OVERVIEW

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Animal movement models for multiple individuals

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Abstract

Statistical models for animal movement provide tools that help ecologists and biologists learn how animals interact with their environment and each other. Efforts to develop increasingly realistic, implementable, and scientifically valuable methods for analyzing remotely observed trajectories have provided practitioners with a wide selection of models to help them understand animal behavior. Increasingly, researchers are interested in studying multiple animals jointly, which requires methods that can account for dependence across individuals. Dependence can arise for many reasons, including shared behavioral tendencies, familial relationships, and direct interactions on the landscape. We provide a synopsis of recent statistical methods for animal movement data applicable to settings in which inference is desired across multiple individuals. Highlights of these approaches include the ability to infer shared behavioral traits across a group of individuals and the ability to infer unobserved social networks summarizing dynamic relationships that manifest themselves in movement decisions.

This article is categorized under:
    Statistical Models > Bayesian Models
    Data: Types and Structure > Time Series, Stochastic Processes, and
        Functional Data
    Data: Types and Structure > Social Networks

KEYWORDS
animal movement, behavior, hierarchical, population inference, social network

1 | INTRODUCTION

Beginning with Dunn and Gipson (1977), then in earnest with Anderson-Sprecher and Ledolter (1991), Blackwell (1997), Brillinger and Stewart (1998), and Turchin (1998) (the first book dedicated to the subject), mathematical and statistical models for animal movement have become extremely active areas of research for both statisticians and quantitative ecologists. The pace of development over the past four decades has only increased. Feature issues and reviews in highly ranked journals (e.g., Hooten, King, & Langrock, 2017; Kays, Crofoot, Jetz, & Wikelski, 2015), new textbooks (e.g., Hooten, Johnson, McClintock, & Morales, 2017), and an outsized representation at scientific conferences (the 2018 International Statistical Ecology Conference featured six separate sessions on movement ecology—a plurality for any single topic) provide evidence that interest in realistic, implementable, and theoretically sound methods for analyzing movement data is higher than ever.

The rapidly expanding volume of innovative research in the field of animal movement modeling makes a general review of the literature impractical. We narrow our attention to an important subset of the broader research field that focuses on the development of methodological tools for the joint study of multiple dependent trajectories. Interest in the aggregate behavior of populations of related individuals, and the direct interspecies and intraspecies interactions that inform animal behavior, has been front and center for movement specialists in wildlife and conservation biology (see, e.g., the recent special issue in Berdahl, Biro, Westley, & Torney, 2018).

We focus on two avenues through which dependence among multiple trajectories can be incorporated into statistical models for animal movement. First, implicit dependence across an observed population of individuals may arise through shared behavior patterns. The tendency of conspecifics to utilize space and resources in similar ways is often well-described through hierarchical models in which parameters that govern behavior are held constant across the population, or treated as random effects arising from a population distribution. Conditioned on these shared effects, individuals are typically assumed to move independent of one another; we therefore refer to the induced joint dependence in these statistical models as "indirect" (Section 2).

Second, dependence among animal paths may arise through direct interactions among socially related individuals. Typically, social interactions are modeled as the tendency of "positively" associated individuals to move toward one another and align their movements toward common goals, though in principle similar approaches could be used to model repulsion or avoidance. These models may also involve indirect dependence through hierarchical structure, but a distinguishing characteristic of this class of models is that individuals' movements are conditionally dependent, with the strength of dependence described by an unobserved graph or social network. We refer to the dependence in these types of statistical models as "direct" (Section 3).

For the purposes of this paper, we emphasize models for animal movement that provide for estimation of the true, unobserved paths of the animals, including both discrete- and continuous-time approaches as well as integrated step selection functions. We refrain from reviewing the closely related literature surrounding resource selection functions and non-integrated step selection functions, as these methods are primarily concerned with describing attributes of habitat selection rather than modeling a trajectory directly. Fundamental references for these topics include Boyce and McDonald (1999), Manly, McDonald, and Thomas (2002), Fortin et al. (2005), Warton and Shepherd (2010), Aarts, Fieberg, and Matthiopoulos (2012), and Avgar, Potts, Lewis, and Boyce (2016); for an introduction, see Hooten, Johnson, et al. (2017, chap. 4). Unlike most traditional resource- and step-selection functions, integrated step selection functions include movement characteristics as predictors and have been shown to be equivalent to modeling movement as a biased correlated random walk (Avgar et al., 2016; Duchesne, Fortin, & Rivest, 2015).

2 | INDIRECT INTERACTIONS

An important source of indirect dependence arises due to collective responses to abiotic and biotic variables that individuals encounter on the landscape. Researchers typically account for this dependence in one of three ways: (a) an individual movement model is independently fit to multiple individuals, followed by a post hoc summary or secondary model, (b) a joint model for all individuals is specified in which behavior is assumed to be constant across individuals (complete pooling), or (c) a joint model is specified in which individual behavior is modeled as a realization from a common distribution (partial pooling). The response variable in the movement model can be either the position process (where the animal is in space), or a deterministic function of position such as velocity, speed, and/or turning angle.

