

RETHINKING HABITAT AND HOW WE STUDY
HUMAN-WILDLIFE RELATIONSHIPS

BY

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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. The first chapter of this manuscript focuses on redeveloping occupancy models to incorporate hypotheses on species diel habitat use. This alternative occupancy framework, called the multi-state diel occupancy model (MSDOM), can evaluate species diel activity against continuous response variables which may impact diel activity within and across seasons or years. We used two case studies on fosa, a mesocarnivore endemic to Madagascar, and coyote in Chicago, USA, 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 altered their diel activity across intensity of human disturbance—in and across years, and by degree of human disturbance. Our results exemplify the importance of understanding animal diel activity patterns and how human disturbance can lead to temporal habitat loss. This adapted model will allow future studies to answer explicit questions in regards to species diel habitat use and direct conservation efforts to protecting habitats over shorter, diel, periods. Chapter two of this manuscript focuses on incorporating human dimension research to understand relationships between people and wildlife. Human dimension research in ecology is especially needed in urban landscapes where more wildlife are living among and adapting to human dominated landscapes. Thus, we focus on understanding the complex drivers of human-wildlife relationships that have become increasingly important for managing both people and wildlife. A common approach to

researching these drivers is via survey questionnaires and the use of Likert items and scales, which require analytical techniques that handle their unique structure. Here, we apply a hierarchical Bayesian modeling framework to conduct ordinal regression that is well suited to Likert response data and allows the evaluation and comparison of model hypotheses. Our case study focuses on two objectives, understanding how people value coyotes and the frequency in which people interact with coyotes. We measured how people value coyotes with a Likert scale on peoples perceived risks and benefits of having coyotes on a landscape and measure frequencies of interactions with two Likert items on people's sightings and incidents (growling, stalking attacking people or owned animals) with coyotes. We investigated how people's demographics, knowledge of coyotes, and relationship with nature impacted the above response variables. We found strong support that decreasing connectedness to nature, fear of coyotes, and incidents between coyotes and owned animals (pets or livestock), negatively impacts people's value of coyotes while pet ownership positively impacted peoples value of coyotes. Additionally, we found value of coyotes to vary across gender and counties; specifically, we found females to value coyotes more positively than males and found people from Bristol and Newport counties to have the most negative value coyotes. We found strong support that animal ownership and fear of coyotes, positively impacted coyote sightings and incidents. Coyote sightings and incidents also varied across counties and occurred most frequently in Bristol and Newport. These results highlight that human demographics and characteristics can shape people's value and interactions with endemic wildlife. Through the application of ordinal regression, we were able to estimate how human demographics and characteristics impact people value of wildlife (positively or

negatively) and how the frequency of interactions vary across groups of people. Through these findings, conservationists and wildlife managers can target mitigation and educational efforts to specific constituents which least value or most interact with coyotes. Importantly, this study highlights the importance of fear in shaping people's value and interactions with coyotes, therefore we encourage more research on assuaging fear of local wildlife.

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PREFACE

The two chapters of this thesis have been provided in the manuscript format of the respective journals they were submitted to. Manuscript 1 (includes Tables, Figures, and References A) follows the *American Naturalist* journal guidelines, and Manuscript 2 (includes Tables, Figures, and References B) follows the *Urban Ecosystems* journal guidelines. The end of each chapter contains references.

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**Rethinking habitat occupancy modeling and the role of diel activity in
an anthropogenic world**

KEYWORDS: camera traps, diel, habitat, multi-state, occupancy, spatial-temporal, temporal activity

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1. INTRODUCTION

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

Understanding a species’ or communities’ 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. (1971) 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). 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 models (Northrup et al., In Press). 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 (Angelieri et al., 2016; Hirzel et al., 2006). 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 (Fidino and Magle, 2017; MacKenzie et al., 2003). 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; Gaston, 2019; Helm et al., 2017). The limited studies that do consider space use and diel activity, predominantly treat them separately (not modeled in a single framework), or observations are associated with categorical predictor variables rather than more informative scales, or continuous predictor variables (e.g. distance from important features, etc.) Thus these models only provide descriptive inferences, as done with circular kernel density methods (Ridout and Linkie, 2009), rather than an explicit estimation of hypothesized effects (James et al, 2013). Therefore, past studies have largely focused on 'average daily conditions rather than those prevailing at the time of day when individuals would tend to be most active' (Gaston, 2019).

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, meso- and large-carnivores have been found to increase their nocturnal activity in urbanized areas (Carter et al., 2012; Gehrt, 2007), 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) who temporally avoid domestic dogs (Farris et al. 2015; Lenth et al. 2008). By modifying behavior across the 24-hour 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 relationship 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 which can incorporate continuous covariates on diel behavior, account for variation in detectability, and 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 and Gallo et al., 2021). As such, we redeveloped static and dynamic occupancy models (Long et al., 2011) in a Bayesian framework to incorporate diel activity information and variation in detection and sampling methodology through the incorporation of random effects (multi-state diel occupancy

models; MSDOM). We exemplify these models by investigating how anthropogenic development and activity may simultaneously alter 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 coyote (*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 (Azzou et al., 2021; Distiller et al., 2020; Gallo et al., 2021).

2. MATERIALS AND METHODS

2.2.1 Multi-state diel occupancy models

2.2.1.1 *Static Model: a single season occupancy analysis*

The MSDOM is a form of the multi-state occupancy model with state uncertainty (MacKenzie et al., 2009; Nichols et al., 2007) 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 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 & 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 multi-state 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.

2.2.1.1.1 Full Model (no covariates)

Let ψ^m be the probability that a site is in occupancy state m where $\boldsymbol{\Psi} = [\psi^1 \ \psi^2 \ \psi^3 \ \psi^4]$ is the state probability vector, $\psi^1 = 1 - \psi^2 - \psi^3 - \psi^4$, and $\mathbf{1} \cdot \boldsymbol{\Psi} = 1$ (see parameter descriptions in Appendix S1). The marginal occupancy probability (regardless of state) is $\psi^\bullet = \psi^2 + \psi^3 + \psi^4$. Then, let, $p_j^{m,l}$ be the probability of observing the occupancy state l , given the true state is m in j survey. 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,

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

Equation 1

Together, the true occupancy state for site i is defined by the latent variable,

$\mathbf{z}_i \sim \text{Categorical}(\boldsymbol{\psi})$ and the observed state in survey j is defined as, $y_{ij} \sim$

$\text{Categorical}(\mathbf{P}_{z_i})$. Taking a Bayesian modeling framework, we can assume diffuse prior

distributions for model parameters as $\boldsymbol{\psi}, \mathbf{P}_4 \sim \text{Dirichlet}(1,1,1,1)$ 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., $p^{2,2}$, $p^{3,3}$, P_4) and occupancy probabilities (i.e., ψ^2 , ψ^3 , ψ^4) across associated M states. Specifically, state 4 ('night & day use') occupancy and detection is not defined by state 2 ('day use') and 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 & day' state may be cathemeral, indicating 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' state given it is present, is $\frac{\psi^3}{\psi^\bullet}$.

2.2.1.1.2 *Reduced Model (no covariates)*

The reduced model is a simpler parameterization that defines the occupancy and detection probabilities of state 4 ('night & day use') as the product of states 2 and 3. Therefore, we assume the diel time periods of 'night & 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 & 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,

$$\psi^1 = (1 - \psi^{\text{Day.M}})(1 - \psi^{\text{Night.M}})$$

$$\psi^2 = \psi^{\text{Day.M}}(1 - \psi^{\text{Night.M}})$$

$$\psi^3 = (1 - \psi^{\text{Day.M}})\psi^{\text{Night.M}}$$

$$\psi^4 = \psi^{\text{Day.M}}\psi^{\text{Night.M}}.$$

Equation 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,

$\mathbf{P} =$

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

Equation 3

We can assume diffuse prior distributions for our reduced model parameters:

$$\psi^{\text{Day.M}}, \psi^{\text{Night.M}}, p^{\text{Day.M}}, p^{\text{Night.M}} \sim \text{Beta}(1,1).$$

2.2.1.1.3 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 multi-state framework for model comparison purposes. Our state occupancy probabilities are then,

$$\begin{aligned} \psi^1 &= 1 - \psi^\bullet \\ \psi^2 &= \frac{\psi^\bullet}{3} \\ \psi^3 &= \frac{\psi^\bullet}{3} \\ \psi^4 &= \frac{\psi^\bullet}{3}, \end{aligned}$$

Equation 4

with the following detection matrix,

$$\mathbf{P} = \begin{bmatrix} 1 & 0 & 0 & 0 \\ 1 - p^\bullet & p^\bullet & 0 & 0 \\ 1 - p^\bullet & 0 & p^\bullet & 0 \\ 1 - p^\bullet & \frac{p^\bullet}{3} & \frac{p^\bullet}{3} & \frac{p^\bullet}{3} \end{bmatrix}.$$

Equation 5

We can assume the following diffuse prior distributions for the null model parameters:

$$\psi^\bullet, p^\bullet \sim \text{Beta}(1,1).$$

2.2.1.1.4 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 ($\mathbf{x}_i^{Day}, \mathbf{x}_i^{Night}, \mathbf{x}_i^{ND}$) that for each site i , are $1 \times Q_m$ (the number of columns) and associated vectors of coefficients ($\alpha^{Day}, \alpha^{Night}, \alpha^{ND}$) 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,

$$\psi_i^1 = \frac{\phi_i^1}{\phi_i^1 + \phi_i^2 + \phi_i^3 + \phi_i^4}$$

$$\psi_i^2 = \frac{\phi_i^2}{\phi_i^1 + \phi_i^2 + \phi_i^3 + \phi_i^4}$$

$$\psi_i^3 = \frac{\phi_i^3}{\phi_i^1 + \phi_i^2 + \phi_i^3 + \phi_i^4}$$

$$\psi_i^4 = \frac{\phi_i^4}{\phi_i^1 + \phi_i^2 + \phi_i^3 + \phi_i^4}$$

$$\phi_i^1 = 1$$

$$\phi_i^2 = e^{\mathbf{x}_i^{Day} \alpha^{Day}}$$

$$\phi_i^3 = e^{\mathbf{x}_i^{Night} \alpha^{Night}}$$

$$\phi_i^4 = e^{x_i^{Day} \alpha^{Day} + x_i^{Night} \alpha^{Night} + x_i^{ND} \alpha^{ND}}.$$

Equation 6

Here, ϕ_i^2 and ϕ_i^3 only contain first-order parameters, which respectively represent the log-odds that a species occupies site i in either state 2 or 3 (i.e., they are associated to a single state). The parameter ϕ_i^4 , however, also contains second-order parameters ($x_i^{ND} \alpha^{ND}$), which represent the log-odds difference a species occupies site i in state ‘night & day’ relative to the aforementioned first-order parameters (see Dai et al., 2013). Thus, the second-order parameters for the ‘night & day’ state allows us to evaluate if this state is different than the day and night states combined. To specify the reduced model, we remove $x_i^{ND} \alpha^{ND}$ 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,

$$\begin{aligned}\phi_i^1 &= 3 \\ \phi_i^2 &= e^{x_i \alpha} \\ \phi_i^3 &= e^{x_i \alpha} \\ \phi_i^4 &= e^{x_i \alpha}.\end{aligned}$$

Equation 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 <https://github.com/bgerber123/multi.state.temporal.activity.git>).

2.2.1.2 *Dynamic Model: across season occupancy analysis*

The dynamic MSDOM considers how site use at the diel scale changes over longer-time scales, 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 occupancy state, $\mathbf{z}_{i,t}$, depends on the state in the previous primary period, $\mathbf{z}_{i,t-1}$, 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 $\boldsymbol{\tau}$ 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.

2.2.1.2.1 *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 datasets to be used.

For the full model, let $\boldsymbol{\tau}$ be

$$\boldsymbol{\tau} = \begin{bmatrix} (1 - \gamma^D)(1 - \gamma^N) & \gamma^D(1 - \gamma^N) & (1 - \gamma^D)\gamma^N & \gamma^D\gamma^N \\ \varepsilon^D(1 - \gamma^{N|D}) & (1 - \varepsilon^D)(1 - \gamma^{N|D}) & \varepsilon^D\gamma^{N|D} & (1 - \varepsilon^D)\gamma^{N|D} \\ (1 - \gamma^{D|N})\varepsilon^N & \gamma^{D|N}\varepsilon^N & (1 - \gamma^{D|N})(1 - \varepsilon^N) & \gamma^{D|N}(1 - \varepsilon^N) \\ \varepsilon^{D|N}\varepsilon^{N|D} & (1 - \varepsilon^{D|N})\varepsilon^{N|D} & \varepsilon^{D|N}(1 - \varepsilon^{N|D}) & (1 - \varepsilon^{D|N})(1 - \varepsilon^{N|D}) \end{bmatrix}$$

,

Equation 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 3 (‘night use’) is $\tau^{2,3} = \varepsilon^D \gamma^{N|D}$, where ε^D is the site extinction probability in the ‘day use’ state and $\gamma^{N|D}$ is the probability of colonization of the ‘night use’ state given ‘day use’ 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 $\mathbf{z}_{i,1} \sim \text{Categorical}(\Psi_i)$ for $t=1$ and $\mathbf{z}_{i,t} \sim \text{Categorical}(\boldsymbol{\tau}_{\mathbf{z}_{i,t-1}})$ for $t > 1$, where $\mathbf{z}_{i,t-1}$ indexes the appropriate row of $\boldsymbol{\tau}$. The observed state is specified like the full static MSDOM, except we indexed the observed data and latent state through time such that $y_{ijt} \sim \text{Categorical}(\mathbf{P}_{\mathbf{z}_{i,t}})$, where \mathbf{P} is Eq. 1 and $\mathbf{z}_{i,t}$ indexes the appropriate row of \mathbf{P} . Finally, we assume the same diffuse prior distributions as the full static MSDOM for $\boldsymbol{\psi}$ and \mathbf{P} while all colonization ($\boldsymbol{\gamma}$) and extinction ($\boldsymbol{\varepsilon}$) parameters have their own respective Beta (1,1) distributions.

