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

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A B S T R A C T

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.

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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 fitting 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:

\[ \mathbf{d}_t = \gamma_t \begin{pmatrix} \cos \phi_t & -\sin \phi_t \\ -\sin \phi_t & -\cos \phi_t \end{pmatrix} \times \mathbf{d}_{t-1} + \mathbf{N}_2 \left( \begin{array}{c} 0 \\ 0 \end{array} \right) \]

\[ \phi_t \sim \text{wC}(0, \text{C}_t) \]

\[ \mathbf{x}_t = \mathbf{x}_{t-1} + \mathbf{d}_t \]

where \( \mathbf{d}_{t-1} \) is the displacement between unobserved locations \( \mathbf{x}_{t-1} \) and \( \mathbf{x}_{t-2} \). \( \gamma_t \) correlates both the magnitude and direction of consecutive displacements. \( \phi \) 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 \( \text{C}_t \) 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 \( \Sigma_t \), composed of \( \sigma^2_{\text{lon},t} \) and \( \sigma^2_{\text{lat},t} \) and 0 variance terms. \( \gamma_t, \text{C}_t, \sigma^2_{\text{lat},t}, \) and \( \sigma^2_{\text{lon},t} \) 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 \( \eta = 0.036 \text{ km} \) and is the variance in latitude and longitude reported by Costa et al. (2010a):

\[ \mathbf{y}_t = \mathbf{x}_t + \mathbf{N}_2 \left( \begin{array}{c} 0 \\ 0 \\ \eta \eta \end{array} \right) \]

We should note that a t-distribution or other long-tailed distribution can be used rather than a 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 \( \{\gamma_t, \text{C}_t, \sigma^2_{\text{lat},t}, \sigma^2_{\text{lon},t}\} \) to the state vector, our process equation becomes:

\[ \mathbf{x}_t = f(\mathbf{x}_{t-1}, \theta_{t-1}) + \Sigma_t \]

where \( \theta_t = \{\gamma_t, \text{C}_t, \sigma^2_{\text{lat},t}, \sigma^2_{\text{lon},t}\} \) and \( \nu_t \) 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 \( \mathbf{S}_k = \{\mathbf{x}_k^{(1)}, \ldots, \mathbf{x}_k^{(N)}\} \), \( k = 1, N \) 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 \( \mathbf{S}_k \) with probabilities proportional to \( w_k^{(i)} \). 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.
For estimating the augmented parameters $\theta_i$, it is necessary to explore a range of parameter values at each prediction step to determine which values are most likely to explain the observation at time $t$. Typically this is done by disturbing parameter estimates $\theta_{i-1}$, that is, adding small amounts of random noise. This noise, $\psi$, is referred to as the disturbance term. A wide range of parameter disturbance and exploration techniques have been developed and implemented (Doucet et al., 2001; Chen et al., 2005; Dowd and Joy, 2011).

Our approach to parameter disturbance and space exploration is relatively straightforward. Elements $\gamma$ and $c$ of $\theta$ range between 0 and 1. For convenience, $\gamma_{t-1}$ and $c_{t-1}$ were logistically transformed to place them on the real line between $-\infty$ and $\infty$. This allows $\psi_t$ to be added as Gaussian noise. However, the nature of movement being modeled tends to cause $\gamma_t$ and $c_t$ to move together, and hence we chose to covary $\nu_t$ and $\psi_t$ and so set the covariance parameter to 0.7. Thus $\nu_t$ and $\psi_t$ tend to move in the same direction, but also differ enough to allow $\gamma_t$ and $c_t$ to move apart. This covariance effectively lowered the number of estimated parameters allowing the system to be solved with fewer particles.

The parameters $\sigma_{t\nu}$ and $\sigma_{t\psi}$ range from 0 to $\infty$. Rather than log transforming them to the real line (this solution did not perform well) we add Gaussian noise to these elements and reset any negative values to 0. This solution is somewhat inelegant and does not explore parameter space very near zero as well as we would like, but in practice worked well as it proved to be much more stable than the log-transformation solution.

All elements of $\nu$ were generated from mixed-normal distributions in order to accommodate rapid, non-linear changes in parameter values that occurred when behavior changed dramatically. The two mixing distributions were centered at 0, but one had a variance 20 times that of the other. This solution was very effective in allowing parameter estimates to tightly track segments where parameters changed little but also be responsive to rapid changes in parameter values.

