REVIEW AND SYNTHESIS

Understanding movement data and movement processes: current and emerging directions

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Abstract

Animal movement has been the focus on much theoretical and empirical work in ecology over the last 25 years. By studying the causes and consequences of individual movement, ecologists have gained greater insight into the behavior of individuals and the spatial dynamics of populations at increasingly higher levels of organization. In particular, ecologists have focused on the interaction between individuals and their environment in an effort to understand future impacts from habitat loss and climate change. Tools to examine this interaction have included: fractal analysis, first passage time, Lévy flights, multi-behavioral analysis, hidden markov models, and state-space models. Concurrent with the development of movement models has been an increase in the sophistication and availability of hierarchical bayesian models. In this review we bring these two threads together by using hierarchical structures as a framework for reviewing individual models. We synthesize emerging themes in movement ecology, and propose a new hierarchical model for animal movement that builds on these emerging themes. This model moves away from traditional random walks, and instead focuses inference on how moving animals with complex behavior interact with their landscape and make choices about its suitability.

INTRODUCTION AND MOTIVATION

Animal movement has been the focus of much theoretical and empirical work in ecology over the last 25 years in part because the movement of individuals provides a spatio-temporal bridge between the individual and the population (Turchin 1998). By studying the causes and consequences of individual movement, ecologists have gained greater insight into spatial dynamics at increasingly higher levels of organization, i.e., patches, populations, communities, and meta-communities (Bowler & Benton 2005). Landscape ecologists have focused on the interaction between individuals and their environment in an effort to understand future impacts from habitat loss and climate change (Bowler & Benton 2005). Wildlife telemetry and GIS have become important conservation and management tools. Researchers in these fields collect spatial data on movement and on the environment to explore how the environment controls the movement behavior of animals; the precise mechanism of this complex interaction is the object of inference. From these different perspectives three issues emerge: (1) developing models for realistic movement behavior (Lima & Zollner 1996; Morales & Ellner 2002; Morales *et al.* 2004; Jonsen *et al.* 2005); (2) inferring how the organism-environment interaction influences movement processes (Morales *et al.* 2004; Forester *et al.* 2007); and (3) inferring movement itself, when the movement data are incomplete or contain substantial error (Newman 1998; Jonsen *et al.* 2003). We suggest that continued progress in movement ecology will require that these components be subsumed into process-based inferential models, i.e., models that have separate stages for the data and the process, and the parameters that govern both (Clark 2005). After reviewing models for animal movement, we describe an approach that accomplishes these goals.

To address the issues facing movement ecologists, a variety of techniques to model movement have been proposed; these range from mathematical diffusion-based approaches to likelihood-based statistical approaches. Skellam's classic work (Skellam 1951) stimulated substantial interest in understanding spatial dynamics of populations (Kareiva 1990; Turchin 1991, 1998). Statistical approaches that focus on the interaction between individuals and their landscape have included: fractal analysis (Dicke & Burrough 1988; Wiens & Milne 1989; Milne 1991); first passage time (Fauchald & Tveraa 2003); Lévy flights (Viswanathan *et al.* 1996); and process-based movement models (Jonsen *et al.* 2003; Morales *et al.* 2004).

In this review, we focus on several issues fundamental to movement ecology. First, we review non-inferential movement models. Because our primary focus is on inferential process-based models, this section is brief. Next, because we feel its development can promote further progress, we then briefly review hierarchical modeling. Third, we review inferential movement models used to address the three main questions outlined above. Finally, we discuss a conceptual model for movement data and processes that builds on process models now in the literature, while exploiting some advantages provided by the hierarchical approach. It includes the organism-environment interaction, a principle interest of movement ecology. Our goals are three-fold: (1) to stress the importance and complexity of movement data; (2) to highlight the techniques used to account for the vagaries of such data; and (3) to promote an integral understanding needed for further progress in this subfield.

MOVEMENT ECOLOGY AND PROCESS MODELS

To analyze and understand a typical movement path, which has distinct movement behaviors (Fig. 1), an ecologist is faced with a potentially confusing variety of models. While we will focus on inferential models that include data and process stages, there are many terms applied to non-inferential models that deserve mention. These include random walks (RW), fractal analysis, first passage time (FPT), Lévy flights, and multi-behavioral approaches. (Random walks and their diffusion approximations have been used and applied so widely in ecology that even briefly reviewing them here would be superficial; for a thorough review see Okubo (1980); Kareiva (1990); Turchin (1998); Okubo & Levin (2002).) Any of these models could be applied to the example track shown in Fig. 1. A random walk model might be fitted to these data with habitat specific parameters (Morales & Ellner 2002; Ovaskainen 2004). Alternatively, a correlated random walk (CRW) might provide the best fit for the 'migrating' phase of the track (Fig. 1) (Jonsen *et al.* 2005). A Lévy flight would pool the

Area restricted search
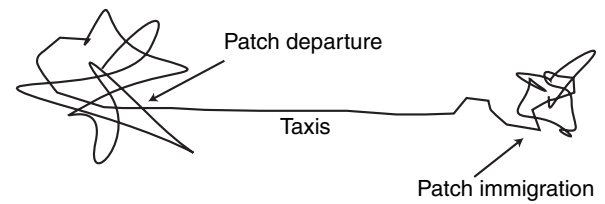
Figure 1 Here we depict a cartoon that captures typical movement behavior, including: area-restricted search, patch-departure, taxis towards a new location, and patch immigration.

observed moves (Fig. 1) and graphically fit the data to see if the steps follow Lévy type behavior (Viswanathan *et al.* 1996). A similar approach would be taken with a multi-behavioral model (Johnson *et al.* 2002b). The many different types of models applied to such data underscore the fact that movement data often look similar (Fig. 1), and models that might fit equally well could involve different assumptions or, at least, be interpreted in different ways.

Calculating a fractal index D from a movement path provides a scale-free measure of the structure in the movement path, or more specifically, a measure of the tortuosity of the movement path (Dicke & Burrough 1988; Milne 1991; With 1994). Typically, $1 \leq D \leq 2$, which corresponds to straight line movement at the lower end, and Brownian motion at the upper end. Since landscape ecologists had used fractals to assess spatial structure in landscapes (Wiens & Milne 1989; Milne 1991), analyzing movement paths with fractal analysis afforded the user a way to observe how D in movement tracks is affected by landscape structure (With 1994). Though these methods have been critiqued on technical and philosophical grounds (Turchin 1996), fractal analysis remains widely used in the movement literature (Fritz *et al.* 2003; Nams 2005, 2006; Tremblay *et al.* 2007) in large part because of the inherent desire of researchers to relate patterns in movement to patterns in the environment.