2.2.1.2.2 *Reduced model (no covariates)*

The reduced dynamic model is similar to the full dynamic model except initial occupancy becomes Eq. 2, $\boldsymbol{\tau}$ lacks conditional parameters, and \mathbf{P} becomes Eq. 3. Therefore, $\boldsymbol{\tau}$ simplifies to

$$\boldsymbol{\tau} = \begin{bmatrix} (1 - \gamma^D)(1 - \gamma^N) & \gamma^D(1 - \gamma^N) & (1 - \gamma^D)\gamma^N & \gamma^D\gamma^N \\ \varepsilon^D(1 - \gamma^N) & (1 - \varepsilon^D)(1 - \gamma^N) & \varepsilon^D\gamma^N & (1 - \varepsilon^D)\gamma^N \\ (1 - \gamma^D)\varepsilon^N & \gamma^D\varepsilon^N & (1 - \gamma^D)(1 - \varepsilon^N) & \gamma^D(1 - \varepsilon^N) \\ \varepsilon^D\varepsilon^N & (1 - \varepsilon^D)\varepsilon^N & \varepsilon^D(1 - \varepsilon^N) & (1 - \varepsilon^D)(1 - \varepsilon^N) \end{bmatrix}.$$

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

2.2.1.2.3 *Null model (No covariates)*

Casting the dynamic MSDOM as a standard multi-season occupancy model requires splitting the associated colonization and extinction probabilities across each respective row of $\boldsymbol{\tau}$ to ensure each row still sums to 1 such that,

$$\boldsymbol{\tau} = \begin{bmatrix} 1 - \gamma & \gamma/3 & \gamma/3 & \gamma/3 \\ \varepsilon & (1 - \varepsilon)/3 & (1 - \varepsilon)/3 & (1 - \varepsilon)/3 \\ \varepsilon & (1 - \varepsilon)/3 & (1 - \varepsilon)/3 & (1 - \varepsilon)/3 \\ \varepsilon & (1 - \varepsilon)/3 & (1 - \varepsilon)/3 & (1 - \varepsilon)/3 \end{bmatrix}.$$

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

2.2.1.2.4 *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,

$$\begin{aligned}
\beta_i^{\gamma^D} &= \mathbf{x}_i^D \mathbf{b}^D & \beta_i^{\gamma^{D|N}} &= \mathbf{x}_i^{D|N} \mathbf{g}^{D|N} \\
\beta_i^{\gamma^N} &= \mathbf{x}_i^N \mathbf{b}^N & \beta_i^{\gamma^{N|D}} &= \mathbf{x}_i^{N|D} \mathbf{g}^{N|D} \\
\beta_i^{\varepsilon^D} &= \mathbf{x}_i^D \mathbf{d}^D & \beta_i^{\varepsilon^{D|N}} &= \mathbf{x}_i^{D|N} \mathbf{h}^{D|N} \\
\beta_i^{\varepsilon^N} &= \mathbf{x}_i^N \mathbf{d}^N & \beta_i^{\varepsilon^{N|D}} &= \mathbf{x}_i^{N|D} \mathbf{h}^{N|D}
\end{aligned}$$

Equation 11

for the dynamic model, $\beta_i^{\gamma^D}$, $\beta_i^{\gamma^N}$, $\beta_i^{\varepsilon^D}$, $\beta_i^{\varepsilon^N}$ are first-order parameters while $\beta_i^{\gamma^{D|N}}$, $\beta_i^{\gamma^{N|D}}$, $\beta_i^{\varepsilon^{D|N}}$, and $\beta_i^{\varepsilon^{N|D}}$ 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 $\boldsymbol{\omega}$ be a matrix with the same dimensions as $\boldsymbol{\tau}$ 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,

$$\boldsymbol{\omega}_i = \begin{bmatrix}
1 & e^{\beta_i^{\gamma^D}} & e^{\beta_i^{\gamma^N}} & e^{\beta_i^{\gamma^D} + \beta_i^{\gamma^N}} \\
e^{\beta_i^{\varepsilon^D}} & 1 & e^{\beta_i^{\varepsilon^D} + \beta_i^{\gamma^N} + \beta_i^{\gamma^{N|D}}} & e^{\beta_i^{\gamma^N} + \beta_i^{\gamma^{N|D}}} \\
e^{\beta_i^{\varepsilon^N}} & e^{\beta_i^{\gamma^D} + \beta_i^{\gamma^{D|N}} + \beta_i^{\varepsilon^N}} & 1 & e^{\beta_i^{\gamma^D} + \beta_i^{\gamma^{D|N}}} \\
e^{\beta_i^{\varepsilon^D} + \beta_i^{\varepsilon^{D|N}} + \beta_i^{\varepsilon^N} + \beta_i^{\varepsilon^{N|D}}} & e^{\beta_i^{\varepsilon^N} + \beta_i^{\varepsilon^{N|D}}} & e^{\beta_i^{\varepsilon^D} + \beta_i^{\varepsilon^{D|N}}} & 1
\end{bmatrix}.$$

2. Equation 12

Dividing each element of a row by its respective row sum (i.e, applying the multinomial logit-link) converts $\boldsymbol{\omega}_i$ to $\boldsymbol{\tau}_i$ (Fidino et al. 2019). The reduced model removes all second-order parameters from $\boldsymbol{\omega}_i$ and becomes,

$$\boldsymbol{\omega}_i = \begin{bmatrix} 1 & e^{\beta_i^{\gamma^D}} & e^{\beta_i^{\gamma^N}} & e^{\beta_i^{\gamma^D} + \beta_i^{\gamma^N}} \\ e^{\beta_i^{\varepsilon^D}} & 1 & e^{\beta_i^{\varepsilon^D} + \beta_i^{\gamma^N}} & e^{\beta_i^{\gamma^N}} \\ e^{\beta_i^{\varepsilon^N}} & e^{\beta_i^{\gamma^D} + \beta_i^{\varepsilon^N}} & 1 & e^{\beta_i^{\gamma^D}} \\ e^{\beta_i^{\varepsilon^D} + \beta_i^{\varepsilon^N}} & e^{\beta_i^{\varepsilon^N}} & e^{\beta_i^{\varepsilon^D}} & 1 \end{bmatrix}.$$

3. Equation 13

The null model, which is a multi-season occupancy model with covariates, $\boldsymbol{\omega}_i$ becomes,

$$\boldsymbol{\omega}_i = \begin{bmatrix} 3 & e^{\beta_i^{\gamma}} & e^{\beta_i^{\gamma}} & e^{\beta_i^{\gamma}} \\ 3 \times e^{\beta_i^{\varepsilon}} & 1 & 1 & 1 \\ 3 \times e^{\beta_i^{\varepsilon}} & 1 & 1 & 1 \\ 3 \times e^{\beta_i^{\varepsilon}} & 1 & 1 & 1 \end{bmatrix},$$

4. Equation 14

where β_i^{γ} and β_i^{ε} 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

Fosa are a medium size carnivore (5.5-9.9 kg; Goodman 2012) in the monophyletic Eupleridae family, which is endemic to Madagascar. Fosa 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 fosa near human settlements and their consumption of livestock has caused conflict with humans (Borgerson, 2016; Kotschwar Logan et al., 2014). Previous studies show their diel activity is largely cathemeral (Farris et al., 2015a; Gerber et al., 2012a). Their ubiquitous occurrence across forests and use of the entire 24-hour period (Gerber et al., In

Press) 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 regions (Gerber et al., 2012a; see Appendix S3; Table 1).

These two parks have unique histories which has 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 which impact fosa in these regions. Given high human activity within forests of Makira (Farris et al., 2015b) compared to Ranomafana (Farris et al., 2017; Gerber et al., 2012b), 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 were low in contrast to those in Makira. The riskiest areas for fosa 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 (see Gerber et al. 2012a for details).

We fit 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 the ‘day use’ state to be used least by fosa due to diurnal human activity near areas of high disturbance. Specifically, we predicted that fosa occupancy during the day would decrease with increasing human disturbance and 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 sunset, while night was defined by hours following civil sunset and before civil sunrise calculated through package `suncalc` (Thieurmel and Elmarhraoui, 2019) in R v 4.0.2. To determine detected diel states of fosa, we used 6-day occasions. All models were coded and fit in JAGS v. 4.0.2 (Plummer, 2003) with the `runjags` package (Denwood, 2016) in R v. 4.0.2. We assessed convergence using the Gelman–Rubin diagnostic (Gelman and Rubin, 1992) to ensure all values were < 1.1 and by visually examining traceplots 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 of parameter estimates included zero and deriving the probability of an effect being less than or greater than zero.

We fit 18 candidate models to two years (two seasons per year) of Ranomafana data (Appendix S3; Table 1): 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 (see Appendix S 3; Table 2). Over the two years, 111 camera traps were deployed 420–670 m apart across four primary, selectively-logged, and fragmented forests sites (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 Appendix S3; Fig 1) 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% credible interval ($\alpha^{\text{Day,Dist.Vill}} = -0.002$; 95% CI = -1.31, 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, 2.95; $P(\alpha^{\text{ND,Dist.Vill}} > 0) = 0.97$), supporting our hypothesis. These results suggest that if fosa use sites during day hours, it is in conjunction with night hours, and the probability of using sites during the day is greater further away from human disturbance. We also found moderate to strong support that night state occurrence declined with increasing distance to village ($\alpha^{\text{Night,Dist.Vill}} = -1.16$; 95% CI = -2.38, -0.02; $P(\alpha^{\text{Night,Dist.Vill}} < 0) = 0.98$). Results from conditional probabilities of use (given fosa are present) revealed similar probabilities (Fig 2B) to those of occurrence. This was due to the widespread distribution of fosa within the study area. We found the probability to detect fosa at night, given it was present during the day and night ($p^{4,3}$), to be the highest detection probability (see Appendix S3; Table 1). Detection of fosa during the day-night state ($p^{4,4}$) 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 6 candidate models to 7 years (two seasons per year) of Makira data (Appendix S3; Table 1): full, reduced, and null model, each with and without the human activity covariate; detection parameters were not modeled with covariates (see Appendix S3; Table 4). From 2008 - 2015, 18–26 camera traps were deployed across seven sites with varying levels of forest degradation (Farris et al., 2015b). We found all models to fit the data ($0.1 > \text{Bayesian GOF p-value} < 0.9$). 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 fosa occupancy was highest during the night state ($\psi^3 = 0.33$; 95% CI = 0.11, 0.60), followed by day, ($\psi^2 = 0.20$; 95% CI = 0.06, 0.44), and night & day state ($\psi^4 = 0.18$; 95% CI = 0.05, 0.41; Fig 3). The large parametric uncertainty of the detection parameters made drawing conclusions difficult, though results indicate fosa are most detectable at night when present during the night & day state (see Appendix S3; Table 5).

Coyote Case Study

Coyote 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, coyote 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 (Gehrt et al., 2007; Way et al., 2004). Therefore, we quantified whether coyote 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). Briefly, 105 cameras were placed along three 50 km transects radiating outward from downtown Chicago, Illinois, USA (see Appendix S3; Table 6). Data were summarized such that each 4-week deployment (e.g., 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 the fosa study. While the static MSDOM (with 4 states) can potentially have 3 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 fit 3 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 & 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 Eq. 3 as the detection matrix, which assumes that the probability of detecting ‘night & 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% credible intervals 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 v 4.3.0 in R v 4.0.3. We evaluated model convergence by inspecting traceplots to ensure proper mixing and using the Gelman-Rubin statistic.

Of the possible 1365 deployments (105 sites across 13 sampling periods), we collected data for 1172 deployments. ‘No use’ was the most observed state ($n = 650$), followed by ‘night use’ ($n = 286$), ‘night & day use’ ($n = 183$), and ‘day use’ ($n = 53$). Overall, the full model (22 parameters, CPO = 3131.46) had the most support, followed by the reduced (16 parameters, CPO = 3209.17) and then the null model (8 parameters, CPO = 3334.52). With the most supported model, the average occupancy probability during the first season was 0.41 for ‘no use’ (95% CI = 0.26, 0.56), 0.18 for ‘day use’ (95% CI = 0.06, 0.33), 0.07 for ‘night use’ (95% CI = 0.01, 0.19), and 0.32 for ‘night & day use’ (95% CI = 0.19, 0.48). Thus, assuming a site was occupied by coyote during the first primary period, coyote were on average, most likely to use sites during the day and night. Across the urbanization gradient, ‘day use’ was more negatively associated to urban intensity ($a_{URB}^D = -1.05$, 95% CI = -1.98, -0.07, $P(a_{URB}^D < 0) = 0.99$) than ‘night use’ ($a_{URB}^N = -0.65$, 95% CI = -1.51, 0.18, $P(a_{URB}^N < 0) = 0.94$). There was some evidence that ‘night & day’ use became more common with increasing urban intensity, but 95% credible intervals for this second-order parameter overlapped 0 ($a_{URB}^{DN} = 1.14$, 95% CI = -0.08, 2.50, $P(a_{URB}^{DN} > 0) = 0.97$). While the initial occupancy parameters demonstrate that ‘day use’ 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 ($\boldsymbol{\tau}$), which describe the processes that bring about coyote occupancy.

While it is equally important to explore the underlying colonization and extinction dynamics of the model, by solving the equation $\delta_i = \delta_i \tau_i$ where $\sum \delta_i = 1$ it is possible to derive the expected probability of each occupancy state at each site (Fidino et al. 2019). Doing so 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 predicted 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 'day use', 'night use' and 'night & day' given coyote presence. For example, $\Pr(\delta_i^N | \text{coyote presence}) = \delta_i^N / (\delta_i^D + \delta_i^N + \delta_i^{DN})$. Plotting these relationships reveals that while 'night & day use' is the most likely category at low levels of urban intensity, it is replaced by 'night' use 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, though this relationship became more pronounced at high levels of urban intensity (Fig. 5). The transitions from 'no use', which are described by γ^D and γ^N , were driven by the strongly negative first-order colonization intercepts for 'day use' ($b_{INT}^D = -2.95$, 95% CI = -3.88, -2.14, $P(b_{INT}^D < 0) = 1.00$) and night use ($b_{INT}^N = -1.47$, 95% CI = -1.85, -1.10, $P(b_{INT}^N < 0) = 1.00$), as well as a negative association between 'night use' and urban intensity ($b_{URB}^N = -0.36$, 95% CI = -0.62, -0.09, $P(b_{URB}^N < 0) = 0.99$). There was weak support that colonization of 'day use' negatively covaried with urban intensity ($b_{URB}^D = -0.28$, 95% CI = -0.74, 0.16, $P(b_{URB}^D < 0) = 0.89$).

While ‘night use’ negatively covaried with urban intensity, the relatively less negative intercept of this level of the model (i.e., $b_{INT}^N > b_{INT}^D$) 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 $\gamma^{D|N}$. At average levels of urban intensity, sites were most likely to transition to ‘night & day use’ (0.53, 95% CI = 0.30, 0.73), followed by ‘night use’ (0.26, 95% CI = 0.08, 0.50), ‘day use’ (0.13, 95% CI = 0.02, 0.30), and then ‘no use’ (0.06, 95% CI = 0.01, 0.17). The large increase in ‘night & day use’ was driven by the positive second-order ‘night use’ colonization parameter ($g_{INT}^{N|D} = 2.82$, 95% CI = 1.60, 4.52, $P(g_{INT}^{N|D} > 0) = 1.00$), whereas the decreasing transition probability of ‘day use’ to ‘night & day use’ was governed by the negative first-order ‘night use’ colonization slope term (b_{URB}^N , listed above). Likewise, first-order ‘day use’ extinction rates were relatively modest ($d_{INT}^D = -0.72$, 95% CI = -2.02, 0.43, $P(d_{INT}^D < 0) = 0.90$) and covaried little with urban intensity ($d_{URB}^D = 0.10$, 95% CI -1.04, 0.85, $P(d_{URB}^D > 0) = 0.54$). As a result, d_{INT}^D and d_{URB}^D generated relatively flat transitions from ‘day use’ to either ‘no use’, ‘night use’, or back to ‘day use’ (Fig. 5).

