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ROBUST STATE–SPACE MODELING OF ANIMAL MOVEMENT DATA

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Abstract. Remotely sensed tracking data collected on animal movement is vastly underutilized due to a lack of statistical tools for appropriate analysis. Features of such data that make analysis particularly challenging include the presence of estimation errors that are non-Gaussian and vary in time, observations that occur irregularly in time, and complexity in the underlying behavioral processes. We develop a state–space framework that simultaneously deals with these features and demonstrate our method by analyzing three seal pathway data sets. We show how known information regarding error distributions can be used to improve inference of the underlying process(es) and demonstrate that our framework provides a powerful and flexible method for fitting different behavioral models to tracking data.

Key words: Argos satellite telemetry; Bayesian; behavior; dispersal; foraging; migration; random walks; switching models; uncertainty; WinBUGS.

INTRODUCTION

The advent of miniaturized satellite transmitters has led to the collection of a plethora of animal movement data. These data are complex both in their underlying biological mechanisms and in their statistical properties. For example, given sufficient time and resolution, any pathway will represent multiple behavioral processes and hence estimation of movement parameters becomes nontrivial. Do we estimate single parameters for the whole pathway, ignoring important behavioral variability? How do we determine where one dominant behavior ends and another begins? Furthermore, many remote sensing devices such as Argos satellite tags (e.g., Austin et al. 2003) and archival tags (e.g., Teo et al. 2004) impose complex error structures on the data that must be dealt with appropriately so that important biological variability can be separated from artificial noise. These issues pose a serious challenge to ecologists studying movement behavior.

Jonsen et al. (2003) proposed a state–space framework for analysis of movement data using a simplistic random walk model fitted to simulated data. State–space models are time-series methods that allow unobserved states and biological parameters to be estimated from data observed with error. A useful feature of these methods is that two principle sources of uncertainty, namely estimation error arising from inaccurate observations and process variability arising from stochasticity in the movement process, can be accounted for separately. Here, we propose a more complex state–space framework that enables one to deal with

biological and statistical complexities associated with satellite tracking data. This is accomplished by formulating movement models appropriate for such data and by using robust statistical methods.

Our focus here is on remotely sensed data collected via the Argos satellite system but the general approach can be applied to other data types; e.g., radio, GPS, or archival telemetry. Argos data are categorized into six quality classes based generally on the number of uplinks from transmitter to satellite, the time between these uplinks, and the time since a previous location was estimated (Austin et al. 2003). The estimation errors associated with these quality classes vary through time and are strongly non-Gaussian. Furthermore, the Argos-derived locations are observed irregularly through time, which imposes an artificial perspective on the movement process(es). We utilize a statistically robust approach that accounts for these features of the data coupled with a correlated random walk model that is appropriate for location data and that can be generalized to handle complexity in the underlying behaviors (e.g., Morales et al. 2004). We illustrate our framework by analyzing three seal data sets that differ in biological and statistical complexity.

METHODS

Our data consist of locations observed through time. These locations may be complex in terms of the underlying biology, but the behavior that we wish to estimate does not derive from the locations in space, it derives from changes in the way animals move. We therefore need to develop a model that estimates unobservable states from locations observed with error, because these are the data typically available. Included in the model are underlying biological dynamics that

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describe changes in move direction and speed, the natural descriptors of animal movement.

Transition equation

The first component of the state–space model is the transition equation, which describes a Markov process where unobservable states evolve over regular time intervals given the previous state, process variability, and biological parameters (see Harvey [1993] for further details). The transition equation describes the dynamics of the movement process being modeled. We start by setting down a transition equation for a simple random walk:

$$\mathbf{x}_{t+1} = \mathbf{x}_t + \boldsymbol{\eta}_t \quad (1)$$

where \mathbf{x}_t is a two-dimensional vector of the unobserved states at time t , i.e., the true locations in terms of latitude and longitude, regularly spaced through time, and $\boldsymbol{\eta}_t$ is the process variability. Assuming zero correlation in the process variances for the two dimensions, Eq. 1 is the simplest type of movement model for location data.