2.4. Irregular observations

Movement models that produce location and parameter estimates on regular time steps have many favorable properties. The most important being that it normalizes the magnitude of observation error relative to the length of displacement, and thus causes observation error to be much more manageable. For example, when irregular observations have very short intervals between observations, these short intervals permit animals to make only very short displacements. However, the observation error will be the same regardless of the displacement length. So where very little time passes between observations the scale of the observation error becomes very large relative to the displacement made by the animal – and thus the signal to noise ratio becomes very small and the biological process may be completely lost in the observation error. The opposite occurs when long periods elapse between observations. Having the signal to noise ratio differ at every time step greatly diminishes the power to robustly resolve behaviors. This problem is particularly troublesome when trying to correlate consecutive displacements, and thus makes fitting CRWs to irregular data difficult.

Examples of SSMs that estimate both temporally regular and irregular time steps have been published (Jonsen et al., 2005; Johnson et al., 2008), but require substantially different process models, with temporally regular models either requiring temporally regular observation or an additional equation to map irregular observations onto the temporally regular CRW framework. Here we choose to use regular time steps to take advantage of the favorable properties of regular location estimates, but also it was required to fit the first order CRW. As such, we modified the process model so that it would predict temporally regular locations from irregular data. Similar modifications have been made to movement SSMs fitted using MCMC, but this is the first time it has been accomplished with particle filters and smoothers.

Before fitting, a desired time step is chosen, in this case we selected 60 min. When selecting an appropriate time step, one must consider both the temporal scale of the behavior of interest, the temporal frequency of tracking observations, and the observation error (see Breed et al. (2009, 2011) for more information about choosing an appropriate time step). Once a time step is chosen, irregular observations are assigned to the temporally nearest regular time step. After identifying which regular time step each tracking observation is nearest to, each regular time step is indexed to, and represented by, a set of irregular observations of length $L$. For the set of tracking observations representing each regular time step, a value $j$ is calculated where $j$ ranges from $-0.5$ to 0.5. This value represents the temporal position of each of the irregular observations relative to the regular time step (negative values before, positive values after): $j_{l,t} = t^*_l - t_l \over \text{interval}$

where $l$ is an element of 1...L, and indexes the set of irregular observations $y_{l,t-1}$, representing the $L$th regular time step, $t^*_l$ is the time of the $L$th irregular observation ($y_{l,t-1}$), $t_l$ is the time of the $L$th regular time step. interval is the regular interval at which $x_l$ and $\theta_l$ are to be estimated. The vector $j$ is the same length as the time series of irregular observations $Y$, and once $j$ has been calculated it can be used to modify the prediction equation (Eq. (3)) to map regular predictions onto irregular observations when calculating the importance weights. The first step is to map the regular predictions onto the set of irregular observations:

$z_{l,t} = x_{l-1} + d_t + d_t \ast j_{l,t}$.

This produces temporally irregular predictions ($z_{l,t}$) at the times of irregular observations ($y_{l,t}$) by adding or subtracting a portion of the temporally regular predicted displacement $d_t$ proportional to the linear interpolation of the difference between the regular time step and irregular observation. In this case we used a simple linear interpolation, but nonlinear functions could be used if necessary or desired.

This allowed a likelihood to be calculated at each irregular prediction $z_{l,t}$ for each irregular observation $y_{l,t}$. The calculated likelihoods, which become the weights ($w_{l,t}$), for the $L$ observations representing each regular prediction $x_l$ can then simply be summed ($\sum w_{l,t}$) because even in the usual situation of temporally regular observations the weights need to be normalized to one before the resampling step. After summing and normalizing the $L$ weights, we have a single weight for the particle representing the temporally regular $x_l$ prediction and its parameters $\theta_l$, and the resampling step proceeds as usual. This way of fitting irregular data to regular time steps is somewhat similar to that used by Jonsen et al. (2005), however, that solution, which worked for MCMC, was not amenable to SMC methods. The approach to handling irregular data described here is relatively elegant and produced results superior to any other approach attempted. Its only requirement is that the first regular time step be at the same time as the first observation.