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

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

3. 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 developed the MSDOM framework to allow species’ diel spatial habitat use to be studied within and across seasons or years. Importantly, our Bayesian occupancy framework allows for the incorporate of continuous covariates while accounting for variation in detectability and sampling methodology, a source of heterogeneity that is typically unmodeled and is required to produce unbiased parameter estimates. The utility of this framework 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, etc. For those who may want to explore this model on archived data, the ability to incorporate random effects can help manage unideal sampling schemes such as unmeasured variation across sites or years of data

collection. We recommend future studies intending to use MSDOM, reflect their sampling methodologies to covariates and diel periods of interest, in addition to model form (static or dynamic). For example, if we hypothesize increasing vehicle traffic will reduce coyote's crepuscular activity and increase night activity across a season, we must first parse camera trap data to consider crepuscular hours. Our sampling design would capture varying traffic intensity, and consider covariates which may impact occurrence and detection, such as distance to forest. We could also adopt additional sampling tools, such as audio recorders, to measure impacts of traffic noise.. Developing studies in this context is critical as we can learn 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 fosa and coyote temporally structure their site-use in response to anthropogenic drivers. Previous studies of fosa in the eastern rainforests have suggested that they are ubiquitously distributed across forested landscapes and are predominantly cathemeral (Gerber et al. 2012b; Farris et al 2015a). By jointly investigating spatial-temporal habitat use of fosa, 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, fosa at Ranomafana were nocturnal near human villages, which occur along the edges of the protected forest. At the forest interior, fosa were cathemeral. These findings indicate that within specific habitats, fosa can be active during day and night hours, but human activity and development limit fosa 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 which were connected to core forest habitat at greater distances from human villages (Farris et al 2015b).

Similar to our findings for fosa, coyote exhibited diel activity across anthropogenic gradients. In contrast with fosa, however, coyote are generally considered to be crepuscular in natural environment (McClennen et al. 2001). We found that coyote 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 coyote, irrespective of diel state, decreased with increasing urban intensity. Thus, while coyote 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 coyote 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, coyote were most likely to use highly urban sites only at night, but were most likely to go locally extinct when this occurred (i.e., transition to state “no use”). Thus, even though coyote were more likely to use highly urban sites at night, the use of these sites is more ephemeral than the urban sites coyote 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 coyote 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 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). Though 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 rituals. Advanced modeling approaches that estimate diel-habitat use will be a valuable asset in supporting successful conservation and land-management strategies in a rapidly changing world.

REFERENCES A

- 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.
- Angelieri, 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 Publications. 224.
- 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* 109:15360–15365.
- CMAP. 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.
- 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., 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.
- 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.
- 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. *J Stat Softw* 43.
- Gallo, T., F. Mason, B. Gerber, A.A. Ahlers, J.L. Angstmann, M. Amaya, D. Drake et al. 2021. Mammals adjust diel activity across gradients of urbanization. *bioRxiv*.
- 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 Hawkins, C.E. In Press. *Cryptoprocta ferox*, fosa. In *The new natural history of Madagascar*. ed. S. M. Goodman. Princeton, Princeton University Press.

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., S.M. Karpanty, and J. Randrianantenaina. 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*. Antananarivo, Madagascar: Association Vahatra.

Goodman, S.M., M.J. Raheirilalao, and S. Wohlhause. 2019. *The terrestrial protected areas of Madagascar: their history, description, and biota*. 3rd ed. Antananarivo: Association Vahatra.

Guisan, A., R. Tingley, J.B. Baumgartner, I. Naujokaitis-Lewis, P.R. Sutcliffe, A.I.T. Tulloch, T.J. Regan, L. Brotons, E. McDonald-Madden, C. Mantyka-Pringle, [T.G. Martin](#), [J.R. Rhodes](#), [R. Maggini](#), [S.A. Setterfield](#), [J. Elith](#), [M.W. Schwartz](#), [B.A. Wintle](#), [O. Broennimann](#), [M. Austin](#), [S. Ferrier](#), [M.R. Kearney](#), [H.P. Possingham](#), [Y.M. Buckley](#). 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 Biological Sciences* 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: London.

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. 2015. 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 Biological Sciences* 372:20160248.

Length, 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., 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.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., 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, M.E. Seamans, and R.J. Gutiérrez. 2009. Modeling species occurrence dynamics with multiple states and imperfect detection. *Ecology* 90:823–835.
- 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*, ed. 2. Academic Press, Cambridge.
- Magle, S. B., M. Fidino, E.W. Lehrer, T. Gallo, M.P. Mulligan, M.J. Rios, A.A. Ahlers, J. Angstmann, A. Belaire, B. Dugelby, A. Gramza, L. Hartley, B. MacDougall, T. Ryan, C. Salsbury, H. Sander, C. Schell, K. Simon, and D. Drake. 2019. Advancing urban wildlife research through a multi-city collaboration. *Frontiers in Ecology and the Environment* 17:232–239.
- McClennen N., R.R. Wigglesworth, 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, S. Federman, C.D. Golden, S.M., S.M. Holmes, M. Irwin, R.L. Jacobs, S. Johnson, T. King, S.M. Lehman, E.E. Louis Jr, A. Murphy, H.N.T. Randriahaingo, H.L.L. Randrianarimanana, J. Ratsimbazafy, O.H. Razafindratsima, and A.L. Baden. 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., E. Vander Wal, M. Bonar, J. Fieberg, M.P. Laforge, M. Leclerc, C. Prokopenko, and B.D. Gerber. In Press. Conceptual and methodological advances in habitat selection modeling: guidelines for ecology and evolution. *Ecological Applications*.
- Odum, E.P. 1975. The Ecosystem. Page 46 *in Ecology: The Link Between the Natural and Social Sciences*, ed 2. Holt, Rinehart, and Winston, New Delhi:Oxford.

Pianka, E.R. 1973. The Structure of Lizard Communities. 2009. *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, Austria.

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.

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. Millspaugh. 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 the Italian Journal of Mammalogy* 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. Zanette, and C.C. Wilmers. 2017. Fear of the human “super predator” reduces feeding time in large carnivores. *Philosophical Transactions of the Royal Society B Biological Sciences* 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.

MANUSCRIPT 2

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Fear and animal ownership drive value of and interactions with coyotes

Keywords

coyote; fear; animal ownership; Likert scale; questionnaire; value; wildlife interactions

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Introduction

More than half of the Earth's land surface has been altered by anthropogenic developments (Ellis et al., 2010). Changing landscapes for agriculture, logging, transportation, development, and energy production, have negatively impacted many species through the removal, fragmentation, and reduction of species' habitat (Living Planet Report, 2018). These types of habitat loss lead to population declines, cascading trophic shifts, and extinction (Bartlett et al., 2016). However, some species have benefitted from these transforming landscapes and have effectively adapted to human dominated habitats, such as urbanized environments. The highest densities of peregrine falcons (*Falco peregrinus*) are now found in New York City, USA and Moscow, Russia (Luniak, 2004); urban mammals, such as squirrel (*Sciurus niger*), deer (*Odocoileus virginianus*), and mice (*Apodemus agrarius*) exhibit higher survival than their rural counterparts (McCleery et al., 2007). Unfortunately, the presence of some wildlife species has stirred public contention with conflict arising where wildlife overlaps with humans (Hussain et al., 2007, Magle et al., 2012).

Human dimensions research and the incorporation of public input into wildlife management decision making has proved a useful tool in the mitigation and management of human-wildlife interactions (Decker et al., 1997; Bath, 1998). As urbanization continues to grow globally (Magle et al., 2012), more species will have to adapt to human dominated landscapes. Thus, understanding the complex drivers of conflict will become increasingly important for managing both people and wildlife. Humans' relationships with wildlife and the role these relationships have managing urban species are shaped by many factors, including people's demographics, lifestyles, or interactions with wildlife

(Knopff et al., 2016; Elliot et al., 2016; Dickman, 2010). For example, Knopff et al., (2016) found that tolerance for cougars (*Puma concolor*) was most strongly shaped by people's intrinsic value for cougars, if they self-identified as a hunter, their age, and perceived risk of cougars. Studies conducted on coyote (*Canis latrans*) have also identified important variables, such as gender, township, fear and perceived risk of coyotes, which influence public attitudes about coyotes and their management (Draheim et al., 2019; Sponarski et al., 2018; Elliot et al., 2016). Identifying these important predictors informs management practices, such as increasing education on wildlife safety and identifying target audiences, such as pet owners (Knopff et al., 2016).

Studies which consider human-wildlife relationships, can also reveal how human behaviors shape and instigate conflict. Findings from large carnivore research, e.g., wolves (*Canis lupus*), bears (*Ursus arctos*), and cougars (*Puma concolor*), have identified livestock carcasses as significant predator attractants, and therefore an important predictor for livestock depredation, a major source of negative carnivore-human interactions (Morehouse et al., 2020). Other human behaviors, such as leaving food sources or unattended pets accessible, have been found to increase negative coyote-human interactions in urban settings (Mitchell, 2017). Identifying behaviors like these helps target specific mitigation efforts, such as organizing and educating people on proper waste or food disposal and heightened care of pets outside (Elliot et al., 2016; Mitchell, 2017).

Questionnaire or survey data have been invaluable to studies of human-wildlife relationships. These instruments frequently rely on scales to collect data from participants, specifically, Likert scales, which consist of questions with natural ordered

responses (e.g., strongly agree, agree, disagree, strongly disagree; Casey et al., 2005; Draheim et al., 2019; Sponarski et al., 2018). Common methods used to analyze scaled data range from descriptive statistics to hypotheses tests (Casey et al., 2005; Knopff et al., 2016; Sponarski et al., 2019). However, few human dimensions studies in ecology have made use of formal modeling that explicitly considers ordered data from commonly used Likert scaling, such as ordinal regression. Ordinal regression is a useful statistical model when considering scales that rank but may not scale equally among values (Larasati et al., 2011). Unlike descriptive and hypothesis testing statistics, ordinal regression can model hypothesized effects of continuous or categorical variables on ordered response variables. This is particularly useful for studies which aim to translate and compare hypotheses into statistical models to evaluate empirical support using data (Burnham et al., 2002). Currently, ecological studies which have modeled Likert data are limited to a single predictive Likert item (Bennett et al., 2018) or making assumptions about the relationship between Likert scale questions (e.g., multiple Likert items which address the same predictor variable) and the difference between the Likert ratings themselves (e.g. the psychological distance between ratings, e.g. strongly disagree – disagree to agree – strongly agree) through methods like averaging ratings (Knopff et al., 2016). By estimating effects under a single ordinal regression framework, variation amongst Likert questions and participants, can be easily account for without reducing and manipulating original response data into new groupings.

Here, we highlight the utility of Bayesian modeling to conduct ordinal regression for human dimension data in ecology. This method accounts for both variation in rating distance and between Likert scale questions, while evaluating and comparing model

hypotheses (Bürkner et al., 2019). We do so with a case study on the coyote, a native North American carnivore. Over the last century, coyotes have expanded their range throughout the Americas, their success likely propelled by the extirpation of apex predators, increased agricultural landcover, and hybridization with eastern wolves and the domestic dog (Hody et al., 2017). These drivers, in conjunction with the generalist nature of coyotes, have allowed them to behaviorally adapt to human-dominated landscapes (Carter et al. 2012; Gehrt 2007), including agricultural, suburban, and urban areas (Hody et al., 2017; Jackman et al., 2015).

Like many carnivore species, coyotes have faced a long and contentious history in America. Since European settlement, coyotes have been persecuted as pests that compete with humans for livestock and wild game (Reynolds et al., 1996). Yet, even with wide-scale government-supported culling programs, coyotes continue to persist across the landscape and cause controversy (Hody et al., 2017, Draheim et al., 2019). This is particularly evident in urban areas where coyotes live in proximity to people and pose threats to humans through risk of zoonotic disease transmission, destruction of property, and the attacking or harassing of livestock, pets, or people (Elliot et al., 2016; Sponarski et al., 2018). However, coyotes also serve important ecological roles as top-down regulators of primary consumers (Benson et al., 2017; Henke et al., 1999). Their diet, predominantly consisting of small mammals and birds, may contribute to some humans' needs as coyotes consume common nuisance species, such as rodents and Canada geese (Gehrt, 2007; Morey et al., 2007). This service may be especially valuable in urban landscapes which lack apex predators and host an abundance of small animal species. With both risks and benefits to coyotes living with people, balancing coyote management

with public concerns remains a challenge for wildlife managers and conservationists in urban spaces (Sponarski et al., 2018).

Our case study specifically focuses on the relationship between people and coyotes in Rhode Island, USA. Coyotes were first sited in Rhode Island in the 1960's and quickly colonized the state due to minimal competition and abundant food resources (Riley, 2021). Currently, coyotes are widespread, but there is lacking data on population estimates statewide. Importantly, coyote presence is contentious; the majority of wildlife complaints reported to the Rhode Island Department of Environmental Management, regard coyotes (Personal Communication, October 2020). Given this contention and history of unsuccessful and, often unsupported, large-scale lethal removal programs nationally (Sponarski et al., 2018), managers and conservationists need other tools to successfully manage coyotes and their relationships with humans. To do this, we investigate how people's demographics and relationship with nature influence their value of and interactions with coyotes; see Methods for hypotheses and predictions.

Methods

Study area

Rhode Island is a developed northeastern coastal state located between the states of Connecticut and Massachusetts, USA. Natural landcover is predominantly deciduous and softwood forest intermixed with high and low intensity human development and agriculture. The state has the second highest human density in the United States (Rhode Island Wildlife Action Plan, 2015) with >10% of the land covered by impervious surface area (Zhou and Wang, 2007) and a population of roughly 1,060,000 (U.S. Census Bureau, 2019). Residents are largely educated with 88.8% having completed a high

school degree and 34.2% completing a bachelor's degree or higher. The median household income is \$67,167.00.

Instrument and Data collection

We collected data through a survey instrument online using Qualtrics Survey Software and advertised widely through news articles and promotional social media pages across Rhode Island. Only participants over the age of 18 were permitted to take the survey. The survey was categorized into six sections: 1) Rhode Island residency, 2) relationship with nature, 3) value, knowledge, and attitudes about coyotes, 4) human-coyote interactions, 5) environmental beliefs, and 6) demographics (full survey here: https://github.com/karivera2194/Coyote_RI). At the start of section three, participants were given a figure depicting an image of a coyote and some basic information about their size and distribution. This was included to encourage participants to correctly recall what a coyote is and their experience with coyotes.

Hypotheses, Predictions, and Variables

Here, we define people's value of the coyote as the strength of an individual's belief in the positive (high value) and negative (low value) role coyotes play on the landscape—which may or may not be representative of coyotes' role in Rhode Island as a whole. To quantify this response variable, we used two five-point Likert scales, one which addressed participants perceived benefits (i.e. 'coyotes have an important role in Rhode Island's ecosystems') and the other, perceived risks of coyotes (i.e. 'coyotes pose a risk to pets') on the landscape (Table 1; full survey on https://github.com/karivera2194/Coyote_RI). The five-point scale ranked as: strongly disagree, disagree, neither agree or disagree, agree, and strongly agree. The risk scale was

reverse-coded so both risk and benefit scales increased with participants increasing value in coyotes (Table 1). To quantify our second objective, interactions with coyotes, we consider two types of interactions separately, sightings and incidents. A sighting is a visual observation of a coyote where an incident is a conflict between a human and a coyote, where a coyote exhibits the following behaviors: growling, stalking, or attacking.

We hypothesized that the major factors contributing to people's value of coyote's are a person's age, gender, county of residence, relationship with nature, knowledge and fear of coyotes, animal ownership, and animal incidents with coyotes (see variable names in Table 1). Animal incidents are defined as instances in which a coyote exhibits the following behaviors towards pets or livestock: growling, stalking, or attacking, as we believe these interactions most impact people's value of coyotes in the state. We predicted that increasing value of coyote's would occur with younger people, those with increased knowledge of coyotes, and those lacking fear. Although pet owners have been found to support coyote presence (Elliot et al., 2016), we predicted that those who have experienced negative animal-coyote interactions would have decreased value of coyotes. We also predicted that people's value of coyote would vary across counties and genders. These predictions were informed by similar studies conducted on human attitudes related to bears and cougars (Piedallu et al., 2015; Thornton et al., 2010; Wechselberger et al. 2005). Previous research on coyotes indicates that value is positively related to relationship with nature and pet ownership (Elliot et al., 2016). We also considered that some factors may interact and affect one's value of coyotes more when they are evaluated together. Specifically, we hypothesized that one's increasing relationship with nature in conjunction with no fear and increased knowledge would significantly increase their

value of coyotes. We also hypothesized that coyote value would decrease dramatically amongst those who have experienced an animal (pet or livestock) incident and fear coyotes. In total, we considered four fundamental statistical models which differ by hypothesized interactions (relationship with nature and fear, or relationship with nature and knowledge) and whether these relationships were strictly additive.

