CONTINUOUS-TIME DISCRETE-SPACE MODELS FOR ANIMAL MOVEMENT

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The processes influencing animal movement and resource selection are complex and varied. Past efforts to model behavioral changes over time used Bayesian statistical models with variable parameter space, such as reversible-jump Markov chain Monte Carlo approaches, which are computationally demanding and inaccessible to many practitioners. We present a continuous-time discrete-space (CTDS) model of animal movement that can be fit using standard generalized linear modeling (GLM) methods. This CTDS approach allows for the joint modeling of location-based as well as directional drivers of movement. Changing behavior over time is modeled using a varying-coefficient framework which maintains the computational simplicity of a GLM approach, and variable selection is accomplished using a group lasso penalty. We apply our approach to a study of two mountain lions (*Puma concolor*) in Colorado, USA.

1. Introduction. Telemetry data have been used extensively in recent years to study animal movement, space use and resource selection [e.g., Fieberg et al. (2010), Hanks et al. (2011), Johnson, London and Kuhn (2011)]. The simplest form of telemetry data consist of a time series of remotely obtained spatial locations of an animal. Typically, an animal or group of animals are captured and fit with a tracking device (e.g., a collar with a GPS) which records the animal's location at specified intervals. The ease with which telemetry data are being collected is increasing, leading to vast improvements in the number of animals being monitored, as well as the temporal resolution at which telemetry locations are obtained [Cagnacci et al. (2010)]. This combination can result in huge amounts of telemetry data on a single animal population under study. Additionally, the processes driving animal movement are complex, varied and changing over time. For example, animal behavior could be driven by the local environment [e.g., Hooten et al. (2010)], by conspecifics or predator/prey interactions [e.g., Merrill et al. (2010), Potts, Mokross and Lewis (2014)], by internal states and needs [e.g., Nathan et al. (2008)], or by memory [e.g., Van Moorter et al. (2009)]. The animal's response to

each of these drivers of movement is also likely to change over time [e.g., Hanks et al. (Hanks et al.), McClintock et al. (2012), Nathan et al. (2008)] as animals respond to changing stimuli (e.g., dirunal cycles) or energy needs.

Examples of recent models for animal telemetry data include the agent-based model of Hooten et al. (2010), the velocity-based framework for modeling animal movement of Hanks et al. (2011), and the mechanistic approach of McClintock et al. (2012). These three approaches use Markov chain Monte Carlo (MCMC) for inference, and both Hanks et al. (2011) and McClintock et al. (2012) allow for time-varying behavior by letting the model parameter space vary, either through a reversible-jump Markov chain Monte Carlo approach [Green (1995)] or the related birth–death Markov chain Monte Carlo approach [Stephens (2000)]. Such methods are computationally demanding and require the user to tune the algorithm to ensure convergence. Our goal is to provide an approach to modeling complex time-varying movement behavior that is both scientifically useful and computationally tractable.

While telemetry data can be collected with relative ease at high resolution, habitat covariates (i.e., landcover) are typically available only in gridded form at a fixed resolution. Traditional analyses that focus on modeling an animal's location often contain redundant information because observations are close enough in time that the spatially available habitat data contains little information to model the fine scale movement. Therefore, constructing an analysis with an eye toward the habitat data scale holds promise for the future of telemetry data.

In this manuscript, we present a continuous-time, discrete-space (CTDS) model for animal movement which allows for flexible modeling of an animal's response to drivers of movement in a computationally efficient framework. We consider a Bayesian approach to inference, as well as a multiple-imputation approximation to the posterior distribution of parameters in the movement model. Instead of a state-switching or change-point model for changing behavior over time, we adopt a time-varying coefficient model. We also allow for variable selection using a lasso penalty. This CTDS approach is highly computationally efficient, requiring only minutes or seconds to analyze movement paths that would require hours using the approach of Hanks et al. (2011) or days using the approach of Hooten et al. (2010), allowing the analysis of longer movement paths and more complex behavior than has been previously possible.

In Section 2, *Continuous-time Markov chain models for animal movement*, we describe the CTDS model for animal movement and present a latent variable representation of the model that allows for inference within a standard generalized linear model (GLM) framework. In Section 3, *Inference on CTDS model parameters using telemetry data*, we present a Bayesian approach for inference and describe the use of multiple imputation [Rubin (1987)] to approximate the posterior predictive distribution of parameters in the CTDS model. In Section 4, *Time-varying behavior and shrinkage estimation*, we use a varying-coefficient approach to model changing behavior over time, and use a lasso penalty for variable selection and

regularization. In Section 5, *Drivers of animal movement*, we discuss modeling potential covariates in the CTDS framework. In Section 6, *Example*: *Mountain lions in Colorado*, we illustrate our approach through an analysis of mountain lion (*Puma concolor*) movement in Colorado, USA. Finally, in Section 7, *Discussion*, we discuss possible extensions to the CTDS approach.

2. Continuous-time Markov chain models for animal movement. Our goal is to specify a model of animal response to drivers of movement that is flexible and computationally efficient. We propose a continuous-time Markov chain (CTMC) model for an animal's CTDS movement through a discrete, gridded space (Figure 1). We then present a latent variable representation of a CTMC model that represents the CTMC as a generalized linear model (GLM), allowing for inference in CTMCs in general and CTDS movement models in particular to be made using GLM theory and computation (e.g., iteratively reweighted least squares optimization routines).

Let the study area be defined as a graph $(\mathbf{G}, \mathbf{A})$ of M spatial vertices $\mathbf{G} = (G_1, G_2, \ldots, G_M)$ connected by "edges" $\mathbf{A} = \{\lambda_{ij} : i \sim j, i = 1, \ldots, M\}$, where $i \sim j$ means that the nodes G_i and G_j are directly connected. For example, in a gridded space each grid cell is a vertex (node) and the edges connect each grid cell to its first-order neighbors (e.g., cells that share an edge). In ecological studies, the spatial resolution of the grid cells in $\mathbf{G}$ will often be determined by the resolution at which environmental covariates that may drive animal movement and selection are available. Discretizing an animal's path across the study area amounts to studying movement at the spatial resolution of the available landscape covariates.

An animal's continuous-time, discrete-space (CTDS) path $\tilde{\mathbf{S}} = (\mathbf{g}, \boldsymbol{\tau})$ consists of a sequence of grid cells $\mathbf{g} = (G_{i_1}, G_{i_2}, \ldots, G_{i_T})$ traversed by the animal and the residence times $\boldsymbol{\tau} = (\tau_1, \tau_2, \ldots, \tau_T)$ in each grid cell. The discrete-space representation $\tilde{\mathbf{S}} = (\mathbf{g}, \boldsymbol{\tau})$ of the movement path allows us to use standard continuous-time Markov chain models to make inference about possible drivers of movement.

