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META-ANALYSIS OF ANIMAL MOVEMENT USING STATE-SPACE MODELS

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Abstract. The study of animal movement and behavior is being revolutionized by technology, such as satellite tags and harmonic radar, that allows us to track the movements of individual animals. However, our ability to analyze and model such data has lagged behind the sophisticated collection methods. We review problems with current methods and suggest a more powerful and flexible approach, state-space modeling, and we illustrate how these models can be posed in a meta-analytic framework so that information from individual trajectories may be combined optimally. State-space models enable us to deal with the complexity of modeling animals interacting with their environment but, unlike other methods, they allow simultaneous estimation of measurement error and process noise that are inherent in animal-trajectory data. A Bayesian framework allows us to incorporate important prior information when available and also allows meta-analytic techniques to be incorporated in a straightforward fashion. Meta-analysis enables both individual and broader-level inference from observations of multiple individual pathways. Our approach is powerful because it allows researchers to test hypotheses regarding animal movement, to connect theoretical models to data, and to use modern likelihood-based estimation techniques, all under a single statistical framework.

Key words: animal movement, analysis of tracking data; Bayesian models, hierarchical; behavior; dispersal; MCMC (Markov chain Monte Carlo) methods; measurement error; meta-analysis of animal movement; migration; process noise; state-space models; WinBUGs analysis.

INTRODUCTION

Animals interact with their environment in complex ways and these interactions can produce complex movement patterns. Understanding how these patterns arise and what their implications are for home-range and territorial dynamics (Moorcroft et al. 1999), habitat use and conservation (Belisle and St. Clair 2001, Block et al. 2001), biological invasions (Lewis and Kareiva 1993), biological control (Jonsen et al. 2001), metapopulation dynamics (Moilanen and Hanski 1998), and community interactions (Ellner et al. 2001) are important issues in ecology.

Our ability to analyze movement patterns, however, has been far outstripped by our ability to collect individual movement data. Technologies such as satellite, archival, and harmonic radar tags enable us to follow marine and terrestrial animal movements over large distances (e.g., Roland et al. 1996, Bergman et al. 2000, Block et al. 2001). There are sources of error inherent in each of these technologies, and innovative methods are required to deal with them while at the same time allowing behaviors to be estimated and hypotheses to be tested formally. In addition, we require meta-analytic tools for combining information from multiple observations of movement trajectories to facilitate broader inference to population, species, and community levels.

Movement pathways, which are time series of location observations, can be analyzed using state-space models (SSMs). SSMs are time-series models that allow unobservable, true states to be inferred from observed data by accounting for errors arising from imprecise observations and from stochasticity in the process being studied. The state-space modeling approach has been used to analyze animal movement (Anderson-Sprecher and Ledolter 1991, Newman 1998, Brillinger 2000, Sibert and Fournier 2001), but a complete description and demonstration of its utility for ecologists is lacking. In addition, the task of fitting SSMs to data can be formidable, requiring both large computational overhead and statistical expertise. Recent advances in statistical methods (Carlin et al. 1992) and freely available application software (WinBUGS, Spiegelhalter et al. 1996), however, have made the task both computationally efficient and accessible for non-statisticians.

Our objectives in this paper are, first, to provide a rationale for the preference of SSMs over more traditional approaches for the analysis of animal trajectory data. Second, to provide a concise description of how SSMs can be fit to animal trajectory data using a Bayesian approach. Third, to illustrate how individual pathways may be combined using meta-analytic techniques so that inferences about population-level behavior can be made and so that parameter estimation for data-poor, individual pathways can be improved.

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Current Approaches

Present methods for the statistical analysis of animal movement pathways primarily determine if observed movements are consistent with random-walk models such as correlated random walks and biased random walks (Kareiva and Shigesada 1983, Turchin 1998). Random-walk analyses (e.g., Kareiva and Shigesada 1983) typically assume that movements are made in homogeneous environments and that animals do not change their behavior drastically (Turchin 1998). Unfortunately, this is rarely the case. Animal behaviors change frequently as new stimuli are encountered and/or as an animal's internal (physiological) state changes. Therefore, movement pathways that span long time periods are likely to contain complex structure that is difficult to compare to a random-walk model. One solution to this problem is to break an observed pathway into separate, homogeneous sections and analyze each in isolation (Turchin 1998, Sibert and Fournier 2001), but this relies on an adhoc determination of appropriate break points. More-appropriate methods should minimize this subjectivity by analyzing the switches in behavior explicitly (Grünbaum 2000).