First passage time (FPT) has deep roots in the physics literature and shares some functional similarity with fractal analysis. In the analysis one centers a window of radius r on the origin (or current location) of a random walker and records how long it takes the walker to leave this circle. This time is the mean first passage time, which scales in non-fractal environments as $T(r) \sim r^2$ (Johnson *et al.* 1992). Like the R_n^2 metric in the diffusion literature (Kareiva & Shigesada 1983), $T(r)$ allows researchers to see how FPT scales with increasing r. Similar to fractal analysis a power law analysis of this scaling behavior suggests a scale-invariant view of the movement process (Johnson *et al.* 1992). Fauchald & Tveraa (2003) extended this analysis by making the link between FPT and search behavior in order

to directly link these movement patterns to landscape patterns. Their hypothesis was that organisms with higher FPT in certain areas would be exhibiting area-restricted search. After empirically detecting search behavior with FPT analysis, Fauchald & Tveraa (2003) could then explore spatial patterns in the environment at these areas of high search intensity.

In the early 1990's the statistical physics community noted how Lévy statistics can be used to study scale invariant patterns observed in kinetic data (Shlesinger *et al.* 1993). In an ecological setting, Viswanathan *et al.* (1996, 1999), were the first researchers to observe and document Lévy flight patterns in searching organisms. Lévy flights are the step lengths (measured in time or in geographic distance) in a movement path and are characterized by a power law distribution $P(l) \sim l^{\mu}$, with $1 < \mu \leq 3$, where l represents the step lengths. Lévy flights differ from Gaussian random walks by the fact that under a power law, longer step lengths are (much) more probable. The case for Lévy flights has been called into question recently by Edwards *et al.* (2007). Their arguments focus on three problems with the initial approach of Viswanathan *et al.* (1996): (1) the lack of a proper data model for observed flights; (2) low resolution data collection that led researchers to conclude erroneously that the albatross were making extremely long flights (when in fact they were still on land); and (3) a non-likelihood based approach to model fitting. Once these problems were addressed, the researchers found no support for flights in four different datasets being drawn from a power-law (Edwards *et al.* 2007), and hence conclude that Lévy flights are not appropriate for movement data. On the other hand, Sims *et al.* (2008), found a good fit between > 1 million records of marine animal dive data and Lévy flights, suggesting that the debate over Lévy flights is yet to play out. Regardless of the outcome of this debate, it is important to note that researchers have used these models to try and explain how a Lévy search *behavior* can be used efficiently by foraging organisms. It has been argued that Lévy flight behavior is selected for as it increases search efficiency (Bartumeus *et al.* 2005).

This treatment of movement data revisits some issues that emerged in the study of long distance dispersal (LDD) and population spread (Okubo & Levin 1989; Kot *et al.* 1996; Clark *et al.* 1999). Fat tailed kernels may fit dispersal data that include rare LDD events, but the extreme behavior should not be over-interpreted. Power functions used to account for this extreme behavior are not proper density functions because they lack finite moments (Clark *et al.* 1999). The infinite variance of a fat-tailed dispersal kernel cannot apply to data, and it makes qualitatively unrealistic predictions (Kot *et al.* 1996; Clark *et al.* 2001, 2003). It makes sense to use a distribution that accounts for occasional fat-tailed movement behavior (Clark *et al.*

1999). Power laws provide '…no understanding of the underlying mechanisms' (Okubo & Levin 1989).

Ecologists increasingly recognize the need for more realistic treatment of behavior in movement models (Lima & Zollner 1996). This need comes in part from empirical work on movement, which highlighted the mismatch between predictions derived from CRWs and observed movement paths (Morales & Ellner 2002). Recognizing the need for a model that fits multiple behavioral modes to movement data, Johnson *et al.* (2002b) employed a model originally developed for the study of foraging or pecking behavior in zebra finches (Sibly *et al.* 1990). This model assumed that behaviors were bouts whose frequency follows a Poisson process. Johnson *et al.* (2002b) fit this model to the frequency of movement rates to determine whether more than one type of (behavioral) movement processes existed in the data, e.g., processes with short and long movements. Despite a recent critique of the approach (Nams 2006), Johnson *et al.* (2006) note that their approach is useful to identify 'behavioral scales of movement.' Johnson *et al.* (2006) point out that more research is needed to detect exact ecological mechanisms that produce the observed movement data.

EMERGING PERSPECTIVES FROM INFERENTIAL MOVEMENT ECOLOGY

Whereas the preceding process models lack a data stage, the models reviewed in this section have stages for both the data and the process. We feel this is a key decomposition, because it allows the user to infer hidden movement processes on the basis of incomplete and/or missing data, multiple data sets, or both. We begin the section with a brief overview of hierarchical modeling, which is followed by a review of how inferential models have been used to: (1) handle complex behaviors; (2) quantify the organism-environment interaction; and (3) understand movement processes in data observed with error.

Hierarchical Bayes for movement data and movement processes

Advances in hierarchical Bayes (HB) have opened up new opportunities for inference on biological processes (Gelfand & Smith 1990; Carlin & Louis 2000; Wikle 2003; Clark 2005, 2007). This inference comes by factoring high dimensional problems into lower dimensional, *conditionally* dependent ones (Berliner 1996; Wikle *et al.* 1998; Clark 2005). Movement data come from a variety of different sensors. Sensors can include ARGOS tags, radio telemetry, GPS tags, and archival tags, each of which has strengths and weaknesses and unique error structures. Because of these error structures, it becomes necessary to separate the data

from the process. Using simple probability rules, we can factor the joint probability distribution of random variables into a series of conditional probability distributions that are easier to compute. One standard factorization breaks the joint distribution into three stages: a data stage, a process stage, and a parameter stage, which yields the following posterior distribution:

$$[process | parameters, data]$$
$$\propto [data | process, parameters][process | parameters][parameters].$$

Such a factorization works well for movement data for the following three reasons. First, movement data are typically recorded with error (Jonsen *et al.* 2003), and using a data stage allows us to account for different error structures. Second, we gain a greater understanding of the processes that drive movement by incorporating the process stage. Finally, having a parameter stage allows for uncertainty in the parameters at all levels of the model. This hierarchical structure allows for structured complexity (Clark 2005).