While we will relax this assumption later to account for temporal autocorrelation in movement behavior, we initially assume that the tth observation (G_{i_t}, τ_t) in the sequence is independent of all other observations in the sequence. Under this
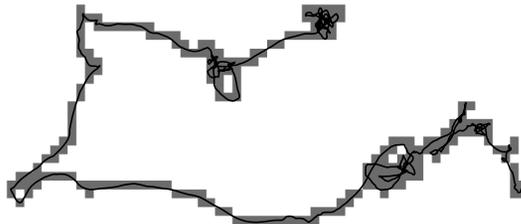

FIG. 1. *Continuous-time continuous-space and continuous-time discrete-space representations of an animal's movement path.*

assumption, the likelihood of the sequence of transitions $\{(G_{i_t} \to G_{i_{t+1}}, \tau_t), t = 1, 2, \ldots, T\}$ is the product of the likelihoods of each individual observation. We will focus on modeling each transition $(G_{i_t} \to G_{i_{t+1}}, \tau_t)$.

If an animal is in cell G_{i_t} at time t, then define the rate of transition from cell G_{i_t} to a neighboring cell G_{j_t} at time t as

$$(1) \qquad \lambda_{i_t j_t}(\boldsymbol{\beta}) = \exp\{\mathbf{x}'_{i_t j_t} \boldsymbol{\beta}\},$$

where $\mathbf{x}_{i_t j_t}$ is a vector containing covariates related to drivers of movement specific to cells G_{i_t} and G_{j_t}, and $\boldsymbol{\beta}$ is a vector of parameters that define how each of the covariates in $\mathbf{x}_{i_t j_t}$ are correlated with animal movement. The total transition rate λ_{i_t} from cell G_{i_t} is the sum of the transition rates to all neighboring cells: $\lambda_{i_t}(\boldsymbol{\beta}) = \sum_{j_t \sim i_t} \lambda_{i_t j_t}(\boldsymbol{\beta})$, and the time τ_t that the animal resides in cell G_{i_t} is exponentially-distributed with rate parameter equal to the total transition rate $\lambda_{i_t}(\boldsymbol{\beta})$:

$$(2) \qquad [\tau_t | \boldsymbol{\beta}] = \lambda_{i_t}(\boldsymbol{\beta}) \exp\{-\tau_t \lambda_{i_t}(\boldsymbol{\beta})\}.$$

When the animal transitions from cell G_{i_t} to one of its neighbors, the probability of transitioning to cell $G_{i_{t+1}}$, an event we denote as $G_{i_t} \to G_{i_{t+1}}$, follows a multinomial (categorical) distribution with probability proportional to the transition rate $\lambda_{i_t i_{t+1}}$ to cell $G_{i_{t+1}}$:

$$(3) \qquad [G_{i_t} \to G_{i_{t+1}} | \boldsymbol{\beta}] = \frac{\lambda_{i_t i_{t+1}}(\boldsymbol{\beta})}{\sum_{j_t \sim i_t} \lambda_{i_t j_t}(\boldsymbol{\beta})} = \frac{\lambda_{i_t i_{t+1}}(\boldsymbol{\beta})}{\lambda_{i_t}(\boldsymbol{\beta})}.$$

Under this formulation, the residence time and eventual destination are independent events, and the likelihood of the observation $(G_{i_t} \to G_{i_{t+1}}, \tau_t)$ is the product of the likelihoods of its parts:

$$
\begin{aligned}
[G_{i_t} \to G_{i_{t+1}}, \tau_t | \boldsymbol{\beta}] &= \frac{\lambda_{i_t i_{t+1}}(\boldsymbol{\beta})}{\lambda_{i_t}(\boldsymbol{\beta})} \cdot \lambda_{i_t}(\boldsymbol{\beta}) \exp\{-\tau \lambda_{i_t}(\boldsymbol{\beta})\} \\
&= \lambda_{i_t i_{t+1}}(\boldsymbol{\beta}) \exp\{-\tau_t \lambda_{i_t}(\boldsymbol{\beta})\}.
\end{aligned}
$$

(4)

2.1. *GLM representation of a continuous-time Markov chain.* We now introduce a latent variable representation of the transition process that is equivalent to (4), but allows for inference within a GLM framework. We note that this latent variable representation is applicable to any continuous-time Markov chain model with transition rates $\{\lambda_{i_t j_t}\}$ and provides a novel approach for inference to this broad class of models. Representing a CTMC model as a GLM allows us to analyze animal movement data using existing computational methods for GLMs (i.e., estimation through iteratively reweighted least squares). Computational efficiency is important as our ability to collect long time series of fine-resolution telemetry data increases.

For each j_t such that $i_t \sim j_t$, define $z_{i_t j_t}$ as

$$z_{i_t j_t} = \begin{cases} 1, & G_{i_t} \to G_{j_t}, \\ 0, & \text{o.w.} \end{cases}$$

and let

(5) $$[z_{i_t j_t}, \tau_t | \boldsymbol{\beta}] \propto \lambda_{i_t j_t}^{z_{i_t j_t}} \exp\{-\tau_t \lambda_{i_t j_t}(\boldsymbol{\beta})\}.$$

Then the product of $[z_{i_t j_t}, \tau_t | \boldsymbol{\beta}]$ over all j_t such that $i_t \sim j_t$ is proportional to the likelihood (4) of the observed transition:

$$
\begin{aligned}
\prod_{j_t : i_t \sim j_t} [z_{i_t j_t}, \tau_t | \boldsymbol{\beta}] &\propto \prod_{j_t : i_t \sim j_t} \lambda_{i_t j_t}^{z_{i_t j_t}} \exp\{-\tau_t \lambda_{i_t j_t}(\boldsymbol{\beta})\} \\
&= \lambda_{i_t i_{t+1}}(\boldsymbol{\beta}) \exp\{-\tau_t \lambda_{i_t}(\boldsymbol{\beta})\} \qquad \text{where } G_{i_t} \to G_{i_{t+1}} \\
&= [G_{i_t} \to G_{i_{t+1}}, \tau_t | \boldsymbol{\beta}].
\end{aligned}
$$

The benefit of this latent variable representation is that the likelihood of $z_{i_t j_t}, \tau_t | \boldsymbol{\beta}$ in (5) is equivalent to the likelihood in a Poisson regression with the canonical log link, where $z_{i_t j_t}$ are the observations and $\log(\tau_t)$ is an offset or exposure term. The likelihood of the entire continuous-time, discrete-space path $\tilde{\mathbf{S}} = (\mathbf{g}, \boldsymbol{\tau})$ can be written as

(6) $$[\tilde{\mathbf{S}} | \boldsymbol{\beta}] = [\mathbf{Z}, \boldsymbol{\tau} | \boldsymbol{\beta}] \propto \prod_{t=1}^{T} \prod_{i_t \sim j_t} \left[\lambda_{i_t j_t}^{z_{i_t j_t}}(\boldsymbol{\beta}) \exp\{-\tau_t \lambda_{i_t j_t}(\boldsymbol{\beta})\} \right],$$

where $\mathbf{Z} = (\mathbf{z}_1, \ldots, \mathbf{z}_T)'$ is a vector containing the latent variables $\mathbf{z}_i = (z_{i_1}, z_{i_2}, \ldots, z_{i_K})'$ for each grid cell in the discrete-space path.