A correlated random walk (CRW) model is a more natural way to think about animal movement because it describes many of the processes that we know to occur and is the basis for more complex behavior (e.g., Turchin 1998, Morales et al. 2004). The CRW for location data is based on the first difference of the locations. In other words, the random walk occurs on the differences in consecutive locations, i.e., the movements, and not on the locations themselves (as is the case in Eq. 1). We begin by writing

$$\mathbf{d}_t \sim \mathbf{T}\mathbf{d}_{t-1} + N_2(0, \boldsymbol{\Sigma}) \quad (2)$$

where \mathbf{d}_{t-1} is the difference between the locations \mathbf{x}_{t-1} and \mathbf{x}_{t-2} , and \mathbf{d}_t is the difference between the locations \mathbf{x}_t and \mathbf{x}_{t-1} . As noted earlier, \mathbf{x}_t is a coordinate vector, and hence \mathbf{d}_t is also a vector. \mathbf{T} is a transition matrix that describes the rotational component of the correlated random walk:

$$\mathbf{T}(\theta) = \begin{pmatrix} \cos \theta & -\sin \theta \\ \sin \theta & \cos \theta \end{pmatrix} \quad (3)$$

where θ is the mean turning angle. N_2 is a bivariate Gaussian distribution with mean 0 and the following covariance matrix:

$$\boldsymbol{\Sigma} = \begin{pmatrix} \sigma_{\text{lon}}^2 & \rho\sigma_{\text{lon}}\sigma_{\text{lat}} \\ \rho\sigma_{\text{lon}}\sigma_{\text{lat}} & \sigma_{\text{lat}}^2 \end{pmatrix} \quad (4)$$

where σ_{lon}^2 is the process variance in longitude, σ_{lat}^2 is the process variance in latitude, and ρ is the correlation coefficient. Eq. 2 describes a random walk that is autocorrelated in both direction and speed. In order to allow for lesser degrees of autocorrelation we add the term γ , with $\gamma = 0$ yielding a simple random walk and $0 < \gamma < 1$ yielding a random walk with correlation in both direction and move speed. We refer to the model

as a first-difference CRW (DCRW). The transition equation for this model is specified as

$$\mathbf{d}_t \sim \gamma\mathbf{T}\mathbf{d}_{t-1} + N_2(0, \boldsymbol{\Sigma}). \quad (5)$$

Complex behavior: switching models

The transition equation (Eq. 5) assumes that the movement pathway can be fully described by a single first difference CRW. However, it is easy to imagine pathways forming as the sum of several distinct behaviors. In order to capture this additional complexity, we can formulate an alternative to Eq. 5 where movement parameters are estimated for each distinct behavior. Suppose that we have two behaviors, where α_1 represents the probability of being in behavioral mode 1 at time t given the same behavioral mode at time $t - 1$, and α_2 represents the probability of being in behavioral mode 1 at time t given behavioral mode 2 at time $t - 1$. This formulation provides the basis of a switching model (DCRWS) where the movement parameters are then indexed by behavioral mode (Morales et al. 2004). Effectively, we have a transition equation for each behavioral mode. This approach can allow for further complexity simply by expanding the number of possible behavioral modes.

Measurement equation

The second component of the state–space formulation relates the unobserved states predicted by the transition equation to the observed data; consequently, it is termed the measurement equation. An implicit assumption here is that the observations are made over regular time intervals that correspond to the time step modeled in the transition equation (Harvey 1993). However, Argos data are observed irregularly through time, thus some sort of a priori data regularization to obtain equal time intervals is usually performed. This can be problematic when none or very few observations occur within a specified interval as one may not have enough information to properly estimate a location. Here we propose an alternative to a priori data regularization by allowing the irregularly observed data to be modeled directly within the state–space framework.

We let i be an index for locations (if any are observed) between time t and $t + 1$; i.e., $i = (0, 1, 2, \dots, n_t)$. We make the simplifying assumption that animals travel in a straight line between \mathbf{x}_{t-1} and \mathbf{x}_t . This poses no difficulty for state transitions with reasonably short time steps, relative to the resolution of the data, and allows us to interpolate a best estimate for each of the irregularly observed locations, $\mathbf{y}_{t,i}$:

$$\mathbf{y}_{t,i} = (1 - j_i)\mathbf{x}_{t-1} + j_i\mathbf{x}_t + \boldsymbol{\varepsilon}_t \quad (6)$$

where j_i is the proportion of the regular time interval between \mathbf{x}_{t-1} and \mathbf{x}_t at which the i th observation is made ($0 < j_i < 1$) and $\boldsymbol{\varepsilon}_t$ is a random variable representing the estimation error. Note that the j_i 's can be calculated from the data if the time of day is recorded with each

observed location. This formulation allows for the possibility of having multiple measurement equations for each transition equation. Note that for regular intervals where no observations exist, we set $i = 1$ and $j_i = 0.5$.