Grünbaum (2000) used an advection–diffusion model that approximated the dynamics of interactions between environment and organisms' internal states to derive population distributions of organisms arising from biased random-walk behaviors. Such theoretical studies provide mathematical links between individual-level movement behaviors and population-level patterns of redistribution. In order to connect theoretical models like Grünbaum's to data, summary statistics such as turning frequencies and squared net displacement (e.g., Kareiva and Shigesada 1983, Grünbaum 1999) are used, but this often requires subjective decisions about how to calculate the statistics from field data (Turchin 1998). A more efficient approach would be to fit a discrete approximation of the model directly to observed data and estimate parameters using likelihood-based statistical techniques.

Only a few studies examine the likelihood of observed movements using modern frequentist methods (Anderson-Sprecher and Ledolter 1991, Newman 1998, Brillinger 2000, Sibert and Fournier 2001) and there are no current applications that utilize Bayesian methods. Such an approach to studying movement trajectories may often require nonlinear methods because animal behaviors, or the changes between behavioral states, are inherently nonlinear. In the simplest case, behavior changes in a simple switch from one type of behavior to another. Time-series models that describe such nonlinearities have been studied extensively in econometrics using nonlinear Kalman filters (Tanizaki 2003) but only recently have they been applied to the analysis of ecological data (Meyer and Millar 1999, Brillinger 2000, de Valpine and Hastings 2002). In the following sections we formulate the nonlinear state-space model and illustrate how it may be implemented using a Bayesian approach that affords efficient computation (Tanizaki 2001) and allows prior information to be incorporated into the analysis. We note that the formulation provided here may also be used for linear cases.

State-space Models

State-space models (SSMs) represent a natural framework to model animal movement. In the past, these models have been applied primarily in the linear case. The nonlinear case, where much of the interesting biology is, previously was not feasible for estimation in most real-world situations. This has changed with the advent of simulation-based estimation methods that allow the integrals inherent in the state-space approach to be estimated (Carlin et al. 1992, Tanizaki 2001). Below we present the standard formulation for a nonlinear state-space model. We use Tanizaki's notation throughout (Tanizaki 2001). Readers interested in greater detail are referred to Tanizaki (2001) and de Valpine and Hastings (2002) and references therein.

Formulation

We consider a marked animal's position to be observed at a series of times $t = 1, 2, \ldots, T$. The locations are observed with error which gives rise to a measurement equation:

$$\mathbf{y}_t = \boldsymbol{h}_t(\boldsymbol{\alpha}_t, \boldsymbol{\varepsilon}_t) \qquad t = 1, 2, \ldots, T \tag{1}$$

where $\mathbf{y}_t$ represents the observed location and $\boldsymbol{\alpha}_t$ (called the ''state variable'' in time-series analysis) is the true location and is not observable. For instance, $\mathbf{y}_t$ may be a two-dimensional vector representing the observed spatial location (e.g., latitude and longitude) of an animal at time t with the error in location at time t given by a two-dimensional vector $\boldsymbol{\varepsilon}_t$.

For many types of geolocation estimate, for example those based upon ambient light intensity (archival tags) or satellite (e.g., ARGOS), the error variance in longitude is not the same as the error variance in latitude (Vincent et al. 2002, Sibert et al. 2003). In these cases, the error variances can be estimated and included in the model describing the measurement equation. If future movement of an animal depends upon the current position, process noise, $\boldsymbol{\eta}_t$ (that is mutually independent of $\boldsymbol{\varepsilon}_t$), and a vector of parameters describing the movement process, $\boldsymbol{\gamma}$, then the dynamics can be described by a transition equation:

$$\boldsymbol{\alpha}_t = \boldsymbol{f}_t(\boldsymbol{\alpha}_{t-1}, \boldsymbol{\eta}_t; \boldsymbol{\gamma}). \tag{2}$$

The purpose of the SSM is to estimate the unobserved locations, $\boldsymbol{\alpha}_t$, using the above two equations and to estimate ecological parameters describing the movement, $\boldsymbol{\gamma}$. Here $\boldsymbol{h}_t(\cdot, \cdot)$ and $\boldsymbol{f}_t(\cdot, \cdot; \cdot)$ are assumed to be known.