3. Inference on CTDS model parameters using telemetry data. We have proposed a CTMC model for animal movement that relies on a complete continuous-time discrete-space (CTDS) movement path $\tilde{\mathbf{S}} = (\mathbf{g}, \boldsymbol{\tau})$. In practice, telemetry data are collected at a discrete set of time points. Let $\mathbf{S} = \{\mathbf{s}(t), t = t_0, t_1, \ldots, t_T\}$ be the observed sequence of time-referenced telemetry locations for an animal. We propose a two-step procedure for inference on $\boldsymbol{\beta}$ in which we first obtain a posterior predictive distribution $[\tilde{\mathbf{S}} | \mathbf{S}]$ of the CTDS path conditioned on the observed telemetry data $\mathbf{S}$. In a Bayesian framework, we specify a Gaussian prior on $\boldsymbol{\beta}$ such that

(7) $$\boldsymbol{\beta} \sim N(\mathbf{0}, \boldsymbol{\Sigma}_\beta)$$

and then the posterior predictive distribution of $\boldsymbol{\beta}$ conditioned only on the telemetry data $\mathbf{S}$ is given by

(8) $$[\boldsymbol{\beta} | \mathbf{S}] = \int_{\mathcal{S}} [\boldsymbol{\beta} | \tilde{\mathbf{S}}][\tilde{\mathbf{S}} | \mathbf{S}] \, d\tilde{\mathbf{S}}.$$

Hooten et al. (2010) and Hanks et al. (2011) use composition sampling to obtain samples from a similar posterior predictive distribution by sampling iteratively from $[\tilde{\mathbf{S}} | \mathbf{S}]$ and $[\boldsymbol{\beta} | \tilde{\mathbf{S}}]$. In addition to this approach (which we will call a fully Bayesian approach), we also consider approximate posterior predictive inference on $\boldsymbol{\beta}$ using multiple imputation [Rubin (1987)].

3.1. *Multiple imputation.*   In the multiple imputation literature [e.g., Rubin (1987, 1996)], $\tilde{\mathbf{S}}$ is treated as missing data, and the posterior predictive path distribution $[\tilde{\mathbf{S}}|\mathbf{S}]$ is called the imputation distribution. The imputation distribution is typically specified as a statistical model for the missing data $\tilde{\mathbf{S}}$ conditioned on the observed data $\mathbf{S}$.

Under the multiple imputation framework, the distribution $[\boldsymbol{\beta}|\mathbf{S}]$ is assumed to be asymptotically Gaussian. This assumption holds under the conditions that the joint posterior is unimodal [see, e.g., Chapter 4 of Gelman et al. (2004) for details]. This distribution can then be approximated using only the posterior predictive mean and variance, which can be obtained using conditional mean and variance formulae

$$(9) \qquad E(\boldsymbol{\beta}|\mathbf{S}) \approx E_{\tilde{\mathbf{S}}|\mathbf{S}}\big(E(\boldsymbol{\beta}|\tilde{\mathbf{S}})\big)$$

and

$$(10) \qquad \mathrm{Var}(\boldsymbol{\beta}|\mathbf{S}) \approx E_{\tilde{\mathbf{S}}|\mathbf{S}}\big(\mathrm{Var}(\boldsymbol{\beta}|\tilde{\mathbf{S}})\big) + \mathrm{Var}_{\tilde{\mathbf{S}}|\mathbf{S}}\big(E(\boldsymbol{\beta}|\tilde{\mathbf{S}})\big).$$

If we condition on $\tilde{\mathbf{S}}$, then the posterior distribution $[\boldsymbol{\beta}|\tilde{\mathbf{S}}]$ converges asymptotically to the sampling distribution of the maximum likelihood estimate (MLE) of $\boldsymbol{\beta}$ under the likelihood $[\tilde{\mathbf{S}}|\boldsymbol{\beta}]$, and we can approximate $[\boldsymbol{\beta}|\tilde{\mathbf{S}}]$ by obtaining the asymptotic sampling distribution of the MLE. This allows us to use standard maximum likelihood approaches for inference, which are well developed and computationally efficient for the GLM formulation in (6).

The multiple imputation estimate $\hat{\boldsymbol{\beta}}_{\mathrm{MI}}$ and its sampling variance are typically obtained by approximating the integrals in (9) and (10) using a finite sample from the imputation distribution. The procedure can be summarized as follows:

1. Draw K different realizations (imputations) $\tilde{\mathbf{S}}^{(k)} \sim [\tilde{\mathbf{S}}|\mathbf{S}]$ from the path distribution (imputation distribution).
2. For each realization, find the MLE $\hat{\boldsymbol{\beta}}^{(k)}$ and asymptotic variance $\mathrm{Var}(\hat{\boldsymbol{\beta}}^{(k)})$ of the estimate under the likelihood $[\tilde{\mathbf{S}}^{(k)}|\boldsymbol{\beta}]$ in (6).
3. Combine results from different imputations using finite sample approximations of the conditional expectation (9) and variance (10) results.

This results in point estimates for $E(\boldsymbol{\beta}|\mathbf{S})$ and $\mathrm{Var}(\boldsymbol{\beta}|\mathbf{S})$, which can be used to construct approximate posterior credible intervals. Combining the multiple imputation approximation with our GLM formulation of the CTDS movement model provides a computationally efficient framework for the statistical analysis of potential drivers of movement.

3.2. *Imputation of continuous-time paths from telemetry data.*   Inference using multiple imputation requires the specification of the imputation distribution $[\tilde{\mathbf{S}}|\mathbf{S}]$, which for telemetry data is the distribution of the continuous-time movement path $\tilde{\mathbf{S}}$ conditioned on the observed telemetry data $\mathbf{S}$. We will consider imputing

continuous-time movement paths by fitting a continuous-time movement model to the observations. Two common continuous-time models for movement data are the continuous-time correlated random walk (CTCRW) of Johnson et al. (2008a) and the Brownian bridge movement model (BBMM) of Horne et al. (2007). Both assume continuous movement paths in time and space, and after estimating model parameters it is straightforward to draw from the posterior predictive distribution of the continuous-time path $[\tilde{\mathbf{S}}|\mathbf{S}]$.