Movement is a complex process that depends on many things. To understand what drives movement at the individual and population levels, models could accommodate up to four elements: (1) a likelihood-based framework that uses distributions with finite moments; (2) complex process models; (3) a way to separate biotic and abiotic forcing, e.g., locomotion vs. advection (a problem that is especially acute in many marine and aerial systems); and (4) the multiple behavioral patterns common to movement data, i.e., spatial memory, site fidelity, directed movement, etc. (Lima & Zollner 1996; Morales *et al.* 2004; Jonsen *et al.* 2005; Armsworth & Roughgarden 2005). With the advent of modern Bayes we are poised for substantive advance in how we think about, analyze, and use movement data; indeed initial forays into this area have been promising (Jonsen *et al.* 2003; Morales *et al.* 2004; Jonsen *et al.* 2005). Such modern analytical tools will allow us to accommodate complexity both in the data and in the process, and will afford us a quantitatively rigorous understanding of this multi-scaled, multi-dimensional process.

Scaling up movement behavior

Lima & Zollner (1996) called for a 'productive union' between behavioral ecologists and landscape ecologists. They argued that though researchers in these two fields studied similar things, i.e., habitat selection and animal movement, they did so at vastly different scales. Because much of the theoretical foundation in ecological diffusion and movement ecology had been developed using invertebrates as study organisms, and because ecologists were increasingly interested in large scale organism-environment interactions, Lima & Zollner (1996)argued that we should develop models with increasing behavioral complexity.

Scale has often been treated spatially (Levin 1992), i.e., does the pattern observed at one spatial domain 'scale-up' to the next. Such scaling in pattern and process is a hallmark of landscape ecology. For movement ecologists, recent developments have highlighted the importance of 'scaling-up' behavior. In their work on beetle movement, Morales & Ellner (2002) examined scaling in experimental model systems (EMS). Though random walk models can successfully describe movement data at one scale, they may fail to accurately predict the data at larger scales. Morales & Ellner (2002) examined whether 'a random walk framework can be used to translate small-scale, within-patch movement data to larger scale spread in heterogeneous landscapes.' What they found was that single mode CRW models fail to capture the observed spatial spread. A better model fit was achieved by incorporating increased behavioral complexity into the movement model. Such behavioral complexity can take the form of a model that accounts for 'state switching' or one that accounts for 'acclimating' (Morales & Ellner 2002). For example, with a state-switch an organism may switch from one behavior type (e.g. foraging) to another (e.g. migrating) (Fig. 1). Their finding has brought about a way of thinking about movement models that includes not just the landscape-heterogeniety/spatial-scale framework, but also the importance of including more detailed and realistic behavior into the movement process (Morales *et al.* 2004; Jonsen *et al.* 2005; Patterson *et al.* 2008).

Ecologists who have incorporated increased behavioral complexity into movement models have accomplished several things: (1) they have obtained better fits to movement data, i.e., for the location and behavioral state (Blackwell 1997; Jonsen *et al.* 2005; Blackwell 2003); (2) they have correlated behaviors with landscape features (Johnson *et al.* 2002a,b; Jonsen *et al.* 2007; Eckert *et al.* 2008); (3) they have estimated hidden movement behavior within discrete habitat patches of different types as well as movement behavior at boundaries (Morales 2002; Ovaskainen 2004; Ovaskainen *et al.* 2008); and (4) they have observed how the environment can influence within-state movements as well as switches between behavioral states (Morales *et al.* 2004; Forester *et al.* 2007).

A second key form of scaling comes from using a hierarchical structure that allows for a probabilistic link from parameters at the individual level to parameters at the population level (Carlin & Louis 2000; Clark 2005). This structure affords one a population level understanding of particular behaviors by borrowing strength across the individual datasets (Clark 2005, 2007). For example, Jonsen *et al.* (2003) show how a hierarchical structure reduces uncertainty around specific movement parameters. Morales *et al.* (2004) (in their Appendix B) present a hierarchical analysis of 10 simulated tracks that depicts individual variation (or 'random effects') within a population. Such

variation can be seen in the individual and population level posterior estimates for specific movement parameters presented by Jonsen *et al.* (2006) (see their Fig. 3). This hierarchical treatment allowed them to infer individual behavior in different movement modes as well as make population level inference, e.g., turtles travel faster during day time while on southward migration.

Despite this progress, much work is needed to account for the types of movement behavior often observed in long-lived species with spatial memory, learned behavior, social structure, etc. (Morales *et al.* 2004; Gautestad & Mysterud 2005; Mueller & Fagan 2008).

Organism-environment interaction

Landscape ecologists and conservation biologists have focused considerable effort on the interaction between individuals and their landscapes. Using GIS, one can overlay a movement track on top of a variety of environmental covariates, e.g., elevation, habitat, sea surface temperature, etc., with the goal of visualizing the observed interaction. This is often a helpful first data exploration step, but typically we want to learn more about the quantitative nature of such interactions. Gaining inference is key to a richer understanding of how the environment controls the observed spatial behavior of individuals. (In terms of behavior, one could argue that this section is inextricably linked with the previous section, as a behavioral state can be a key determinant of organism-environment interaction. While we review them separately here, we acknowledge the importance of such a link, and we take up their synthesis further in the model section.)

Many recent efforts have quantified the relationship between movement patterns and landscape patterns. Ovaskainen (2004) used a diffusion approach to model movement in heterogeneous landscapes. His model was comprised of multiple CRWs with habitat-specific parameters, boundary behavior, and mortality. A diffusion coefficient, $D_i(t)$, was fitted that varied with time and habitat type i. The boundary behavior component consisted of a biased movement toward a specific habitat type. The model is connected to the data via maximum likelihood and the set of partial differential equations are solved numerically with a finite element scheme. Though there was not support for a habitat-specific $D_i(t)$ in the butterfly data, the model provides a way to estimate these parameters. The model has been further developed in Ovaskainen *et al.* (2008) to include a Bayesian approach in lieu of the MLE approach of Ovaskainen (2004). This approach yielded separate sex- and habitat-specific movement rates (in patch vs. in matrix), whose median was similar, but with a broader range of diffusion rates of butterflies in the patches (Ovaskainen *et al.* 2008).