We hypothesized that the major factors contributing to people's interactions (sightings and incidents) with coyotes are county, relationship with nature, animal ownership (pets and livestock), knowledge, and fear of coyotes. We predicted that interactions would vary amongst counties, which may be due to coyote or human abundance (Poeseel et al., 2017), habitat structure, or people's awareness of coyote presence. We also predicted that increasing interactions would occur with people's increasing relationship with nature, animal ownership, decreased knowledge of coyotes, and lack of fear of coyotes. We predicted that people who feel closer to nature, own pets, and do not fear coyotes likely spend more time outdoors where they may interact with coyotes. Therefore, we predicted that those who are fearful and have a distant relationship with nature will experience significantly less coyote sightings. We also predicted that the importance of people's knowledge of coyotes will vary depending on their relationship with nature. Those with reduced knowledge of coyotes were expected to have more incidents with coyotes than those who are more educated on the species. In total, we consider three fundamental statistical models for each sightings and incidents, which differ in their hypotheses about interacting or additive relationships.

To evaluate our hypotheses, we used binary, multiple-choice, and scale questions to collect data on participants' demographics, environmental values, animal ownership,

knowledge of coyotes, fear of coyotes, and incidence between owned animals and coyotes (see Table 1). We measured participants relationship or ‘interconnectedness’ with nature using Schultz’ (2001) ‘Inclusion of Nature of Self’ (*INS*) scale—adapted from Aron et al. (1992); this scale is positively related to one’s biospheric values (Schultz 2001).

Analysis

We followed Bürkner et al. (2019) by adapting a multilevel cumulative modeling framework to evaluate value of coyotes by jointly analyzing Likert scales of coyote benefits and risks and use separate cumulative models to evaluate coyote-human sightings and incidents. Response variables were linked to predictor variables using a probit link function, assuming residuals follow a Normal distribution and that the variance between response ratings did not differ across categories and measures of predictor variables (Bürkner et al., 2019). In our value analyses, we accounted for variation between Likert items, as well as variation in participants perceived distance between Likert ratings in this model (e.g. Participant A may perceive a larger difference between Agree and Strongly Agree, than Participant B; see full survey on: https://github.com/karivera2194/Coyote_RI) using random intercepts, where all the thresholds in the cumulative ordinal model vary (Bürkner et al., 2019). We fitted models using the *Brms* package in R (version 2.16.1) and compared their support using leave-one-out-cross-validation (LOOCV; Vehtari et al., 2017), which estimates pointwise out-of-sample prediction accuracy; lower values indicate more empirical support for a model. For each model, we used diffuse Gaussian prior distributions and 10,000 Markov chain Monte Carlo iterations using three chains to evaluate convergence. Based on the

Gelman–Rubin diagnostic (Gelman and Rubin, 1992) and visually examining traceplots of the posterior distributions, we found models converged.

We quantified support for estimated effects by reporting the proportion of posterior samples which were >0 as an indication of the probability that the effect is positive. Proportional values >0.9 indicated strong support for a positive effect, or conversely <0.1 indicated strong support for a negative effect. Probabilities >0.7 indicated moderate support of a positive effect and <0.3 indicated moderate support for a negative effect. Further, we used the magnitude of estimated effects to compare the relative influence of hypothesized variables.

Results

The self-selected survey was conducted over two months, 6 October 2020 to 6 December 2020, with a total of 980 participants. Screening techniques were applied to reduce inadequate and unusable responses (https://github.com/karivera2194/Coyote_RI), leaving 971 valid participants. Participation occurred across all Rhode Island counties with over-representation in Newport (30.18% of RI's total population lives in Newport but only 14.73% of surveys came from here), Washington (11.92% of RI to 7.83% of surveys), and Bristol slightly so (4.61% of RI to 6.49% of surveys). The remaining counties were under-represented—Kent (15.5% of RI to 9.68% of surveys) and Providence (60.13% of RI to 27.81% of surveys). Participants were highly educated compared to state averages with 78.37% of participants having a bachelor's degree or higher compared to 34.2% of Rhode Island's population possessing bachelors degrees. This may be partially due to high impact advertisement on the University of Rhode Island's webpage, increasing University student and staff participation. The median household income for participants

ranged from \$75,000 –\$99,999 and was higher than the state’s median of \$67,167. The majority of participants who disclosed their gender were female (46.5% to 33.4% male) and <1% of the participants identified as gender non-binary.

We found the most supported model for value of coyotes to be one in which there was an interaction between the variables *fear* and *animal.incident* (see Appendix S1; Table 1). We found our hypotheses that peoples age and knowledge of coyotes are major factors contributing to value of coyotes, to be unsupported with estimated medians close to zero (Table 2; Figure 1). We did find support that increasing connectedness to nature directly related to increasing value of coyotes with strong support of positive effects. Specifically, we found people’s increasing connectedness to nature (variable *INS* >1) to increase people’s value of coyotes compared to people who responded with a low connection with nature (*INS* of 1). Further, posterior medians generally increased with increasing connectedness to nature, but not enough for a clear statistical difference. As we hypothesized, we found people’s value of coyotes to vary amongst genders and counties. We also found strong support that the conditional effects of incidents between owned animals and coyotes and peoples fear of coyotes, to negatively impact participants value of coyotes. When these variables (*age* and *knowledge*) were considered in addition, their effect was even stronger (Table 2). However, we did not find support for their interaction with a median close to zero. Lastly, we found considerable variation via our two random effects used to estimate variation in Likert scores across questions (0.73; 95% CI = 0.67, 0.79) and individuals (1.06; 95% CI = 0.62, 1.98).

We found the most supported model for coyote sightings to be one which considered only additive effects (no interactions were supported; Appendix S1; Table 2;

Figure 2). Our hypotheses that one's connectedness with nature and knowledge of coyotes to affect coyote sightings, were unsupported with medians close to zero (Table 3). The coefficients with the strongest statistical support were people's resident county, animal ownership, and fear of coyotes (Table 3, Figure 2). Our hypothesis that coyote sightings varied across counties was supported. There was strong support against our hypothesis that fear of coyotes would decrease people's sightings of them, as fear actually had a positive effect on sightings. However, we did find strong support for our hypothesis that animal owners had increased coyote sightings as ownership had a positive effect on sightings (Table 3).

We found the most supported model for incidents with coyotes to have an interaction between the variables *fear* and *animal.owner* (Appendix S1; Table 3). We found moderate support that knowledge of coyotes had a weak effect on incidents with a median close to zero (Table 4). Additionally, we did not find support that increasing connectedness with nature affected incidents with coyotes and no clear directional pattern existed. The coefficients with the strongest statistical support were people's county of residence, animal ownership, fear of coyotes and an interaction between people's fear and animal ownership (Table 4, Figure 3). Our hypothesis that human-coyote incidents varied across counties was supported. We also found strong support that fear of coyotes and animal ownership impact incidents with coyotes positively. Fear of coyotes had the strongest conditional effect on incidents, while the interaction between animal ownership and fear of coyotes was larger than the conditional effect of animal ownership, but smaller than fear of coyotes considered independently (Table 4). Thus, animal ownership does not greatly influence how this population of people fear coyotes.

Discussion

Human dimension studies in ecology are increasingly important as species are forced to interact with people and survive within anthropogenic landscapes (Decker et al., 1997). Survey questionnaires are an effective and low cost means to understand how people are interacting and valuing wildlife species. This is especially important for contentious wildlife species whose presence may present risks on the landscape though they may still serve an important ecological function. However, using survey data is complex, as people's psychological interpretations of questions and available responses can vary.

We highlight hierarchical Bayesian ordinal regression modeling as a useful approach to incorporate and estimate sources of variation. Further, ordinal regression is appropriate for handling the unique structure of Likert items and scales, which do not follow common numerical data analyses assumptions, despite being commonly treated as such (Burkner et al., 2019). Lastly, the Bayesian ordinal regression modeling framework allows for explicit linking of data to relevant model hypotheses. By applying this model to a case study of coyote-human relationships in Rhode Island, we were able to determine which variables most impact people's value of and interactions with coyotes and how (directionally) they impact these response variables.

As a self-selected, online survey, our sample of responses comes with inherent biases. Sampled demographics, such as wealth and education, were above state averages and may have biased our results relative to the total population of Rhode Island. County representation also varied, therefore we suggest future studies to integrate online and in-person advertisements to be more inclusive across these demographics. However, our survey did obtain a wide distribution of participant's age despite findings of decreased

internet use in older age classes (65-74; Ferri-García et al., 2020). Increased internet use across ages could be tied to the COVID-19 pandemic which was largely impacting Rhode Island residents at the time of this survey. Methods to account for self-selection bias were not included in this case study, however we recommend future studies to consider methods like propensity score adjustment (PSA), which uses auxiliary information collected from an unrelated study to reduce bias from confounding factors (Ferri-García et al., 2020).

We found strong support that both people's fear and incidents between owned animals and coyotes negatively impacted people's value of coyotes, and when considered together, have an even stronger impact on their value. We consider that fear of coyotes may impact participants interpretation of what is considered an incident, as studies have found people to be most fearful of coyote attacks on pets (Draheim et al., 2019) and fear has been shown to increased risk perceptions (Bruskotter et al., 2013). We found that differences in value of coyotes existed amongst genders, specifically, males valued coyote less so than females. This difference may be a driver in why men tend to support more lethal methods of coyote management (Draheim et al., 2019). We also found differences in value amongst Rhode Island counties where, interestingly, Newport was the only county which valued coyotes less than Bristol. Although this model explains how value of coyotes differs amongst categorical groups, it does not explain why. However, the Cooperative Coyote Research Project, which aims to develop 'science-based coexistence and management strategies' for coyotes in Rhode Island (<http://theconservationagency.org/narragansett-bay-coyote-study/>), has already conducted extensive research of coyote ecology in this area. Newport and surrounding islands have

experienced heightened interactions with coyotes, predominantly driven by direct and indirect supplemental feeding (Mitchell, 2017). These heightened negative interactions are likely driving decreased human value of coyotes. It is also possible that additional media attention from these incidents and project efforts have increased coyote visibility in this region.

Coyote sightings were only moderately increased by people's fear and animal ownership. It is possible that the demographics of people who fear coyotes, have a heightened awareness of coyote activity, again increasing coyote visibility. We believe results of animal ownership positively affecting coyote sightings could be due to owners spending more time outdoors walking their pet, as dogs were the most commonly owned pet. This could lead to increasing interactions with wildlife, like coyotes. Most notably, the counties which experienced the most frequent coyote sightings were Newport and Bristol, the same counties which least value coyotes. This provides further evidence that these counties have heightened awareness of coyotes which may be driven by increased interactions.

Similar to findings related to sightings, those who fear coyotes experienced increased frequencies of incidents between people and coyotes. We believe in addition to this groups heightened awareness of coyote presence, fear is driving varied interpretations of coyote incidents. For example, although a coyote passing through someone's backyard may inflict fear in observers, this experience is not considered an 'incident', as no aggressive behavior was observed (stalking, growling, attacking). Such perceptions may have influenced the positive effect animal ownership had on incident

frequency, though this could also be related to animal owners spending more time outdoors with pets.

Coyote-human interactions have generated significant concerns in the state of Rhode Island which has led to the creation of educational resources provided by the Rhode Island Department of Environmental Management (RIDEM) and the Cooperative Coyote Research Project. These materials include coyote conflict mitigation (such as hazing and pet safety practices in addition to identifying coyote attractants), management guides, and coyote reporting tools (Riley, 2021). These materials serve as thorough resources for Rhode Island residents and our methods and results provide guidance on what populations of people are in greatest need of these resources. Our results specifically highlight the importance of communicating with pet and livestock owners. We recommend managers and conservationists to collaborate with veterinary and animal clinics in addition to pet or feed stores to disseminate information on animal safety, mitigation tools, and hazing techniques. It is important to note that the presence of domestic dogs can reduce the effectiveness of hazing with voice, body, and/or approaching coyotes (Bonnell et al., 2017), therefore owners may consider arming themselves with additional tools like pepper spray (Miller et al., 2001) and follow best practice methods to move away from an unfazed coyote. We note that although pepper spray is legal to buy, carry, and ship in Rhode Island, managers and conservationist should consider leading workshops on the safe and effective use of such products in cooperation with local law enforcement. Given our findings that fear of coyotes largely impact people's value of and interactions (real or perceived) with coyotes, we encourage coyote management tools which encourage appropriate risk assessment and best dissuade

fear. We recommend further publicizing of the ‘coyote interaction assessment’ chart by RIDEM (Riley et. al., 2021) and promote pet and livestock owners to consider additional hazing tools such as blow-horns or pepper spray when outside with their animals. As outlined in RIDEM’s management and response guide, coyote removal (lethal and relocation) is an ineffective tool for long-term management, and efforts are better spent fostering communities of ‘educated’ coyotes which have a healthy fear of humans (Riley, 2021). The fostering of such communities is driven by people. Therefore, it is crucial we continue to implement quantitative techniques to better direct management and conservation efforts which advocate for coexistence and fostering of positive relationships, not just with coyote, but other urban wildlife.

References B

- Aron, A., Aron, E. N. & Smollan, D. (1992). Inclusion of other in the self scale and the structure of interpersonal closeness. *Journal of Personality and Social Psychology*, 63, 596-612.
- Bartlett, L.J., Bartlett LJ, T. Newbold, D.W. Purves, D.P. Tittensor, & M.B.J. Harfoot. (2016). Synergistic impacts of habitat loss and fragmentation on model ecosystems. *Proceedings of the Royal Society B*, 283: 20161027.
- Bath, A. J. (1988). The role of human dimensions in wildlife resource research in wildlife management. *Ursus*, 10, 345–349.
- Bennett, N. J. *et al.* (2019). Local support for conservation is associated with perceptions of good governance, social impacts and ecological effectiveness. *Conservation Letters*. <https://doi.org/10.1111/conl.12640>
- Benson, J.F., Loveless, K.M., Rutledge, L.Y., & Patterson, B.R. (2017). Ungulate predation and ecological roles of wolves and coyotes in eastern North America. *Ecological Applications*, 27, 718–733.
- Bonnell, M.A., Breck, S.W. (2017). Using resident-based hazing programs to reduce human-coyote conflicts in urban environments. *Human-Wildlife Interact* 11:146–155.
- Bruskotter, J. & Wilson, R. S. (2014). Determining where the wild things will be: using psychological theory to find tolerance for large carnivores. *Conservation Letters*, 7, 158–165.
- Burnham, K. P. & Anderson, D. R. (2002). Model selection and inference: a practical information- theoretic approach, 2nd edn. Springer, Berlin Heidelberg New York.
- Bürkner, Paul & Matti Vuorre. (2018). Ordinal regression models in psychology: A tutorial. *PsyArXiv*. September 15, 2018.
- Carter, Neil, Binoj Shrestha, Jhamak Karki, Narendra Pradhan, & Jianguo Liu. (2012). “Coexistence between Wildlife and Humans at Fine Spatial Scales.” *Proceedings of the National Academy of Sciences*, 109: 15360–65.
- Casey, A.L., Krausman, P.R., Shaw, W.W. & Shaw, H.G. (2005) Knowledge of and attitudes towards mountain lions: a public survey of residents adjacent to Saguaro National Park, Arizona. *Human Dimensions of Wildlife*, 10, 29–38.
- Decker, D.J., and Chase, L.C. (1997). Human Dimensions of Living with Wildlife: A Management Challenge for the 21st Century. *Wildlife Society Bulletin*, 1973-2006 25, 788–795.