A particular challenge for analyzing many kinds of movement data is the need to deal with extreme observations in an objective fashion (e.g., Fig. 1A). In current analyses of movement data, extreme observations are typically removed a priori, for example, by filtering on a maximum rate of travel (e.g., McConnell et al. 1992, Austin et al. 2003). This may be reasonable for very large deviations. The problem, however, is what to do with less obvious deviations; how do we determine if they are erroneous? One approach to dealing with these deviations has been to throw out all the poor-quality data (classes B, A, and 0), but, for diving animals, this represents approximately 90% of the data (e.g., Vincent et al. 2002). Even more sophisticated filtering approaches result in data loss (Austin et al. 2003). These data can be tremendously expensive to collect, so utilizing state-space filtering methods are clearly advantageous because they do not remove “noisy” data, they account for the noise in the data.

We choose to use independent t distributions to model both the latitude and longitude components of estimation error in Eq. 6. That is, for estimation errors in latitude of quality class q ($q = 1, \dots, 6$) we let $\varepsilon_{t, \text{lat}, q} \sim t(0, \tau_{\text{lat}, q}, \nu_{\text{lat}, q})$, where $\tau_{\text{lat}, q}$ is the scale parameter and $\nu_{\text{lat}, q}$ is the df (and similarly for the longitude estimation error). The t distribution is robust in the sense that it has the effect of making extreme values less unlikely under the model, thereby minimizing their influence on parameter estimation. Note that the Gaussian distribution is a special case of the t distribution as $\nu \rightarrow \infty$. At this point, our robust state-space model for irregularly observed data is fully described by Eqs. 5 and 6.

Rather than estimate the parameters of each t distribution directly within the state-space model, we obtain independent estimates a priori by making use of published data derived from Argos-tagged gray seals, *Halichoerus grypus* (Fabricius 1791), that were caged at a known location (Vincent et al. 2002). A total of 425 locations for four caged seals were observed, four of which were extreme observations (i.e., >100 km from the true location; three in quality class 0 and one in quality class 2). See Vincent et al. (2002) for a complete description of the data. For the sets of maximum likelihood estimates (six quality classes in two directions), we produced plots of the likelihood surface with 95% confidence regions (see Appendix A, Fig. A1). The 95% confidence regions suggest that only the best location quality class, 3, is approximately Gaussian in both directions, all others are better modeled by a t distribution. Resulting point estimates (see Appendix A, Table A1) are subsequently treated as known parameters used within the state-space model. Given that not all Argos tags function equally (M. C. James, *per-*