Code that performs the calculation of $j_l$ fits the CRW with augmented parameters in an SIR particle smoother as described above, and a sample of 1000 h of GPS data from a California sea lion are available as a compressed package of Matlab files as an online supplement to this article.
3. Simulation

We performed a simulation study to validate our model’s ability to recover known parameters by fitting it to two different simulated tracks. In both cases, tracks were simulated using a CRW of the same form as in Eq. (1). The simulated tracks differed in how parameters driving the CRW evolved. In Design 1 they drifted gradually on a sine wave, and in Design 2 they switched between two discrete states. Each simulation was iterated forward $T=600$ time steps to produce simulated tracks. As real tracking observations are irregular, we linearly interpolated along the simulated pathways at lengths of time randomly drawn from the positive side of a zero-centered Gaussian distribution to produce a temporally irregular time-series of observations. The variance of this distribution was set such that, on average, 2 observations were made for each position simulated from the CRW. We chose to simulate twice as many observations as location estimates in order to approximately match the number of observations we had for each regular location estimate we made for our real GPS tracking data. At each irregular observation time, bivariate Gaussian noise was added according to Eq. (4). This resulted in simulated tracks with irregular observation times and GPS-like spatial accuracy as might be collected from real tracked animals.

For Design 1, parameters were set to oscillate through two cycles of a sine wave and the values of $\gamma_t$, $c_t$, and $\Sigma_t$ were set proportional to its value at time $t$ such that:

$$\gamma_t = \frac{1 + \sin \left( \frac{4\pi t}{T} \right)}{2}$$

$$c_t = \frac{1 + \sin \left( \frac{4\pi t}{T} \right)}{2}$$

$$\Sigma_t = \begin{bmatrix} 0.001 + 0.01 \times \frac{1 + \sin \left( \frac{4\pi t}{T} \right)}{2} & 0 \\ 0 & 1 \end{bmatrix} \times \begin{bmatrix} 1 & 0 \\ 0 & 1 \end{bmatrix}$$

(8)
where \( t \) is the current time step, \( t=1 \ldots T \) and \( \Sigma_t \) is the variance–covariance matrix of the process noise. This simulation produces a track with slowly varying movement patterns. Note that parameters were varied with the same sine wave and so were in phase with each other.

Whether fitting our PS to simulated or real data, the PS was executed 50 times using 1000 particles each in order to fully explore the state and parameter space and to be robust to Monte Carlo error. For the sine wave simulations, it was necessary to obtain 50 different simulated datasets because process noise often overwhelmed and confounded the slowly varying parameters for a few time steps (Fig. 1a–c). When averaged across the 50 simulations, the driving sine process is clearly recovered and the stochastic jumps blend out (Fig. 1d and e). In real data, stochastic spikes would represent unexplained behavior which could temporarily mask larger scale processes.

Estimates of \( \gamma_t \) and \( c_t \) generally track the parameters used to generate the simulation well, but the time-series of parameter estimates are a bit more shoulderled than the sine wave (Fig. 1d). This suggests that when \( \gamma_t \) and \( c_t \) are small they are overwhelmed by process noise in all simulations. This makes sense, as when these parameters are 0 or small, the process is driven mostly or entirely by \( \Sigma_t \) and is a pure random walk with \( \gamma \) and \( c \) having only subtle effects compared to \( \Sigma \).

Estimates of \( \Sigma_t \) varied by about a factor of 3, which was smaller than the factor of 11 amplitude of the driving sine wave (Eq. (8)). The

\[ \begin{align*}
\gamma &= 0.98, \\
c &= 0.98
\end{align*} \]
phase of the estimates was also offset from the sine wave driving them. This phase shift, combined with the small estimates of $\Sigma$ relative to those used to drive the simulation, suggests some of the process noise is confounding with and being explained by other parameters. However, the structural parameters are nonetheless following the simulation, and the overall result of this validation suggest that parameter estimates with biological meaning can be accurately estimated, even if they vary slowly.

In simulation Design 2, parameters evolved by discretely switching between two states based on a fixed transition probability (e.g. Morales et al., 2004; Jonsen et al., 2005). The parameters of each state were fixed: for state 1 $\gamma_1 = 0.9, c_1 = 0.98, \sigma_{x,1} = \sigma_{y,1} = 1$ km; for state 2 $\gamma_2 = 0, c_2 = 0, \sigma_{x,2} = \sigma_{y,2} = 0.1$ km. This simulation produced tracks with obvious discrete changes in movement.