The CTCRW model of Johnson et al. (2008a) relies on an Ornstein–Uhlenbeck velocity process. If the animal's location and velocity at an arbitrary time t are $\mathbf{s}(t)$ and $\mathbf{v}(t)$, respectively, then the CTCRW model can be specified as follows, ignoring the multivariate notation for simplicity,

$$dv(t) = \gamma\big(\mu - v(t)\big)\,dt + \sigma\,dW(t),$$

$$s(t) = s(0) + \int_0^t v(u)\,du,$$

where μ is a drift term corresponding to long-time scale directional bias in movement, γ controls the rate at which the animal's velocity reverts to μ, and σ scales $W(t)$, which is standard Brownian motion. This model can be discretized and formulated as a state-space model, which allows for efficient estimation of model parameters from telemetry data and simulation of quasi-continuous discretized paths $\tilde{\mathbf{S}}$ at arbitrarily fine time intervals via the Kalman filter [Johnson et al. (2008b)]. If a Bayesian framework is used for inference on $\{\mu, \gamma, \sigma\}$, then Johnson et al. (2008a) show how to obtain the posterior distribution $[\mu, \gamma, \sigma|\mathbf{S}]$ and approximate the posterior predictive distribution of the animal's continuous path $\tilde{\mathbf{S}}$ using importance sampling.

The CTCRW model is a flexible and efficient model for animal movement that has been successfully applied to studies of aquatic [Johnson et al. (2008a)] and terrestrial [Hooten et al. (2010)] animals, and can represent a wide range of movement behavior, as well as account for location uncertainty when telemetry locations are observed with error. As such, we will use the CTCRW model as our primary imputation distribution. In the supplemental article [Hanks, Hooten and Alldredge (2015)], we consider the Brownian bridge model as an alternative path imputation distribution and compare it to the CTCRW model.

3.3. *Links to existing methods.* We note that the transition probabilities in (1) are similar in form to step selection functions [e.g., Boyce et al. (2002)] in multinomial logit discrete-choice models for movement data. The key distinction between the step selection function approach and the approach of Hooten et al. (2010) (and, by extension, the approach we present) is the imputation of the continuous path between telemetry locations. Imputing the continuous path distribution allows us to examine movement and resource selection between telemetry locations, providing a more complete picture of an animal's response to landscape features and other potential drivers of movement.

The transformation of the movement path from continuous space to discrete space results in a compression of the data to a temporal scale that is relevant to the resolution of the environmental covariates that may be driving movement and selection. Under the discrete-space, discrete-time dynamic occupancy approach of Hooten et al. (2010), each discrete-time location is modeled as arising from a multinomial distribution reflecting transition probabilities from the animal's location at the previous time. If the animal is in cell $G_{i_{t-1}}$ at time $t-1$, then define the probability of transitioning to the jth cell at the tth time step as P_{ij_t} and the probability of remaining in cell i as P_{ii_t}. Hooten et al. (2010) recommend choosing a temporal discretization Δt of the continuous movement path fine enough to ensure that the animal remains in each cell for a number of time steps before transitioning to a neighboring cell. If an animal is moving slowly relative to the time it takes to traverse a grid cell in $\mathbf{G}$, then there will be a long sequence of locations within one grid cell before a transition to a neighboring grid cell is made. In this situation the CTDS approach can be much more efficient than the discrete-time discrete-space approach of Hooten et al. (2010). For sufficiently small Δt, discrete-time transition probabilities are approximated by $P_{ij_t} \approx \lambda_{i_t j_t} \Delta t$ and $P_{ii_t} \approx 1 - \lambda_{i_t} \Delta t$. Under this model, the probability of the animal remaining in cell G_i for time equal to τ_t and then leaving cell G_i is

$$\lambda_{i_t} \Delta t \prod_{t=1}^{\tau_t/(\Delta t)} P_{ii_t} = \lambda_{i_t} \Delta t\, P_{ii}^{\tau_t/\Delta t} = \lambda_{i_t} \Delta t (1 - \lambda_{i_t} \Delta t)^{\tau_t/\Delta t}.$$

Letting $\Delta t \to 0$ results in

$$(11) \qquad \lim_{\Delta t \to 0} \lambda_{i_t} \Delta t (1 - \lambda_{i_t} \cdot \Delta t)^{\tau_t/\Delta t} = \lambda_{i_t} \exp\{-\tau_t \lambda_{i_t}\}.$$

Likewise, taking the limit as $\Delta t \to 0$, the probability of transitioning from cell G_i to G_k, given that the animal is transitioning to some neighboring cell, is

$$(12) \qquad \lim_{\Delta t \to 0} \frac{P_{ik_t}}{\sum_j P_{ij_t}} = \lim_{\Delta t \to 0} \frac{\lambda_{i_t k_t} \cdot \Delta t}{\lambda_{i_t} \cdot \Delta t} = \frac{\lambda_{i_t k_t}}{\lambda_{i_t}},$$

and (5) is obtained by multiplying the right-hand sides of (11) and (12). Thus, the CTDS specification could be obtained by using the sufficient statistics $(\tau_t, \{\lambda_{i_t j_t}\})$ of the discrete-time, discrete-space approach of Hooten et al. (2010) in the limiting case as $\Delta t \to 0$. This data compression is especially relevant for telemetry data, in which observation windows can span years or even decades for some animals.

4. Time-varying behavior and shrinkage estimation. In this section we describe how covariate effects can be allowed to vary over time using a varying-coefficient model and how variable selection can be accomplished through regularization.

4.1. *Changing behavior over time.* Animal behavior and response to drivers of movement can change significantly over time. These changes can be driven by external factors such as changing seasons [e.g., Grovenburg et al. (2009)] or predator/prey interactions [e.g., Lima (2002)], or by internal factors such as internal energy levels [e.g., Nathan et al. (2008)]. The most common approach to modeling time-varying behavior in animal movement is through state switching, typically within a Bayesian framework [e.g., Forester, Im and Rathouz (2009), Getz and Saltz (2008), Gurarie, Andrews and Laidre (2009), Jonsen, Flemming and Myers (2005), Merrill et al. (2010), Morales et al. (2004), Nathan et al. (2008)]. Often, the animal is assumed to exhibit a number of behavioral states, each characterized by a distinct pattern of movement or response to drivers of movement. The number of states can be either known and specified in advance [e.g., Jonsen, Flemming and Myers (2005), Morales et al. (2004)] or allowed to be random [e.g., Hanks et al. (2011), McClintock et al. (2012)].