2.1 | Nonintegrated estimation

Historically, many applications of movement models have treated all individuals as statistically independent. This was primarily for two reasons: researchers were focused on developing and explaining a novel, individual-based movement model (e.g., Buderman, Hooten, Ivan, & Shenk, 2016; Hooten, Johnson, Hanks, & Lowry, 2010; Johnson, London, Lea, & Durban, 2008; Jonsen, Flemming, & Myers, 2005; Morales, Haydon, Frair, Holsinger, & Fryxell, 2004), or computational limitations associated with fitting movement models to multiple individuals in an integrated framework prohibited implementation (Hooten, Buderman, Brost, Hanks, & Ivan, 2016). However, biological research is increasingly concerned with aggregated descriptions of behavior across a population or sub-population of individuals (as determined by, e.g., sex, age, or reproductive status), necessitating the development of new methodologies.

Biologists are often interested in "hot spots" on the landscape that are important to multiple individuals as the identification of these critical regions can aid in conservation decision making. For example, a researcher might begin by separately fitting a movement model to the observed locations of multiple individuals, then sum or average results from the movement analysis across individuals to create a map of important stopover habitats or movement corridors (e.g., Buderman, Hooten, Ivan, & Shenk, 2018; Sawyer, Kauffman, Nielson, & Horne, 2009, see Figure 1). Ideally, these maps properly depict uncertainty in estimates of the true movement path, especially if there is large measurement error (Buderman, Hooten, Ivan, & Shenk, 2018).

Although they are not typically used to create maps of hot spots, integrated step selection analyses (iSSAs; see Avgar et al., 2016) are an alternative method used to quantify the impact landscape features have on movement behavior for both individuals and populations. For example, Prokopenko, Boyce, and Avgar (2017), DeMars and Boutin (2018), and Scrafford, Avgar, Heeres, and Boyce (2018) performed independent iSSAs on multiple individuals and then calculated population-level movement rate and habitat selection coefficients by re-sampling or weighting individual-level estimates.
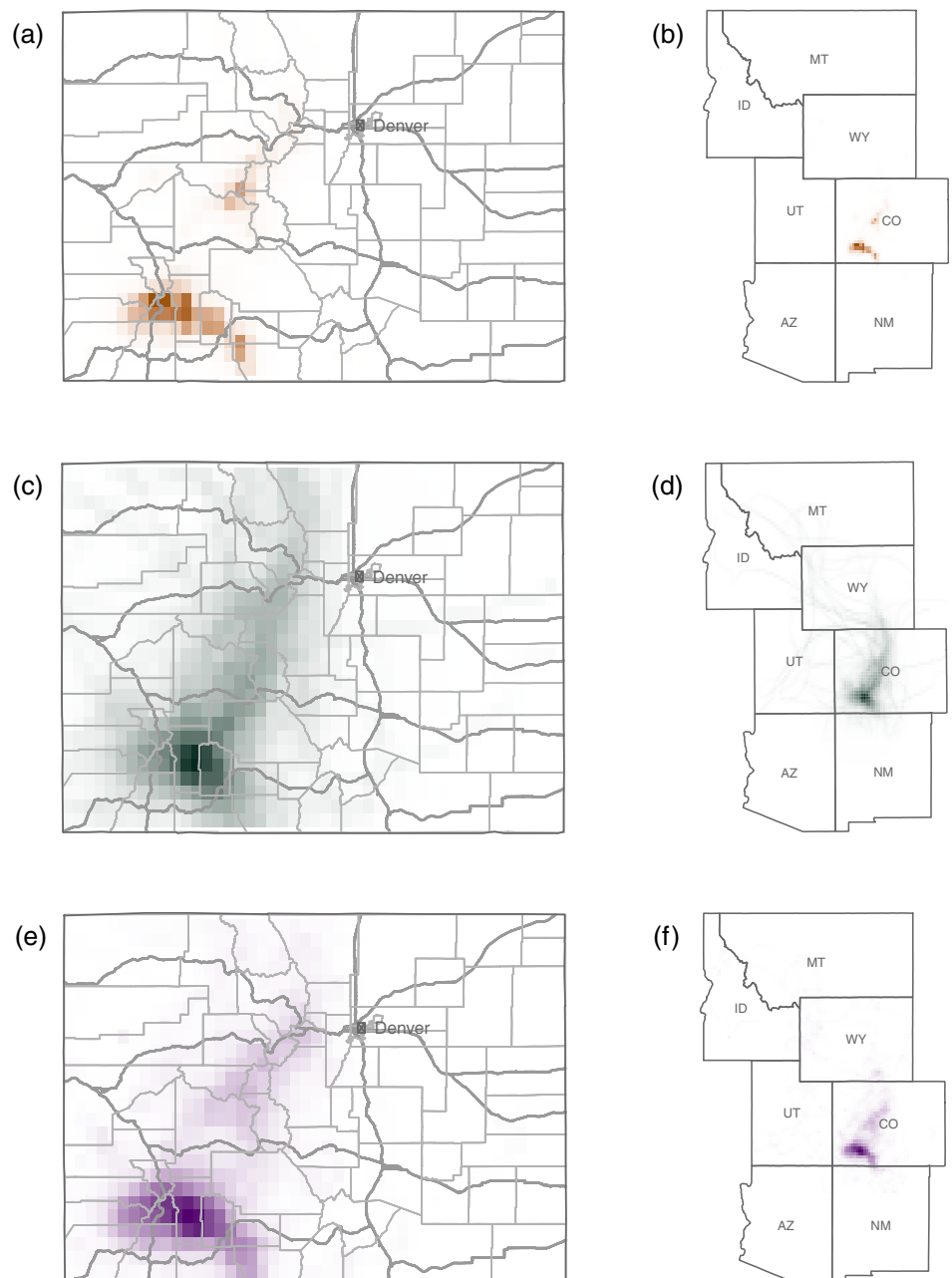

