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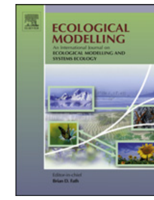

State-space methods for more completely capturing behavioral dynamics from animal tracks

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ABSTRACT

State-space models (SSMs) are now the tools of choice for analyzing animal tracking data. A wide variety of such data are being collected worldwide and modeled using state-space methods to better understand population dynamics, animal behavior and physical and environmental processes. The central goal of such analyses is the estimation of biologically interpretable static parameters. Most approaches implement some form of MCMC or Kalman filter to estimate these parameters. We demonstrate the utility in allowing time-varying (rather than static) parameters to more completely capture dynamic features of the processes of interest, in this case the behavioral dynamics of tracked marine animals. We develop and demonstrate a parameter augmented sequential Monte Carlo method (also referred to as an augmented particle filter or particle smoother (PF or PS)) that allows straightforward estimation of both static and time-varying parameters from tracking data. We focus specifically on temporally irregular GPS data describing marine animal movement with the goal of better understanding the underlying behavioral dynamics. Using tracking data from California sea lions (*Zalophus californianus*) we demonstrate the approach's ability to detect subtle yet biologically relevant changes in behavior.

1. Introduction

Electronic animal tracking technology is rapidly developing such that increasingly fine scale observations of location, motion, and internal physiological state are now possible. At the same time, remote sensing technology has greatly increased the resolution of corresponding environmental information (Costa et al., 2010b). Unfortunately the development of statistical methods for analyzing such data has proceeded more slowly, lagging behind technological developments. Fortunately, because of their ability to separately model process noise and observation error, state-space methods have emerged as an accepted and leading framework for modeling and analysis of animal tracking data.

In their simplest form SSMs involve linear processes and Gaussian distributed errors, making it possible to formulate exact likelihood equations based on the Kalman filter (KF) recursions. This approach has been widely implemented to estimate both parameters and states (often locations) from tracking data (e.g. Nielsen et al., 2006; Johnson et al., 2008). However most tracking data, particularly for animals, have elements of non-Gaussianity and nonlinearity making alternatives to the KF necessary. Approximation schemes (e.g. extended and unscented KF) have been developed (e.g. Johnson et al., 2008) and Markov chain Monte Carlo (MCMC) methods successfully implemented to estimate parameters and states in non-linear and/or non-Gaussian SSMs for tracking data (Jonsen et al., 2005; Patterson et al., 2008). An excellent alternative to MCMC and KF approaches are Sequential Monte Carlo (SMC) methods. For ecological problems, these approaches have not been widely implemented (Ionides et al., 2006; Dowd and Joy, 2011), but they have many advantages to MCMC and KF methods including online or real time calculation, computational efficiency, and relatively straightforward implementation of highly nonlinear and/or non-Gaussian models.

SMC methods are a set of simulation algorithms designed for sequentially updating a posterior distribution or likelihood. Commonly referred to as particle filters and smoothers (PFs and PSs), they have been developed independently in many fields, as described in Doucet et al. (2001). PF and PS methods have been demonstrated for state estimation in animal movement analyses (e.g. Royer et al., 2005; Andersen et al., 2007), but they have not been used to estimate movement parameters. In PFs and PSs, the posterior distribution (or likelihood) is represented using a finite set of samples which are generated from the model being fitted, the *particles*, and these can be used to estimate any property of the posterior distribution (or likelihood) in an ordinary Monte Carlo

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estimation framework. Techniques for performing this SMC updating include rejection sampling, importance sampling and sampling importance resampling. Desirably, all allow online estimation and are relatively simple to implement using interpreted languages such as R or Matlab.

In an effort to capture behavioral dynamics from animal tracking data, SSMs have recently been demonstrated (Royer et al., 2005; Jonsen et al., 2005) to switch among discrete behavioral *modes* where each mode is described by a static set of parameters. However, behavioral modes must be explicitly constructed a priori as part of the model structure. Usually only two and rarely three modes are included before they confound or it becomes necessary to define additional states based on the region used in addition to the movement dynamics (Kim and Nelson, 1999; McClintock et al., in press). Here we show that by including time-varying parameters in our SSMs we can obtain a richer picture of both model performance and animal behavior than can be obtained from so-called "switching models". Gurarie et al. (2009) successfully estimated time-varying parameters from tracking data, but that analysis used a mix of standard time-series methods and did not explicitly account for measurement error. Instead it required an ad hoc pre-filtering of the data that was not robust to measurement error.

We describe and demonstrate an SSM with time-varying parameters that captures nonlinear time-varying behavioral dynamics that were previously inaccessible from animal tracks. The model is fitted using a Sequential Importance Resampling (SIR) PS with time-varying parameters estimated via state augmentation (Doucet et al., 2001; Durbin and Koopman, 2001). A similar method was recently demonstrated for animal diving data which possesses many convenient properties (high resolution, precision, accuracy, and temporal regularity) that are not generally available for animal tracking data like that considered here (Dowd and Joy, 2011). The ability of our augmented PS implementation to detect subtle yet biologically relevant behavioral dynamics from data with much less convenient characteristics than Dowd and Joy (2011) is demonstrated using 3 California sea lion tracked by GPS.

