Guest Editor's Introduction to the Special Issue on "Animal Movement Modeling"

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In this introduction, we provide a brief overview to statistical models for animal trajectories and then summarize the set of invited articles that comprise the issue.

INTRODUCTION

The study of individual animal trajectories is ancient, with a written record dating back more than 2000 years (Nussbaum 1978). The mathematics of trajectories also have a long history (Turchin 1988), but rigorous statistical methods development for animal trajectory data (i.e., telemetry data) only dates back approximately 50 years (e.g., Dunn and Gipson 1977). In more recent times, the technology to collect a massive amount and variety of telemetry data has increased dramatically, leading to unprecedented information on the spatial ecology of animal populations (Cagnacci et al. 2010; Kays et al. 2015). The sheer availability, variety, and volume of telemetry data sets present golden opportunities for the development of new statistical methods that can provide deeper, more meaningful inference about animal ecology. However, the volume, veracity, and velocity of the data coupled with the complexity of the trajectory processes and underlying animal behaviors themselves present formidable challenges for statisticians.

Whereas there are several examples of recent compilations pertaining to animal movement, including a new journal devoted to the subject, this special issue on Animal Movement Modeling is timely in that it captures an important subset of the new and innovative developments in statistical methodology and practice associated with the analysis of animal telemetry data. This special issue contains nine articles aimed at topics clustered naturally

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into two main categories: continuous-time models and discrete-time models. Most telemetry data associated with animal tracking involve a spatial component (geographic position) and a temporal component (temporal position). Associated statistical models for telemetry data usually are formulated in discrete time or continuous time in the way the temporal dynamics are expressed (McClintock et al. 2014). A third category that could be associated with either time formulation is the class of models for point processes (e.g., Johnson et al. 2013), but these methods (e.g., resource selection and step selection models) are not explicitly represented in this special issue. For more details on the use of point process models for animal telemetry data, see Hooten et al. (2017) and Hooten and Johnson (2017a) for overviews, and Johnson et al. (2013) and Brost et al. (2015) for specific examples.

This special issue contains a variety of approaches that address important issues within each type of time formulation, including multi-scale temporal processes, interactions among conspecifics, computational efficiency improvements using multistage modeling procedures, barriers and constraints to movement, intractable movement model likelihoods, and movement in patchy landscapes. The articles in this special issue involve applications to a diverse set of organisms including insects, mammals (both marine and terrestrial), reptiles, and fish.

In what follows, we summarize each article in this special issue in the context of either discrete-time or continuous-time formulations. We also provide background on the prior research in this area and highlight the novel contributions of the special issue articles.

DISCRETE-TIME MODELS

Statistical models for temporally referenced data are most commonly formulated in discrete time. These include time series models with autoregressive and moving average formulations. The simplest discrete-time model one might envision for animal telemetry data is a first-order vector random walk model $\mathbf{s}_t = \mathbf{s}_{t-1} + \boldsymbol{\varepsilon}_t$, where $\mathbf{s}_t$ represents the animal position at time t and $\boldsymbol{\varepsilon}_t$ are white noise vectors with variance σ^2. Of course, such a model relies on independence and nonstationarity assumptions as well as regularly spaced data that are collected at a resolution that is well modeled by the random walk. This simple time series model is surprisingly easy to fit to data, but does not account for measurement error and is purely phenomenological. It may also contain dynamics that are not smooth enough to characterize real animal trajectories. Jonsen et al. (2005) proposed to use a generalized version of the random walk model for the velocity process (i.e., the first-order difference of position in time) which provided more generality and smoothness to the resulting trajectories, better accommodating real data. This new model was couched in a hierarchical statistical modeling framework and therefore better able to explicitly incorporate a measurement error process.

Taking a different approach, Morales et al. (2004) proposed a mixture model for telemetry data that was based on a transformation of the velocity data to polar coordinates—effectively the animal's step lengths and turning angles—and classified the data into a set of "states" depending on their characteristics. This approach has persisted in the literature, and the general concept of state-switching models still serves as a dominant theme for animal movement modeling approaches (e.g., Langrock et al. 2012; McClintock et al. 2012; Patterson et al.

2017). This special issue contains five articles focused on methods and practical guidance associated with discrete-time animal movement models. These articles provide a wide range of novel statistical contributions that are directed at solving long-standing questions pertaining to animal movement modeling.