FIGURE 1 Population-level spatial quantities of residence time (a,b), speed (c,d), and tortuosity (e,f). For reference, county boundaries and major roads are shown for Colorado (a,c,e). Not included are rare movements to eastern states (Nebraska, Kansas, and Iowa) (Reprinted with permission from Buderman, Hooten, Ivan, and Shenk (2018). Copyright 2018 John Wiley & Sons Ltd; and refers to quantities related to Canada lynx movement)

2.2 | Two-stage models

Hierarchical models are often used as part of a two-stage modeling framework in which a movement model is first fit independently to each individual, and then a derived variable related to the movement is used as the response in a hierarchical or mixed-model regression. For example, observed locations, $\mathbf{s}_i$, of individual $i = 1, ..., m$ are often modeled conditionally as realizations from a probability distribution with parameters that describe the true location of the individual, μ_i, and measurement error, σ^2, as

$$\mathbf{s}_i \mid \mu_i \sim F_s(\mu_i, \sigma^2). \tag{1}$$

A common form for F_s is a multivariate distribution in which the observation made at any given time, $\mathbf{s}_i(t)$, is bivariate Gaussian-distributed with mean $\mu_i(t)$ and covariance matrix $\sigma^2\mathbf{I}$. The true location of the individual arises from a distribution described by parameters θ_i given by

$$\mu_i \mid \theta_i \sim F_\mu(\theta_i). \tag{2}$$

Common specifications are discrete- and continuous-time state-space models, and Gaussian processes (see Hooten, Johnson, et al., 2017, chaps. 5 and 6 for a review).

At the second stage, a function of the true location, $g(\hat{\mu}_i)$ (e.g., speed, turning angle, velocity), is regressed on landscape covariates, $\mathbf{X}_i$, as

$$g(\hat{\mu}_i) = f(\mathbf{X}_i, \beta) + \varepsilon_i. \tag{3}$$

Most often the functional relationship is taken to be linear (i.e., $f(\mathbf{X}_i, \beta) = \mathbf{X}_i\beta$).

A simple implementation of a two-stage model for aggregated behavior might be the following. At the first stage, a trivial model is implicitly specified for the observed data in which measurement error is assumed to be zero (i.e., $\mathbf{s}_i = \mu_i$). In the second stage, instantaneous speeds, turning angles, or movement-related coefficients are calculated using the position process and used as a response variable in a linear (e.g., Barocas, Hefner, Ucko, Merkle, & Geffen, 2018; Raynor, Beyer, Briggs, & Joern, 2017; Smith, Donadio, Pauli, Sheriff, & Middleton, 2019) or generalized additive model (e.g., Kohl et al., 2018). Individual-level predictors, $\mathbf{X}_i$, could include, for example, sex, age, and breeding status. Because the functions of observed locations are typically calculated for each individual's sequential set of observations, it is often necessary to use a mixed-model framework with random intercepts to account for repeated measures within each individual such that

$$\begin{aligned} g(\hat{\mu}_i) &= \beta_{0i} + \mathbf{X}_i\beta + \varepsilon_i \\ \beta_{0i} &\sim F_{\beta_0}. \end{aligned} \tag{4}$$

Deviations from the population-level effect of a covariate can also be incorporated using random slopes (e.g., Buderman, Hooten, Alldredge, Hanks, & Ivan, 2018), such that

$$\begin{aligned} g(\hat{\mu}_i) &= \beta_{0i} + \mathbf{X}_i\beta_i + \varepsilon_i \\ \beta_i &\sim F_\beta. \end{aligned} \tag{5}$$

To avoid identifiability issues, random slopes should only be utilized for covariates that have variation within an individual.

The movement model just described in which $\mathbf{s}_i = \mu_i$ assumes that there is no measurement error, and often it is implicitly assumed that individuals move in a straight line between observations. In practice, these assumptions may not be valid, and the uncertainty in the true location, both at observation times and between them, will manifest itself in derived metrics. As an example, consider an application relating movement to landscape characteristics measured on a regular grid (e.g., vegetation cover type, elevation, presence of human structures). If the pixel sizes of the grid are

much larger than confidence regions for the true position of individuals at a given time, ignoring measurement error will usually have a negligible impact on the inferred effect of landscape on movement behavior. However, if uncertainty about the true location is comparable to the scale of the individual pixels in the grid on which covariates are measured, there will be uncertainty about what type of landscape individuals actually move through, and inference can be strongly affected by ignoring measurement error. Variation in animal ecology and behavior, monitoring technology, sampling interval, and desired inference make it difficult to provide general guidance for when one cannot ignore measurement error, but see Brost, Hooten, Hanks, and Small (2015), Frair et al. (2010), Hurford (2009), Noonan et al. (2019) for some specific applications that incorporate measurement error.