Dickman AJ. (2010). Complexities of conflict: the importance of considering social factors for effectively resolving human–wildlife conflict. *Animal Conservation*, 13:458–66.

Draheim, M. M., Parsons, E. C. M., Crate, S. A., & Rockwood, L. L. (2019). Public perspectives on the management of urban coyotes. *Journal of Urban Ecology*, 5:1– 13.

Elliot, E.E., Vallance, S., & Molles, L.E. (2016). Coexisting with coyotes (*Canis latrans*) in an urban environment. *Urban Ecosystems*, 19, 1335–1350.

Ellis, E.C., Kees Klein Goldewijk, Stefan Siebert, Deborah Lightman, & Navin Ramankutty. (2010). Anthropogenic Transformation of the Biomes, 1700 to 2000. *Global Ecology and Biogeography* 19 (5): 589–606. <https://doi.org/10.1111/j.1466-8238.2010.00540.x>.

Ferri-García R, Rueda MDM. (2020). Propensity score adjustment using machine learning classification algorithms to control selection bias in online surveys. *PLoS One*, 15:e0231500.

Gehrt, Stanley D. & McGraw, M. (2007). Ecology of coyotes in urban landscapes. *Wildlife Damage Management Conferences -- Proceedings*, April.

A Gelman, DB Rubin. (1992). Inference from iterative simulation using multiple sequences (with discussion). *Statistical Science*, 7: 457-511.

Henke, S.E. & Bryant, F.C. (1999). Effects of coyote removal on the faunal community in western Texas. *Journal of Wildlife Management*, 63:1066–1081.

Hody JW, Kays R (2018) Mapping the expansion of coyotes (*Canis latrans*) across North and Central America. *ZooKeys* 759: 81–97. <https://doi.org/10.3897/zookeys.759.15149>

Hussain, A., J. B. Armstrong, D. B. Brown, & J.Hogland. (2007). Land-use pattern, urbanization, and deer–vehicle collisions in Alabama. *Human–Wildlife Conflicts*, 1:89–96.

Jackman, J. L., & Rutberg, A. (2015). Shifts in attitudes toward coyotes on the urbanized east coast: The cape cod experience, 2005–2012. *Human Dimensions of Wildlife*, 20(4), 333–348. doi:10.1080/10871209.2015.1027973

Knopff, A.A., Knopff, K.H., & St. Clair, C.C. (2016). Tolerance for cougars diminished by high perception of risk. *Ecological Society*, 21.

Larasati, A., DeYong, C., & Slevitch, L. (2011) Comparing Neural Network and Ordinal Logistic Regression to Analyze Attitude Responses. *Service Science* 3(4):304-312.

- Luniak, M. (2004). Synurbanization — adaptation of animal wildlife to urban development. *Proceedings of the 4th International Symposium on Urban Wildlife Conservation* (eds WW Shaw, LK Harris, L Vandruff), 50– 55. Tucson, AZ.
- Magle, S. B., Hunt, V. M., Vernon, M., & Crooks, K. R. (2012). Urban wildlife research: past, present, and future. *Biological Conservation*, 155, 23–32.
- McCleery, R.A., Lopez, R.R., Silvy, N.J., & Gallant, D.L. (2008). Fox squirrel survival in urban and rural environments. *Journal of Wildlife Management*, 72: 133–137.
- Miller, D.S. (2001). Review of oleoresin capsicum (pepper) sprays for self-defense against captive wildlife. *Zoo Biology*, 20(5): 389-398.
- Mitchell, N. (2017). Best Management Practices for Coexistence with Coyotes on Aquidneck and Conanicut Islands (pp. 1–7). Jamestown, RI: The Conservation Agency.
- Morehouse, A. T., Hughes, C., Manners, N., Bectell, J., & Bruder, T. (2020). Carnivores and communities: A case study of human-carnivore conflict mitigation in Southwestern Alberta. *Frontiers in Ecology and Evolution*, 8(2), 1–15.
- P.S. Morey, E.M. & Gese, S. Gehrt. (2007). Spatial and temporal variation in the diet of coyotes in the Chicago metropolitan area. *American Midland Naturalist.*, 158: 147-161.
- Poessel, S. A., Gese, E. M. & Young, J. K. (2017). Environmental factors influencing the occurrence of coyotes and conflicts in urban areas. *Landscape and Urban Planning*, 157, 259–269.
- Preatoni, D., Mustoni, A., Martinoli, A., Carlini, E., Chiarenzi, B., Chiozzini, S. et al. (2005) Conservation of brown bear in the Alps: space use and settlement behavior of reintroduced bears. *Acta Oecologica*, 28, 189–197.
- Rhode Island Wildlife Action Plan Executive Summary. (2015). Chapter 2: “Rhode Island’s Fish and Wildlife Habitat”. <http://www.dem.ri.gov/programs/fish-wildlife/wildlifehuntered/swap15.php>
- Reynolds, J.C., & S.C. Tapper. (1996). Control of mammalian predators in game management and conservation. *Mammal Review*, 26:127–56
- Riley, Sarah. (2021). *Understanding the Eastern Coyote, a Management and Response Guide*. Rhode Island Department of Environmental Management Division of Fish & Wildlife, West Kingston, RI.
- P.W. Schultz. (2001). Assessing the structure of environmental concern: Concern for the self, other people, and the biosphere. *Journal of Environmental Psychology*, 21: 327-339

- Sponarski, C.C., Miller, C., & Vaske, J.J. (2018). Perceived risks and coyote management in an urban setting. *Journal of Urban Ecology*, 4.
- Sullivan, G.M., & Artino, A.R. (2013). Analyzing and interpreting data from Likert-type scales. *Journal of Graduate Medical Education*, 5(4):541–542.
- Thornton, C., & Quinn, M.S., (2010). Risk Perceptions and Attitudes Toward Cougars in the Southern Foothills of Alberta. *Human Dimensions of Wildlife*, 15 (5): 359–72. <https://doi.org/10.1080/10871200903582626>.
- “U.S. Census Bureau Quickfacts: Rhode Island.” (2019). QuickFacts Rhode Island, United States Census Bureau, 1 July 2019, <https://www.census.gov/quickfacts/RI>.
- Vehtari, A., Gelman, A. & Gabry, J. (2017). Practical Bayesian model evaluation using leave-one-out cross-validation and WAIC. *Statistics and Computing*, 27, 1413–1432. <https://doi.org/10.1007/s11222-016-9696-4>
- Wechselberger M., Rigg R. and Bet'ková S. (2005). An investigation of public opinion about the three species of large carnivores in Slovakia: brown bear (*Ursus arctos*), wolf (*Canis lupus*) and lynx (*Lynx lynx*). *Slovak Wildlife Society*, 89.
- World Wildlife Fund. “Living Planet Report 2018”. July 20, 2020. <https://www.worldwildlife.org/pages/living-planet-report-2018>.
- Zhou, Y. & Wang, Y. (2007). An assessment of impervious surface areas in Rhode Island. *Northeastern Naturalist*, 14: 643-650.

TABLE 1B.

Category	Variable	Type	Definition
Response variables for coyote value	Benefits of coyote	4 Likert scale questions Strongly disagree – strongly agree	1 = low value of coyote, 5 = high value
	Risks of coyote	4 Likert scale questions Strongly disagree – strongly agree	5 = low value of coyote, 1 = high value
Response variable for coyote sighting	Coyote sighting	Likert frequency item Never – daily	6 = high sighting frequency, 1 = low sighting frequency
Response variables for coyote incident	Coyote incident	Likert frequency item Never – daily	6 = high incidence frequency, 1 = low incidence frequency
All predictive variables	age	Continuous	Years of age
	gender	Non-ordered categorical	Male, female, and non-binary
	county	Non-ordered categorical	County where participants predominantly reside
	INS (Inclusion of Nature of Self)	Continuous between 1 -5	Measure of biospheric values; 1 = low biospheric values, 5 = high values
	animal.ownership	Binary	1 = owns an animal, 0 = does not
	knowledge	Continuous between 1 - X	Knowledge of coyotes; 1 = correct response, 0 = incorrect response or 'I don't know' response
	animal.incidence	Binary	Incident where coyote growled, stalked, or attacked livestock or pets; 1 = incident occurred, 0 = incident did not occur
	fear	Likert question Strongly disagree – strongly agree	5 = high fear of coyote, 1 = low fear

TABLE 2B.

Model Coefficient	Medians	SD	Lower 95% CI	Upper 95% CI	Probability > 0
age	0.00	0.00	-0.01	0.00	0.14
gender_female	0.18	0.08	0.03	0.33	0.99
gender_non.binary	-0.30	0.35	-1.00	0.38	0.20
knowledge	0.04	0.02	-0.01	0.09	0.95
fear	-0.85	0.10	-1.03	-0.66	0.00
animal_incident	-0.52	0.16	-0.84	-0.21	0.00
animal.owner	0.12	0.09	-0.05	0.30	0.91
fear:animal.incident	0.06	0.28	-0.49	0.60	0.58
INS_2	1.35	0.38	0.57	2.09	1.00
INS_3	1.34	0.38	0.58	2.08	1.00
INS_4	1.50	0.37	0.75	2.21	1.00
INS_5	1.67	0.37	0.93	2.38	1.00
INS_6	1.72	0.37	0.98	2.44	1.00
countyKent	0.16	0.19	-0.20	0.52	0.79
countyNewport	-0.21	0.17	-0.54	0.13	0.11
countyProvidence	0.27	0.16	-0.05	0.58	0.95
countyWashington	0.24	0.16	-0.09	0.55	0.93

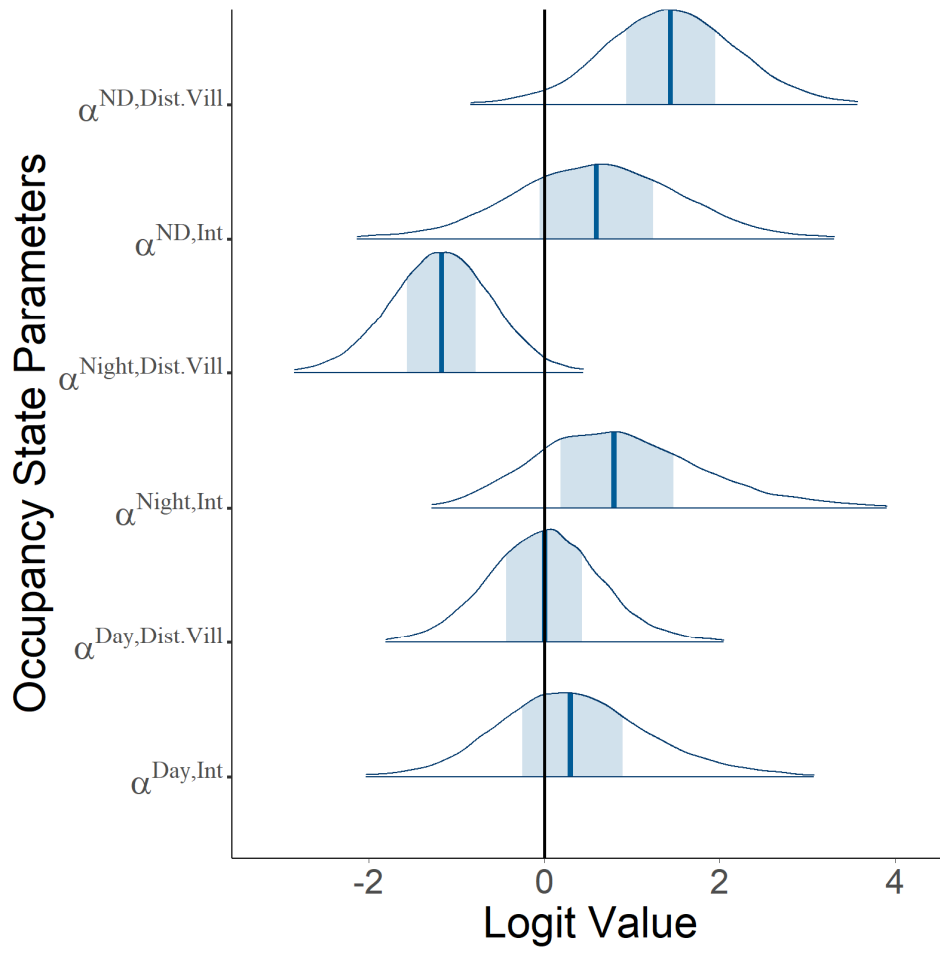
TABLE 3B.

Model coefficient	Medians	SD	Lower 95% CI	Upper 95% CI	Probability > 0
animal.owner	0.30	0.10	.10	0.50	1.00
fear	0.15	0.10	-0.05	0.35	0.93
knowledge	0.06	0.03	-0.00	0.11	0.98
INS_6	-0.09	0.34	-0.76	0.59	0.40
INS_5	0.03	0.34	-0.63	0.70	0.53
INS_4	-0.05	0.34	-0.73	0.62	0.43
INS_3	-0.11	0.36	-0.82	0.61	0.37
INS_2	-0.10	0.37	-0.82	0.63	0.39
countyWashington	-0.32	0.18	-0.66	0.02	0.03
countyProvidence	-0.59	0.18	-0.94	-0.24	0.00
countyNewport	-0.03	0.19	-0.41	0.34	0.43
countyKent	-0.34	0.21	-0.74	0.06	0.04

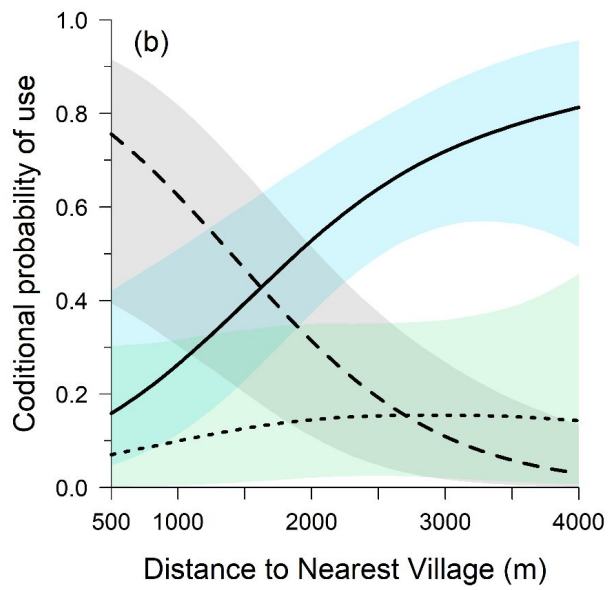
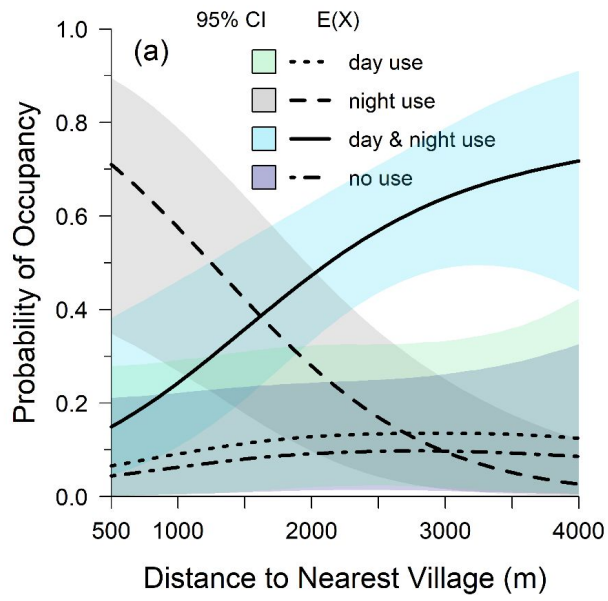
TABLE 4B.