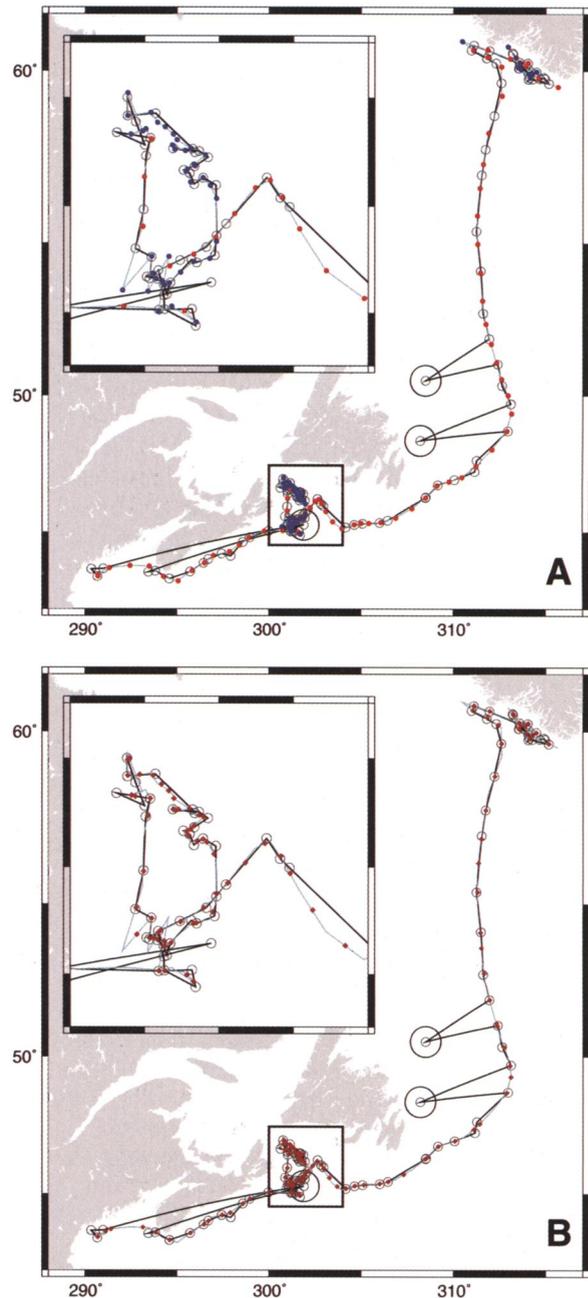


FIG. 1. (A) Plot of hooded seal track data, with observed locations as open circles and state estimates from the DCRWS (first-difference correlated random walk switching) model as red and blue filled circles. Red circles are state estimates associated with migrating behavior, and blue circles are state estimates associated with foraging behavior. The black line is the straight-line path between observations and the gray line is the straight-line path between state estimates. (B) Plot of hooded seal track data, with observed locations as open circles and interpolated locations as red diamonds. Inset panels show details of the foraging bout highlighted in the main panels. The black line is the straight-line path between observations and the gray line is the straight-line path between interpolated locations. Note the three extreme observations indicated by the large circles. The track (in both panels) originated off Maine, USA (bottom left), and terminated south of Greenland (top right).

sonal communication) and we only have independent data for one tag type (Vincent et al. 2002), we also include an additional scale parameter that we estimate directly within the model. This parameter serves to inflate or deflate (uniformly) the standard errors of the t distributions as determined by the data.

Data analysis

To illustrate the utility of our state–space framework, we consider three movement pathways, each posing distinct challenges for analysis. The first data set is of a juvenile male hooded seal, *Cystophora cristata* (Erleben 1777), (Fig. 1A) where a location was observed almost every day but at varying times of day. With the exception of three extreme values (Fig. 1, large circles), estimation error appears small but there appears to be more than one underlying behavioral process (e.g., foraging and migrating). The data are *available online*.⁴

The second and third data sets are of adult gray seals tagged off of Sable Island (seals 617 and 2986 from Austin et al. 2003; Fig. 2A is female 617, Fig. 2B is male 2986). Transmitters on these individuals were set to record locations every second day on which multiple locations were observed over varying time intervals. The male gray seal data set represents a case of numerous dubious observations, some clearly extreme and others less so (Fig. 2A, open circles). The female data set represents a combination of both complex behavior and numerous extreme observations (Fig. 2B).

We utilize the freely available software packages, WinBUGS and R, to fit the DCRW and DCRWS state–space models to the data (software *available online*).^{5,6} WinBUGS enables Bayesian analysis of statistical models via Markov Chain Monte Carlo estimation methods. Nonlinear and/or non-Gaussian state–space models utilize Bayes' rule as an updating algorithm (Jonsen et al. 2003), consequently WinBUGS is suitable for fitting state–space models. Because our analysis is Bayesian in nature, we specify priors for all unknown parameters. We use vague priors throughout, specifically, uniform priors for θ and α , a Wishart prior for Σ , and a Beta prior for γ . We note here that the current functionality of WinBUGS requires $\nu \geq 2$ and as a consequence all estimates of $\nu < 2$ were constrained to be 2. This constraint will have little effect because, in the relevant cases, a t distribution with $\nu = 2$ is still a marked improvement over the Gaussian distribution. WinBUGS code for both models including details of these priors are included in the Supplement. Upon fitting the state–space models, we obtain parameter estimates, estimates of the unobserved states, and interpolated estimates of the observed locations. For ease of presentation, we display interpolated location