One way to relax the assumptions of zero measurement error and linear increments is by fitting a continuous-time movement model (e.g., Buderman et al., 2016; Horne, Garton, Krone, & Lewis, 2007; Johnson et al., 2008) to each individual in stage one. Uncertainty in the true movement processes, μ_i, can then be propagated forward into the second stage by sampling trajectories from the fitted distribution in stage one (e.g., Buderman, Hooten, Ivan, & Shenk, 2018). In some cases, a movement model acknowledging measurement error is used in the first stage; however, uncertainty in the true position process is not propagated forward to the second stage. It is common, often for computational reasons, to treat a single path summarizing fits from the first stage (e.g., the posterior mean in a Bayesian framework, or the trajectory that maximizes the likelihood) as the true position process in the second stage (Buderman, Hooten, Ivan, & Shenk, 2018; Prokopenko et al., 2017). When it is not feasible to propagate exact uncertainty through from stage one to two, it is often still possible to account for measurement uncertainty approximately using bootstrapping or multiple imputation in which small number of realizations of μ_i in stage one represent the overall variability in the true movement process (Buderman, Hooten, Alldredge, et al., 2018; Hanks, Hooten, & Alldredge, 2015; Hanks, Hooten, Johnson, & Sterling, 2011; McClintock, 2017; Scharf, Hooten, & Johnson, 2017; Tremblay, Robinson, & Costa, 2009).

2.3 | Complete pooling

A further step toward obtaining population-level inference is complete pooling within a single-stage movement model. With this method, individuals can not deviate from the population-level behavior parameters, and inference is made on those shared parameters, θ:

$$\mu_i \,|\, \theta \sim F_\mu(\theta). \tag{6}$$

$$\theta \sim F_\theta. \tag{7}$$

For example, Brennan et al. (2018) used the same modeling framework as Buderman, Hooten, Alldredge, et al. (2018), described in more detail below, but were only interested in population-level behavior and therefore did not model individual-level deviations from the population process.

The hidden Markov model (HMM) for animal movement is quickly becoming a popular and easily accessible tool for ecologists due to a number of packages for the R statistical programming environment that facilitate their implementation (McClintock & Michelot, 2018; Michelot, Langrock, & Patterson, 2016). HMMs are dependent mixture models in which observations of an individual arise from state-dependent distributions whose sequence in time can be described as a first order Markov process. Many of the analyses using HMMs for animal movement have used complete pooling to obtain information on a shared state transition probability matrix and state-dependent distributions for metrics such as speed, depth, and turning angle (e.g., Leos-Barajas et al., 2017; McClintock, Russell, Matthiopoulos, & King, 2013; Michelot et al., 2017). Jonsen (2016) refers to this method as a joint estimation approach, and demonstrated that movement parameters and state variables can be estimated with greater precision by pooling information across all individuals as opposed to independently fitting the movement model to each individual.

Implementation of HMMs typically proceeds under the assumption that the data represent regularly spaced observations in time made without error. When these assumptions are violated, it is possible to obtain approximately valid inference using multiple imputations as outlined at the end of Section 2.2. The quality of the approximation depends on both the severity of the measurement error and the nature of the statistical inference (see McClintock, 2017; Scharf et al., 2017, for an assessment of multiple imputations in the context of animal movement).

2.4 | Partial pooling

The most flexible approach that accounts for indirect interactions between individuals allows for partial pooling of information across observed individuals. Partial pooling methods allow for individually varying behavioral parameters that arise from a population distribution. The model formulation can be interpreted as a two-stage approach formalized in a single, holistic hierarchical structure (as in Berliner, 1996). At the data level, the model is identical to the two-stage specification, which we repeat here for clarity:

$$\mathbf{s}_i \mid \mu_i \sim F_s\big(\mu_i, \sigma^2\big). \tag{1}$$

$$\mu_i \mid \theta_i \sim F_\mu(\theta_i). \tag{2}$$

However, in contrast with two-stage approaches which rely on post hoc analyses of independent movement models, partial pooling continues the hierarchy to include a population distribution, $F_\theta(\psi)$ for the individual behavior parameters, θ_i such that

$$\theta_i \mid \psi \sim F_\theta(\psi). \tag{8}$$

$$\psi \sim F_\psi. \tag{9}$$

The distribution F_θ dictates the degree of individual variation within the population. Partial pooling thus allows for interpretation at both the individual (θ_i) and population (ψ) levels. One caveat is that the inclusion of a nonlinear transformation of θ in Equation (1) can have an unexpected effect on the interpretability of ψ (for a more in-depth discussion of the differences between subject-specific and population-averaged responses, especially in the context of non-Gaussian data, see Fieberg, Rieger, Zicus, & Schildcrout, 2009). In addition, the shared population-level distribution, F_ψ, induces positive dependence across θ_i, which can reduce the effective degrees of freedom in the model and result in improved inference for individual parameters in data-poor applications by borrowing strength across the population (see Figure 2).

Partial pooling has been implemented in a number of movement modeling frameworks. One such approach was developed by Jonsen, Myers, and James (2006), which is an extension of the discrete-time correlated random walk model by Jonsen et al. (2005). In this model, the individual-specific terms for drift (directed movement) and process variation each arise from a distribution shared among all individuals. Buderman, Hooten, Alldredge, et al. (2018) expanded
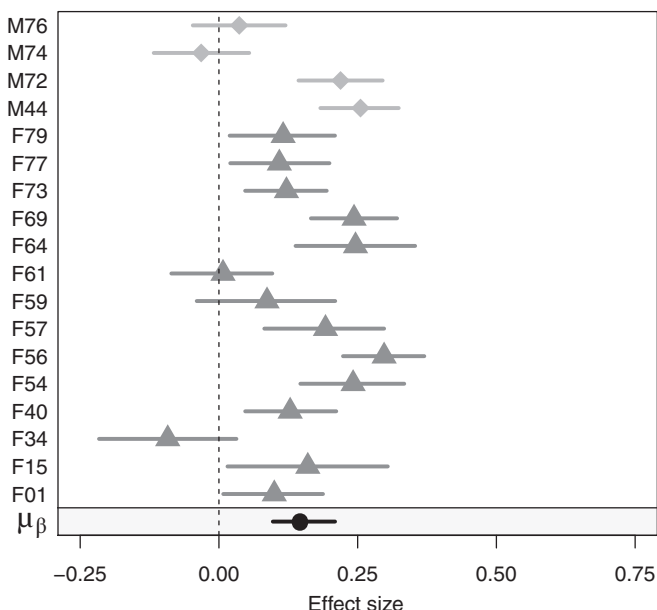