State-switching models are an intuitive approach to modeling changing behavior over time, but there are limits to the complexity that can be modeled using this approach. Allowing the number of states to be unknown and random requires a Bayesian approach with a changing parameter space. This is typically implemented using reversible-jump MCMC methods [e.g., Green (1995), Hanks et al. (2011), McClintock et al. (2012)], which are computationally expensive and can be difficult to tune. Our approach is to use a computationally efficient GLM (6) to analyze parameters related to drivers of animal movement. Instead of using the common state-space approach, we employ varying-coefficient models [e.g., Hastie and Tibshirani (1993)] to model time-varying behavior in animal movement. A similar approach to modeling time-varying behavior in animal movement was taken by Breed et al. (2012).

For simplicity in notation, consider the case where there is only one covariate x in the model (1) and no intercept term. The model for the transition rate will typically contain an intercept term and multiple covariates $\{x\}$, and the varying-coefficient approach we present generalizes easily to this case. In a time-varying coefficient model, we allow the parameter $\beta(t)$ to vary over time in a functional (continuous) fashion. The transition rate (1) then becomes

$$\lambda_{i_t j_t}(\beta(t)) = \exp\{x_{i_t j_t}\beta(t)\},$$

where t is the time of the observation and x_{ij} is the value of the covariate related to the exponential rate of moving from cell i to cell j. We model the functional regressor $\beta(t)$ as a linear combination of n_{spl} spline basis functions $\{\boldsymbol{\phi}_k(t), k = 1, \ldots, n_{\text{spl}}\}$:

$$\beta(t) = \sum_{k=1}^{n_{\text{spl}}} \alpha_k \boldsymbol{\phi}_k(t).$$

Under this varying-coefficient specification, (1) can be rewritten as

$$\lambda_{i_t j_t} = \exp\{x_{i_t j_t} \beta(t)\}$$

(13)
$$= \exp\left\{ x_{i_t j_t} \sum_{k=1}^{n_{\mathrm{spl}}} \alpha_k \boldsymbol{\phi}_k(t) \right\}$$

$$= \exp\{\boldsymbol{\psi}'_{i_t j_t} \boldsymbol{\alpha}\},$$

where $\boldsymbol{\alpha} = (\alpha_1, \ldots, \alpha_{n_{\mathrm{spl}}})'$ and $\boldsymbol{\psi}_{i_t j_t} = x_{i_t j_t} \cdot (\phi_1(t), \ldots, \phi_{n_{\mathrm{spl}}}(t))'$. The result is that the varying-coefficient model can be represented by a GLM with a modified design matrix. This specification provides a flexible framework for allowing the effect of a driver of movement (x) to vary over time that is computationally efficient and simple to implement using standard GLM software. For our asymptotic arguments in Section 3.1 to hold, we will only consider the case where n_{spl} is fixed and the temporal variation in the $\beta(t)$ models periodic (e.g., diurnal) changes in movement behavior.

4.2. *Regularization.* The model we have specified is likely to be overparameterized, especially if we utilize a varying-coefficient model (13). Animal movement behavior is complex, and a typical study could entail a large number of potential drivers of movement, but an animal's response to each of those drivers of movement is likely to change over time, with only a few drivers being relevant at any one time. Under these assumptions, many of the parameters α_k in (13) are likely to be very small or zero. Multicollinearity is also a potential problem, as many potential drivers of movement could be correlated with each other.

The most common approach to these issues is penalization or regularization [e.g., Hooten and Hobbs (2015), Tibshirani (1996)]. We propose a shrinkage estimator of $\boldsymbol{\alpha}$ using a lasso penalty [Tibshirani (1996)]. The typical maximum likelihood estimate of $\boldsymbol{\alpha}$ is obtained by maximizing the likelihood $[\mathbf{Z}, \boldsymbol{\tau} | \boldsymbol{\alpha}]$ from (6) or, equivalently, by maximizing the log-likelihood $\log[\mathbf{Z}, \boldsymbol{\tau} | \boldsymbol{\alpha}]$. The lasso estimate is obtained by maximizing the penalized log-likelihood, where the penalty is proportional to the sum of the absolute values of the regression parameters $\{\alpha_k\}$:

(14)
$$\hat{\boldsymbol{\alpha}}_{\mathrm{lasso}} = \max_{\boldsymbol{\alpha}} \left\{ \log[\mathbf{Z}, \boldsymbol{\tau} | \boldsymbol{\alpha}] - \gamma \sum_{k=1}^{K} |\alpha_k| \right\}.$$

As the tuning parameter γ increases, the absolute values of the regression parameters $\{\alpha_k\}$ are "shrunk" to zero, with the parameters that best describe the variation in the data being shrunk more slowly than parameters that do not. Cross-validation is typically used to set the tuning parameter γ at a level that optimizes the model's predictive power.

Shrinkage approaches such as the lasso are well developed for GLMs, and computationally-efficient methods are available for fitting GLMs to data [e.g.,

Friedman, Hastie and Tibshirani (2010)]. Recent work has also applied the lasso to multiple imputation estimators [e.g., Chen and Wang (2011)]. The main challenge in applying the lasso to multiple imputation is that a parameter may be shrunk to zero in the analysis of one imputation but not in the analysis of another. If the lasso is used for variable selection, a group lasso penalty [Yuan and Lin (2006)] can be specified in which a group of parameters is constrained to either all equal zero or all be nonzero together. In the case of multiple imputation, we consider the joint analysis of all imputations and constrain the set of $\{\alpha_p^{(k)}, k = 1, \ldots, K\}$, where p indexes the parameters in the model and k indexes the imputations, to either all equal zero or all be nonzero together. This group lasso sets the requirement that a parameter must either be zero for all imputations or nonzero for all imputations. One simple approach to implementing this group lasso is to combine all imputations and analyze the aggregate paths as if they were independent observed paths. This amounts to the stacked lasso estimate of Chen and Wang (2011) and is reminiscent of data cloning [Lele, Nadeem and Schmuland (2010)]. We note that this approach does not yield straightforward estimates of the uncertainty about the lasso estimates. We will focus on a full Bayesian analysis with lasso prior to characterize the uncertainty in $\boldsymbol{\alpha}$ under a lasso approach.

In a full Bayesian analysis we consider specifying a shrinkage prior distribution on $\boldsymbol{\alpha}$ such that the posterior mode of $\boldsymbol{\alpha}|\mathbf{S}$ is identical to the lasso estimate (14). Instead of the Gaussian prior in (7), we follow Park and Casella (2008) and consider a hierarchical prior specification:

$$(15) \qquad \alpha_k|\sigma_k^2 \sim N(0, \sigma_k^2), \qquad k = 1, \ldots, K,$$

where the prior on σ_k^2 is conditioned on the shrinkage parameter γ:

$$(16) \qquad [\sigma_k^2|\gamma^2] \propto \gamma^2 \exp\{-\gamma^2\sigma_k^2/2\}, \qquad k = 1, \ldots, K.$$

Then, marginalizing over the σ_k^2 gives a Laplace prior distribution on α conditioned only on γ:

$$[\alpha_k|\gamma] = \int_0^\infty [\alpha_k|\sigma_k^2][\sigma_k^2|\gamma]\, d\sigma_k^2$$

$$\propto \int_0^\infty \frac{1}{\sqrt{2\pi\sigma_k^2}} \exp\{-\alpha_k^2/(2\sigma_k^2)\}\gamma^2 \exp\{-\gamma^2\sigma_k^2/2\}\, d\sigma_k^2$$

$$= \frac{\gamma}{2} \exp\{-\gamma|\alpha_k|\},$$

where the last step uses the representation of the Laplace distribution as a scale mixture of Gaussian random variables with exponential mixing density [e.g., Park and Casella (2008)]. Maximizing the resulting log-posterior predictive distribution for $\boldsymbol{\alpha}$ gives us the lasso estimate (14).