⁴ (<http://whale.wheelock.edu/whalenet-stuff/StopHoods04/>)

⁵ (<http://www.mrs-bsu.cam.ac.uk/bugs/winbugs/contents.shtml>)

⁶ (<http://www.R-project.org/>)

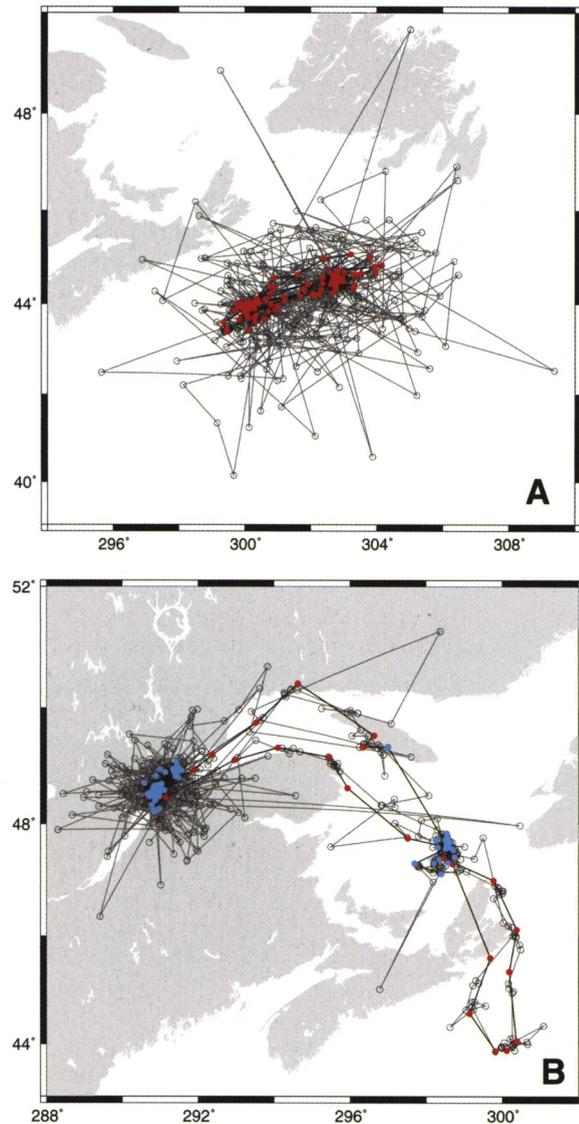


FIG. 2. (A) Plot of gray seal 617 track data, with state estimates from the DCRW model overlaid in red. (B) Plot of gray seal 2986 track data, with state estimates from the DCRWS model overlaid in red and blue. Red circles are state estimates associated with migrating behavior, and blue circles are state estimates associated with foraging behavior. Both seals' tracks originated and terminated at Sable Island, Nova Scotia, Canada.

estimates for the hooded seal example only (Fig. 1B). Using the hooded seal data set, we also present a comparison of movement parameters derived from the state estimates with those obtained from the original data after regularization (Appendix B).

RESULTS

Both models deal similarly with the extreme observations highlighted in Figs. 1A and 2 by producing reasonable state estimates. The three extreme observations highlighted in Fig. 1A are clearly downweight-

TABLE 1. Posterior medians and 95% credible limits for parameters estimated from the DCRWS (first difference correlated random walk switching) model.

| Parameter | Data set | | | | | | | | |
|----------------|-------------|-------|-------|---------------|-------|-------|----------------|-------|-------|
| | Hooded seal | | | Gray seal 617 | | | Gray seal 2986 | | |
| | 0.025 | 0.5 | 0.975 | 0.025 | 0.5 | 0.975 | 0.025 | 0.5 | 0.975 |
| θ_1 | -0.07 | 0.04 | 0.16 | -3.11 | -1.81 | 3.13 | -0.33 | -0.07 | 0.19 |
| θ_2 | -3.13 | -2.70 | 3.13 | -3.11 | -1.76 | 3.12 | -3.10 | 1.92 | 3.09 |
| γ_1 | 0.71 | 0.83 | 0.94 | 0.06 | 0.52 | 0.98 | 0.50 | 0.76 | 0.99 |
| γ_2 | 0.07 | 0.62 | 0.94 | 0.01 | 0.34 | 0.97 | 0.01 | 0.15 | 0.52 |
| α_1 | 0.45 | 0.85 | 0.96 | 0.05 | 0.43 | 0.91 | 0.04 | 0.23 | 0.56 |
| α_2 | 0.03 | 0.09 | 0.20 | 0.07 | 0.59 | 0.96 | 0.80 | 0.93 | 0.98 |
| σ_{lon} | 0.09 | 0.13 | 0.20 | 0.34 | 0.49 | 0.71 | 0.19 | 0.26 | 0.35 |
| σ_{lat} | 0.04 | 0.06 | 0.09 | 0.07 | 0.09 | 0.14 | 0.11 | 0.15 | 0.20 |