FIGURE 2 Posterior means and 95% equi-tailed credible intervals for the individual- (each named row) and population-level (μ) effects of distance to nearest potential kill site on cougar motility. Population-level effects represent the mean coefficient across all individuals (Reprinted with permission from Buderman, Hooten, Alldredge, et al. (2018). Copyright 2018 BioMed Central Ltd)

on the individual-level model proposed by Hanks et al. (2015) to account for deviations from the estimated population-level effects of landscape variables on cougar movement rates and directionality. Although the model formulation in Hanks et al. (2015) fits within the partial pooling paradigm, the authors made use of a computationally efficient two-stage approximate model fitting procedure that is similar to the two-stage approaches discussed in Section 2.2. When a Bayesian implementation is used, the posterior distribution for individual-level parameters can be summarized alongside the posterior distribution of the population-level mean of the parameter's distribution to provide a useful visualization of individual variation (Figure 2).

As we discussed above, many HMMs have been implemented in a complete pooling framework. Langrock et al. (2012) proposed using mixed-effects HMMs for animal movement, but noted that fitting such a model in a likelihood framework is computationally demanding, particularly when there are a large number of individuals, and recommended using a combination of individual covariates and a small number of random effects. In subsequent work, McKellar, Langrock, Walters, and Kesler (2014) used a random effect to capture individual heterogeneity in the state transition probabilities that was not explained by the available covariates, but employed a computationally efficient semi-parametric approach to estimate the random effect. Because the current software available for fitting HMMs is fit using maximum likelihood (Michelot et al., 2016), adoption of Bayesian mixed-effects HMMs has been slow, despite Morales et al. (2004) noting that hierarchical models would be useful for assessing the degree of individual variability in movement behavior in a HMM framework (referred to as a state-space model in their work) and subsequent implementation in Eckert et al. (2008).

Although they represent a more holistic modeling approach, which can both improve estimation for parameters sharing a common distribution and account for uncertainty in both the data collection and movement process (Gelman et al., 2013), examples of formal hierarchical models for animal movement have not been widely adopted due to computational limitations (Hanks et al., 2011; Langrock et al., 2012) or features of the modeling framework. For example, for the semiparametric location process model developed in Buderman et al. (2016), it does not make ecological sense to share location information across individuals, particularly if they are a wide-ranging and solitary species (Buderman, Hooten, Ivan, & Shenk, 2018). However, it is possible to share the data generating process (e.g., information about measurement error) across individuals, which can improve inference on the true, unobserved locations of the individuals.

With regard to computational limitations, Hooten et al. (2016) applied an algorithm for Bayesian meta-analysis that was originally developed by Lunn, Barrett, Sweeting, and Thompson (2013) to a number of animal space-use and movement models. Although this method is described as a two-stage approach, it is more rigorous and formally hierarchical than the two-stage approaches discussed above. However, it remains in limited use because it currently requires the user implementing their own Markov chain Monte Carlo sampler (but see Northrup, Rivers, Yang, & Betts, 2019). Similarly, obtaining individual- and population-level inference for conditional logistic regression models (the framework used to perform iSSA) was previously accomplished with a two-stage approach using the expectation–maximization algorithm (Craiu, Duchesne, Fortin, & Baillargeon, 2011, 2016). Recent work by Muff, Signer, and Fieberg (2019) proposes a more computationally efficient method for fitting conditional logistic regression models by reformulating them as a Poisson regression with stratum-specific intercepts modeled as a random effect; this development should facilitate performing iSSA in a hierarchical framework.

3 | DIRECT INTERACTIONS

Increasingly, biologists and ecologists understand and describe social relationships in animal populations using graphical structures. Graphs, or networks, provide a useful way of summarizing relationships among many individuals (vertices) through the quantification of pairwise connections (edges). Edges may be binary or continuous, directed or undirected, static or dynamic, and are therefore suitable for a wide variety of applications. Graphs are often summarized using a binary $m \times m$ adjacency matrix, $\mathbf{A}$, in which a value of 1 indicates an edge between vertices matching the corresponding row and column, and a 0 indicates the absence of an edge (for a general review of networks, see A. Goldenberg, Zheng, Fienberg, & Airoldi, 2010; for a text specific to animal social networks, see Croft, James, & Krause, 2008). The methods presented in this section can all be understood as means for studying the edges in a graph that represents biologically relevant connections within a population. The graph itself may be of fundamental interest, or it may represent a random effect that must be acknowledged as a potential confounder.