Model coefficient	Medians	SD	Lower 95% CI	Upper 95% CI	Probability > 0
countyKent	-0.53	0.29	-1.10	0.05	0.04
countyNewport	-0.12	0.25	-0.61	0.37	0.30
countyNot_shared	-1.20	0.65	-2.59	-0.02	0.02
countyProvidence	-0.46	0.23	-0.92	0.00	0.03
countyWashington	-0.48	0.23	-0.92	-0.04	0.02
INS_2	-0.36	0.45	-1.24	0.51	0.22
INS_3	-0.54	0.46	-1.45	0.34	0.12
INS_4	-0.47	0.42	-1.30	0.36	0.14
INS_5	-0.19	0.41	-1.00	0.61	0.32
INS_6	-0.41	0.42	-1.22	0.40	0.17
knowledge	0.05	0.04	-0.04	0.13	0.85
fear	1.41	0.33	0.79	2.07	1.00
animal.owner	0.53	0.23	0.09	1.01	0.99
fear:animal.owner	-0.64	0.35	-1.32	0.04	0.03

FIGURE 1A.



FIGURUE 2A.



FIGURUE 3A.

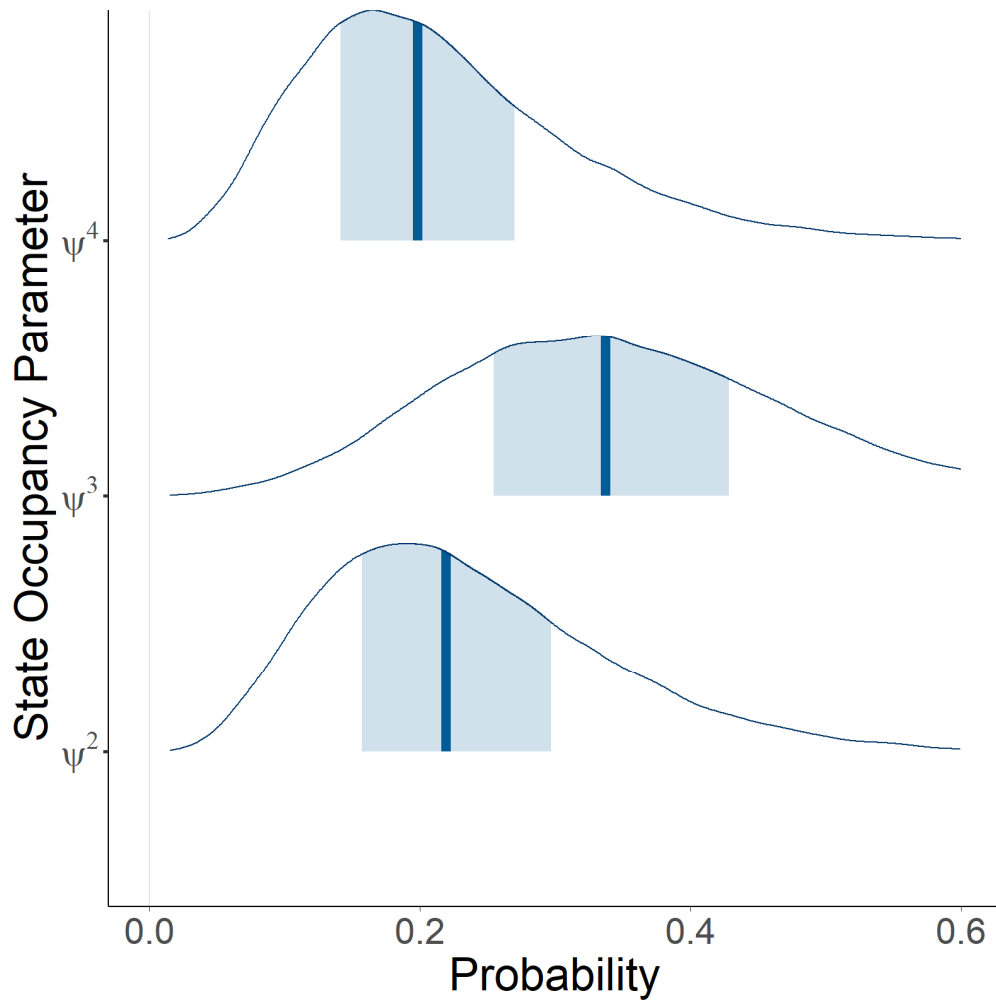


FIGURE 4A.

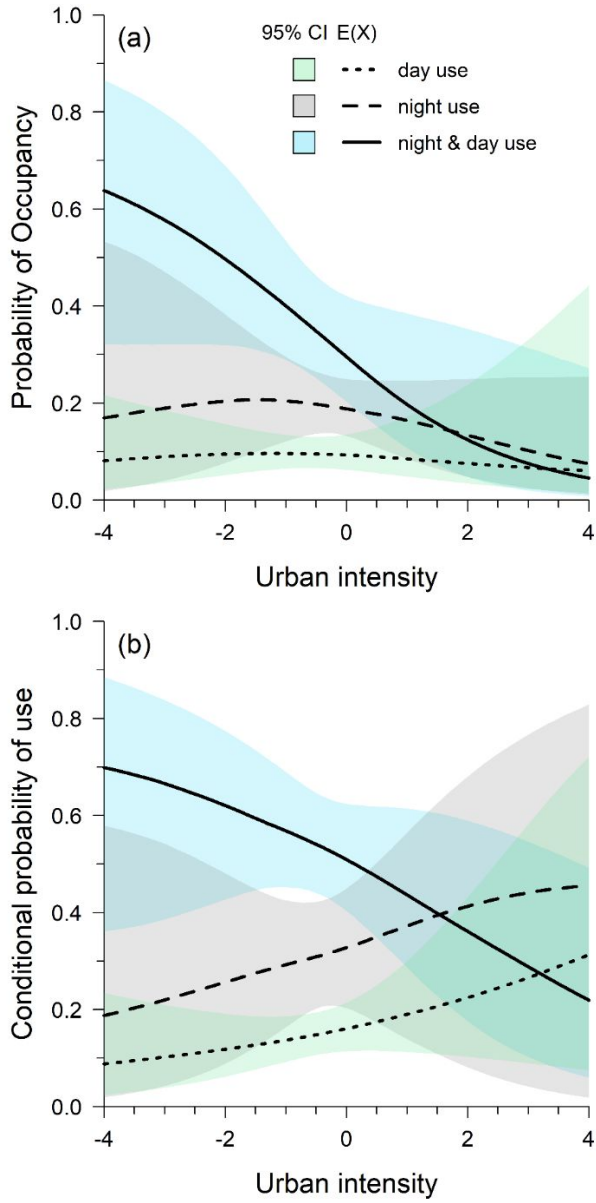


FIGURE 5A.

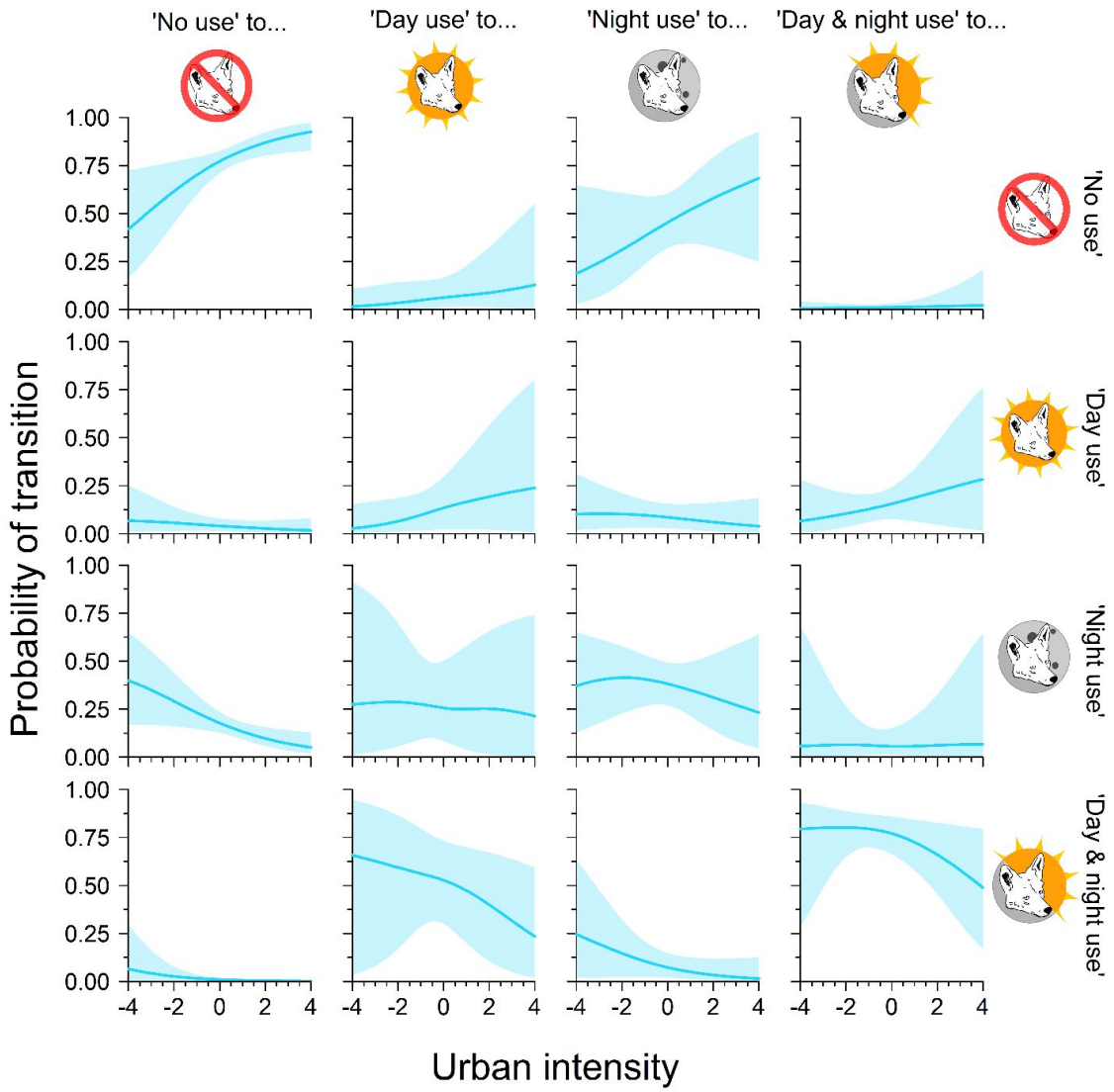


FIGURE 1B.

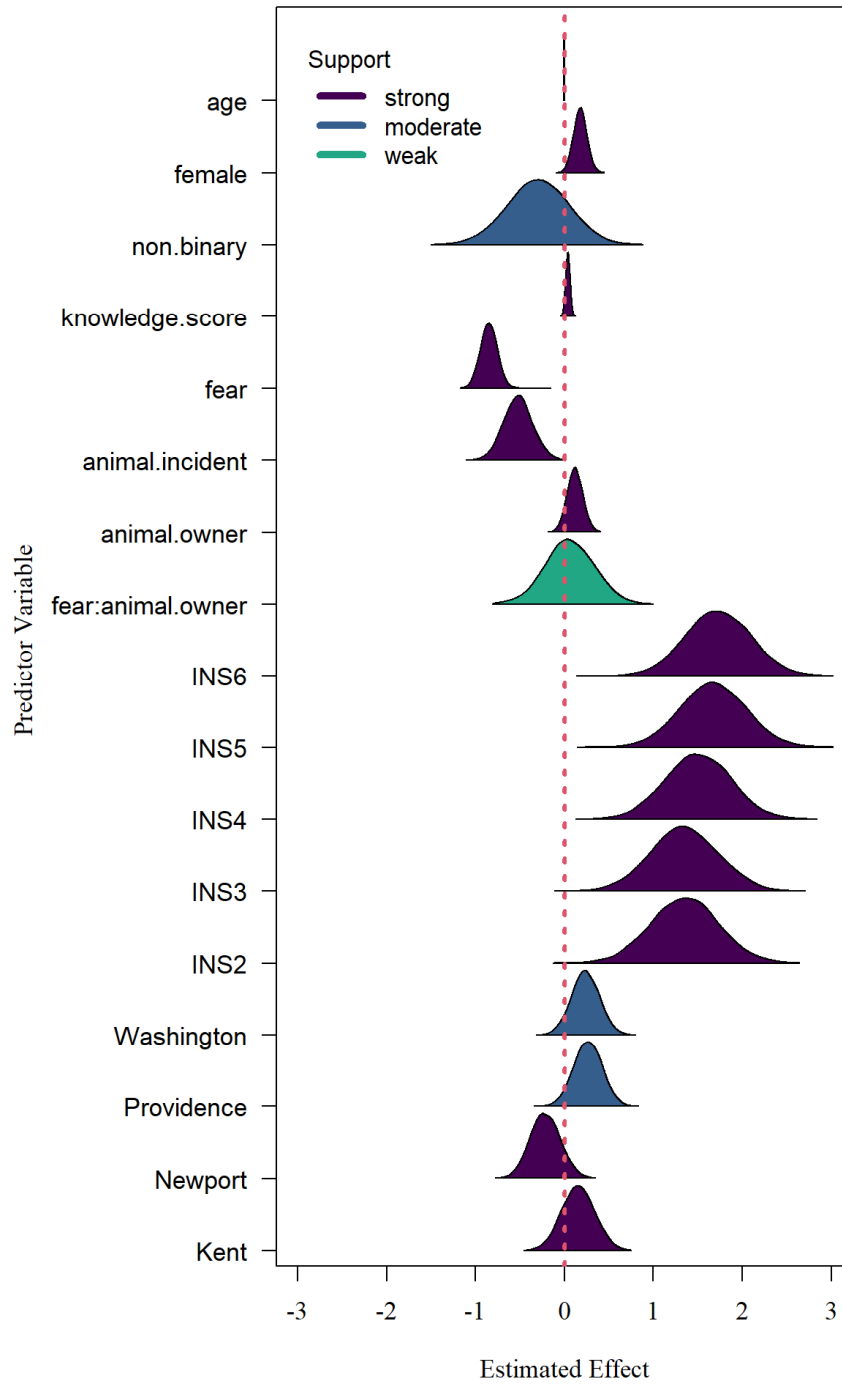


FIGURE 2B.

