.98 to -0.07 , $\text{Pr}(a_{\text{URB}}^{\text{D}} < 0) = 0.99$) than the night-use state ($a_{\text{URB}}^{\text{N}} = -0.65$, 95% CI = -1.51 to 0.18 , $\text{Pr}(a_{\text{URB}}^{\text{N}} < 0) = 0.94$). There was some evidence that the night-and-day-use state became more common with increasing urban intensity, but 95% CIs for this second-order parameter overlapped zero ($a_{\text{URB}}^{\text{DN}} = 1.14$, 95% CI = -0.08 to 2.50 , $\text{Pr}(a_{\text{URB}}^{\text{DN}} > 0) = 0.97$). While the initial occupancy parameters demonstrate that the day-use state decreases with increasing levels of urban intensity, it is only a snapshot of the underlying

process. The dynamic MSDOM provides new ways to assess this relationship through additional manipulations of the latent-state transition probability matrix (τ), which describe the processes that bring about coyote occupancy.

While it is important to explore the underlying colonization and extinction dynamics of the model, it is possible to derive the expected probability of each occupancy state at each site as well by solving the equation $\delta_i = \delta_i \tau_i$, where $\sum \delta_i = 1$. Here, δ_i is the normalized first left eigenvector of τ_i and represents the stationary occupancy probability of each state at site i given τ_i (Fidino et al. 2019). Solving this equation simplifies the $I \times M \times M$ transition matrix into $I \times M$ occupancy probabilities and therefore can highlight the overall pattern across an environmental gradient. We applied this equation to the entire posterior of $\tau_{i,t}$ and generated stationary occupancy states at hypothetical sites across Chicago's urbanization gradient. Following this, the probability of use of the different coyote occupancy states, conditional on coyote presence, can be derived by calculating the conditional probability of the day-use state, the night-use state, and the night-and-day-use state given coyote presence. For example, $\text{Pr}(\delta_i^{\text{N}} | \text{coyote presence}) = \delta_i^{\text{N}} / (\delta_i^{\text{D}} + \delta_i^{\text{N}} + \delta_i^{\text{DN}})$. Plotting these relationships reveals that while the night-and-night-use state is the most likely category at low levels of urban intensity, it is replaced by the night-use state as urban intensity increases, assuming coyotes are present (fig. 4).

The transitions among different states can be plotted out and interpreted through the parameters that describe them (fig. 5). For example, sites without coyotes were most likely to stay in the no-use state across all levels of urban intensity, although this relationship became more pronounced at high levels of urban intensity (fig. 5). The transitions from the no-use state, which are described by γ^{D} and γ^{N} , were driven by the strongly negative first-order colonization intercepts for the day-use state ($b_{\text{INT}}^{\text{D}} = -2.95$, 95% CI = -3.88 to -2.14 , $\text{Pr}(b_{\text{INT}}^{\text{D}} < 0) = 1.00$) and the night-use state ($b_{\text{INT}}^{\text{N}} = -1.47$, 95% CI = -1.85 to -1.10 , $\text{Pr}(b_{\text{INT}}^{\text{N}} < 0) = 1.00$), as well as a negative association between the night-use state and urban intensity ($b_{\text{URB}}^{\text{N}} = -0.36$, 95% CI = -0.62 to -0.09 , $\text{Pr}(b_{\text{URB}}^{\text{N}} < 0) = 0.99$). There was weak support that colonization of the day-use state negatively covaried with urban intensity ($b_{\text{URB}}^{\text{D}} = -0.28$, 95% CI = -0.74 to 0.16 , $\text{Pr}(b_{\text{URB}}^{\text{D}} < 0) = 0.89$). While the night-use state negatively covaried with urban intensity, the relatively less negative intercept of this level of the model (i.e., $b_{\text{INT}}^{\text{N}} > b_{\text{INT}}^{\text{D}}$) made night use the most likely diel category for coyotes to colonize along the gradient of urban intensity (fig. 5).

When a site was in the night-use state, transitions are described by ϵ^{N} and γ^{DN} . At average levels of urban intensity, sites were most likely to transition to the no-use