Social relationships in animal populations often affect behavior in numerous ways, including what areas on the landscape individuals choose to utilize and when. It is therefore natural to expect to see signatures of socials networks

in observations of animal trajectories. The most commonly studied manifestations of interacting species have tended to center around "positive" relationships, such as a tendency for socially connected individuals to occupy proximate locations in space and time, and/or to coordinate their movements along parallel trajectories (e.g., Bode et al., 2012). We use the term positive for these types of interactions as they often correspond to cooperative, rather than competitive relationships, and typically yield positive linear correlations between the position processes of pairs of individuals (although one counterexample to this terminology occurs when two related individuals are attracted toward one another, which can result in a negative cross correlation in the position process).

As we describe in the following subsections, the general progress of methodological research for social network-based analyses of animal movement data has proceeded along a conventional route, beginning with techniques for exploring and summarizing movement data, followed by the development of moderately complex generative models, up to the present moment in which researchers are actively developing sophisticated models for movement that are able to capture impressively realistic and subtle behaviors for a wide range of applications. A useful way to organize the existing available methods is into (a) descriptive approaches, (b) generative models conditioned on a known network, and (c) generative models conditioned on an unknown network.

3.1 | Descriptive

Descriptive approaches generally consist of summary statistics computed directly from the observed positions of a population of individuals. Long, Nelson, Webb, and Gee (2014) provide a review and critical evaluation of many commonly used statistics intended to reveal meaningful social interactions from telemetry data. Frequently, researchers studying animal social networks adopt proximity-based definitions of relationships; two individuals that spend a sufficient amount of time less than some fixed minimum distance apart are deemed to be connected and assigned an edge in the network (e.g., S. Z. Goldenberg, de Silva, Rasmussen, Douglas-Hamilton, & Wittemyer, 2014). The resulting graph is a summary of the data that might be interpreted as a point estimate in the space of possible social networks. In some situations, networks defined this way represent a helpful, inexpensively computed description of the population. However, Scharf et al. (2016) showed that networks defined based on proximity alone can sometimes lead to spurious connections in the inferred network that generative models are able to avoid. Figure 3 shows dynamic, pairwise connections among a seven killer whales. A proximity-based network includes connections across killer whale subtypes (A, B1, and B2), which contradicts expert knowledge of wildlife biologists that whales from different subtypes do not share social ties. The network estimated using the generative model of Scharf et al. (2016) did not identify any connections across subtypes.

In addition, networks defined as direct functions of the observed positions do not always acknowledge the presence of measurement error in the data, which can also lead to spurious and/or missed social relationships. When descriptive statistics are unable to reliably answer research questions, mechanistic models for animal movement that incorporate a social network as a collection of latent variables are required.

3.2 | Known network

Generative models conditioned on a known network represent statistical models for jointly dependent trajectories that rely on strong assumptions about the unobserved social network that drives the dependence across individuals. Namely, a network, $\mathcal{G}$, summarized by a time-indexed adjacency matrix, $\mathbf{A}(t)$, is assumed to be known with certainty throughout the study period. A general hierarchical framework given by Equation (1) and

$$\mu \mid \mathcal{G} \sim F_\mu(\mathcal{G}) \tag{10}$$

includes a model for the observed locations given the true trajectories, μ_i, coupled with a model for all m trajectories, $\mu = (\mu_1, ..., \mu_m)$, given the network. These approaches are most useful when there is a priori scientific knowledge about the underlying social network, and the primary goal is to account for network-related effects on movement to avoid confounding them with other relevant drivers of movement.

Often the social network that describes the pairwise relationships in these applications is assumed to be completely connected (i.e., $A_{ij}(t) = 1$ for all t, $i \neq j$). For example, Russell, Hanks, and Haran (2016) developed a statistical model for the group movement of guppies in which all individuals are assumed to be socially connected and the effect of the