Let $\mathbf{Y}_t$ contain all observations from time 0 through to time t. Define $p_y(\mathbf{y}_t|\boldsymbol{\alpha}_t)$ as the density function derived

from the measurement equation, and define $p_\alpha(\boldsymbol{\alpha}_t|\boldsymbol{\alpha}_{t-1}; \boldsymbol{\gamma})$ as the density function derived from the transition equation. State-space models can be formulated recursively by ''filtering.'' This process consists of two steps, the first of which takes information from all the previously observed data, $\mathbf{Y}_{t-1}$, to predict the new location. This is the prediction equation and is given by

$$p(\boldsymbol{\alpha}_t|\mathbf{Y}_{t-1}; \boldsymbol{\gamma}) = \int p_\alpha(\boldsymbol{\alpha}_t|\boldsymbol{\alpha}_{t-1}; \boldsymbol{\gamma})p(\boldsymbol{\alpha}_{t-1}|\mathbf{Y}_{t-1}; \boldsymbol{\gamma})\, d\boldsymbol{\alpha}_{t-1}. \quad (3)$$

The second step updates the new information provided by $\mathbf{y}_t$ with the previous information provided by $\mathbf{Y}_{t-1}$. This update equation is Bayes rule and is given by

$$p(\boldsymbol{\alpha}_t|\mathbf{Y}_t; \boldsymbol{\gamma}) = \frac{p_y(\mathbf{y}_t|\boldsymbol{\alpha}_t)p(\boldsymbol{\alpha}_t|\mathbf{Y}_{t-1}; \boldsymbol{\gamma})}{\int p_y(\mathbf{y}_t|\boldsymbol{\alpha}_t)p(\boldsymbol{\alpha}_t|\mathbf{Y}_{t-1}; \boldsymbol{\gamma})\, d\boldsymbol{\alpha}_t}. \quad (4)$$

Filtering is conducted for times $t = 1, 2, \ldots, T$ from an initial, known position (i.e., where the animal was released), which is given by $p(\boldsymbol{\alpha}_1|\mathbf{Y}_0; \boldsymbol{\gamma}) = p_\alpha(\boldsymbol{\alpha}_1|\boldsymbol{\alpha}_0)$.

The likelihood for γ is the probability of observing each of the $\mathbf{y}_t$'s, given the previous observed positions and explanatory variables:

$$L(\boldsymbol{\gamma}; \mathbf{Y}_T) = p(\mathbf{Y}_T; \boldsymbol{\gamma}) = \prod_{t=1}^{T} p(\mathbf{y}_t|\mathbf{Y}_{t-1}; \boldsymbol{\gamma}) = \prod_{t=1}^{T}\left[\int p(\mathbf{y}_t|\boldsymbol{\alpha}_t)p(\boldsymbol{\alpha}_t|\mathbf{Y}_{t-1}; \boldsymbol{\gamma})\, d\boldsymbol{\alpha}_t\right]. \quad (5)$$

This is called the ''innovation'' for the likelihood function. Note that the likelihood is the denominator of Eq. 4, and thus does not require extra evaluation. The likelihood can be calculated for any $\boldsymbol{\gamma}$ and set of observed positions. Solutions in the general, nonlinear case are difficult to obtain and typically require the use of Monte Carlo or numerical methods to resolve the multiple integrals that are inherent in the likelihood.

There are two basic approaches to the problem of fitting SSMs to data: a Bayesian approach and a frequentist approach. In a Bayesian approach, it is possible to use Markov chain Monte Carlo (MCMC) methods to solve this problem (Carlin et al. 1992, Tanizaki 2003). This is the solution used here. The frequentist approach requires a linearization and use of the extended Kalman filter (e.g., Anderson-Sprecher and Ledolter 1991) or numerical integration (de Valpine and Hastings 2002).

One advantage of the Bayesian approach is that prior information can be formally incorporated into the analysis by specifying prior distributions for the variables of interest. For example, this may be information regarding the measurement error of our instruments, knowledge of the variance in the movement process itself, or information regarding some of the biological parameters contained in the vector $\boldsymbol{\gamma}$. An additional advantage exists when meta-analysis is desired because this amounts to a straightforward extension of the model—the addition of hyper-prior distributions. Hyper-prior distributions are simply prior distributions on the parameters of prior distributions (Carlin and Louis 1996).

In the following sections we illustrate how SSMs can be fit in a Bayesian context to animal movement data using a freely available software package, WinBUGS version 1.3 (available online)[4] (Spiegelhalter et al. 1996).