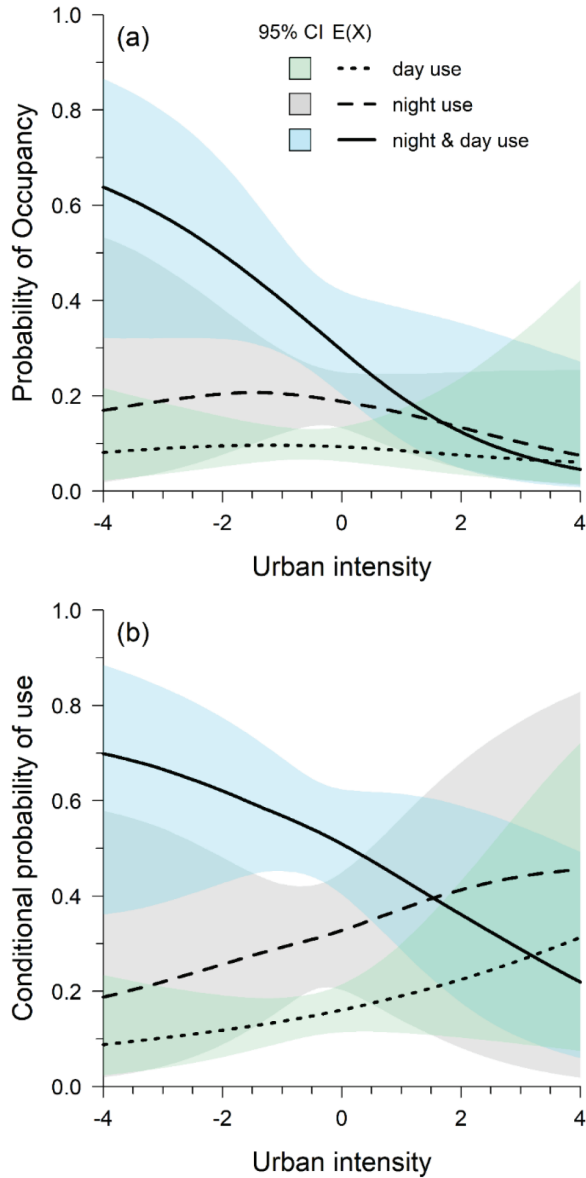


Figure 4: A, As urban intensity increases, coyote occupancy decreases and the most likely diel state changes from the night-and-day-use state to the night-use state. Horizontal black lines represent the expected occupancy probability of coyotes (*Canis latrans*) in each diel category, while shaded ribbons represent 95% credible intervals. State 1 (no use) was excluded. B, If coyotes are present at a site, this panel illustrates the most likely diel state the species will take along a gradient of urban intensity. Horizontal black lines represent the conditional probability of use for each diel state, and shaded ribbons are 95% credible intervals. State 1 (no use) was excluded. All probabilities were estimated from 13 sampling periods of camera trapping data from 1,172 deployments at 105 unique sites between July 2016 and July 2019 in Chicago, Illinois.

state (0.53, 95% CI = 0.30 to 0.73), followed by the night-use state (0.26, 95% CI = 0.08 to 0.50), the day-use state (0.13, 95% CI = 0.02 to 0.30), and then the night-and-day-use state (0.06, 95% CI = 0.01 to 0.17). The large increase in the night-and-day-use state was driven by the positive second-order night-use colonization parameter ($g_{\text{INT}}^{\text{NID}} = 2.82$, 95% CI = 1.60 to 4.52, $\text{Pr}(g_{\text{INT}}^{\text{NID}} > 0) = 1.00$), whereas the decreasing transition probability of the day-use state to the night-and-day-use state was governed by the negative first-order night-use colonization slope term ($b_{\text{URB}}^{\text{N}}$, listed above). Likewise, first-order day-use extinction rates were relatively modest ($d_{\text{INT}}^{\text{D}} = -0.72$, 95% CI = -2.02 to 0.43, $\text{Pr}(d_{\text{INT}}^{\text{D}} < 0) = 0.90$) and covaried little with urban intensity ($d_{\text{URB}}^{\text{D}} = 0.10$, 95% CI = -1.04 to 0.85, $\text{Pr}(d_{\text{URB}}^{\text{D}} > 0) = 0.54$). As a result, $d_{\text{INT}}^{\text{D}}$ and $d_{\text{URB}}^{\text{D}}$ generated relatively flat transitions from the day-use state to the no-use state, the night-use state, or back to the day-use state (fig. 5).

Finally, for the night-and-day-use state, transitions are described by $e^{\text{D|N}}$ and $e^{\text{N|D}}$. Second-order parameters associated with these probabilities were both strongly negative ($h_{\text{INT}}^{\text{D|N}} = -1.89$, 95% CI = -3.67 to -0.17, $\text{Pr}(h_{\text{INT}}^{\text{D|N}} < 0) = 0.99$; $h_{\text{INT}}^{\text{N|D}} = -1.79$, 95% CI = -2.70 to -0.98, $\text{Pr}(h_{\text{INT}}^{\text{N|D}} < 0) = 1.00$). When these second-order parameters are combined with the relatively small influence urban intensity had on first-order extinction parameters (i.e., $d_{\text{INT}}^{\text{D}}$ and $d_{\text{INT}}^{\text{N}}$), sites in the night-and-night-use state were by far more likely to remain in this state (fig. 5).