FIGURE 3 Selection of the 21 possible pairs of seven individuals in the killer whale study. The plots displayed are for all (inter-type) pairs of killer whales that include the sole individual of type B1. The dotted line shows the proximity-based network defined such that individuals are deemed connected whenever they are separated by a distance less than 10 km. The solid line in each plot shows the inferred probability of a social connection during the 1 week study period (i.e., Pr $(A_{ij}(t) = 1)$), and the gray region depicts uncertainty as one standard deviation above and below the probability computed using samples from the posterior distribution (Reprinted with permission from Scharf et al. (2016). Copyright 2016 Institute of Mathematical Statistics)
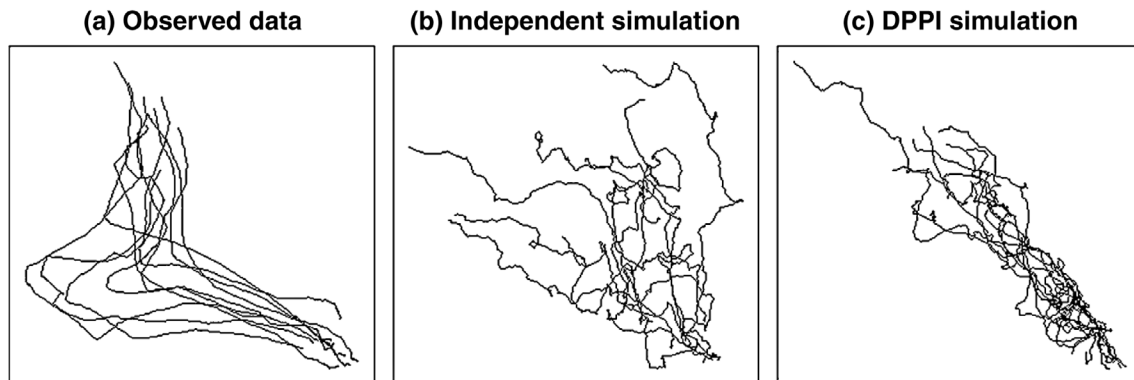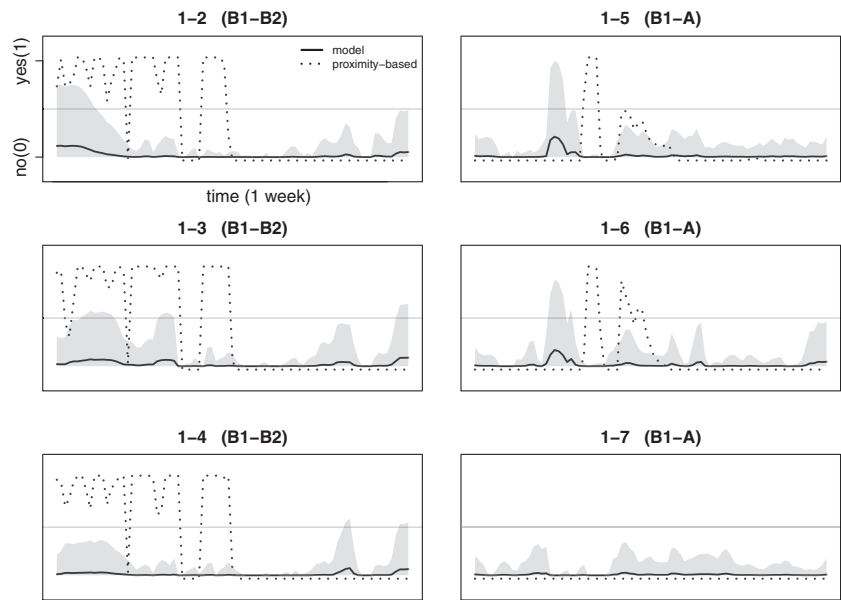

FIGURE 4 Group movement paths. (a) Plotted paths of a shoal of 10 guppies from Bode et al. (2012). (b) Plotted paths of a simulated realization from the CTCRW model without interactions. (c) Plotted paths of a simulated realization from the DPPI model with the attraction-repulsion point process interaction function (Reprinted with permission from Russell et al. (2016); Copyright 2016 Springer Nature)

relationships in the movement model depends on the proximity of each pair of individuals (see Figure 4). Previously, Brillinger, Preisler, and Wisdom (2011) described a simpler, but qualitatively similar, approach for the movement of a pair of elk. In both of these examples, the network has edge set that contains all $\binom{m}{2}$ possible pairs of vertices throughout the study period.

The fundamental challenge to defining a useful model for directly interacting individuals is describing mathematically how social connections manifest themselves in movement. Notationally, this means specifying $F_\mu(\mathcal{G})$ in Equation (10). For example, Calabrese et al. (2018) specified a model for joint movement in which trajectories evolved according to an additive combination of an overall drift and a random walk correlated across connected individuals. Trajectories arising from this model will tend to progress along parallel increments for connected individuals, even after accounting for an overall drift shared by the entire population, where the strength of the tendency to move in parallel is controlled by a correlation coefficient, $\rho \in [0, 1]$. The nonzero elements in the matrix denoted **D** in this article give the locations of 1's in the adjacency matrix of the social network. Scharf, Hooten, Johnson, and Durban (2018) specified a similar model for joint movement in which the random walk was correlated both in time and across individuals, though without the inclusion of a drift component.

Appropriately defining the link between the social network and movement is important for two reasons. First, it ensures that the movement model will achieve a reasonably good model fit, which is necessary to support any claims of scientific learning gained through application of the methodology. Second, it inherently defines the meaning of the

social network. A single study population may be usefully described with several possible social networks, all of which may differ in structure. The networks researchers can learn about through the study of movement will necessarily describe social connections that inform behavioral decisions on the part of the individuals about what locations on the landscape they should visit, and when.

Whether implicitly or explicitly, defined empirically or a priori, the network of relationships in these models is assumed to be known. In the next section, we provide a survey of recent methods for applications in which the network is unknown and must be inferred from the movement data.

3.3 | Unknown network

The additional modeling challenge that must be met to infer a latent social network from movement data is carefully defining the space of networks that could plausibly occur in the study population. Statistically, this means specifying a distribution over the support of possible $\mathcal{G}$ as a new layer in the hierarchical model denoted by

$$\mathcal{G} \,|\, \xi \sim F_{\mathcal{G}}(\xi). \tag{11}$$

Network spaces are inherently complex and high-dimensional; directly specifying interpretable parametric families of probability distributions is not typically possible. Simply specifying a uniform distribution across all possible networks often leads to hard to explore solution spaces, and fails to exclude scientifically incompatible networks.

Researchers have reduced the complexity of possible network configurations in various ways. For example, the joint model for movement introduced in Calabrese et al. (2018) is based on a time-varying network that at any time, t, is either completely connected ($\rho > 0$ using the authors' notation) or completely empty ($\rho = 0$). This assumption may be reasonable for applications involving herding species and reduces the number of network parameters to be estimated at each time point from $\binom{m}{2}$ to 1. In addition, the authors imposed a smoothness criterion on the time-evolution of the network to limit the frequency with which the connections change in time, further reducing the dimensionality. Two early contributions to the literature, Langrock et al. (2014) and Niu, Blackwell, and Skarin (2016), did not explicitly adopt the perspective of estimating a social network describing pairwise relationships; however, the methodologies yield a graphical interpretation that is closely related to other approaches. In both approaches, the movements of a small group of reindeer are described using a state-space formulation in which behavior is conditioned on a latent state variable defining whether an individual is "connected" or not. Connected individuals represent so-called "followers" whose movement is biased toward a single "leader," which is an abstracted point in space that may or may not correspond to an unobserved individual in the population. At a given time point, the graph to be estimated has a very particular form: it consists of a single central node with edges connecting the followers (sometimes called a "star" in the graph theory literature). Thus, the number of parameters to be estimated at each time point is reduced to m.