Morales *et al.* (2004); Forester *et al.* (2007); Eckert *et al.* (2008) all provide examples of how state-space models can be used to quantify the interaction between the organism and environment. Unlike the approach of Ovaskainen (2004) and Ovaskainen *et al.* (2008), these models specifically model the dynamics of a time-series of movement steps. Morales *et al.* (2004) provide a framework for incorporating the influence of abiotic structure on movement processes and such hidden states. They assumed fixed observation error, and explored several models of increasing complexity. Though Morales *et al.* (2004) caution that even these models were probably insufficient to capture the full behavior of elk, the analysis provided an example linking likelihood-based movement models of increasing behavioral sophistication with remotely-sensed landscapes. From an ecological standpoint, Morales *et al.* (2004) were able to quantitatively separate 'encamped' vs. 'exploratory' movements as well as the habitat preferences among elk in the encamped state. Such an approach allows us to answer an ecological question; under what conditions do certain movement types occur? In lieu of a switching approach, Forester *et al.* (2007) accommodate a multi-scale movement process in the transition equation of the state-space model by accounting for (1) the immediate response of elk to the environment and (2) a longer and temporally autocorrelated index of the behavioral state of the animal. Eckert *et al.* (2008) combined the approach of Jonsen *et al.* (2005) with that of Morales *et al.* (2004) to first filter the sightings, and then quantitatively determine how oceanographic covariates influence movement states. Not only were several of these measured covariates used differently by turtles in different movement states, Eckert *et al.* (2008) also found that turtles of different size classes had different persistence in 'fast swimming' modes. Lastly, Johnson *et al.* (2008), in a continuous time CRW model, include a drift term that allows for inference on movement that is influenced by ocean currents. From an inferential standpoint the continuous time formulation allows for precise spatio-temporal matching between animal locations and environmental covariates.

Moorcroft *et al.* (1999, 2006) use telemetry data to parameterize mechanistic home ranges in coyotes. Whereas traditional home range analysis largely ignores the mechanisms that drive movement, and hence space-use by animals, Moorcroft's modeling approach used both a process stage and a data stage to connect movement data to the environment. Using a system of coupled partial differential equations whereby movement is built on two simple biologically-based rules, Moorcroft *et al.* (1999) provided steady-state equilibrium estimates of pack-specific home ranges. In a later model, Moorcroft *et al.* (2006) compare a model where space-use is topographically restricted to one where space-use is prey-driven, and find

that the prey-driven model provides a better fit to the data. This model offers several compelling features: (1) it is spatially explicit; (2) it is likelihood-based; and (3) the movement rules are biologically meaningful. The model offers a snapshot of animal distribution that accounts for individual movement, pack-level distribution, landscape features, attraction towards home range, and conspecific avoidance. While these are not billed as movement models, the take home message is clear; more focus on the organism-environment interaction typically yields a better understanding of space use in animals.

Lastly, non-inferential models have been applied to movement data to explore the population level consequences of organism-environment interactions of moving individuals (Morales *et al.* 2005; Mueller & Fagan 2008). The modeling approach here used artificial neural networks and genetic algorithms (ANN/GA) to build upon a more traditional individual based model. Morales *et al.* (2005) explored how the same set of movement decisions in different simulated landscapes led to different emergent movement behavior. For example, heterogeneous landscapes led to increased variability in movement. Whereas Morales *et al.* (2005) focused more on organism-environment interactions, Mueller & Fagan (2008) focus on how movements of individuals in response to the distribution of resources translates to population level distribution. Mueller & Fagan (2008) note that this modeling approach can accommodate three typical types of movement behavior: non-oriented, oriented, and memory based. Dalziel *et al.* (2008) extend the approach of Morales *et al.* (2005) by combining likelihood with an ANN/GA framework to examine the effect of resources, spatial memory, and distance on elk movements.

Process-based inference in the face of messy data

Proceeding from a simple hierarchical decomposition of the data, the process, and the parameters, we can ask increasingly complicated questions about the features driving movement processes. This theme was first noted in the ecological movement literature by Jonsen *et al.* (2003), who argued that (especially in marine settings) movements are observed incompletely, infrequently, and with error. Accounting for this error via a state-space formulation enables one to probabilistically filter these movement tracks. It should be noted that state-space models for movement existed prior to these, but were found primarily in the statistical literature (Anderson-Sprecher & Ledolter 1991; West & Harrison 1997; Newman 1998; Sibert & Fournier 2001). Perhaps more importantly, while ecologists' introduction to SSMs comes from the statistical and econometrics literature, the field of origin for state-space modeling is control engineering, e.g., Kalman (1960), or section 2.1.6 in Hinrichsen & Pritchard (2005).

The strength of a state-space model framework is that it allows uncertainty in both the process and in the observation to be accounted for separately in the estimation process. The model can be thought of as two 'time series running in parallel' (Newman 1998) – one for the process and one for the observations. For the process model, one typically assumes the underlying true state x changes over time, but is hidden from observation, i.e., x is a latent state variable requiring estimation:

$$x_t = f(x_{t-1}) + \epsilon_t,$$

where the dynamic state variable (typically) evolves according to a Markov process with inherent error that allows for stochasticity (sensu Berliner 1996). Here ϵ_t denotes error that is not accounted for by the process model $f(x)$. The model structure for the observations y also includes an observation model with error ω_t:

$$y_t = g(x_t) + \omega_t,$$

where again we assume a generic observation model $g(x)$.

This framework, though seemingly simple, accommodates a great deal of structure in both the data and the process (Clark & Bjørnstad 2004; Jonsen *et al.* 2005; Patterson *et al.* 2008). For animal movement data, this flexibility is key because movement is comprised of multiple behavioral patterns, and multi-scaled interactions with the environment (Patterson *et al.* 2008). The movement data themselves are typically derived from some telemetry method (e.g., ARGOS, GPS, light sensing archival tags, radio tracking) all of which are marked by complicated non-Gaussian error in the observation (Jonsen *et al.* 2005; Royer *et al.* 2005; Jonsen *et al.* 2006). State-space models can be solved numerically with a Kalman filter approach (Newman 1998; Forester *et al.* 2007). Alternatively, a hierarchical form allows for more complex relationships.