With regard to detectability, if a site was in the day-use state, the probability of detecting that state was 0.15 (95% CI = 0.12 to 0.18) at average levels of urban intensity and covaried little with urban intensity ($f_{\text{URB}}^{\text{D}} = 0.03$, 95% CI = -0.20 to 0.22, $\text{Pr}(f_{\text{URB}}^{\text{D}} > 0) = 0.56$). The ability to detect the night-use state was, on average, double that of the day-use state (0.30, 95% CI = 0.28 to 0.33) but was minimally and negatively associated with urban intensity ($f_{\text{URB}}^{\text{N}} = -0.13$, 95% CI = -0.24 to -0.01, $\text{Pr}(f_{\text{URB}}^{\text{N}} < 0) = 0.99$). When a site was in the night-and-day-use state, at average levels of urban intensity we were most likely to observe the site as the no-use state (0.59, 95% CI = 0.56 to 0.62), followed by the night-use state (0.26, 95% CI = 0.23 to 0.28), the day-use state (0.10, 95% CI = 0.09 to 0.12), and then the night-and-day-use state (0.04, 95% CI = 0.04 to 0.05).

Discussion

The study of animal-habitat relationships has often focused on identifying spatial drivers of species occurrence while largely ignoring when species use habitat within the diel period. We specified the MSDOM to allow species' diel spatial habitat use to be studied within and across

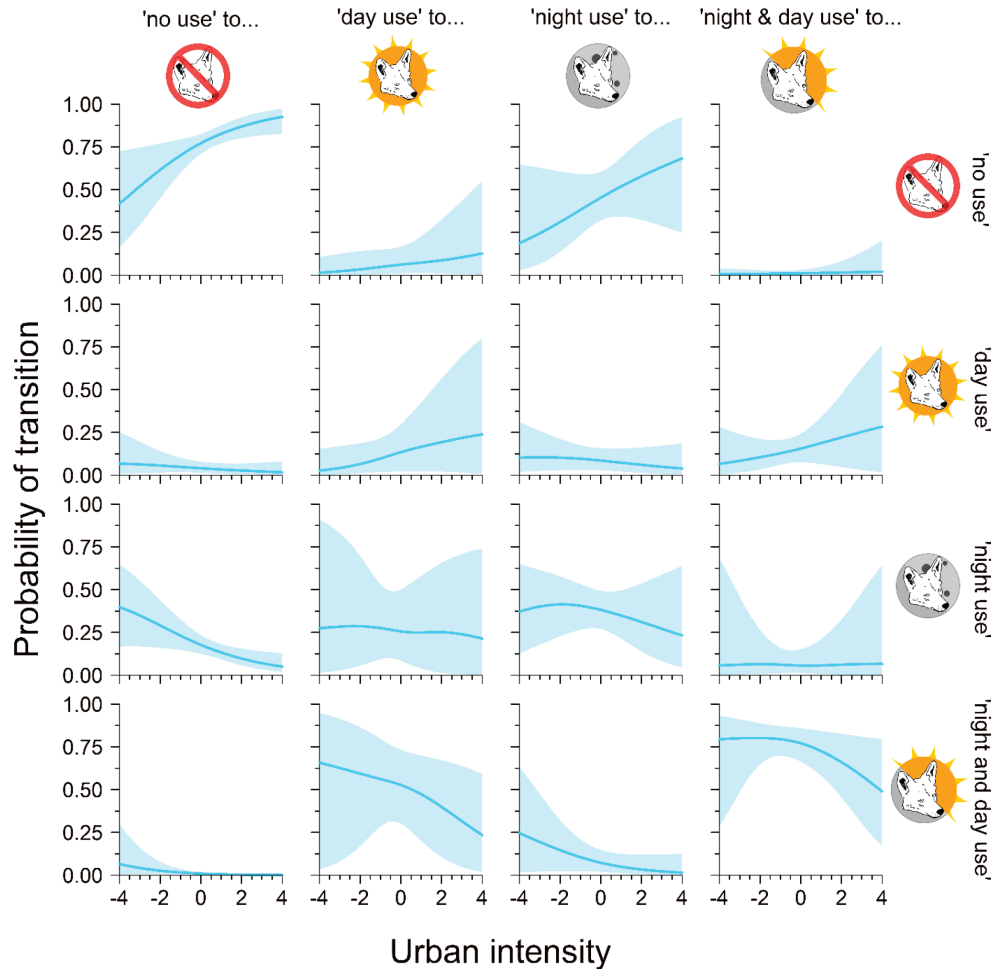


Figure 5: Transition probabilities among each of the four diel coyote (*Canis latrans*) states as a function of urban intensity estimated from 13 sampling periods of camera trapping data collected in Chicago, Illinois, from 1,172 deployments at 105 unique sites between July 2016 and July 2019. Horizontal lines indicate the median estimate, while shaded ribbons represent 95% credible intervals.