The issue of scale has been a long-standing concern in the study of animal space use. Johnson (1980) is often credited with developing a framework for thinking about spatial scale in studies of space use and resource selection, and others have tackled similar scale issues in the temporal domain (e.g., Hooten et al. 2014). However, temporal multi-scale specifications in a state-switching hidden Markov model framework have not been addressed, until now. In this special issue, Leos-Barajas et al. (2017) tackle the problem by using multiple latent processes operating at different time scales within an HMM framework. Leos-Barajas et al. (2017) formulate an HMM using a nested structure where the data depend on a fine-scale hidden Markov process, which in turn depends on a coarse-scale process. In this way, they are capable of capturing patterns in animal behavior that manifest themselves at multiple scales (e.g., migration as long-term behavioral strategy versus foraging or resting behavior as short-term behaviors). They apply their models to study harbor porpoises and garter snakes and their shifts in behavior over time.

Discrete-time movement models from the class of HMM are proliferating in the literature, due at least in part to the availability of statistical software to fit the models to data and their intuitive nature (Michelot et al. 2016). However, discrete-time formulations have an associated set of challenges. Among them is the fact that telemetry data are often irregularly spaced in time and often subject to measurement error. While these features of the data can be accommodated in hierarchical implementations of HMMs, they add to the computational requirements to fit the models to larger datasets. Similar challenges have been addressed in continuous-time models for animal movement using imputation approaches (Hooten et al. 2010; Hanks et al. 2015; Scharf et al. 2017). In this special issue, McClintock (2017) assesses the performance of multistage model fitting procedures using data imputation approaches within HMMs. Using interpolated tracks resulting from an initial model fit to the data and then a second-stage HMM that integrates over the uncertainty in the tracks, McClintock (2017) found it naturally solves the irregular time issue for the data and performs well for parameter estimation. He does note that, in certain pathological situations with large measurement error and low temporal resolution in the data, biases can arise in parameter estimation.

A common issue with clustering models in general, and state-switching animal movement models in particular, is that the number of clusters (or states) can be notoriously difficult to estimate. Morales et al. (2004) used DIC to select among the relatively small set of parsimonious candidate models they considered, but in more recent studies, it became apparent that traditional model selection procedures have tended to select models that are too complex (i.e., involve too many states; see Langrock et al. 2015; DeRuiter et al. 2017; Li and Bolker 2017). In this special issue, Pohle et al. (2017) perform a thorough inspection of model selection issues arising in state-switching models, in particular HMMs. They demonstrate why traditional model selection criteria tend to favor state-switching models with overly complex state architectures and provide step-by-step practical guidance for selecting a suitable number of states. They illustrate their procedure using telemetry data from muskox in Greenland involving several different behaviors.

Agent-based models (ABMs) have been used to mimic a variety of ecological processes and have been applied in movement analyses to test null hypotheses about animal behavior and space use. However, only recently have ABMs appeared in the statistical animal movement modeling literature, both in the individual-level (Hooten et al. 2010) and population-level (Hooten and Wikle 2010) contexts. In each previous case, however, the model formulations were tractable enough that the likelihood could be calculated analytically. However, it is relatively easy to construct simulation-based stochastic ABMs that result in intractable likelihoods. In such cases, typical parametric Bayesian methods are difficult or impossible to apply. In this issue, McDermott and Wikle (2017) specify an ABM for multiple individuals that mechanistically involves interactions among several trajectories. They develop an approximate Bayesian computation (ABC) approach to fit the ABM to observational data on a set of guppies moving in an experimental setting.

Several new developments in collective movement have appeared in recent years (e.g., Scharf et al. 2016), but few have used explicit potential function specifications (Russell et al. 2016). Potential functions have been traditionally used in continuous-time stochastic differential equation (SDE) models (Brillinger 2010). In this issue, Russell et al. (2017) describe a collective movement model based on potential functions that is motivated by an SDE, but implemented in discrete time. They couple individuals together in their model using dependent latent behavioral states and apply their models to study the movement of carpenter ants in an experimental setting where individuals can leave or stay in the study area during the observational period. In this case, the data are collected by observing the positions of individual ants over time.

CONTINUOUS-TIME MODELS

Traditionally, continuous-time movement models are similar to discrete-time formulations in that they involve parameterizations of the position process directly, but with infinitely many small steps. Integrating the sequence of steps results in a stochastic process with long-range structure, and formal specifications of such processes are referred to as Wiener processes or Brownian motion (Hooten et al. 2017). Johnson et al. (2008) imposed additional smoothness on the resulting stochastic processes by letting a stationary form of Brownian motion (i.e., the Ornstein–Uhlenbeck process) describe the velocity process and then integrating it a second time to result in the position process. This idea to use an integrated form of Brownian motion inspired a class of generalized models using basis function specifications to yield different amounts and types of smoothness in the process to model more realistic animal movement trajectories (Hooten and Johnson 2017b). In this special issue, there are four articles focused on modeling trajectories in continuous time.