State-space models have greatly advanced the way we think about movement ecology (Patterson *et al.* 2008). True movement is observed neither continuously, nor with complete accuracy. A state-space model accounts for this by making the true movement data conditionally dependent on the movement process, and the observed data conditionally dependent on the true data. This is especially important in the marine realm where the quality of locations returned by satellite or archival tags is often much lower than on land (Jonsen *et al.* 2003; Royer *et al.* 2005).

These models for movement have allowed for inference that would not be possible under a traditional non-likelihood based approach. Jonsen *et al.* (2005) showed how one can use all the data in a probabilistic framework to build models that partition movement data (observed with error) into different behavioral modes. Jonsen *et al.* (2006) used hierarchical SSMs to infer varying rates of travel speed in leatherback turtles as a function of time of year and

breeding status. Jonsen *et al.* (2007) linked posterior estimates of behavioral mode with *in situ* observations of diving behavior in leatherback turtles.

While all of these state-space models represent an advance in our ability to model these types of data, there is room for improvement (Patterson *et al.* 2008). Notably, we see a real need for biologically-based transition processes that occur at different scales, and that account for biotic and abiotic interactions on the movement processes. Instead of filtering or classifying the locations and overlaying them on the environment (Johnson *et al.* 2002b; Jonsen *et al.* 2006), we propose that such environmental interactions or forces be estimated as part of the movement processes themselves. Including forces within the transition equation may help explain movement behaviors in long lived mammals who undergo migration, have spatial memory, experience matrilineal learning, are attracted to conspecifics, etc. (Morales *et al.* 2004).

SYNTHESIS AND FUTURE DIRECTIONS

Though movement data are key to a variety of ecological processes, there is room for refinement. The models reviewed here have addressed several different and important aspects of these processes. For example, the random walk/diffusion framework has told us a great deal about the spatial dynamics of populations. Findings here have been key not only to our understanding of the ecology of these systems, but they have also been instrumental in our understanding of how populations might respond spatially to threatened or fragmented landscapes (Kareiva & Wennergren 1995). With the advent of metapopulation biology and landscape ecology, we saw a resurgence in interest in spatial processes at the individual level. Researchers in these fields began to focus on questions of the following form: How does an organism perceive its landscape? How does it move through that landscape? What happens to these processes with fragmentation? Many of the phenomenological models (fractal analysis, first passage time, Lévy flights) address these lines of inquiry. These three families of models share many similarities in that they examine how patterns in the movement data correspond to patterns in the environment, but these models typically do not include separate data and process stages. As a result, it is easy to see how different combinations of movements could lead to the same observed phenomenon. More importantly, though many of these models arose out of a desire to understand organism-environment interactions, none of these models has an ability to test for how landscape features actually influence the movement process. In addition, though our technological progress in wildlife telemetry has progressed considerably since the late 1980's (Cooke *et al.* 2004; Godley *et al.* 2008) many of these observations are still made with

error (Hays *et al.* 2001). Accounting for error in the observations, especially with marine organisms, is critical.

A movement model needs to do several different things simultaneously. First and foremost it can be grounded in biology, that is, it uses biological information about behaviorally-based movement processes as opposed to simply looking for variance in movement patterns. The model can accommodate multiple spatial and temporal scales, and it can inclued the multiple inputs that a moving individual is constantly evaluating (Dall *et al.* 2005). It should be likelihood-based, and could be structured according to hierarchy. Lastly, the model should be flexible, adaptable, and useful for prediction.

Hierarchical Bayes represents an advance in our ability to model movement for the following three reasons: (1) a traditional HB structure accounts separately for error in the process and the observations; (2) it offers a full likelihood-based framework for testing model fit; and (3) it affords the user the ability to borrow strength across the dataset while estimating parameters. Clearly state-space models have taken full advantage of this structure. By employing a hierarchical structure one can straightforwardly, if not necessarily *easily*, conduct inference on movement processes. Without such a structure, it is difficult to make inference on the movement process underlying the inherently messy movement data.

Given the emerging questions in movement ecology as well as the importance of thinking hierarchically, we present an example model that incorporates advances that many of previous models. Recall Fig. 1, which depicted a typical movement path structured by a combination of short moves in one area and long directed moves towards another area. These types of paths occur throughout movement ecology, and ecologists have long applied models to better understand such paths.

To date, most movement models, especially those RW-based inferential models reviewed here, have modeled the state of the animal, each of which has particular parameter distributions (Blackwell 1997; Morales *et al.* 2004; Jonsen *et al.* 2005). In cases where the state is a function of the environment (Morales *et al.* 2004; Forester *et al.* 2007), the environment has been fixed and typically the movement data are taken as known. There has been little attempt to model the state of the map in large part because of algorithmic challenges. In WinBUGS (Lunn *et al.* 2000) 'sampling' the environment (e.g., extracting spatially and temporally explicit values from remotely-sensed covariates) in cases where true movement observations are unknown, and/or where the environment is dynamic (e.g., marine settings) is not possible. Because of the importance of incorporating biotic and abiotic forces into the process component of the model, the model described here addresses both the state of the moving individual and its response to the state of the map over which it moves (Fig. 2, 3).

Like random walk-based movement models, resource selection functions (RSF) (Manly & McDonald 2002) have been important in animal ecology. They are useful for wildlife managers as large-scale predictive tools because they answer the questions most managers want to know – namely how likely are we to observe an animal in any given cell in a landscape? Accordingly, they have earned a well-deserved place in animal ecology and conservation biology (Johnson *et al.* 2004). RSFs are a way to relate observed habitat selection of individuals to a broader understanding of habitat suitability across larger spatial and temporal scales (Manly & McDonald 2002). Many RSF papers use telemetry data as the input, where visitation is a function of resources. These visitations, or locations, are typically not treated as autocorrelated moves. Loarie *et al.* developed and implemented a temporally explicit RSF for moving pronghorn (*Antilocapra americana*) (Fig. 2) (Loarie, S.R., M.J. Suitor, R.S. Schick, C.J. Loucks, P. Jones, C. Gates, and J.S. Clark, Natural and artificial barriers to pronghorn movement choices in the Northern Great Plains, [*manuscript a, in prep*]). In this case, the RSF is embedded within the process equation.