seasons or years. Importantly, this model allows for continuous covariates and accounts for variation in detectability and sampling methodology, a source of heterogeneity that is typically unmodeled when analyzing diel activity and is necessary to produce unbiased parameter estimates. The utility of the MSDOM is especially pertinent to studying species at risk to human activities where researchers may want to consider additional anthropogenic covariates, such as noise, artificial lighting, and so on. For those who may want to explore this model with archived data, the ability to incorporate random effects can help accommodate variable sampling schemes, such as unmeasured variation across sites or sampling seasons. MSDOM is best suited for camera trap data or other passive 24-h (or relevant diel time periods) detection/nondetection sampling techniques. While our case studies show that MSDOMs can be used with large and small data sets, it is important to temper expectations with sparse

detections (many zeros in the detection history), rare species, or fewer sites (e.g., <50). When these issues arise, it may be best to avoid the full model implementation and reduce parameter complexity using the reduced model. Alternatively, prior information may be incorporated, especially on the detection components, or multiple studies can be linked together (e.g., our fosa examples) to increase statistical power. Likewise, if these issues create problems when fitting a dynamic MSDOM, the model could be further simplified to estimate occupancy in each time step instead of local colonization and extinction via an autologistic parameterization, following Kass et al. (2020). Doing so may make it possible to leverage smaller, long-term camera trap data sets to address questions about a species' diel activity.

We recommend that future studies intending to use MSDOMs consider diel periods and covariates that are specific to their hypotheses and model form (static or

dynamic). We also greatly encourage pairing camera traps to other remote data-logging devices. For example, remote ambient light data loggers could be used in conjunction with camera traps to determine how fine-scale variation in artificial light at night is related to a species' diel behavior. Likewise, acoustic recorders could be deployed with camera traps to explore how anthropogenic noise is associated with a species' diel activity. Developing studies in this context is critical to learning how species shift their activity away from diel periods of high risk (Gaynor et al. 2018; Gaston 2019). Such behavioral shifts are likely not without important ecological costs and may go undetected under previous model forms but can be detected with the MSDOM.

Our case studies highlight that spatial habitat is not used equally across diel time. We found that fosas and coyotes temporally structure their site use in response to anthropogenic drivers. Previous studies of fosas in the eastern rain forests have suggested that they are ubiquitously distributed across forested landscapes and are predominantly cathemeral (Gerber et al. 2012*b*; Farris et al. 2015*a*). By jointly investigating the spatial-temporal habitat use of fosas, we found that they do occur widely across forested sites but vary when they use a site based on its proximity to anthropogenic activity. For example, fosas at Ranomafana were nocturnal near human villages, which occur along the edges of the protected forest. At the forest interior, fosas were cathemeral. These findings indicate that within specific habitats, fosas can be active during day and night hours, but human activity and development limit fosas to roughly half of their potential activity period. However, the level and type of human disturbance is important in predicting fosa diel activity, as we did not find support that human activity affected diel occurrence at Makira; this is likely due to predictable diurnal human activity and locations of camera sites that were connected to core forest habitat at greater distances from human villages (Farris et al. 2015*b*).

Similar to our findings for fosas, coyotes exhibited variation in diel activity across anthropogenic gradients. In contrast with fosas, however, coyotes are generally considered to be crepuscular in natural environment (McClennen et al. 2001). We found that coyotes used sites during the day and night at low levels of urban intensity. However, as urban intensity increased, diel use of sites transitioned to be nocturnal. In combination with this, we found that the marginal occupancy of coyotes, irrespective of diel state, decreased with increasing urban intensity. Thus, while coyotes occupy less habitat in the core of Chicago, the habitat they do occupy is generally used at night.

A special feature of the dynamic MSDOM is that the transition matrix provides additional information on diel use, which helps disentangle the expected occupancy

patterns in how coyotes used diel time across space. For example, while it was relatively rare for coyotes to use highly urban sites during the day and night, their probability to persist from one season to the next in this state was high. Conversely, coyotes were most likely to use highly urban sites only at night but were most likely to become locally extinct when this occurred (i.e., transition to the no-use state). Thus, even though coyotes were more likely to use highly urban sites at night, the use of these sites is more ephemeral than the urban sites coyotes use throughout the entire diel period. Because urban coyotes typically have home ranges roughly twice the size of their rural counterparts (Gese et al. 2012), we suspect that in the urban core coyotes use pockets of primary habitat during the day and night and venture out to secondary or tertiary habitat patches exclusively at night, when human activity levels are low.

As the definition of habitat has evolved to better recognize the value of time, so too should our modeling approaches. Our MSDOM achieves this and can measure the effect of continuous covariates to quantify change in diel behavior across space and through time. Although understanding habitat use of species has been critical in making informed conservation and management decisions (Guisan et al. 2013), current land-planning tools are often limited to spatial considerations (Gaynor et al. 2018). Although progress has been made in protecting habitats used over longer timescales, such as seasons, we lacked informative tools to protect habitat during critical diel periods, such as when sensitive species are feeding or performing mating displays. Advanced modeling approaches that estimate diel habitat use will be an asset in supporting successful conservation and land management strategies in a rapidly changing world.