Notes: Column heads indicate quantiles: 0.5 (median) and 0.025, 0.975 (95% credible limits). Subscripts 1 and 2 index the migrating and foraging behavioral modes, respectively. Process variability was assumed to be constant between the behavioral modes but differed between latitude and longitude. Mean turning angle (θ) is measured in radians; σ_{lon} and σ_{lat} represent process variance measured in units of degrees longitude and latitude, respectively; γ determines the degree of correlation in both move speed and direction; and α_1 is the probability of being in behavioral mode 1 at time t , given the same behavioral mode at time $t - 1$; α_2 is the probability of being in behavioral mode 1 at time t , given behavioral mode 2 at time $t - 1$.

ed and more subtle filtering is also evident wherever the interpolated locations are displaced from the observed locations (Fig. 1B). Much more dramatic filtering is evident for the gray seal data (Fig. 2), where a substantial portion of the observations are clearly erroneous.

Comparisons of DCRWS estimates for the two behavioral modes (Table 1) suggest the DCRWS model is a better fit to both the hooded seal and gray seal 2986 data but not to gray seal 617. The 95% credible limits of $\hat{\gamma}_1$ and $\hat{\gamma}_2$ for gray seal 2986 show minimal overlap and those for $\hat{\theta}_1$ and $\hat{\theta}_2$ suggest substantially different concentrations about the median (Table 1). Similarly, for the hooded seal data, the $\hat{\theta}$'s indicate forward movement with only small turns when migrating and frequent course reversals when foraging (Table 1). Although the 95% limits of the $\hat{\gamma}$'s for the hooded seal do overlap substantially, the pattern does suggest more persistent movements when migrating than when foraging. There appears to be insufficient data on foraging movements to reliably estimate γ_2 for the hooded seal. For gray seal 617, both the $\hat{\gamma}$'s and $\hat{\theta}$'s overlap substantially, suggesting that the DCRW model is a better fit to these data (Table 1). The presence of distinctly different behaviors is quite apparent in Figs. 1 and 2B, but much less so in Fig. 2A.

The process variance estimates indicate that there is considerably more variation in east–west movements than in north–south movements; compare σ_{lon} vs. σ_{lat} estimates (Table 1). For the hooded seal, this is substantiated by the fact that there are relatively uniform step lengths as the seal traveled north (approximately 50° and 60° N) and more variable step lengths as it traveled east (approximately 70° to 50° W) and foraged along the Greenland coast (60° N; Fig. 1B). The dif-

ferences are even more dramatic for gray seal 617 (Table 1), although they are difficult to visualize (Fig. 2A).

For both the hooded seal and gray seal 2986, movement is highly persistent in direction and speed while migrating (compare γ 's, Table 1) and course reversals and changes in speed are more prevalent while foraging (compare θ 's and γ 's, Table 1). Estimates of the switching rates between behaviors reveal a high probability of remaining in either the migrating or foraging mode (α_1 and $1 - \alpha_2$, respectively, Table 1) for the hooded seal. For gray seal 2986, there is an intermediate probability of remaining in the migrating mode (α_1 , Table 1) and a high probability of remaining in the foraging mode ($1 - \alpha_2$, Table 1).