The hyperparameter γ controls the amount of shrinkage in the Bayesian lasso. While a prior distribution could be assigned to γ, we take an empirical approach

and estimate γ using cross-validation in the penalized likelihood approach (14) to the lasso. This estimate can then be used to set the value of the hyperparameter γ in the Bayesian lasso analysis.

5. Drivers of animal movement. We now provide some examples showing how a range of hypothesized drivers of movement could be modeled within the CTDS framework. We consider two distinct categories for drivers of movement from cell G_i to cell G_j: location-based drivers ($\{p_{ki}, k = 1, 2, \ldots, K\}$), which are determined only by the characteristics of cell G_i, and directional drivers ($\{q_{lij}, l = 1, 2, \ldots, L\}$), which vary with direction of movement. Under a time-varying coefficient model for each driver, the transition rate (1) from cell G_i to cell G_j is

$$(17) \qquad \lambda_{ij}(\boldsymbol{\beta}(t)) = \exp\left\{\beta_0(t) + \sum_{k=1}^{K} p_{ki}\beta_k(t) + \sum_{l=1}^{L} q_{lij}\beta_l(t)\right\},$$

where $\beta_0(t)$ is a time-varying intercept term, $\{\beta_k(t)\}$ are time-varying effects related to location-based drivers of movement, and $\{\beta_l(t)\}$ are time-varying effects related to directional drivers of movement. We consider both location-based and directional drivers in what follows.

5.1. *Location-based drivers of movement.* Location-based drivers of movement can be used to examine differences in animal movement rates that can be explained by the environment an animal resides in. For example, if the animal is in a patch of highly desirable terrain, surrounded by less-desirable terrain, a location-based driver of movement could be used to model the animal's propensity to stay in the desirable patch and move quickly through undesirable terrain. In the CTDS context, location-based drivers would be covariates dependent only on the characteristics of the cell where the animal is currently located. Large positive (negative) values of the corresponding $\beta_k(t)$ would indicate that the animal tends to transition quickly (slowly) from a cell containing the cover type in question.

5.2. *Directional bias in movement.* In contrast to location-based drivers, which describe the effect that the local environment has on movement rates, directional drivers of movement [Brillinger et al. (2001), Hanks et al. (2011), Hooten et al. (2010)] capture directional bias in movement patterns.

A directional driver of movement (or bias effect in our GLM) is defined by a vector which points toward (or away) from something that is hypothesized to attract (or repel) the animal in question. Let $\mathbf{v}_l$ be the vector corresponding to the lth directional driver of movement. In the CTDS model for animal movement, the animal can only transition from cell G_i to one of its neighbors $G_j : j \sim i$. Let $\mathbf{w}_{ij}$ be a unit vector pointing from the center of cell G_i in the direction of the center of cell G_j. Then the covariate q_{lij} relating the lth directional driver of movement to

the transition rate from cell G_i to cell G_j is the inner product of $\mathbf{v}_l$ and $\mathbf{w}_{ij}$:

$$q_{lij} = \mathbf{v}'_l \mathbf{w}_{ij}.$$

Then p_{lij} will be positive when $\mathbf{v}_l$ points nearly in the direction of cell G_j, negative when $\mathbf{v}_l$ points directly away from cell G_j, and zero if $\mathbf{v}_l$ is perpendicular to the direction from cell G_i to cell G_j.

6. Example: Mountain lions in Colorado. We illustrate our CTDS random walk approach to modeling animal movement through a study of mountain lions (*Puma concolor*) in Colorado, USA. R code to download all needed files and replicate this analysis is available from the R-forge website (http://r-forge.r-project.org/projects/ctds/). As part of a larger study, a female mountain lion, designated AF79, and her subadult cub, designated AM80, were fitted with global positioning system (GPS) collars set to transmit location data every 3 hours. We analyze the location data **S** from two weeks (14 days) of location information for these two animals (Figure 2).
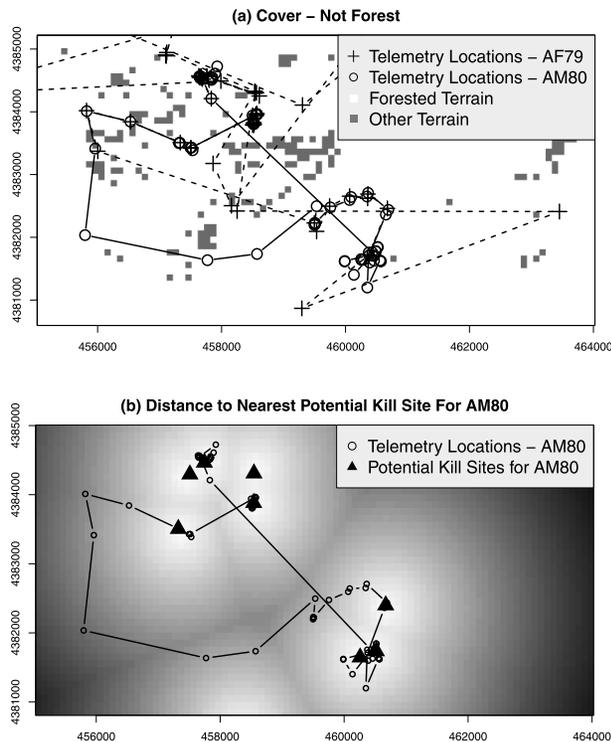

FIG. 2. *Telemetry data for a female mountain lion (AF79) and her male cub (AM80). A location-based covariate was defined by landcover that was not predominantly forested (a). Potential kill sites were identified, and a directional (bias) covariate defined by a vector pointing toward the closest kill site (b) was also used in the CTDS model.*

We fit the CTCRW model of Johnson et al. (2008a) to both animals' location data using the "crawl" package [Johnson (2011)] in the R statistical computing environment [R Core Team (2013)].