The model was fit 50 times to the same simulated dataset. Parameters occasionally failed to track short bouts of transiting, but were generally responsive to switches. $\Sigma$ tended to be somewhat underestimated, suggesting parameters confound some with process noise and observation error. Overall, parameters closely tracked the behavioral switches of the simulated track (Fig. 2). The fit structural parameters $\gamma$ and $c$ were with in 10% of the values used to simulate the track 93% of the time and location estimates were nearly perfect.

4. Application

We fit our model to GPS tracking data collected from California sea lions (Zalophus californianus). In early November 2008, 10 adult female sea lions were captured on San Nicolas Island (33.27° N, 119.57° W) and instrumented with Wildlife Computers Mk10-AF Argos linked GPS tags following methods described in Weise and Costa (2007). These tags produced tracks of high temporal resolution (1000–2000 locations over 2.5 months) and low spatial error as reported in Costa et al. (2010a). Animals were recaptured, tags removed, and GPS locations downloaded in February 2009.

California sea lion movement patterns vary widely among individuals, but are generally characterized by central place foraging from one or several haul out sites. Foraging trips range from 1 to 2 days covering a few tens of kilometers to several weeks covering thousands of kilometers. Variance in trip length tends to be between rather than within individuals. We chose 3 tracks to demonstrate our model, one animal making short trips, one making intermediate length trips, and one making very long trips. We fit the model to these 3 tracks 50 times using 1000 particles each time. As before, parameter estimates from the 50 runs were then averaged to produce a grand mean and 95% CI for both parameter and location estimates. In all cases, distinct changes in $\gamma_1$ and
$c_i$ were clear. The model detected rapid, more or less instantaneous switches between two distinct movement types most of the time (Fig. 3) and appeared robust to Monte Carlo error (Fig. 4a–d). The effective number of particles used to estimate parameters and states varied considerably, but ranged between 300 and 5000 of the 50,000 total particles (50 runs using 1000 particles) used to explore the state-space (Fig. 4e).

The parameter $\Sigma_t$ was elevated at the onset of directed movements, intermediate in the middle of directed movements, and low at haulout and in foraging areas (Fig. 3c and e). Though $\Sigma_t$ was low at both haulout and at foraging areas, the behavior differed subtly. In particular, at haulout, $\sigma_{lat}$ and $\sigma_{lon}$ assume the same value and have much lower variance. While swimming at sea, these patterns in the $\Sigma$ parameter estimates were not present, making it possible to discriminate haulout from foraging behaviors at sea using only the $\Sigma_t$ parameter. Our current state augmented SIR PS does not allow us to sample the parameter space adequately when $\Sigma_t$ approaches 0. Improvements here will make such subtle behavioral discriminations even clearer.

One sea lion made very long foraging trips, and parameter estimates from this animal suggest a more complicated behavioral scenario. Segments of track include less discrete behavioral phases. In these segments, occurring during three long midwinter trips (beginning 1400 h after deployment in Figs. 5a and 6a and b), the animal moved persistently in a particular direction, but did so slowly and with more meanders than the discrete travel segments of the other two individuals. Parameters during these trips were less discrete, intermediate and highly variable. Conversely, trips made by this animal in autumn, as well as trips made by the other two sea lions, were characterized by repeated visits to small foraging areas, with very direct transit between these areas and haulout sites. These trips appeared to be structured based on previous foraging experience and memory and had very discrete parameter phases. Unproductive winter months may have disrupted a predictable foraging landscape available in autumn, requiring prolonged search oriented foraging trips to find prey resources. Analysis of a larger dataset is needed to carefully test this hypothesis.

![Fig. 4. State and parameter estimates from individual 1000 particle simulations (black line), and the grand mean of 50 simulation (red line) for latitude (a), longitude (b), $c$ (c), $c$ (d), and $\text{neff}$, the number of effective particles (e) for the track shown in Fig. 3. The individual simulations mix well. Only the first 1000 time steps shown. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of the article.)](image-url)
Fig. 5. Analysis of 2 additional California sea lion tracks. Parameter estimates for $\gamma$ are indicated by the intensity of red, with more saturated reds representing $\gamma$ values closer to 1 and blacker shades nearer 0. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of the article.)

Fig. 6. Parameter estimate time-series for the 2 California sea lion tracks shown in Fig. 5. Panels a and b correspond to the track shown in Fig. 5a and panels c and d correspond to the track shown in Fig. 5b.
5. Discussion

5.1. Time-varying parameters

Time-varying parameters within an SSM are a key advantage as they accommodate non-stationary statistical properties. Using a simple autoregressive time-series approach Curarie et al. (2009) demonstrated how much information could be extracted from movement data if parameters are allowed to vary in time. Though powerful and exciting, their model could be embedded in an SSM, as we have done here, so as to improve its robustness with respect to observation error.