We can further develop this temporally explicit RSF model by considering multi-state movement paths, i.e., a resident state with no directional movement; and a state

Figure 2 A movement path for a migrating pronghorn in Alberta, Canada. The path begins at $t = 1$ and ends at $t = 186$. Each location is 4 h apart. The red areas are estimates of three missing locations. The arrow from $t = 100$ to $t = 101$ illustrates a single choice. The choice set for this choice includes the 445 pixels centered on the animal's location at time $t = 100$. The background shows greenness and a river. (Figure from Loarie *et al.*, manuscript a, in prep.).

depicted by movement towards another location (Fig. 1). In either state, movements are predicated in space and time in response to habitat suitability, where the response has some functional form based on environmental covariates. In the moving state, moves are predicated on the location of the destination, i.e., taxis, and on environmental covariates along the path. In this model moves are conditioned upon two hidden processes: behavior and organism-environment interaction (Fig. 3).

Formally, the event that an individual i in state m at time $t-1$ moves from location j to k at time t is given by:

$$z_{ijk,t,m} = I(s_{i,t-1,m} = j, s_{i,t,m} = k) \quad (1)$$

Here t refers to discrete time intervals; see Johnson *et al.* (2008) for a continuous time formulation of state-space movement model. The indicator function $I()$ is 1 when its argument is true, and 0 otherwise. Thus, $s_{i,t,m} = k$ is the time specific location k of individual i on the map. It follows that the observed move $z_{ijk,t,m}$ by the individual is from location $s_{i,t-1,m} = j$ to $s_{i,t,m} = k$; s is simply a two dimensional vector of cartesian coordinates. This movement event has probability distribution:

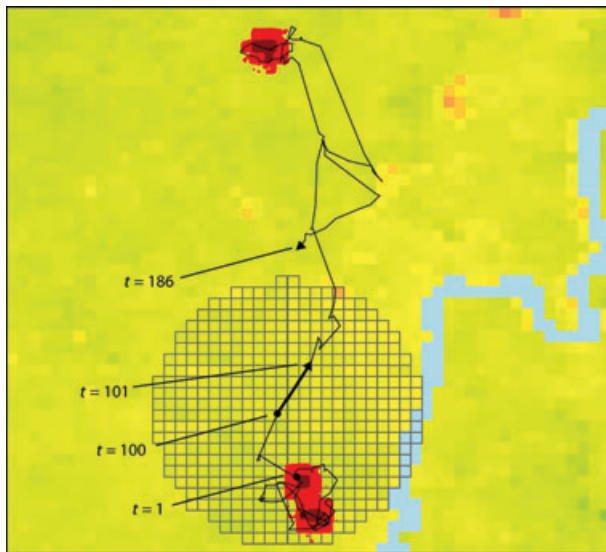$$\Pr[z_{ijk,t,m}] = \text{Multinom}(z_{ijk,t,m}|1, \theta_{ijk,t-1,m}) \quad (2)$$

This says the observed move results when the animal chooses *one* location with probability θ from a set of available locations. This set depends on the state-specific suitability of habitat cells. This probability θ describes suitability h of location k, which varies in time, i.e. the choice set,

$$\theta_{ijk,t-1,m} = \frac{h_{jk,t-1,m}}{\sum_{k=1}^{N} h_{jk,t-1,m}}. \quad (3)$$

The relative suitability of location k given that individual i is in j is a function of covariates, e.g., $\text{logit}(h_{jk,t-1,m}) = \mathbf{X}_{jk,t-1}\mathbf{B}_m$. Here $\mathbf{X}_{jk,t-1}$ describes the landscape covariates of choice k at time $t-1$ for an individual located at j, and $\mathbf{B}_m$ contains the state-specific movement parameters for individual covariates, i.e.,
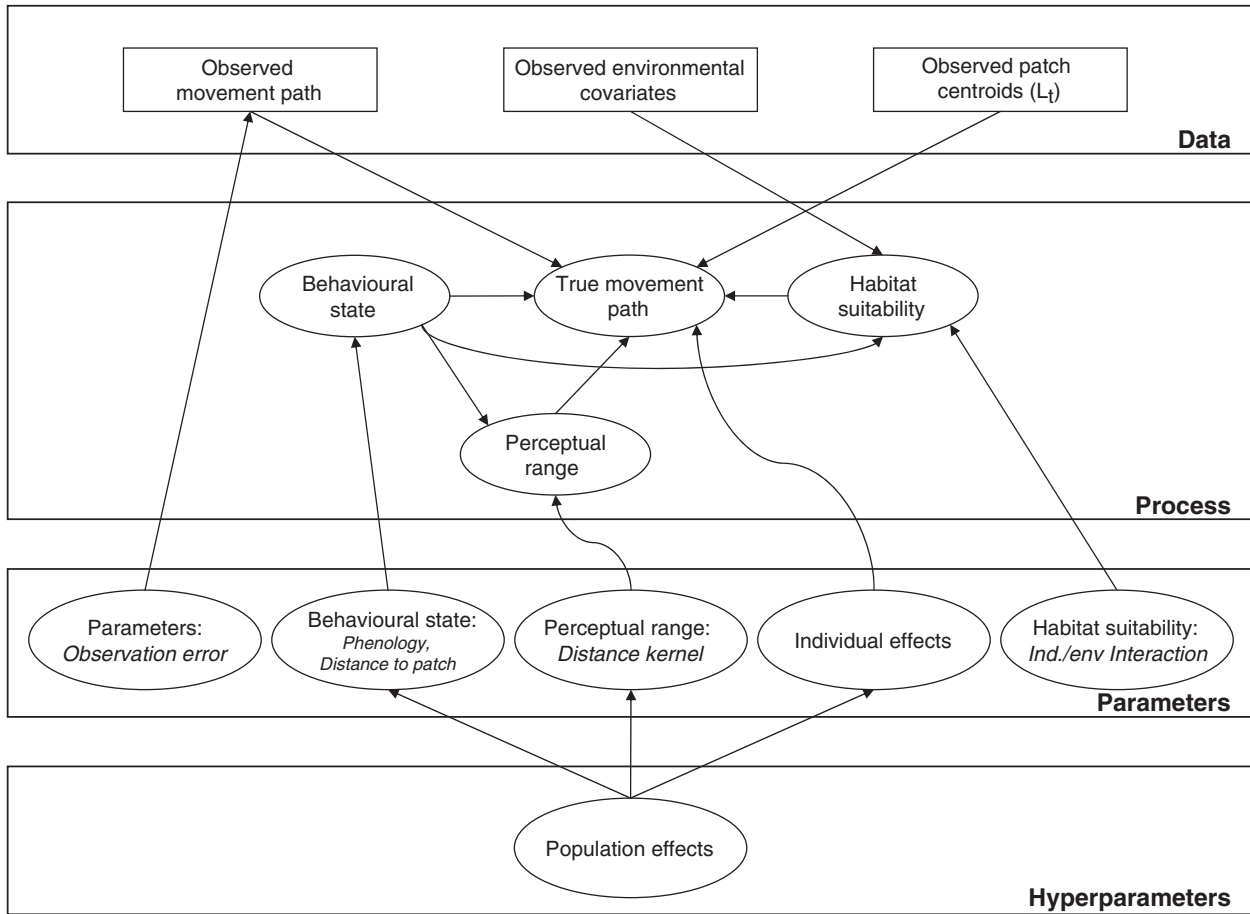
$$\mathbf{X}_{jk,t-1}\mathbf{B}_m = x_{1jk,t-1}\beta_{1,m} + x_{2jk,t-1}\beta_{2,m} + x_{3jk,t-1}\beta_{3,m} + \dots . \quad (4)$$