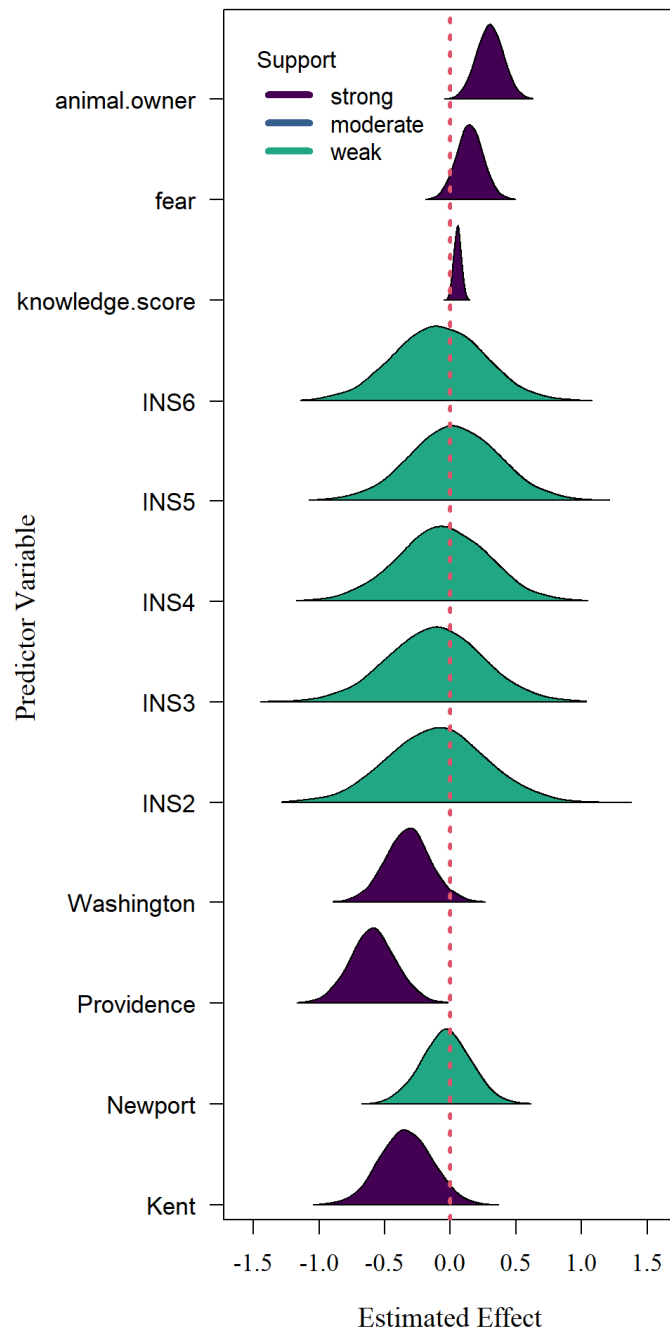
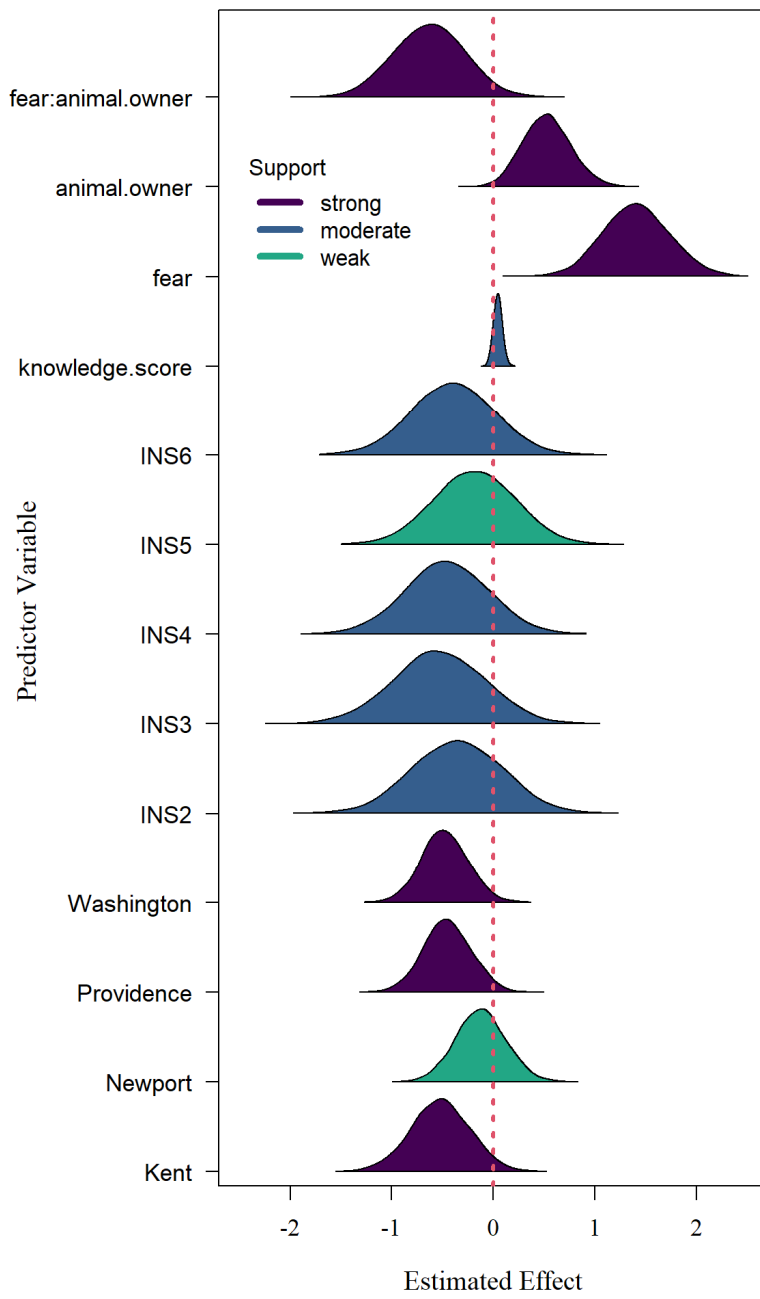


FIGURE 3B.



APPENDICES

APPENDIX S1 – Chapter 1

Parameter type	Verbal description
ψ	Probability of occupancy vector for the $M = 4$ states, which sums to one. The full model assumes that state 4 ('day & night') is independent whereas the reduced model assumes state 4 is the product of states 2 ('day') and 3 ('night', Eq. 2). The null model assumes states 2, 3, and 4 are all equal (Eq. 4). For all models, states 2, 3, and 4 are estimated from the data while state 1 is obtained through subtraction such that $\psi^1 = 1 - \psi^2 - \psi^3 - \psi^4$.
P	Probability of detection matrix for the $M = 4$ states, which is $M \times M$ with the observed states along the column and true states along the rows. Rows sum to one. The full model assumes that there is no relationship among state-specific detection probabilities, and so detection probabilities in state 4 ('day & night') are not defined by the detection probabilities of state 2 ('day') or 3 ('night', Eq. 1). Conversely, the reduced model assumes that the detection probabilities in state 4 are related to states 2 and 3, or their complementary probability, depending on the observed state (Eq. 3). The null model assumes the probability of detecting states 2, 3, or 4 are identical (eq. 5).
τ	The $M \times M$ transition probability matrix of the dynamic MSDOM. The true state at sampling period $t-1$ is along the rows and the possible states to transition to are along the columns. Each row sums to 1. Transitions are composed of local colonization (γ) and extinction (ε) probabilities. To reduce model complexity, the full (Eq. 8), reduced (Eq. 9), and null (Eq. 10) models assume all transitions are defined by the product of local colonization and extinction probabilities, though they do so in different ways (described below).
γ	The probability of local colonization between sampling period $t-1$ and t . The full model (Eq. 8) has four colonization probabilities: the probability an unoccupied site transitions to state 2 ('day', γ^D) or state 3 ('night', γ^N), the conditional probability a site transitions to state 2 given state 3 at $t-1$ ($\gamma^{D N}$), and the conditional probability a site transitions to state 3 given state 2 at $t-1$ ($\gamma^{N D}$). The reduced model (Eq. 9), removes the conditional probabilities present in the full model and therefore assumes that transitions between day and night are composed of γ^D and γ^N . The null model (Eq. 10) assumes day and night transitions are the same so there is a single colonization probability (γ).

ϵ The probability a local extinction between sampling period $t-1$ and t . The full model (Eq. 8), has four extinction probabilities: the probability state 2 ('day') transitions to any other state (ϵ^D), the probability state 3 ('night') transitions to any other state (ϵ^N), the conditional probability day is not included at time t given state 4 ('day & night') at time $t-1$ ($\epsilon^{D|N}$), and the conditional probability night is not included at time t given state 4 at time $t-1$ ($\epsilon^{N|D}$). The reduced model (Eq. 9) removed the conditional probabilities present in the full model and therefore assumes that transitions between day and night are composed of ϵ^D and ϵ^N . The null model (Eq. 10) assumes day and night transitions are the same so there is a single extinction probability (ϵ).

Table 1. A high-level description of the types of model parameters for the multi-state diel occupancy model (MSDOM). For this description, we assume that there are $M = 4$ states which represent whether the species is 1) not present, 2) present during the day only, 3) present during the night only, and 4) present during the day & night.

Parameters	Relevant Model	Verbal Description
$p^{2,2} = p^{\text{DAY}}$	Full	Probability of detecting a species during the day only, given it was present only during the day. Part of matrix P.
$p^{3,3} = p^{\text{Night}}$	Full	Probability of detecting a species at night only, given it was present only at night. Part of matrix P.
$p^{4,1} = p^{\text{ND1}}$	Full	Probability of not detecting a species, given it was present during the day and night. Part of matrix P.
$p^{4,2} = p^{\text{ND2}}$	Full	Probability of detecting a species during the day only, given it was present during the day and night. Part of matrix P.
$p^{4,3} = p^{\text{ND3}}$	Full	Probability of detecting a species during the night only, given it was present during the day and night. Part of matrix P.
$p^{4,4} = p^{\text{ND4}}$	Full	Probability of detecting a species during the day and night, given it was present during the day and night. Part of matrix P.
$p^{\text{Day.M}}$	Reduced	Probability of detecting a species during the day, regardless of use or lacking use at night. Part of matrix P.
$p^{\text{Night.M}}$	Reduced	Probability of detection a species at night, regardless of use or lacking use during the day. Part of matrix P.
$\psi^{\text{Day.M}}$	Reduced	Probability of using a site during the day, regardless of use or lacking use at night. Part of probability of occupancy vector.

$\psi^{\text{Night.M}}$	Reduced	Probability of using a site at night, regardless of use or lacking use during the day. Part of probability of occupancy vector.
ψ^1	Full, Reduced, Null	Probability a species is not present. Part of probability of occupancy vector.
ψ^2	Full, Reduced, Null	Probability a species is present during the day only. Part of probability of occupancy vector.
ψ^3	Full, Reduced, Null	Probability a species is present during the night only. Part of probability of occupancy vector.
ψ^4	Full, Reduced, Null	Probability a species is present during the day & night. Part of probability of occupancy vector.
ψ^\bullet	Full, Reduced, Null	The probability a site is occupied, regardless of state. Part of probability of occupancy vector.
p^\bullet	Null	The probability of detection, regardless of state. Part of matrix P.

Table 2. Verbal descriptions and model relevancy of fundamental model parameters for the static (single season) multi-state diel occupancy model.

Parameters	Relevant Model	Verbal Description
$p_t^{2,2} = p_t^{\text{DAY}}$	Full	Probability of detecting a species in season t during the day only, given it was present only during the day. Part of matrix P.
$p_t^{3,3} = p_t^{\text{Night}}$	Full	Probability of detecting a species in season t at night only, given it was present only at night. Part of matrix P.
$p_t^{4,1} = p_t^{\text{ND1}}$	Full	Probability of not detecting a species in season t , given it was present during the day and night. Part of matrix P.
$p_t^{4,2} = p_t^{\text{ND2}}$	Full	Probability of detecting a species in season t , during the day only, given it was present during the day and night. Part of matrix P.
$p_t^{4,3} = p_t^{\text{ND3}}$	Full	Probability of detecting a species in season t , during the night only, given it was present during the day and night. Part of matrix P.
$p_t^{4,4} = p_t^{\text{ND4}}$	Full	Probability of detecting a species in season t , during the day and night, given it was present during the day and night. Part of matrix P.
$p_t^{\text{Day.M}}$	Reduced	Probability of detecting a species in season t , during the day, regardless of use or lacking use at night. Part of matrix P.
$p_t^{\text{Night.M}}$	Reduced	Probability of detection a species in season t , at night, regardless of use or lacking use during the day. Part of matrix P.
$\psi_1^{\text{Day.M}}$	Reduced	Probability of using a site in season 1, during the day, regardless of use or lacking use at night. Part of probability of occupancy vector.

$\psi_1^{\text{Night.M}}$	Reduced	Probability of using a site in season 1, at night, regardless of use or lacking use during the day. Part of probability of occupancy vector.
ψ_1^1	Full, Reduced, Null	Probability a species is not present in season 1. Part of probability of occupancy vector.
ψ_1^2	Full, Reduced, Null	Probability a species is present during the day only in season 1. Part of probability of occupancy vector.
ψ_1^3	Full, Reduced, Null	Probability a species is present during the night only in season 1. Part of probability of occupancy vector.
ψ_1^4	Full, Reduced, Null	Probability a species is present during the day & night in season 1. Part of probability of occupancy vector.
ψ^\bullet	Full, Reduced, Null	The probability a site is occupied, regardless of state. Part of probability of occupancy vector.
p^\bullet	Null	The probability of detection, regardless of state. Part of matrix P.
γ^D	Full, Reduced	The probability a site is colonized and used in the day only. Part of the probability of local colonization between sampling period $t-1$ and t .
γ^N	Full, Reduced	The probability a site is colonized and used in the night only. Part of the probability of local colonization between sampling period $t-1$ and t .
$\gamma^{N D}$	Full	The probability a site is colonized and used in the night only, given it was used previously in the day only. Part of the probability of local colonization between sampling period $t-1$ and t .
$\gamma^{D N}$	Full	The probability a site is colonized and used in the day only, given it was used previously in the

		night only. Part of the probability of local colonization between sampling period $t-1$ and t .
ε^D	Full, Reduced	The probability a site is no longer used in the day only. Part of the probability of local extinction between sampling period $t-1$ and t .
ε^N	Full, Reduced	The probability a site is no longer used in the night only. Part of the probability of local extinction between sampling period $t-1$ and t .
$\varepsilon^{N D}$	Full	The probability a site is no longer used in the night only, given it was used previously in the day only. Part of the probability of local extinction between sampling period $t-1$ and t .
$\varepsilon^{D N}$	Full	The probability a site is no longer used in the day only, given it was used previously in the night only. Part of the probability of local extinction between sampling period $t-1$ and t .

Table 3. Verbal descriptions and model relevancy of fundamental model parameters for the dynamic (multi-season) multi-state diel occupancy model. Descriptions also include matrix, vector, and probability affiliations described in Table 1.

Derived Parameter	Relevant Model	Verbal Description
$\psi^4 / (\psi^2 \times \psi^3)$	Full Static and Dynamic	This day-night interaction factor quantifies the tendency for a site to be used during the day and night more than (>1) or less (<1) than expected; this will be exactly 1 in the reduced model, as it's part of the assumption of the model. This parameter is akin to a species interaction factor of co-occurrence models (MacKenzie et al., 2004).
$\frac{\psi^2}{\psi^\bullet}$	Full and Reduced Static and Dynamic	The probability of temporal use at a site during the day only, given the site is used.
$\frac{\psi^3}{\psi^\bullet}$	Full and Reduced Static and Dynamic	The probability of temporal use during the night only, given the site is used.
$\frac{\psi^4}{\psi^\bullet}$	Full and Reduced Static and Dynamic	The probability of temporal use during the day & night, given the site is used.