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Statement of Authorship

K.R., M.F., and B.D.G. conceptualized the manuscript, and K.R., M.F., B.D.G., and Z.J.F. wrote the first draft. K.R. and B.D.G. conducted data and model analysis and data visualization for the fosa case studies. M.F. conducted data and model analysis and data visualization for the coyote case study. B.D.G., Z.J.F., S.B.M., and A.M. supported field data

methodologies and collection. All authors reviewed and edited the manuscript.

Data and Code Availability

All data and code can be found at <https://github.com/bgerber123/multi.state.diel.occupancy.model> (<https://doi.org/10.5281/zenodo.6014030>; Gerber et al. 2022). All data have been archived in the Dryad Digital Repository (<https://doi.org/10.5061/dryad.bvq83bk9w>; Rivera 2022).

Literature Cited

- Anderson, S. R., and J. J. Wiens. 2017. Out of the dark: 350 million years of conservatism and evolution in diel activity patterns in vertebrates. *Evolution* 71:1944–1959.
- Angelier, C. C. S., C. Adams-Hosking, K. M. P. M de B. Ferraz, M. P. de Souza, and C. A. McAlpine. 2016. Using species distribution models to predict potential landscape restoration effects on puma conservation. *PLoS ONE* 11:e0145232.
- Azzou, S. A. K., L. Singer, T. Aebischer, M. Caduff, B. Wolf, and D. Wegmann. 2021. A sparse observation model to quantify species distributions and their overlap in space and time. *Ecography* 44:1–13.
- Bekoff, M., and E. Gese. 2003. Coyote (*Canis latrans*). USDA National Wildlife Research Center, staff publication 224.
- Bennie, J., J. P. Duffy, R. Inger, and K. J. Gaston. 2014. The biogeography of time partitioning in mammals. *Proceedings of the National Academy of Sciences of the USA* 111:13727–13732.
- Borgerson, C. 2016. Optimizing conservation policy: the importance of seasonal variation in hunting and meat consumption on the Masoala Peninsula of Madagascar. *Oryx* 50:405–418.
- Campomizzi, A. J., J. A. Butcher, S. L. Farrell, A. G. Snelgrove, B. A. Collier, K. L. Gutzwiller, M. L. Morrison, and R. N. Wilkins. 2008. Conspecific attraction is a missing component in wildlife habitat modeling. *Journal of Wildlife Management* 72:331–336.
- Carter, N., B. Shrestha, J. Karki, N. Pradhan, and J. Liu. 2012. Coexistence between wildlife and humans at fine spatial scales. *Proceedings of the National Academy of Sciences of the USA* 109:15360–15365.
- CMAP (Chicago Metropolitan Agency for Planning). 2016. High-resolution land cover, Cook County, 2010. October 8, 2014. Accessed March 16, 2020. <https://datahub.cmap.illinois.gov/dataset/high-resolution-land-cover-cook-county-2010>.
- Dai, B., S. Ding, and G. Wahba. 2013. Multivariate Bernoulli distribution. *Bernoulli* 19:1465–1483.
- Denwood, M. J. 2016. runjags: an R package providing interface utilities, model templates, parallel computing methods and additional distributions for MCMC models. *JAGS Journal of Statistical Software* 71:25.
- Distiller, G. B., D. L. Borchers, R. J. Foster, and B. J. Harmsen. 2020. Using continuous-time spatial capture-recapture models to make inference about animal activity patterns. *Ecology and Evolution* 10:11826–11837.
- Elliot, E. E., S. Vallance, and L. E. Molles. 2016. Coexisting with coyotes (*Canis latrans*) in an urban environment. *Urban Ecosystems* 19:1335–1350.