For covariate data, we used a landcover map of the state of Colorado created by the Colorado Vegetation Classification Project (http://ndis.nrel.colostate.edu/coveg/), which is a joint project of the Bureau of Land Management and the Colorado Division of Wildlife. The landcover map contained gridded landcover information at 100 m square resolution. The area traveled by the two animals in our study was predominantly forested. To assess how the animals' movement differed when in terrain other than forest, we created an indicator covariate where all forested grid cells were assigned a value of zero, and all cells containing other cover types, including developed land, bare ground, grassland and shrubby terrain, were assigned a value of one [Figure 2(a)]. This covariate was used as a location-based covariate in the CTDS model.

For the subadult male AM80, we created a set of potential kill sites (PKS) by examining the original GPS location data [Figure 2(b)]. Knopff et al. (2009) classified a location as a PKS if two or more GPS locations were found within 200 m of the site within a six-day period. We added an additional constraint that at least one of the GPS locations be during nighttime hours (9 pm to 6 am) for the point to be classified a PKS. We then created a covariate raster layer containing the distance to the nearest PKS for each grid cell [Figure 2(b)]. A directional covariate defined by a vector pointing toward the nearest PKS was included in the CTDS model.

To examine how the movement path of the mother AF79 affected the movement path of the cub AM80, we included a directional covariate in the CTDS model for AM80 defined by a vector pointing from the cub's location to the mother's location at each time point.

We also included a directional covariate pointing in the direction of the most recent movement at each time point. This covariate measures the strength of correlation between moves and thus the strength of the directional persistence shown by the animal's discrete-space movement path. The CTCRW imputation distribution assumes an underlying correlated movement model, while the Brownian bridge model does not. See the online supplement for details [Hanks, Hooten and Alldredge (2015)].

6.1. *Comparison of methods under time-homogeneous model.*   We first compare a full Bayesian analysis of the path of AM80 to the multiple imputation approximation to the posterior mean (9) and variance (10). For this first analysis, we do not assume any time-varying behavior, but rather model the cub's mean response over time to the landscape, identified PKSs and the movement path of AF79. For both the full Bayesian analysis and the multiple imputation approximations we used the CTCRW imputation distribution. We used a Markov chain Monte Carlo algorithm to draw 20,000 samples from the posterior predictive distribution of $\beta|\mathbf{S}$ for AM80. We discarded the first 5000 as burn-in and used the remaining

TABLE 1

Results on regression parameters related to movement behavior. Entries are Bayesian posterior predictive means ($\hat{\beta}$) and standard deviations (s.e.) for the fully Bayesian analysis (Bayes), and multiple imputation approximations to the same for the multiple imputation analyses. Results are shown for varying numbers of imputations K from the continuous-time correlated random walk (CTCRW) path imputation distribution [$\tilde{\mathbf{S}}|\mathbf{S}$]. Starred entries indicate parameters with a 95% Bayesian credible interval that does not overlap zero

			Forest cover		Dist. to PKS		Dist. to AF79		CRW	
Method	[$\tilde{\mathbf{S}}|\mathbf{S}$]	K	$\hat{\beta}$	s.e.	$\hat{\beta}$	s.e.	$\hat{\beta}$	s.e.	$\hat{\beta}$	s.e.
Bayes	CTCRW	NA	0.326	0.197	0.297*	0.043	0.059	0.048	0.398*	0.0518
MI	CTCRW	50	0.326	0.197	0.297*	0.043	0.059	0.048	0.398*	0.051
MI	CTCRW	10	0.334	0.197	0.305*	0.042	0.063	0.050	0.399*	0.0487
MI	CTCRW	5	0.372	0.154	0.293*	0.040	0.076	0.061	0.407*	0.043
MI	CTCRW	2	0.228	0.168	0.300*	0.046	0.035	0.055	0.431*	0.040

samples to approximate the posterior predictive distribution. Posterior means and standard deviations are shown in Table 1. Each parameter whose posterior predictive distribution's 95% equal-tailed credible interval does not overlap zero is marked with a star in Table 1. We then applied the multiple imputation approach to approximate the posterior distribution using the $K = 2, 5, 10$ and 50 continuous paths drawn from the CTCRW imputation distribution: [$\tilde{\mathbf{S}}|\mathbf{S}$]. The resulting mean and posterior standard deviations are given in Table 1. We constructed symmetric asymptotically normal 95% confidence intervals for each regression parameter, and mark each estimate with a star in Table 1 when the confidence interval does not overlap zero. The multiple imputation results approximate the mean and variance of the posterior predictive distribution in this example with reasonable precision, even when very few imputations are used, and when $K = 50$ imputed paths are used, the multiple imputation approximation yields results that are nearly identical to the results from the fully Bayesian analysis.

The results show that much of the subadult male's movement can be explained by a correlated random walk with attractive points at PKSs [Figure 2(b)]. The results also show that the animal's movement behavior is fairly homogeneous when in forested and in nonforested terrain. These results are consistent for all approaches using the CTCRW imputation distribution.

6.2. *Simulation study.* We conducted a simulation study motivated by our data analysis to examine our ability to find the correct subset model using multiple imputation with lasso penalty. We are interested in identifying which parameters affect animal movement and directional bias, and so focus on a group lasso penalty which will force estimates for regression parameters to be either zero or nonzero in all imputations. An alternative approach would be to obtain a lasso estimate of

Simulation study results. A simulation study was conducted, by setting the true covariate effects for "Not forest," "Direction to nearest PKS" and "Distance to AF79" to various values motivated by the estimates in Section 6.1. We then simulated a CTDS random walk under the true parameters, and thinned the simulated path to "observed" locations at four-hour intervals (to simulate regular telemetry observations). The resulting simulated observations were fit using our proposed approach using the CTCRW model to impute continuous-time paths and a lasso penalty on the fitted GLM. This simulation study was repeated for the case when the true covariate effects are all zero. In each case, 1000 paths were simulated and fit, with the results summarized below

Covariate	True value	Proportion $\hat{\beta} \neq 0$	Proportion $\hat{\beta} = 0$	Min	Max
Not forest	0.000	0.000	1.000	0.000	0.000
Direction to PKS	0.300	0.634	0.866	0.000	0.217
Distance to AF79	0.000	0.000	1.000	0.000	0.000
Not forest	0.000	0.000	1.000	0.000	0.000
Direction to PKS	0.000	0.002	0.998	0.000	0.016
Distance to AF79	0.000	0.000	1.000	0.000	0.000

the regression parameters (14) for each imputated path, and then combine them using the standard combining rules.