Brillinger (2010) described a suite of approaches to incorporate spatial covariates in continuous-time models using potential surfaces that control the rate and direction of the trajectory on the surface. Potential surface models can be challenging to implement because they involve a gradient of the potential function that is not analytically tractable for realistically complex model specifications. Thus, in this special issue, Scharf et al. (2017) examined imputation approaches that involve multistage model fitting procedures similar to those explored by McClintock (2017; also in this special issue) and previously used in continuous-time discrete-space models (Hooten et al. 2010; Hanks et al. 2015). Scharf et al. (2017) applied what they refer to as "process imputation" to fit potential function models using a two-stage procedure. In the first stage, they interpolated the data (with uncertainty) using a simplified continuous-time movement model like the functional movement model of Buderman et al. (2016) and then integrated over the posterior predictive track distribution when fitting the potential function model in the second stage of the procedure. They found that imputation approaches account for complicated measurement error processes and work remarkably well for recovering interpretable model parameters, but appear to show bias for other nuisance model parameters that are not usually used for inference. They demonstrate their approach using telemetry data from northern fur seals near Alaska, USA.

Few true barriers completely impede the movement of airborne animals like birds. However, terrestrial and aquatic animals are often constrained to land and waterscapes. In such cases, it can be critical to formally account for barriers to movement when analyzing telemetry data to make inference on space use and resource selection. For example, in a study of harbor seals in Alaska, USA, Brost et al. (2015) found dramatic differences in inference when properly accounting for barriers to movement using a spatio-temporal point process model. In continuous-time stochastic process models, some approaches to account for barriers to movement have been suggested, but few, if any, are used in practice. In this special issue, Hanks et al. (2017) investigated approaches to account for barriers to movement using reflected SDEs. In reflected SDEs, Brownian motion is reflected when it encounters a boundary and the reflection process is specified mathematically in the model. Hanks et al. (2017) examined the performance of their model in simulation and demonstrate it using Steller sea lion telemetry data in a marine environment with many boundaries in the form of a complex shoreline and several islands that impede the movement of the sea lions.

While state-switching models have become popular in discrete-time movement analyses, continuous-time models have mostly focused on track interpolation and the influence of spatial covariates on movement via potential functions. Because true animal trajectories are continuous in time and individuals may switch behaviors among a finite set of potential states (e.g., resting, foraging, migrating), there is a need for continuous-time formulations of state-switching models. Parton and Blackwell (2017) explored such models in this special issue. Specifically, they developed models for steps and turns, in the same spirit as Morales et al. (2004) and McClintock et al. (2012), but using continuous-time stochastic process specifications. They used data augmentation approaches to fit the models and apply them to the movement trajectories of elk based on the telemetry data analyzed by Morales et al. (2004) and show how their inference is similar but relevant for the continuous-time domain.

So far, in this special issue, all of the articles have focused on the continuous-space setting. By contrast, Morales et al. (2017) are interested in transitions among patches of habitat in a discrete-space domain. While previous statistical models for discrete-space transitions have appeared in the literature (e.g., Hooten et al. 2010; Hanks et al. 2015), they have been formulated for a regular grid of pixels in which the individual animal resides. In this special issue, Morales et al. (2017) constructed a transition model that provides inference on patch transitions in a landscape with irregularly sized and shaped patches. Their model also accounts for memory and is based on earlier theoretical work by Ovaskainen and Cornell (2003). They applied their model to understand the movement of domestic sheep in experimental paddocks.

CONCLUSION

In summary, this special issue is comprised of a variety of modern approaches for statistically modeling animal movement processes. The field of animal movement modeling is evolving rapidly, and new forms of telemetry data require new statistical methods. Thus, it is a golden era for statisticians to make useful contributions to the field by finding ways to obtain new types of inference based on telemetry data and efficient ways to analyze massive tracking data sets. The future of animal movement modeling will continue to see a need for advancements in models for multiple individuals (Langrock et al. 2014; Hooten et al. 2016) while incorporating measurement error, environmental covariates, and real-time tracking data. Also, the analyses of auxiliary telemetry data such as accelerometer data that can provide deeper insights into animal behavior and health are still nascent (Leos-Barajas et al. 2017), and reconciling these data with more traditional spatially referenced tracking data will be key for tying animal movement models to management and conservation decision making.

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REFERENCES

Brillinger, D.R. (2010), Modeling spatial trajectories. In Gelfand, A. E., P. J. Diggle, M. Fuentes, and P. Guttorp, editors, Handbook of Spatial Statistics, chapter 26, pages 463-475. Chapman & Hall/CRC, Boca Raton, Florida, USA.