2. Methods

We implement an SSM with time-varying parameters to describe both the behavioral dynamics (and associated noise) and measurement error present in animal tracking data. The behavioral dynamics are captured in the SSM's process equation, in this case a correlated random walk (CRW) that describes the movement process of the animal through time. The observation equation then relates predictions made by the process equation to the observations. In the framework of an SSM fit using a PF or PS, the observation equation becomes the importance distribution from which the likelihood of simulations (particles) from the process model are calculated. These likelihoods become the particle weights.

2.1. Process equation

We use a CRW model similar to the single state first-difference CRW model described in Jonsen et al. (2005) as the process equation of our SSM:

$$\mathbf{d}_t = \gamma_t \begin{pmatrix} \cos\phi_t & -\sin\phi_t \\ -\sin\phi_t & -\cos\phi_t \end{pmatrix} \times \mathbf{d}_{t-1} + N_2\left(\mathbf{0}, \begin{bmatrix} \sigma^2_{lon,t} & 0 \\ 0 & \sigma^2_{lat,t} \end{bmatrix}\right) \tag{1}$$

$$\phi_t \sim wC(0, c_t) \tag{2}$$

$$\mathbf{x}_t = \mathbf{x}_{t-1} + \mathbf{d}_t \tag{3}$$

where $\mathbf{d}_{t-1}$ is the displacement between unobserved locations $\mathbf{x}_{t-1}$ and $\mathbf{x}_{t-2}$. γ_t correlates both the magnitude and direction of consecutive displacements. ϕ is the turn angle and is described by a wrapped Cauchy (wC) distribution with the mean turn angle fixed at 0 and an estimated concentration parameter c_t ranging between 0 and 1. The wrapped Cauchy distribution is quite standard for turn angle estimation (Turchin, 1998; Morales et al., 2004; Yackulic et al., 2011), and is an important improvement on the CRW described by Jonsen et al. (2005), which used bounded uniform distributions to estimate turn angles. Bivariate Gaussian process error is included with mean **0** and variance–covariance matrix Σ_t; composed of $\sigma^2_{lon,t}$ and $\sigma^2_{lat,t}$ and 0 covariance terms. γ_t, c_t, $\sigma_{lat,t}$, and $\sigma_{lon,t}$ are 4 time-varying parameters, the inclusion of which represents a more significant departure from Jonsen et al. (2005) and similar switching models. In all previous SSMs of animal movement, static parameters have been estimated for entire tracks and behavior was modeled as switching between discrete modes. Switching models are powerful, but animal movement with continuous time-dynamic parameters is a more general approach (Gurarie et al., 2009).

2.2. Observation equation

The observation equation relates the unobserved locations $\mathbf{x}_t$ to the locations $\mathbf{y}_t$ observed by GPS, where η = 0.036 km and is the variance in latitude and longitude reported by Costa et al. (2010a):

$$\mathbf{y}_t = \mathbf{x}_t + N_2\left(\mathbf{0}, \begin{bmatrix} \eta & 0 \\ 0 & \eta \end{bmatrix}\right) \tag{4}$$

We should note that a t-distribution or other long-tailed distribution can be used rather than a simple Gaussian distribution. However, we found for our GPS data that a Gaussian worked better than a t-distribution for the observation error equation. To fit our model we used the SIR PS described by Arulampalam et al. (2002), with a fixed lag of 15 time steps for the smoother. Time-varying parameters were estimated by augmenting them to the state vector using methods outlined in Doucet et al. (2001) and Durbin and Koopman (2001). By augmenting the four time-varying parameters (c_t,γ_t, $\sigma_{lat,t}$, $\sigma_{lon,t}$) to the state vector, our process equation becomes:

$$\begin{pmatrix} \mathbf{x}_t \\ \boldsymbol{\theta}_t \end{pmatrix} = \begin{pmatrix} f(\mathbf{x}_{t-1}, \boldsymbol{\theta}_{t-1}) \\ \boldsymbol{\theta}_{t-1} \end{pmatrix} + \begin{pmatrix} \Sigma_t \\ \boldsymbol{\nu}_t \end{pmatrix} \tag{5}$$

where $\boldsymbol{\theta}_t$ = (c_t, γ_t, $\sigma_{lat,t}$, $\sigma_{lon,t}$), and $\boldsymbol{\nu}_t$ is the disturbance term for parameter augmentation.

2.3. Parameter augmentation

The PS implemented here is based on importance resampling. In this case, $\mathbf{x}_k$ is simulated sequentially from some importance distribution $f_k(\mathbf{x}_k|\mathbf{x}_{1:k-1}, \mathbf{y}_{1:k})$, and the whole trajectory $\mathbf{x}_{1:k}$ is given an importance weight w_k. N such sequences are simulated from the CRW process model in parallel, giving a weighted particle set $S_k = (\mathbf{x}^{(i)}_{1:k}, w^{(i)}_k)$, $i = 1, N$ at each time point t_k. We use the observation equation (Eq. (4)) as the importance distribution with which to assign the importance weight to each particle (and the parameter set augmented to it) based on the tracking observation at that time. As time evolves, the variance of particle weights will increase and eventually the system will be represented by only one or a few particles. A standard method to avoid this is to resample from S_k with probabilities proportional to $w^{(i)}_k$. Resampling greatly reduces particle degeneracy, but it can still occur. To assure it did not, we assessed degeneracy by monitoring the particle variance and effective particle number at each time step.