Demonstration

An environmentally dependent linear state-space model

The following example uses simulated data to illustrate our general approach to fitting state-space models (SSMs) to movement data. By using simulated data we can compare parameter estimates to their true values, thereby assessing the performance of SSMs, which cannot be done using field data. We consider a marine situation where a leatherback turtle, *Dermochelys coriacea* (Vandelli 1761), moves in an environmentally dependent manner with its behavior governed by differences in sea surface temperature. This simulation is purposefully simplified to ease the illustration of the statistical approach. More complex models could be fit to appropriate data.

Sea surface temperature, which we denote s_t, is assumed to be sampled along with location, which is consistent with current tagging technologies (e.g., archival and ARGOS satellite tags). We further assume that movements in the north–south and east–west directions are independent draws from the same normal distribution whose variance, σ_η^2 is related to temperature in the following way:

$$\sigma_\eta = \sigma\exp(-\beta_{s_t}). \quad (6)$$

Note that the biological component of the SSM, γ, is fully parameterized by β; β determines how quickly the distance moved, at each step t, declines with increasing temperature. Note, also that σ represents the process noise implicit in the movements. This component of the model acknowledges a stochastic component to the turtle's movement. We include measurement error in our simulated data through the introduction of a random variable, $\varepsilon_t \sim \mathcal{N}(0, \tau^2)$, where $\mathcal{N}$ denotes the normal distribution.

We have specified all of the components of our SSM and now present the transition and measurement equations for this example:

[4] URL: ⟨http://www.mrc-bsu.cam.ac.uk/bugs/winbugs/contents.shtml⟩.

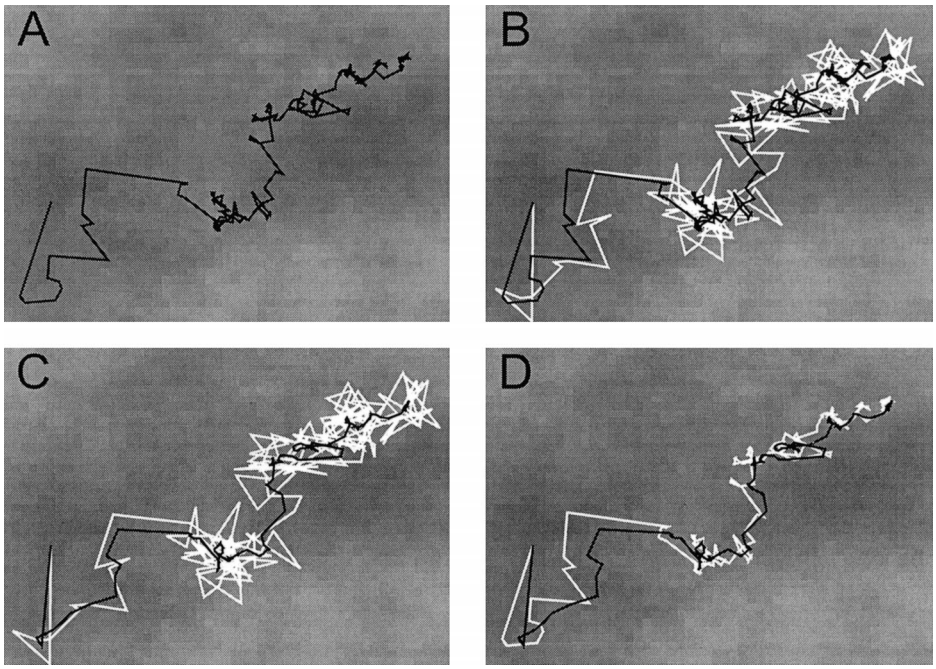

FIG. 1. Graphical results of fitting a state-space model (SSM) to simulated movement data of a marine turtle. (A) The true pathway (black) overlaid on the sea surface temperature (s_t) field. (B) The true pathway (black) and the ''observed'' pathway (white) for comparison. The difference between these two pathways represents the error associated with measuring the position of the turtle at discrete points in time. (C) Plots of the estimated (black) and observed (white) pathways, overlaid. (D) Plots of the estimated (black) and true (white) pathways, overlaid. The estimated pathway accounts for measurement-error and process-noise components estimated by the SSM. Darker areas on the s_t field represent colder temperatures.

$$\boldsymbol{\alpha}_{t+1} = \boldsymbol{\alpha}_t + \boldsymbol{\eta}_t \tag{7}$$

$$\mathbf{y}_t = \boldsymbol{\alpha}_t + \boldsymbol{\varepsilon}_t \tag{8}$$

where $\eta_t \sim \mathcal{N}(0, \sigma\exp[-\beta_{S_t}])$ and $\varepsilon_t \sim \mathcal{N}(0, \sigma_\varepsilon)$. Note that $\boldsymbol{\alpha}_t$, $\mathbf{y}_t$, $\boldsymbol{\eta}_t$, and $\boldsymbol{\varepsilon}_t$ are two-dimensional vectors accounting for movement in the north–south and east–west directions.