Brost, B.M., M.B. Hooten, E.M. Hanks, and R.J. Small. (2015), Animal movement constraints improve resource selection inference in the presence of telemetry error. Ecology, 96:2590-2597.

Buderman, F.E., M.B. Hooten, J.S. Ivan, and T.M. Shenk. (2016), A functional model for characterizing long distance movement behavior. Methods in Ecology and Evolution, 7:264-273.

Cagnacci, F., L. Boitani, R.A. Powell, and M.S. Boyce. (2010), Animal ecology meetings GPS-based radiotelemetry: A perfect storm of opportunities and challenges. Philosophical Transactions of the Royal Society of London B: Biological Sciences, 365:2157-2162.

DeRuiter, S.L., R. Langrock, T. Skirbutas, J.A. Goldbogen, J. Calambokidis, A.S. Friedlaender, and B.L. Southall. (2017), A multivariate mixed hidden Markov model for blue whale behaviour and responses to sound exposure. Annals of Applied Statistics, 11:362-392.

Dunn, J.E. and P.S. Gipson. (1977), Analysis of radio-telemetry data in studies of home range. Biometrics, 33:85-101.

Hanks, E.M., M.B. Hooten, and M. Alldredge. (2015), Continuous-time discrete-space models for animal movement. Annals of Applied Statistics, 9:145-165.

Hanks, E.M, D.S. Johnson, and M.B. Hooten. (2017), Reflected stochastic differential equation models for constrained animal movement. Journal of Agricultural, Biological and Environmental Statistics, doi:10.1007/s13253-017-0291-8.

Hooten, M.B., D.S. Johnson, E.M. Hanks, and J.H. Lowry. (2010), Agent-based inference for animal movement and selection. Journal of Agricultural, Biological and Environmental Statistics, 15:523-538.

Hooten, M.B., E.M. Hanks, D.S. Johnson, and M.W. Alldredge. (2014), Temporal variation and scale in movement-based resource selection functions. Statistical Methodology, 17:82-98.

Hooten, M.B., F.E. Buderman, B.M. Brost, E.M. Hanks, and J.S. Ivan. (2016), Hierarchical animal movement models for population-level inference. Environmetrics, 27:322-333.

Hooten, M.B. and D.S. Johnson. (2017b), Basis function models for animal movement. Journal of the American Statistical Association, 112:578-589.

Hooten, M.B., D.S. Johnson, B.T. McClintock, and J.M. Morales. (2017), Animal Movement: Statistical Models for Telemetry Data. Chapman and Hall/CRC.

Hooten, M.B. and D.S. Johnson. (2017a), Modeling Animal Movement. Gelfand, A.E., M. Fuentes, and J.A. Hoeting (eds). In Handbook of Environmental and Ecological Statistics. Chapman and Hall/CRC.

Hooten, M.B. and C.K. Wikle (2010), Statistical agent-based models for discrete spatio-temporal systems. Journal of the American Statistical Association, 105:236-248.

Johnson, D.H. (1980), The comparison of usage and availability measurements for evaluating resource preference. Ecology, 61:65-71.

Johnson D.S., J. London, M. Lea, and J. Durban. (2008), Continuous-time correlated random walk model for animal telemetry data. Ecology, 89:1208-1215.

Johnson, D.S., M.B. Hooten, and C.E. Kuhn. (2013), Estimating animal resource selection from telemetry data using point process models. Journal of Animal Ecology, 82:1155-1164.

Jonsen, I., J. Flemming, and R. Myers. (2005), Robust state-space modeling of animal movement data. Ecology, 45:589-598.

Kays, R., M. Crofoot, W. Jetz, and M. Wikelski. (2015), Terrestrial animal tracking as an eye on life and planet. Science, 384(6240):aaa2478.

Langrock, R., J.G.C. Hopcraft, P.G. Blackwell, V. Goodall, R. King, M. Niu, T.A. Patterson, M.W. Pedersen, A. Skarin, and R.S. Schick. (2014), Modelling group dynamic animal movement. Methods in Ecology and Evolution, 5:190-199.

Langrock, R., T. Kneib, A. Sohn, and S.L. DeRuiter. (2015), Nonparametric inference in hidden Markov models using P-splines. Biometrics, 71:520-528.

Langrock, R., R. King, J. Matthiopoulos, L. Thomas, D. Fortin, and J. Morales. (2012), Flexible and practical modeling of animal telemetry data: Hidden Markov models and extensions. Ecology, 93:2336-2342.