Let L_t be the x,y location of the destination patch centroid, and $\mathbf{B}_m$ is a vector of parameters, $\beta_{1,m}$, $\beta_{2,m}$, etc., indexed for each movement state ($m = 0, m = 1$). Here we include directionality to a new location L_t as a covariate (Fig. 4). Imagine that in the 'resident' state, the movement depends on the density of conspecifics, elevation and distance to a road (Fig. 4). Hence, directionality to L_t is weak. Now consider the state switch that changes the importance of the covariates. Distance and direction to the

Figure 3 Following Clark (2005) we diagram the conceptual model in four stages: a data stage, a process stage, a parameter stage, and a hyperparameter stage. Conceptually we propose making inference on the true (hidden) movement process based on (hidden) habitat suitability, (hidden) behavioral state, and perceptual range. The data stage consists of the observed path, a set of spatially and temporally explicit covariates, and inferred patch centroids (the location L_t). Though L_t is taken as known, it could be estimated. The process stage for the model consists of a true movement path that is based on an estimated behavioral state, a relationship to the dynamic covariates, and an estimated perceptual range. Finally we have parameters for the data, the process, and a hyperparameter stage that accounts for population level effects.

new location L_t may become more important. That is, when $m = 0$ the covariates are related to local habitat suitability, e.g., $\beta_{1,m=0}$ relates to conspecific density, $\beta_{2,m=0}$ relates to elevation, etc. (Fig. 4). Following the state switch, $(m = 1)$, the habitat suitability is governed by a new set of parameters. Advection towards L_t becomes important and the animal balances taxis with local choices while moving.

This suite of behaviors covers the classic example of area-restricted search in a favorable location $(m = 0)$, followed by taxis towards the next destination $(m = 1)$. More importantly we now have a direct way to gain inference on these behaviorally and map-dictated processes and the parameters that govern them.

The full model summary is as follows:

$$p(\mathbf{B}_m, m|\mathbf{z}) \propto \prod_{i=1}^{n} \prod_{t=1}^{T} Multinom(z_{ijk,t,m}|1, \theta_{ijk,t-1,m}) \times N_t(\mathbf{B}_m|0, \sigma^2), \qquad (5)$$

where $\mathbf{z}$ are the observed data, and m is the vector of behavioral states. For the priors we use non-informative truncated multivariate normals for $\mathbf{B}_m$ centered on zero with large variance, σ^2. Loarie *et al.* (see Loarie, S.R., R.S. Schick, M.J. Suitor, C.J. Loucks and J.S. Clark, Environmental constraints on pronghorn migratory behavior in the Northern Great Plains, [manuscript b, in prep]) applied this model to explore how habitat suitability and movement choices differ between the "resident" and "migrating" phase in pronghorn antelope. The model combines environmental covariates greenness, snow,
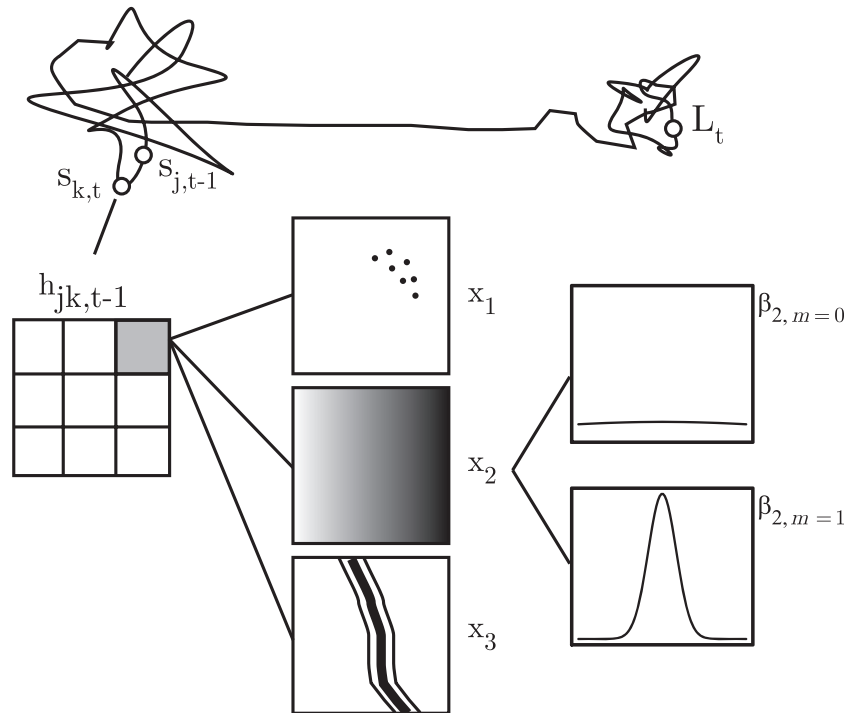
Figure 4 Here we repeat the movement path from Fig. 1 in an effort to highlight the potential results from the conceptual model. Movement behaviors depicted include: area-restricted search, taxis towards a new location L_t, and area-restricted search at the new location. Consider the following organism-environment interaction scenario addressed by the model. An animal moves from location $s_{j,t-1}$ to $s_{k,t}$; here s_k corresponds to a two dimensional vector of cartesian location coordinates of location k. For visual clarity, we drop the index for individual and state. These moves are made according to some normalized habitat suitability $h_{jk,t-1}$, which describes the suitability of the landscape at position k given that the animal is currently at j. This suitability is comprised of a state-specific vector of covariates $\mathbf{X}_{jk,t-1,m}$. $h_{jk,t-1}$ can be based on any number of covariates; here we depict (1) location of conspecifics x_1, (2) elevation x_2, and (3) distance to a road x_3. Once the animal has switched movement states, moves are still evaluated based on covariates, but now we explicitly model taxis as a function of direction to L_t (here taken as known-though it could be estimated). Lastly, the cartoon documents what state-specific posterior estimate of the β's could look like (two boxes at right). For example, in the each movement state the animal evaluates suitability that includes elevation. In the resident state values across a wider range are plausible, while in a moving state, the values are much more constrained.