Table 4. Verbal descriptions and model relevancy of derived model parameters for the multi-state diel occupancy model.

APPENDIX S3 – Chapter 1

1. Fosa Dataset

Region	Site ID	Year	Total Cameras	Survey Dates	Season
Makira	SITE 1	2008	20	Sept 2 – Nov 13	Cool, Dry
	SITE 1	2010	24	Sept 16 – Nov 16	Cool, Dry
	SITE 1	2011	24	Aug 20 – Oct 20	Cool, Dry
	SITE 1	2012	24	Aug 1 – Oct 16	Cool, Dry
	SITE 1	2013	24	Sept 7 – Nov 20	Cool, Dry
	SITE 1	2015	24	Sept 11 – Nov 9	Cool, Dry
	SITE 2	2011	24	Mar 20 – May 23	Warm, Wet
	SITE 2	2012	24	Jun 9 – July 23	Cold, Dry
	SITE 2	2013- 2014	24	Nov 16 – Jan 7	Hot, Wet
	SITE 3	2009	20	Mar 4 – May 4	Warm, Wet
	SITE 4	2009	19	Aug 21 – Oct 27	Cool, Dry
	SITE 5	2009- 2010	18	Nov 20 – Jan 27	Hot, Wet
	SITE 6	2010- 2011	24	Dec 9 – Feb 18	Hot, Wet
SITE 7	2011	24	Jun 9 – Aug 13	Cold, Dry	
Ranomafana	VAL-SAH	2008	53	June – Oct	Cold, Dry
	SAH-CVB	2007	42	June – Aug	Cold, Dry

Table 1. Details on seven survey regions used for analysis of fosa in the Makira Natural Park and Ranomafana National Park Regions. Survey dates refer to the first date cameras were set for the specific site and year followed by the last date cameras were removed.

Incorporating multiple camera surveys for the fosa case studies

We modeled the variation among data collection years and survey areas differently for the Makira and Ranomafana datasets. For the Makira data, we accounted for this variation by treating each model parameter as a random effect across survey areas (e.g., for s survey areas, $\alpha_s^{Day} \sim \text{Normal}(\mu_{\alpha^{Day}}, \sigma_{\alpha^{Day}})$); as such, model parameter estimates reported in the main text are the population-level mean effects (inference for across survey areas for each parameter). We did not treat each survey independently as this would allow ‘Site 1’ to have an oversized influence on parameter estimates as it was surveyed six times. Survey areas with multiple years of surveys (e.g., ‘Site 1’) were modeled together based on preliminary findings for a lack of difference among years. Specifically, we evaluated across year differences within a survey area by treating surveys as a categorical variable in a stacked occupancy design (see Monterroso et al., 2020). Models without survey year variation were more supported by CPO. With only two surveys at Ranomafana, we only used a stacked occupancy design, treating survey as a categorical variable, and compare models with and without this variable.

References

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.

Model	Model description	CPO	Δ CPO
<i>M1.full</i>	Full model with distance to town covariate	838.50	0.00
<i>M4.red</i>	Reduced model with distance to matrix covariate	843.12	4.62
<i>M9.red.no.covs</i>	Reduced model with no covariates	843.64	5.14
<i>M8.full2.no.covs</i>	Full model with no covariates and categorical effect	843.74	5.24
<i>M2.full</i>	Full model with distance to matrix covariate	843.76	5.26
<i>M4.red2</i>	Reduced model with distance to matrix covariate and categorical effect	844.58	6.08
<i>M3.red</i>	Reduced model with distance to town covariate	844.65	6.15
<i>M2.full2</i>	Full model with distance to matrix covariate and categorical effect	844.68	6.18
<i>M9.red2.no.covs</i>	Reduced model with no covariates and categorical effect	844.82	6.32
<i>M1.full2</i>	Full model with distance to town covariate and categorical effect	845.50	7.00
<i>M3.red2</i>	Reduced model with distance to town covariate and categorical effect	845.99	7.49
<i>M8.full.no.covs</i>	Full model with no covariates	846.11	7.61
<i>M6.null</i>	Null model with distance to matrix covariate	916.25	77.75
<i>M7.null</i>	Null model with no covariates	916.27	77.77
<i>M5.null</i>	Null model with distance to town covariate	917.00	78.50
<i>M7.null2</i>	Null model with no covariates and categorical effect	917.00	78.50
<i>M6.null2</i>	Null model with distance to matrix covariate and categorical effect	917.19	78.69
<i>M5.null2</i>	Null model with distance to town covariate and categorical effect	917.80	79.295612

Table 2. Conditional predictive ordinate outputs for Ranomafana data. Lower values indicate a more supported model.

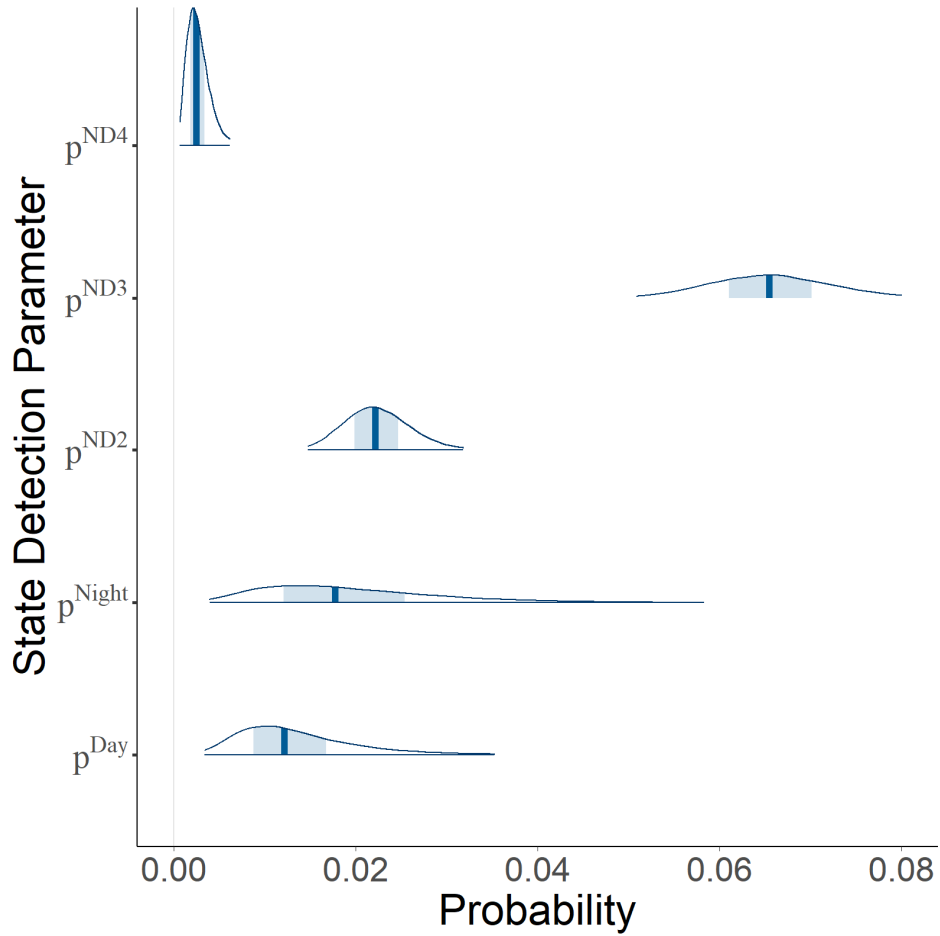


Figure 1. Posterior distributions of fosa state detection probability for the most supported model using the Ranomafana National Park data. The light blue shaded area represents 50% probability density and the dark blue line indicates the posterior mode. Note, p^{ND1} is not plotted.

Parameter	Mode	Credible Interval	
		Lower 95%	Upper 95%
p^{Day}	0.01	0.01	0.00
p^{Night}	0.02	0.02	0.00
p^{ND1}	0.91	0.91	0.89
p^{ND2}	0.02	0.02	0.02
p^{ND3}	0.07	0.07	0.05
p^{ND4}	0.00	0.00	0.00

Table 3. Posterior quantities for detection probabilities of Ranomafana National Park from the best fit model. Credible intervals were calculated using the highest posterior density interval.

Model	Model description	CPO	ΔCPO
<i>M1.full.no.covs</i>	Full model with no covariates	1155.65	0.00
<i>M2.full.covs</i>	Full model with covariates	1158.05	2.40
<i>M1.red.no.covs</i>	Reduced model with no covariates	1173.68	18.03
<i>M2.red.covs</i>	Reduced model with covariates	1175.35	19.70
<i>M1.null.no.covs</i>	Null model with covariates	1215.40	59.75
<i>M2.null.covs</i>	Null model with no covariates	1216.78	61.13

Table 4. Conditional predictive ordinate outputs for Makira data. Lower values indicate a more supported model.

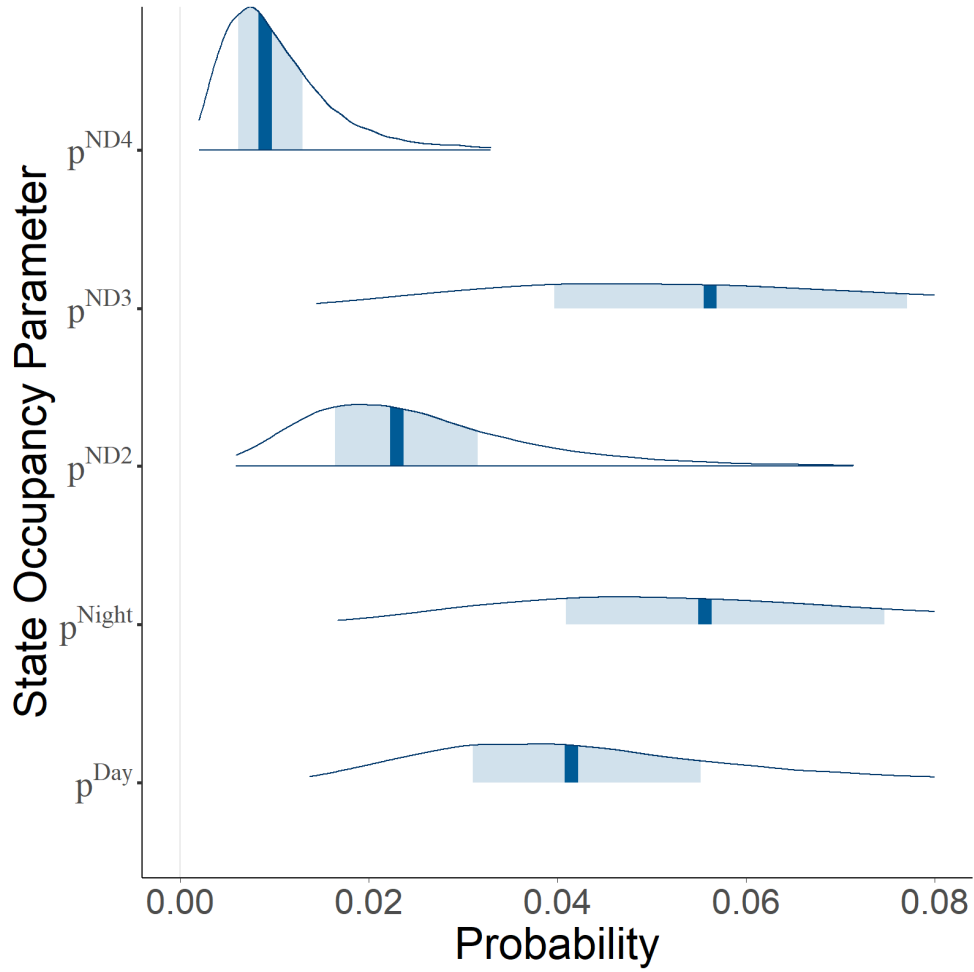


Figure 2. Posterior distributions of fosa state detection probability for the most supported model using the Makira Natural Park data. The light blue shaded area represents 50% probability density and the dark blue line indicates the posterior mode. Note, p^{ND1} is not plotted.

Parameter	Mode	Credible Interval	
		Lower 95%	Upper 95%
p^{Day}	0.04	0.01	0.09
p^{Night}	0.05	0.02	0.12
p^{ND1}	0.29	0.14	0.47
p^{ND2}	0.02	0	0.05
p^{ND3}	0.05	0.01	0.12
p^{ND4}	0.01	0	0.02

Table 5. Posterior results for detection probabilities of the Makira region from the best fit model. Credible intervals were calculated using the highest posterior density interval.

2. Coyote Dataset

Camera	Bushnell Trophy Cam Standard Edition and HD models
Model numbers (and their count)	1199435 (8), 119436 (12), 1193537C (2), 119363C (19)
Mode	Camera
Image Size:	5M Pixel
Capture Number	1
Photo Video Size	NA
Video Length	NA
Interval	30 seconds
Sensor Level	Normal
Format	Execute (format memory card every time before deploying camera trap or replacing memory card)
TV Out	NTSC
Time Stamp	On
Set Clock	24hr, year-month-day
Field Scan	Off
Video Sound	NA
Default Set	Cancel

Table 6. Settings of motion-triggered camera traps and examples of lure treatments used in

The camera trap settings used on the camera traps for Fidino et al., The Effect of Lure on Detecting Mammals with Camera Traps. Wildlife Society Bulletin.

Data collection for Dynamic Modeling

To capture seasonal variation in occupancy, cameras were placed for a minimum of 4 consecutive weeks in January, April, July, and October. Cameras were placed in urban greenspace such as city parks, cemeteries, golf courses, and natural areas, and sampling locations were 1 km apart at a minimum.

APPENDIX S1 – Chapter 2

Model	Model variation	LOOC V
1 + age+county+gender+image.relation.nature+knowledge.score+fear*animal.incident+animal.owner	interaction	0.0
1 + age+county+gender+image.relation.nature*knowledge.score+fear+ animal.owner+animal.incident	interaction	-1.0
1 + age + county + gender + image.relation.nature + fear + knowledge.score + animal.owner + animal.incident	additive	-1.4
1 + age+gender+county+image.relation.nature*fear+knowledge.score+ animal.incident+animal.owner	interaction	-2.1

Table 1. Leave-one-out-cross-validation outputs for coyote *sightings*. Lower values indicate a more supported model.

Model	Model variation	LOOC V
1 + county+image.relation.nature+fear+knowledge.score+animal.owner	additive	0.0
1 + county+image.relation.nature*knowledge.score+fear+animal.owner	interaction	1.7
1 + county+image.relation.nature*fear+knowledge.score+animal.owner	interaction	2.4

Table 2. Leave-one-out-cross-validation outputs for coyote *sightings*. Lower values indicate a more supported model.

Model	Model variation	LOOCV
1 + county+image.relation.nature+knowledge.score+fear* animal.owner	interaction	0.0
1 + county+image.relation.nature+fear+knowledge.score+ animal.owner	additive	1.9
1 + county+image.relation.nature*knowledge.score+fear+ animal.owner	interaction	3.2

Table 3. Leave-one-out-cross-validation outputs for coyote *incidents*. Lower values indicate a more supported model.