In order to take a Bayesian approach to fitting our SSM to the simulated data we specify prior distributions for β, σ, and τ. These priors represent our knowledge of the system before analyzing the current data. Here, we assume that no prior information regarding β and σ is available and assign appropriately vague priors for each; $\beta \sim \mathcal{N}(0, 1 \times 10^3)$ and $\log \sigma \sim \mathcal{N}(0, 1 \times 10^3)$.

We assume that we do have some prior knowledge regarding measurement error, $\boldsymbol{\varepsilon}_t$, and can incorporate this additional information by specifying an informative prior for τ. Prior information of this sort is likely to exist for many analyses using real data (e.g., Vincent et al. 2002). Here we assume that the measurement-error variance, τ, is known and thus specify an informative prior, $\tau \sim \mathcal{N}(2, 0.1)$. For simplicity, we assume that τ is identical in the north–south and east–west directions.

We simulate a single trajectory with the following parameter values: $\beta = 0.90$, $\sigma = 1.0$, $\tau = 2.0$. This pathway is the true pathway of an animal that, in real applications, is unobservable because observation methods are imprecise. Hereafter we refer to this simulated pathway as the ''true pathway.'' Fig. 1A shows the true pathway (black) overlaid on the s_t field and Fig. 1B includes the observed pathway (white), which contains measurement error. We want to estimate the true locations at times $t = 1, 2, \ldots, T$ while accounting for measurement error and also understand something about how the turtle responds to its environment.

The SSM was fit to the data using WinBUGS versions 1.3 (see footnote 4). WinBUGS performs Bayesian analyses for complex statistical models using MCMC techniques and it is ideally suited to fitting SSMs (Meyer and Millar 1999). The WinBUGS code for fitting the SSM to the simulated data is provided in the Appendix. Simulation code (requires S-Plus 6.0, PC version, or higher [Insightful Corporation, Seattle, Washington, USA]) for generating pathways, along with instructions and additional required data, is available in Supplement 1.

After fitting the SSM to the observed data we obtain a ''most probable'' pathway that accounts for the estimated measurement error and process noise components (Fig. 1C and D: black lines). The ''most probable'' pathway is obtained from the means, medians, or modes of the univariate posterior distributions for $\mathbf{y}_t$; in this case we have plotted the means because the posterior distributions are symmetric. The means and

TABLE 1. Comparison of the true parameters and their corresponding estimates for a single marine turtle's simulated trajectory; estimated values are given as the posterior mean (with 1 SD) and the median, along with 2.5% and 97.5% credible limits [CL].

Parameter†	True	Mean (1 SD)	2.5% CL	Median	97.5% CL
β	0.9	0.8716 (0.1208)	0.6403	0.8696	1.1130
σ	1.0	1.0090 (0.1192)	0.7968	1.0020	1.2650
τ	2.0	2.0020 (0.0866)	1.8370	1.9980	2.1750

Note: Values were estimated from 4000 samples, after a 5000-sample burn-in (Spiegelhelter et al. 1996) with every 10th sample retained to reduce autocorrelation.

† Parameters: β = coefficient that describes how rapidly the distance moved declines with increasing water temperature; σ = process-noise variance; τ = measurement-error variance.

medians are reported as standard output in WinBUGS and the modes can be calculated from output generated by convergence diagnostic packages such as BOA (Bayesian output analysis) and CODA (convergence diagnostic and output analysis). We used BOA Version 1.0.0 for S-PLUS and R (available online).[5] Clearly, we now have an improved estimate of the true pathway (Fig. 1: panel C cf. panel D). The SSM produces good estimates of the parameters σ (process noise), τ (measurement error variance), and β (Table 1).

Meta-analysis of behavior from many pathways

Meta-analytic techniques allow us to gain valuable insight about a population by combining information collected on individuals. The essential idea of Bayesian meta-analysis is to consider some of the parameters of a statistical model as random variables. An advantage of meta-analytic models is that parameter estimates from individual data sets can be improved over those that would be obtained by fitting separate models to each data set (Myers et al. 1999, Worm and Myers 2003). The resulting models often are referred to as ''hierarchical random-effects models'' or ''hierarchical Bayesian models'' (e.g., Sauer and Link 2002).