- Ellington, E. H., E. M. Muntz, and S. D. Gehrt. 2020. Seasonal and daily shifts in behavior and resource selection: how a carnivore navigates costly landscapes. *Oecologia* 194:87–100.
- Ellis, E. C., K. K. Goldewijk, S. Siebert, D. Lightman, and N. Ramankutty. 2010. Anthropogenic transformation of the biomes, 1700 to 2000. *Global Ecology and Biogeography* 19:589–606.
- Enright, J. T. 1970. Ecological aspects of endogenous rhythmicity. *Annual Review of Ecology and Systematics* 1:221–238.
- Farris, Z. J., B. D. Gerber, S. Karpanty, A. Murphy, V. Andrianjakarivelo, F. Ratelolahy, and M. J. Kelly. 2015a. When carnivores roam: temporal patterns and overlap among Madagascar's native and exotic carnivores. *Journal of Zoology* 296:45–57.
- Farris, Z. J., B. D. Gerber, K. Valenta, R. Rafaliarison, J. C. Razafimahaimodison, E. Larney, T. Rajaonarivelo, Z. Randriana, P. C. Wright, and C. A. Chapman. 2017. Threats to a rainforest carnivore community: a multi-year assessment of occupancy and co-occurrence in Madagascar. *Biological Conservation* 210:116–124.
- Farris, Z. J., C. D. Golden, S. Karpanty, A. Murphy, D. Stauffer, F. Ratelolahy, V. Andrianjakarivelo, C. M. Holmes, and M. J. Kelly. 2015b. Hunting, exotic carnivores, and habitat loss: anthropogenic effects on a native carnivore community, Madagascar. *PLoS ONE* 10:e0136456.
- Fidino, M., and S. B. Magle. 2017. Using Fourier series to estimate periodic patterns in dynamic occupancy models. *Ecosphere* 8:e01944.
- Fidino, M., J. L. Simonis, and S. B. Magle. 2019. A multistate dynamic occupancy model to estimate local colonization–extinction rates and patterns of co-occurrence between two or more interacting species. *Methods in Ecology and Evolution* 10:233–244.
- Fiske, I., and R. Chandler. 2011. unmarked: an R package for fitting hierarchical models of wildlife occurrence and abundance. *Journal of Statistical Software* 43, <https://doi.org/10.18637/jss.v043.i10>.
- Gallo, T., M. Fidino, B. D. Gerber, A. A. Ahlers, J. L. Angstmann, M. Amaya, D. Drake, D. Gay, E. W. Lehrer, M. H. Murray, and T. J. Ryan. 2021. Mammals adjust diel activity across gradients of urbanization. *bioRxiv*, <https://doi.org/10.1101/2021.09.24.461702>.
- Gaston, K. J. 2019. Nighttime ecology: the “nocturnal problem” revisited. *American Naturalist* 193:481–502.
- Gaynor, K. M., C. E. Hojnowski, N. H. Carter, and J. S. Brashares. 2018. The influence of human disturbance on wildlife nocturnality. *Science* 360:1232–1235.
- Gehrt, S. D. 2007. Ecology of coyotes in urban landscapes. *Wildlife Damage Management Conferences—Proceedings* 63.
- Gelman, A., and D. B. Rubin. 1992. Inference from iterative simulation using multiple sequences. *Statistical Science* 7:457–472.
- Gerber, B. D., and C. E. Hawkins. Forthcoming. *Cryptoprocta ferox*, fosa. In S. M. Goodman, ed. *The new natural history of Madagascar*. Princeton University Press, Princeton, NJ.
- Gerber, B. D., S. M. Karpanty, and J. Randrianantenaina. 2012a. Activity patterns of carnivores in the rain forests of Madagascar: implications for species coexistence. *Journal of Mammalogy* 93:667–676.
- Gerber, B. D., F. Mason, and K. Rivera. 2022. bgerber123/multi.state.diel.occupancy.model: Zenodo archive MSDOM. *American Naturalist*, Zenodo, <https://doi.org/10.5281/zenodo.6011753>.
- . 2012b. The impact of forest logging and fragmentation on carnivore species composition, density and occupancy in Madagascar's rainforests. *Oryx* 46:414–422.