Particularly important for animal movement processes is the inclusion of time-varying process noise ($\Sigma_t$ in this model). All previous SSM implementations for tracking data, including those that switch between behavioral states, assume constant process noise throughout a track (e.g. Morales et al., 2004; Jonsen et al., 2005). This is not biologically realistic, as process noise will necessarily change as an animal's behavior changes. Sleeping animals, for example, generally do not move. The movement process stops, and the stochastic element of movement will also necessarily stop. More generally, one might hypothesize that process noise should be high or low based upon some a priori understanding of how animals behave. Such hypotheses could be tested with a model that estimates time-varying process noise like the one we demonstrate here.

In the case of California sea lions, process noise dropped to the lowest allowable value at haulout, which is exactly what one would predict as haul-out is a resting state. $\Sigma_t$ spiked at the initiation of transits and was low but variable during apparent foraging bouts, making it possible to discriminate several meaningful behavioral conditions with this parameter.

5.2. Future directions

Ionides et al. (2006) demonstrated the strengths of parameter augmented SIR particle filters for fitting complex, non-linear SSMs to ecological time series data, and more recently Dowd and Joy (2011) implemented the method to analyze marine animal diving data. However, parameter augmented PF of PS methods have largely remained untapped for analysis of real systems, with most published examples fit to simulated data. 2-d animal tracking data are more challenging to fit with the SIR method than the 1-d data time-series fit by Ionides et al. (2006) or Dowd and Joy (2011). The difficulty stems from the temporal irregularity of observations, higher spatial error, and an extra dimension in the data. Having overcome these issues, the SIR implementation presented here offers several key advantages over other SSM fitting methods.

While extremely useful in its current state, the models demonstrated here are also scaffolding on which to build models that incorporate a wide range of mechanisms that might control movement. Moving away from regime switching models to time-varying parameters opens the door to a much wider range of model forms and the flexibility should afford easier construction of models that test behavioral hypotheses.

In particular, incorporation of time-varying parameters that track persistence in compass heading and speed would be highly informative of navigation ability. Models could still retain first-order autocorrelation in displacements and turn angle to estimate immediate behavioral condition. Incorporating parameters that relate environmental conditions to movement parameters has been a long standing goal of mechanistic movement model development. There are some examples of CRWs that relate environment to movement parameters (Schultz and Crone, 2001; Morales et al., 2004; Schick et al., 2008), but environmental data of sufficient temporal and spatial resolution are not usually available to inform movement, particularly in the marine environment.

There are sufficient environmental data around the Channel Islands, however, to test some interesting behavioral hypotheses. Around the Channel Islands, sea lions must negotiate a strong, complex, and dynamic tidal current field. Adding a parameter relating current vectors to movement should illuminate the degree to which sea lions take advantage of, or otherwise coordinate, transiting movement with favorable tidal and current conditions, a behavior that could save them thousands of calories per transit between haulout and foraging areas. Work is now progressing to adapt our model to this problem. As part of that work, we are developing a better sampling scheme for $\Sigma_t$ so that process noise close to 0 can be more accurately estimated.

Here we chose to use a temporally regular process model, but it would be straightforward to build a continuous time process model in the PS framework (e.g. Johnson et al., 2008). Temporally regular steps have a number of favorable properties and tend to be more robust to irregularities in parameter estimates introduced when extremely short periods pass between observations and the observation error disproportionately increases relative to the scale of the movement process. However, some prefer continuous time models because of their simplicity of implementation, and the PS framework we describe can accommodate such models.

At present, there is some limitation on the number of parameters that can be estimated using SMC methods, but alternatives such as coding one’s own MCMC sampler with dozens of parameters is no trivial task, and platforms like WinBUGS are not transparent and the available models restrictive. Modeling at its best is about reducing systems to small numbers of meaningful parameters to achieve an elegant reduction of complexity that fits into a theoretical framework that can be meaningfully interpreted. The flexibility in the PS method for tracking data allows for fitting transparent and elegant models of movement behavior in a state-space framework that produce meaningful and biologically interpretable results.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.ecolmodel.2012.03.021.

References