It is quite simple to extend SSMs to perform meta-analysis when they are developed in a Bayesian framework as it essentially amounts to introducing additional prior distributions (hyper-priors). For more detail on meta-analytic techniques using hierarchical Bayesian models the reader is referred to Carlin and Louis (1996).

To illustrate our approach we extend the turtle example from the previous section by considering 15 individual pathways (50 observations each). We let β_i represent the temperature-dependent movement parameter for individual i and we assume the parameters β_i are independent samples from a normal distribution: $\beta_i \sim \mathcal{N}(\mu_\beta, \sigma_\beta^2)$.

We assign vague hyper-prior distributions to reflect our ignorance about the unknown hyper-parameters μ_β and σ_β^2. We simulate the pathways by setting the true hyper-prior values as shown in Table 2. Upon fitting the hierarchical model we obtain estimates of the hyper-parameters μ_β and σ_β. Results of this meta-analysis are presented in Table 2. The estimated parameters describing the distribution of the β_i's are quite reasonable (Table 2). The WinBUGS code for fitting the meta-analytic SSM to the simulated data is provided in Supplement 2.

To illustrate the advantage of simultaneously modeling the individual pathways for improved individual parameter estimation, we generate an additional 15 10-observation and 15 100-observation pathways, for a total of three sets of 15 pathways with 10, 50, or 100 observations. The same simulation code used to generate pathways in the first example was also used here. The codes, instructions, and required data are provided in Supplement 2. All pathways were generated using the same true values for β and, therefore, differed only in the number of location observations. We analyzed the pathways by (1) fitting the meta-analytic model described above to each group and (2) fitting a separate SSM to each of the individual pathways. The results presented in Fig. 2 demonstrate that parameter estimates for β generated from the individual analyses have a larger standard error than the corresponding estimates generated from the meta-analytic model and that this standard error is largest for the 10-observation pathways (Fig. 2). Note, however, that for the 10-observation group the among-pathway variation is underestimated (Fig. 2); this may be due to the small number of pathways considered.

DISCUSSION

In this paper we have presented an underutilized and, hitherto, technically difficult statistical framework for the analysis of animal trajectory data—state-space modeling (SSM). In particular, we illustrate the relative ease with which SSMs can be fit in a Bayesian context using freely available software. An additional advan-

TABLE 2. Comparison of the true and estimated parameter values from the meta-analytic model; estimated values are given as the posterior mean (with 1 SD) and median, along with 2.5% and 97.5% credible limits [CL].

Parameter†	True	Mean (1 SD)	2.5% CL	Median	97.5% CL
μ_β	0.867	0.846 (0.093)	0.669	0.844	1.032
σ_β	0.234	0.204 (0.090)	0.143	0.279	0.500

Notes: For this meta-analysis of marine turtle movement behavior, we generated three sets of 15 pathways: one set based on 10 observations per pathway, one on 50 observations per pathway, and one on 100 observations per pathway. Estimates are based on 4000 samples from the joint posterior, after a 5000-sample burn-in with every 10th sample retained to reduce autocorrelation.

† Parameters: μ_β and σ_β = hyper-parameters (mean and 1 SD, respectively) describing the distribution of β_i values.

[5] URL: ⟨http://www.public-health.uiowa.edu/boa/⟩.