- Gese, E. M., P. S. Morey, and S. D. Gehrt. 2012. Influence of the urban matrix on space use of coyotes in the Chicago metropolitan area. *Journal of Ethology* 30:413–425.
- Golden, C. D. 2009. Bushmeat hunting and use in the Makira Forest, north-eastern Madagascar: a conservation and livelihoods issue. *Oryx* 43:386–392.
- Goodman, S. M. 2012. Les carnivora de Madagascar. Association Vahatra, Antananarivo.
- Goodman, S. M., M. J. Raheerilalao, and S. Wohlhause. 2019. The terrestrial protected areas of Madagascar: their history, description, and biota. 3rd ed. Association Vahatra, Antananarivo.
- Guisan, A., R. Tingley, J. B. Baumgartner, I. Naujokaitis-Lewis, P. R. Sutcliffe, A. I. T. Tulloch, T. J. Regan, et al. 2013. Predicting species distributions for conservation decisions. *Ecology Letters* 16:1424–1435.
- Hammer, R. B., S. I. Stewart, R. L. Winkler, V. C. Radeloff, and P. R. Voss. 2004. Characterizing dynamics spatial and temporal residential density patterns from 1940–1990 across the North Central United States. *Landscape and Urban Planning* 69:183–199.
- Helm, B., M. E. Visser, W. Schwartz, N. Kronfeld-Schor, M. Gerkema, T. Piersma, and G. Bloch. 2017. Two sides of a coin: ecological and chronobiological perspectives of timing in the wild. *Philosophical Transactions of the Royal Society B* 372:20160246.
- Hirzel, A. H., G. Le Lay, V. Helfer, C. Randin, and A. Guisan. 2006. Evaluating the ability of habitat suitability models to predict species presences. *Ecological Modelling* 199:142–152.
- Hody, J. W., and R. Kays. 2018. Mapping the expansion of coyotes (*Canis latrans*) across North and Central America. *ZooKeys* 759:81–97.
- Hooten, M. B., and N. T. Hobbs. 2015. A guide to Bayesian model selection for ecologists. *Ecological Monographs* 85:3–28.
- James, G., D. Witten, T. Hastie, and R. Tibshirani. 2013. An overview of statistical learning. Page 1 *in* An introduction to statistical learning with applications in R. Springer, New York.
- Kass, J. M., M. W. Tingley, T. Tetsuya, and F. Koike. 2020. Co-occurrence of invasive and native carnivores affects occupancy patterns across environmental gradients. *Biological Invasions* 22:2251–2266.
- Kearney, M. 2006. Habitat, environment, and niche: what are we modelling? *Oikos* 115:186–191.
- Kilgo, J., R. Labisky, and D. Fritzen. 1998. Influences of hunting on the behavior of white-tailed deer: implications for conservation of the Florida panther. *Conservation Biology* 12:1359–1364.
- Kotschwar Logan, M., B. D. Gerber, S. M. Karpanty, S. Justin, and F. N. Rabenahy. 2014. Assessing carnivore distribution from local knowledge across a human-dominated landscape in central-southeastern Madagascar. *Animal Conservation* 18:82–91.
- Kronfeld-Schor, N., M. E. Visser, L. Salis, and J. A. van Gils. 2017. Chronobiology of interspecific interactions in a changing world. *Philosophical Transactions of the Royal Society B* 372:20160248.
- Lenth, B. E., R. L. Knight, and M. E. Brennan. 2008. The effects of dogs on wildlife communities. *Natural Areas Journal* 28:218–227.
- Long, R. A., T. M. Donovan, P. MacKay, W. J. Zielinski, and J. S. Buzas. 2011. Predicting carnivore occurrence with noninvasive surveys and occupancy modeling. *Landscape Ecology* 26:327–340.
- MacKenzie, D. I., L. L. Bailey, and J. D. Nichols. 2004. Investigating species co-occurrence patterns when species are detected imperfectly. *Journal of Animal Ecology* 73:546–555.
- MacKenzie, D. I., J. D. Nichols, J. E. Hines, M. G. Knutson, and A. B. Franklin. 2003. Estimating site occupancy, colonization, and local extinction when a species is detected imperfectly. *Ecology* 84:2200–2207.
- MacKenzie, D. I., J. D. Nichols, G. B. Lachman, S. Droege, J. A. Royle, and C. A. Langtimm. 2002. Estimating site occupancy rates when detection probabilities are less than one. *Ecology* 83:2248–2255.
- MacKenzie, D. I., J. D. Nichols, J. A. Royle, K. H. Pollock, L. Bailey, and J. E. Hines. 2017. *Occupancy estimation and modeling: inferring patterns and dynamics of species occurrence*. 2nd ed. Academic Press, Cambridge.
- MacKenzie, D. I., J. D. Nichols, M. E. Seamans, and R. J. Gutiérrez. 2009. Modeling species occurrence dynamics with multiple states and imperfect detection. *Ecology* 90:823–835.
- Magle, S. B., M. Fidino, E. W. Lehrer, T. Gallo, M. P. Mulligan, M. J. Rios, A. A. Ahlers, et al. 2019. Advancing urban wildlife research through a multi-city collaboration. *Frontiers in Ecology and the Environment* 17:232–239.
- Martin, C. W., L. K. Reynolds, W. A. S. Tiffany, and S. Kopetman. 2021. Diel variability and influence of artificial light on fish and macroinvertebrate communities in Gulf of Mexico seagrass beds. *Estuaries and Coasts* 44:431–441.
- McClennen, N., R. R. Wigglesworth, and S. H. Anderson. 2001. The effect of suburban and agricultural development on the activity patterns of coyotes (*Canis latrans*). *American Midland Naturalist* 146:27–36.
- Mitchell, S. C. 2005. How useful is the concept of habitat? a critique. *Oikos* 110:634–638.
- Morano, S., K. M. Stewart, T. Dilts, A. Ellsworth, and V. C. Bleich. 2019. Resource selection of mule deer in a shrub-steppe ecosystem: influence of woodland distribution and animal behavior. *Ecosphere* 10:e02811.
- Morelli, T. L., A. B. Smith, A. N. Mancini, E. A. Balko, C. Borgerson, R. Dolch, Z. J. Farris, et al. 2020. The fate of Madagascar's rainforest habitat. *Nature Climate Change* 10:89–96.
- Nichols, J. D., J. E. Hines, D. I. Mackenzie, M. E. Seamans, and R. J. Gutiérrez. 2007. Occupancy estimation and modeling with multiple states and state uncertainty. *Ecology* 88:1395–1400.
- Northrup, J. M., and B. D. Gerber. 2018. A comment on priors for Bayesian occupancy models. *PLoS ONE* 14:e0212346.
- Northrup, J. M., E. Vander Wal, M. Bonar, J. Fieberg, M. P. Laforge, M. Leclerc, C. Prokopenko, and B. D. Gerber. 2022. Conceptual and methodological advances in habitat-selection modeling: guidelines for ecology and evolution. *Ecological Applications* 32:e02470.
- Odum, E. P. 1975. The ecosystem. Page 46 *in* *Ecology: the link between the natural and social sciences*. 2nd ed. Holt, Rinehart, & Winston, New Delhi.
- Pianka, E. R. 1973. The structure of lizard communities. *Annual Review of Ecology and Systematics* 4:53–74.
- Plummer, M. 2003. JAGS: a program for analysis of Bayesian graphical models using Gibbs sampling. *Proceedings of the 3rd International Workshop on Distributed Statistical Computing*, Vienna.
- Ridout, M. S., and M. Linkie. 2009. Estimating overlap of daily activity patterns from camera trap data. *Journal of Agriculture, Biological, and Environmental Statistics* 14:322–337.