Leos-Barajas, V., E.J. Gangloff, T. Adam, R. Langrock, J.M. Morales, F.M. van Beest, and J. Nabe-Nielsen. (2017a), Multi-scale modeling of animal movement and general behavior data using hidden Markov models with hierarchical structures. Journal of Agricultural, Biological and Environmental Statistics, doi:10.1007/s13253-017-0282-9.

Leos-Barajas, V., T. Photopoulou, R. Langrock, T.A. Patterson, Y. Watanabe, M. Murgatroyd, and Y.P. Papastamatiou. (2017b), Analysis of animal accelerometer data using hidden Markov models. Methods in Ecology and Evolution, 8:161-173.

Li, M. and B. Bolker. (2017), Incorporating periodic variability in hidden Markov models for animal movement. Movement Ecology, 5:1.

McClintock, B.T. (2017), Incorporating telemetry error into hidden Markov models of animal movement using multiple imputation. Journal of Agricultural, Biological and Environmental Statistics, doi:10.1007/s13253-017-0285-6.

McClintock, B.T., D.S. Johnson, M.B. Hooten, J.M. Ver Hoef, and J.M. Morales. (2014), When to be discrete: the importance of time formulation in understanding animal movement. Movement Ecology, 2:21.

McClintock, B.T., R. King, L. Thomas, J. Matthiopoulos, B. McConnell, and J. Morales. (2012), A general discrete-time modeling framework for animal movement using multistate random walks. Ecological Monographs, 82:335-349.

McDermott, P., and C.K. Wikle. (2017), Hierarchical nonlinear spatio-temporal particle models for animal movement. Journal of Agricultural, Biological and Environmental Statistics, doi:10.1007/s13253-017-0289-2.

Michelot, T., R. Langrock, and T.A. Patterson. (2016), moveHMM: An R package for analysing animal movement data using hidden Markov models. Methods in Ecology and Evolution, 7:1308-1315.

Morales, J.M., D. Haydon, J. Friar, K. Holsinger, and J. Fryxell. (2004), Extracting more out of relocation data: Building movement models as mixtures of random walks. Ecology, 85:2436-2445.

Morales, J., A. di Virgilio, M. Delgado, and O. Ovaskainen. (2017), A general approach to model movement in (highly) fragmented patch networks. Journal of Agricultural, Biological and Environmental Statistics, doi:10.1007/s13253-017-0298-1.

Nussbaum, M. (1978), Aristotle's De Motu Animalium: Text with Translation, Commentary, and Interpretive Essays. Princeton University Press, Princeton, New Jersey, USA.

Ovaskainen, O. and S.J. Cornell. (2003), Biased movement at a boundary and conditional occupancy times for diffusion processes. Journal of Applied Probability, 40:557-580.

Parton, A., and P.G. Blackwell. (2017), Bayesian inference for continuous time animal movement based on steps and turns. Journal of Agricultural, Biological and Environmental Statistics, doi:10.1007/s13253-017-0286-5.

Patterson, T.A., A. Parton, R. Langrock, P.G. Blackwell, L. Thomas, and R. King. (2017), Statistical modelling of individual animal movement: an overview of key methods and a discussion of practical challenges. Advances in Statistical Analysis, doi:10.1007/s10182-017-0302-7.

Pohle, J., R. Langrock, F.M. van Beest, and N.M. Schmidt. (2017), Selecting the number of states in hidden Markov models: pragmatic solutions illustrated using animal movement. Journal of Agricultural, Biological and Environmental Statistics, doi:10.1007/s13253-017-0283-8.

Russell, J.C., E.M. Hanks, M. Haran, and D.P. Hughes. (2016), A spatially-varying stochastic differential equation model for animal movement. arXiv:1603.07630.

Russell, J., E.M. Hanks, and D. Hughes. (2017), Modeling collective animal movement through interactions in behavioral states. Journal of Agricultural, Biological and Environmental Statistics, doi:10.1007/s13253-017-0296-3.

Scharf, H.R., M.B. Hooten, B.K. Fosdick, D.S. Johnson, J.M. London, and J.W. Durban. (2016), Dynamic social networks based on movement. Annals of Applied Statistics, 10:2182-2202.

Scharf, H., M.B. Hooten, and D.S. Johnson. (2017), Evaluating process imputation approaches in continuous-time animal movement models. Journal of Agricultural, Biological and Environmental Statistics, doi:10.1007/s13253-017-0294-5.

Turchin, P. (1998), Quantitative Analysis of Movement. Sinauer Associates, Inc. Publishers. Sunderland, Massachusetts, USA.