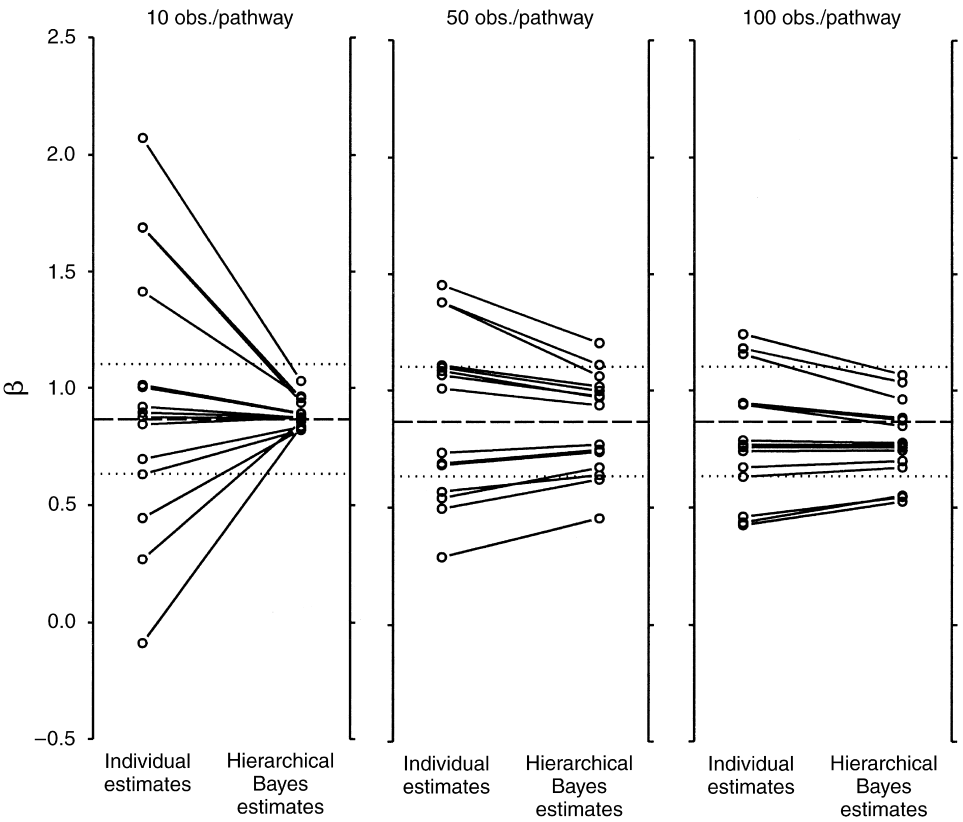

FIG. 2. Comparison of parameter estimates for β made by fitting the state-space model (SSM) to each of the individual pathways and by fitting a hierarchical random-effect SSM to all the pathways simultaneously. The three panels illustrate the comparison for pathways of 10 observations, 50 observations, and 100 observations. Dashed horizontal lines indicate the true mean of the distribution for β, and dotted horizontal lines indicate 1 SD from the true mean for β, the coefficient that describes how rapidly the distance moved declines with increasing sea surface temperature.

tage to the Bayesian approach is that SSMs can be extended easily to include meta-analytic techniques that allow individual pathways to be combined optimally. Using our framework, any discrete individual-based movement model can be fit to appropriate trajectory data.

State-space models have a number of attractive features that have the potential to revolutionize the analysis of animal movement data. First, movement data typically contain temporal dependencies that violate assumptions of independence upon which more traditional methods rely. SSMs account for the temporal dependence by conditionally modeling the observed data given unknown states and specifying a function for the transition between those states. In addition, these models can easily handle missing location data.

Second, no other current statistical method can simultaneously account for the measurement error and process noise typically found in many types of ecological data, in such an intuitive fashion. The removal of measurement error is of particular benefit for improving location estimates from archival, radio-transmitter, harmonic-radar, and acoustic tags. In contrast, removal of process noise may be of most benefit when the intervals between observed locations are short relative to the scale of the process being modeled. For example, we might expect a high degree of apparent stochasticity in observed movements if a model of large-scale migration was fit to a pathway of appropriate spatial extent but with very frequent, e.g., hourly, location observations.

Third, SSMs provide a rigorous statistical framework, not only for estimating model parameters but also for testing hypotheses about animal movements. For this reason, we view the state-space framework as a uniquely flexible tool that, with widespread adoption, has the potential to advance the analysis of animal movement in a fashion analogous to that of ANOVA for the analysis of ecological experiments (Underwood 1981). Alternative biological models may be fit within a state-space model and compared using information criteria such as the deviance information criterion (DIC) (Spiegelhalter et al. 2002) or Bayes factors (Carlin and Louis 1996).

Our example using simulated data illustrates how the influence of environmental variables on movement be-

havior may be examined in the state-space framework and we anticipate that similarly framed models fit to real data will yield interesting results. Furthermore, the ability to combine environmental covariates with theoretical movement models, such as biased random walks that describe area-restricted search behavior, will provide insight into what constitutes important habitat features for foraging animals and how those animals locate their habitats. This approach may be particularly relevant for marine systems where habitat features are more difficult to delineate than in terrestrial environments.