roads, and rivers with direction and distance of movement. During the migratory phase, results described not only the rapid northerly movement, but also the increased tendency to move into snow covered areas and to cross roads than when in the resident phase. By incorporating dynamic spatial covariates (e.g., greenness, snow cover) Loarie *et al.* (manuscript b, in prep) quantified a balance of processes affecting local movement in combination with migratory dynamics at coarse scales. For the full development, implementation, and application of this model to data, we refer the reader to Loarie *et al.* (*manuscript b, in prep*).

Several key differences emerge in a comparison to a RW-based process model. Here we explicitly model how the state, location, and suitability for the individual and the landscape govern choices the animal makes about moving from place to place (Fig. 4). That is to say, instead of a multiple CRW model, which yield posterior estimates of random movement in different landscape types, here we model how those landscape types actually influence the

movements (see the boxes for the β's in Fig. 4). In comparison to a biased CRW (Marsh & Jones 1988), which accounts for directed random movement to a location, the model presented here accounts for the timing of that influence (i.e., the states), as well as choices along the path towards L_t (Fig. 4). Of course uncertainty arises in many places in movement modeling, including the uncertainty in suitability h. There exists a range of how well we know any individual covariate. Certain habitat classification maps derived from a remotely sensed product can propagate errors in spatial location, reflectance, and the classification itself. In some cases these errors can be larger than the errors in animal location. Accounting for this error could be important, and while it increases the dimensionality of the model, it can readily be accomplished in the model proposed above.

One of the primary algorithmic difficulties faced by a practicing movement ecologist is the interface between the map and the animal. At each time step the animal samples and

monitors its environment and its behavioral state and then makes movement decisions (Gautestad & Mysterud 2005). In a Gibbs sampling framework the proposed location must sample the 'map' and this sampling is not straightforward with the widely used program WinBUGS (Lunn *et al.* 2000). We note this because as WinBUGS code for movement models is increasingly published with the papers (Morales *et al.* 2004; Jonsen *et al.* 2005), it can be relatively easy to apply these models to movement data. When faced with a dynamic map, missing data and observation error we can use R, Matlab, or other computing languages.

Many models (analytical, phenomenological, or statistical) include efforts to account for difficult components of an average movement ecology problem. The model presented here is incrementally more sophisticated. We do believe that it builds on the strengths of previous models, while offering an important new component: the response of a moving individual to a dynamic environment. In addition to sampling the map, the process component differs from inferential models that are based on random walks (e.g., Blackwell 1997; Jonsen *et al.* 2005; Morales *et al.* 2004; Ovaskainen 2004), including instead a multinomial choice model. We are interested in how the animal is choosing to move as a function of the environment and behavioral state. Rather than basing state-specific moves on random walks [including correlated random walks, biased correlated random walks (Marsh & Jones 1988), or multiple random walks (Morales *et al.* 2004)], in this model the animal is actively monitoring the state of the map in addition to its own internal state and making state-specific choices. One way to think of this is as a resource selection function embedded within a movement model. Whereas Moorcroft & Barnett (2008), used RSF's embedded within a mechanistic home range model, here we have one embedded within a movement path. In addition to the model presented here, others have taken a similar approach. Christ *et al.* (2008) have developed a similar RSF-type approach using a likelihood that is based on a bivariate normal, as opposed to the multinomial approach used here. Their model also includes a home range component. From an inferential standpoint, when fit to telemetry data the model developed by Christ *et al.* (2008) outputs a utilization distribution from posterior estimates of site fidelity and habitat selection. With such an RSF-type framework, we can easily propose multiple behaviorally explicit movement process models complete with switching models, and let the data be the arbiter of the models. In addition we can begin to ask behavioral and landscape specific questions about the organism-environment interaction. For example, the extension to multiple states, each with a behavioral and/or (dynamic) landscape-mediated switch probability is straightforward. We feel that this framework addresses many of the key themes for ecological inference in movement systems, while remaining flexible enough to be tailored to multiple tagging technologies in both marine and terrestrial systems.

CONCLUSIONS

We have argued that further progress in movement ecology can focus effort on the movement process itself. Without separating the data from process, inference is difficult. In addition, we have argued for the need to understand both the state of the organism as well as the state of the environment through which it moves. Clearly it is important to account for complexity in the data and the process, especially where this process is in response to the environment. HB offers a structure that accounts for this complexity by factoring multidimensional problems into simpler conditionally dependent ones. We have stressed a need to formulate biologically-based process models that a) account for multiple behavior types, b) incorporate what we know about how the environment drives movement processes, and c) account for the often messy data we collect on movement. While we have stressed the need for more biology in the movement process, we also recognize the importance of a data stage, i.e., a way to handle observation error. Though tagging technology continues to improve, certain tag types (e.g., archival tags) have large observation error that must be accounted for explicitly. By also accounting for the 'map,' we better understand how the landscape (or seascape) affects individuals.

We believe that implementing the conceptual framework outlined here will lead to greater ecological insight about why animals move. Learning more about how multi-scaled interactions with the environment influence movement will enhance our understanding of the effects of habitat fragmentation and loss on population size and structure. With a better understanding of the movement mechanisms, we can take advantage of the huge tagging datasets now available to gain much needed insight into the ecology and conservation of mobile species.

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