We first simulated a CTDS movement path using the forest cover and direction to nearest PKS covariates from our mountain lion analysis, as well as a simulated covariate meant to mimic the directional effect of the conspecific (AF79). Various combinations of true parameter values were specified, and a full CTDS path was simulated for a two-week period (equal to the observation period of the mountain lions in our study). We then simulated telemetry data from the CTDS path by recording the simulated location only every four hours. The resulting simulated telemetry locations were used to estimate the movement parameters using our approach with a CTCRW imputation distribution and lasso penalty, with the lasso tuning parameter chosen by 10-fold cross-validation using the "glmnet" package [Friedman, Hastie and Tibshirani (2010)] in R. This was repeated 1000 times for each set of parameters. The results are shown in Table 2.

Our approach is very accurate at estimating model parameters as equal to zero when the true parameter is zero. When the true value of the parameter related to the directional gradient toward the nearest PKS is positive (0.30), the approach correctly estimates this parameter as positive 86.6% of the time, and never incorrectly estimates this parameter as being negative.

From this simulation study we see that our proposed approach with lasso penalty provides a conservative estimate of the relationship between an animal's observed movement and the potential drivers of animal movement in the model (17).

6.3. *Time-varying behavior.* We next examine changing movement behavior over time using a varying-coefficient model for each covariate in the model, where
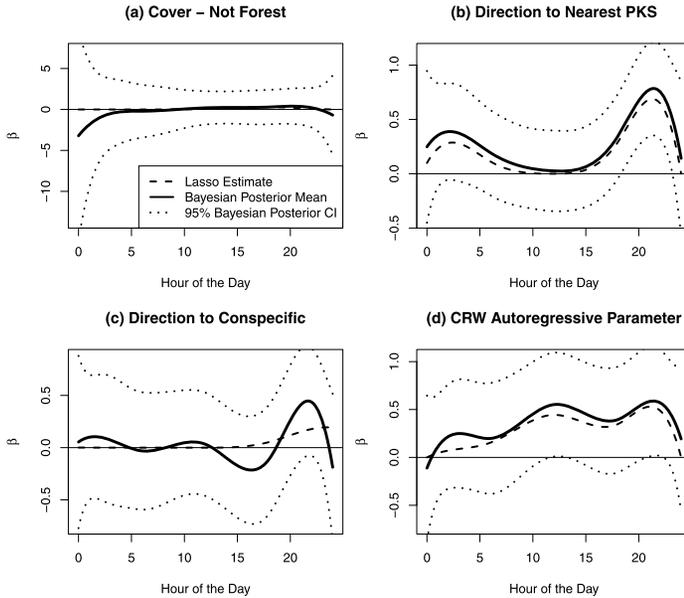
FIG. 3. *Time-varying results for the location-based and directional covariates in the continuous-time discrete-space model for a male mountain lion (AM80) obtained using a lasso shrinkage prior. The x-axis is time of day in hours. The y-axis is the effect size.*

behavior was allowed to vary with time of day. For all covariates we specified a B-spline basis expansion with regularly-spaced spline knots at 6 hour intervals over the course of a 24 hour period. Observations over multiple days (14 days in this study) are replications in this model and allow for inference about diurnal changes in movement behavior.

For this analysis, we fit the CTDS model with CTCRW imputation distribution and a lasso penalty. After estimating the model parameters and choosing the lasso tuning parameter using cross-validation, we used the chosen lasso tuning parameter γ as a hyperparameter in the full Bayesian model with lasso shrinkage prior (15)–(16). The resulting posterior predictive mean and equal-tailed 95% credible interval bounds for $\boldsymbol{\beta}(t)$ are shown in Figure 3.

In Figure 3(b) the peak in the value of the $\beta(t)$ associated with movement toward the nearest PKS indicates the animal shows some preference for returning to a PKS near dusk (8 pm). The confidence bands of the other parameters include zero throughout the day, indicating that we lack evidence that the animal's response to the relevent covariates is synchronous with the diurnal cycle.

7. Discussion. While we have couched our CTDS approach in terms of modeling animal movement, we can also view this approach in terms of resource selection [e.g., Manly, McDonald and Thomas (2002)]. Johnson et al. (2008a) describe

a general framework for the analysis of resource selection from telemetry data using a weighted distribution approach where an observed distribution of resource use is seen as a reweighted version of a distribution of available resources, and the resource selection function (RSF) defines the preferential use of resources by the animal. Warton and Shepherd (2010) describe a point process approach to resource selection that can be fit using a Poisson GLM, similar to the CTDS model we describe here. In the context of Warton and Shepherd (2010), the CTDS approach can be viewed as a resource selection analysis with the available resources at any time defined as the neighboring grid cells. The transition rate (17) of the CTDS process to each neighboring cell contains information about the availability of each cell, as well as the RSF that defines preferential use of the resources in each cell.

One alternative to our continuous time model for animal movement is the spatio-temporal point process modeling approach of Johnson, Hooten and Kuhn (2013), where the movement process is considered as a set of points that exist in space and time, instead of as a dynamic process occurring in space and time. In the spatio-temporal point process context, telemetry points can arise in a space that is both geographical and temporal, and Johnson, Hooten and Kuhn (2013) integrate over the temporal dimension and arrive at a marginal spatial point process model. Our approach is explicitly dynamic in that it models actual transition probabilities as function spatio-temporally varying environmental and ecological conditions. Furthermore, we allow for additional flexibility and predictive ability in our approach through the use of regularization.

Representing a CTMC model for CTDS animal movement in terms of a Poisson GLM likelihood (6) allows for the possibility of inference under a wide variety of statistical approaches. An alternative to our Bayesian approach based on MCMC, generalized additive modeling approaches and software [e.g., Wood (2011)], as well as approximate Bayesian approaches such as integrated nested Laplace approximations [INLA, Rue, Martino and Chopin (2009)], could be used for inference on time-varying parameters in (13).

The use of directional drivers of movement has a long history. Brillinger et al. (2001) model animal movement as a continuous-time, continuous-space random walk where the drift term is the gradient of a "potential function" that defines an animal's external drivers of movement. Tracey, Zhu and Crooks (2005) use circular distributions to model how an animal moves in response to a vector pointing toward an object that may attract or repel the animal. Hanks et al. (2011) and McClintock et al. (2012) make extensive use of gradients to model directed movements and movements about a central location. In our study of mountain lion movement data, we used directional drivers of movement to model conspecific interaction between a mother (AF79) and her cub (AM80). Interactions between predators and prey could also be modeled using directional covariates defined by vectors pointing between animals. Some movements based on memory could also be modeled using directional covariates. For example, a directional covariate defined by a vector pointing to the animal's location one year prior could be used

to model seasonal migratory behavior. The ability to model both location-based and directional drivers of movement make the CTDS framework a flexible and extensible framework for modeling complex behavior in animal movement.

SUPPLEMENTARY MATERIAL

Alternate path imputation distribution (DOI: 10.1214/14-AOAS803SUPP; .pdf). This supplement contains details of a Brownian bridge path imputation distribution and its use with our CTDS approach to modeling animal movement.

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