A key idea implicit in combining environmental covariates with biased random-walk models is that an animal's behavior is modeled as a dynamic variable that changes as a function of the animal's internal (e.g., physiological) state and/or the environment (Grünbaum 2000). Dynamic state variable models are especially useful for determining optimal behaviors in an evolutionary context, and a great deal of work in behavioral ecology has focused on these problems (Clark and Mangel 2000). State-space models have been used to fit population models with dynamic variables to time-series data (Zeng et al. 1998), and a similar approach could be used to fit dynamic foraging models (e.g., Grünbaum 2000) to movement-trajectory data. Although our example does not explicitly include an internal state variable one could be incorporated into the SSM, perhaps by temperature–movement relationship (β) to be governed by the turtle's level of satiety.

Our approach to fitting SSMs relies on Bayesian methods that are becoming widespread in the ecological literature (e.g., O'Hara et al. 2002, Sauer and Link 2002). There are a number of well-documented issues that must be considered when using Bayesian methods, such as specifying appropriate prior distributions, model sensitivity to prior distributions, and testing for convergence of the MCMC (Markov Chain Monte Carlo) algorithm (Carlin and Louis 1996, Punt and Hilborn 1997, Brooks and Roberts 1998) and we urge the reader to become familiar with these. Despite these issues, the Bayesian approach to state-space modeling, using MCMC sampling, is simpler to implement in comparison to numerical approaches (Tanizaki 2001). The task is simplified further with the advent of software such as WinBUGS (Spiegelhalter et al. 1996) that allows users to concentrate on appropriate model specification, selection of prior distributions, testing for convergence, and interpretation. We refer the interested reader to Meyer and Millar (1999) for a detailed discussion of the WinBUGS software and its application to state-space modeling.

Summary

The state-space modeling approach illustrated here allows researchers not only to build and fit empirically based movement models to data but also to develop and statistically compare theoretical models to empirical data. The ability to conduct both approaches under a common framework has the potential to advance our understanding of animal movement and how it contributes to many ecological processes. In addition, we have shown that SSMs can easily be formulated in a meta-analytic framework, thus allowing valuable trajectory data to be combined optimally so that higher-level processes may be inferred from individual paths. We envisage that future work using these methods will allow the development of widely applied and sophisticated movement models that, in turn, will contribute to a broader and more mechanistic understanding of animal movement processes.

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APPENDIX

The WinBUGS code required to fit the state-space model is presented in the single-pathway example. The appendix can be typed verbation into WinBUGS.

```
model rwalk; {
# Random Movement Dependent Upon the Environment

# Process Error (eta_t):
# eta_t ~ N(mean = 0, variance = (sigma*exp(−beta*
temp))^2)
# Vague prior for the precision.
isigma~dlnorm (0, .001)

# convert isigma to sigma (Note: Changes the precision to
the standard deviation)
sigma <−1/sqrt(isigma)

# beta describes how rapidly movement variance declines
with increasing temperature
# beta~N(mean = 0, variance = 1000): Vague prior for beta
beta~dnorm(0, .001)

# Observation error (epsilon_t):
# epsilon_t~N(mean = 0, variance = tau^2)
# Informative prior for the precision.
itau~dlnorm(−1.386294, 10)

# convert itau to tau (Note: Changes the precision to the
standard deviation)
tau<−1/sqrt(itau)

# Initializations:
# Y = True locations (alpha_t)
# Y1 = Observed locations (y_t)

# In order to get first true location equal to the observed
location (i.e., where released) we do the following:
Y[1,1]~dnorm(Y1[1,1] ,100000000)
Y[1,2]~dnorm(Y1[1,2] ,100000000)
```

```
isig.temp[1,1]<-0
isig.temp[1,2]<-0

# Interate transition equation
for (i in 2:N){ # cycles through locations
   for (j in 1:2){ # two dimensions (x & y directions)

      isig.temp [i,j]<-(isigma*pow(exp(-1*beta*temp
      [i-1]),-2))
      Y[i,j]~dnorm(Y[i-1,j] ,isig.temp[i,j])
   }
}

# Iterate measurement equation
for (i in 1:N){
   for (j in 1:2){
      Y1[i,j]~dnorm(Y[i,j],itau)
   }
   }
}
```

SUPPLEMENT 1

The S-Plus (6.0 for Windows [Insightful Corporation, Seattle, Washington, USA]) code used to generate simulated pathways for both examples together with a data set for the sea surface temperature (s_t) field is available in ESA's Electronic Data Archive: *Ecological Archives* E084-080-S1.

SUPPLEMENT 2

The WinBUGS code required to fit the meta-analytic state-space model (SSM) presented in the second example is available in ESA's Electronic Data Archive: *Ecological Archives* E084-080-S2.