DISCUSSION

The general framework developed here emphasizes the flexibility and power of a state–space approach. Although we have illustrated our approach using Argos satellite data, the methods are applicable for any remotely sensed movement data, including those obtained via GPS, radio, and archival tags. Indeed, issues of robustness and/or irregularly sampled data are common (although not equivalent) among these data types and must be dealt with in an objective, statistically sound manner. We suggest that, wherever possible, researchers conduct and include in their publications the results of experiments that quantify estimation errors for their tracking devices under conditions typically encountered in the field.

Our state–space framework has several useful features. First, when ancillary data are available, the state–space framework can explicitly model the known error distribution(s) of the locations via the measurement equation. Here, we chose to deal with errors in Argos

locations by estimating parameters of the error distributions from an independently collected data set and subsequently holding these parameters fixed in the state-space model. We find that the t distribution is more appropriate than the Gaussian for modeling these errors. In a Bayesian context, even when quantitative information regarding error distributions do not exist, e.g., radio telemetry data, prior distribution(s) can be constructed to reflect qualitative knowledge of conditions that may affect estimation errors. Second, information regarding an animal's position is not lost when it is obscured by substantial estimation error. Ad-hoc filters necessarily remove such locations potentially leading to substantial information loss (see Austin et al. 2003, for an evaluation of some ad-hoc filters). In addition, ad-hoc filters do not deal with estimation error present in locations that pass the filter, whereas all locations are filtered in the state-space framework and this leads to more reliable parameter estimation. Third, credible limits can be obtained for each state estimate, thereby providing an explicit quantification of uncertainty. This is particularly useful when overlays of filtered pathways on spatial environmental data are desired (e.g., Luschi et al. 2003). Finally, our framework is the basis for detailed analyses such as inferring switches between behavioral states (Morales et al. 2004) and more general estimation of behavioral parameters (Jonsen et al. 2003).

When dealing with location data, we believe that specifying a random walk on the differences between locations is a more sensible approach for modeling animal movement from location data than simply a random walk on the locations themselves. This makes intuitive sense because the differences in location represent much of the behavior in which ecologists are interested, i.e., speed of travel and direction. We show, via the switching (DCRWS) model, that the first difference CRW model can be generalized to deal with more complex types of movement. Switching models are perhaps most useful for quantifying movements over long time periods or in heterogeneous environments where the data likely represent a complex composite of two or more distinct behaviors (Morales et al. 2004). In most cases, visualization of the movement pathways may be adequate to confirm the presence of multiple behaviors but estimation provides not only movement parameters for each of the behavioral components but also an objective method for apportioning the data among these components. When desired, this approach will obviously facilitate more detailed analyses on the individual behavioral components.

Unlike Morales et al. (2004), who also fit switching models to movement data (by first calculating turning angles and movement speeds), we do not assume that estimation error is negligible. We have shown here that accounting for estimation error requires robust, flexible methods that can be achieved in a state-space framework. In order to take the approach of Morales et al.

(2004), who calculated turning angles and movement speeds from GPS location data, one would necessarily need to first decompose the errors in location before one could directly model turning angles and movement speeds. Using our state-space framework, such a decomposition is unnecessary because we can derive turning angle and movement rate distributions directly from the state estimates.

CONCLUSION

Our proposed state-space framework represents a significant improvement, in terms of removing noisy data, over current traditional, non-likelihood-based methods. However, the true value of the state-space approach lies in its ability to directly model movement behavior in a flexible and reliable manner with robust methods for dealing with the error structure of the data. Future work will need to focus on (1) improving our knowledge of Argos error distributions; (2) incorporating biological and environmental constraints on movements directly into the DCRW models; and (3) modeling the effect of internal states and environmental covariates on movement behavior. Ultimately, we wish to utilize our framework to link movement data to quantitative models of animal movement behavior, such as home range and territorial dynamics, foraging behavior, and migration (e.g., Grünbaum 1998, Clark and Mangel 2000, Morales et al. 2004).

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APPENDIX A

Likelihood surface plots and ML point estimates of Argos error distribution parameters are available in ESA's Electronic Data Archive: *Ecological Archives* E086-156-A1.

APPENDIX B

A description of the data regularization procedure and a comparison of movement parameters are available in ESA's Electronic Data Archive: *Ecological Archives* E086-156-A2.

SUPPLEMENT

The code and sample data for state-space analysis of Argos movement data are available in ESA's Electronic Data Archive: *Ecological Archives* E086-156-S1.