Rivera, K., M. Fidino, Z. J. Farris, S. B. Magle, A. Murphy, and B. D. Gerber. 2022. Multi-state diel occupancy model, Dryad, data set, <https://doi.org/10.5061/dryad.bvq83bk9w>.

Rota, C. T., M. A. R. Ferreira, R. W. Kays, T. D. Forrester, E. L. Kalies, W. J. McShea, A. W. Parsons, and J. J. Millsbaugh. 2016. A multispecies occupancy model for two or more interacting species. *Methods in Ecology and Evolution* 7:1164–1173.

Rovero, F., F. Zimmermann, D. Berzi, and P. Meek. 2013. “Which camera trap type and how many do I need?” a review of camera features and study designs for a range of wildlife research applications. *Hystrix* 24:148–156.

Segurado, P., and M. B. Araújo. 2004. An evaluation of methods for modelling species distributions. *Journal of Biogeography* 31:1555–1568.

Smith, J. A., J. P. Suraci, M. Clinchy, A. Crawford, D. Roberts, L. Y. Zarette, and C. C. Wilmsers. 2017. Fear of the human “super predator” reduces feeding time in large carnivores. *Philosophical Transactions of the Royal Society B* 284:20170433.

Thieurmel, B., and A. Elmarhraoui. 2019. Suncalc. R package version 0.5.0.

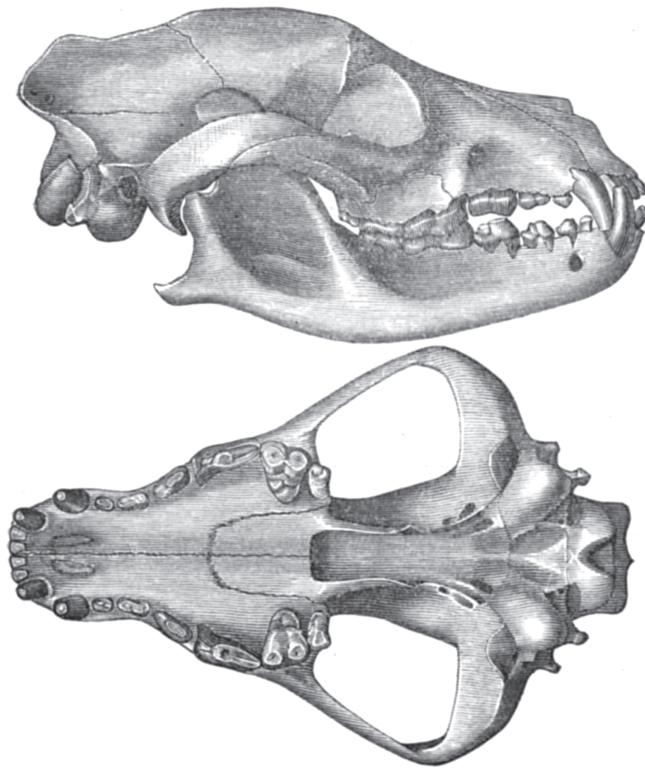
Way, J. G., I. M. Ortega, and E. G. Strauss. 2004. Movement and activity patterns of eastern coyotes in a coastal, suburban environment. *Northeastern Naturalist* 11:237–254.

References Cited Only in the Online Enhancements

Broms, K. M., M. B. Hooten, and R. M. Fitzpatrick. 2016. Model selection and assessment for multi-species occupancy models. *Ecology* 97:1759–1770.

Monterroso, P., F. Díaz-Ruiz, P. M. Lukacs, P. C. Alves, and P. Ferreras. 2020. Ecological traits and the spatial structure of competitive coexistence among carnivores. *Ecology* 101:e03059.

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“In all three species the premolars are very robust, as though to aid the sectorials in crushing bones, as they do in the hyænas.” Figured: “*Ælurodon sævus* Leidy. . . . From the Loup Fork beds of Nebraska.” From “On the Extinct Dogs of North America” by E. D. Cope (*The American Naturalist*, 1883, 17:235–249).