More recently, Scharf et al. (2018) developed a continuous-time movement model for killer whales in which a dynamic, weighted network describes how strongly connected individuals align their trajectories in parallel directions. The approach allows for more flexible social networks than those in Langrock et al. (2014), Niu et al. (2016), and Calabrese et al. (2018), which may be necessary for species whose social connections are not well-described by complete or star graphs. The model for the network relies on a latent-space formulation first proposed for networks by Hoff, Raftery, and Handcock (2002) in which the probability density for a particular network configuration at a given time is a function of the proximity of an arrangement of m actors in a d-dimensional social space. The parameterization of the probability distribution for the dynamic graph evaluated at a given time points is thus reduced from $\binom{m}{2}$ to md, where d is typically much less than m (often 2 or 3, which admits intuitive visualizations of the social space). A similar model was applied in Hooten, Scharf, Hefley, Pearse, and Weegman (2018) to migrating Sandhill cranes.

In both Scharf et al. (2018) and Hooten et al. (2018), the authors demonstrated that accounting for dependence across individuals provided opportunities for reducing the uncertainty in the true path taken by an individual. Essentially, positive correlation among connected individuals allows for relatively precise estimation of infrequently observed individuals' positions, provided regular observations are made about their socially connected counterparts. Figure 5 shows the reduction in uncertainty about the true location of Sandhill cranes over time after accounting for a latent, dynamic, weighted network of relationships.
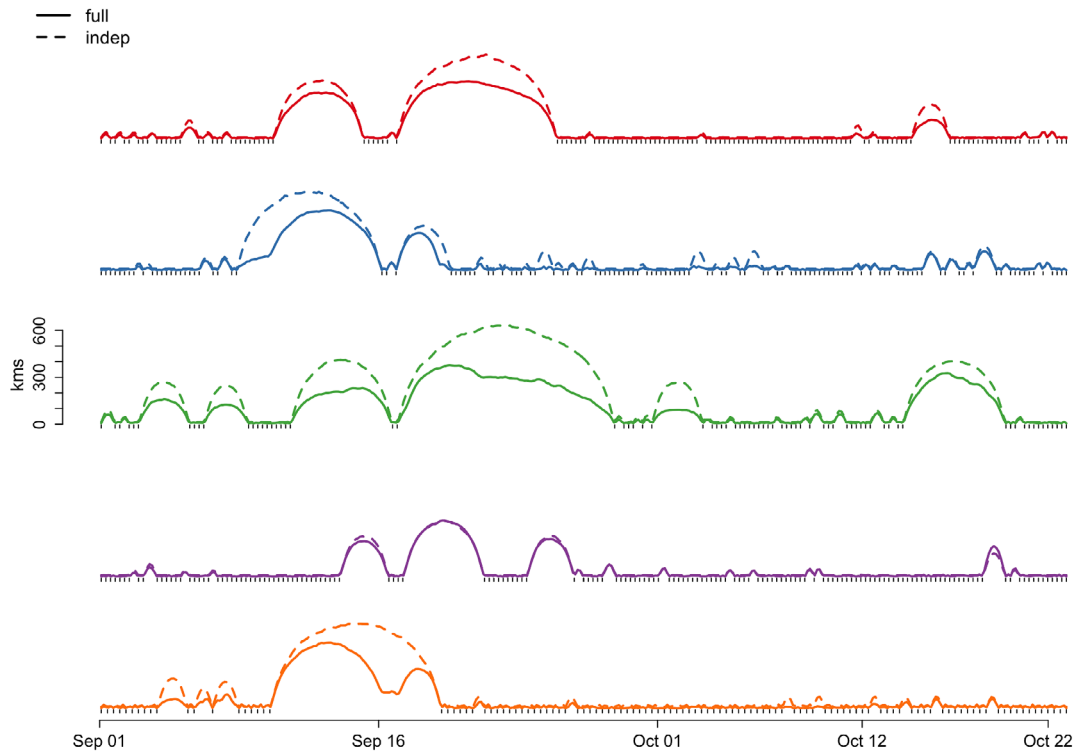
FIGURE 5 Location uncertainty for five individual cranes over time indicated by the radius of the 95% credible circle for $\mu_j(t)$ on the y-axis. The dashed lines represent the uncertainty inferred from models fit independently to each individual, whereas the solid lines represent the uncertainty resulting from the migratory network model. Rug plots show observation times (Reprinted with permission from Hooten et al. (2018). Copyright 2018 John Wiley & Sons Ltd)

FIGURE 6 Points and lines in the bottom of the figure represent the effects of attraction (dashed line) and alignment (dotted line) between individual i and its "ego-network" (polygons), defined as the collection all individuals that share a connection with i (Reprinted with permission from Scharf et al. (2016). Copyright 2016 Institute of Mathematical Statistics)
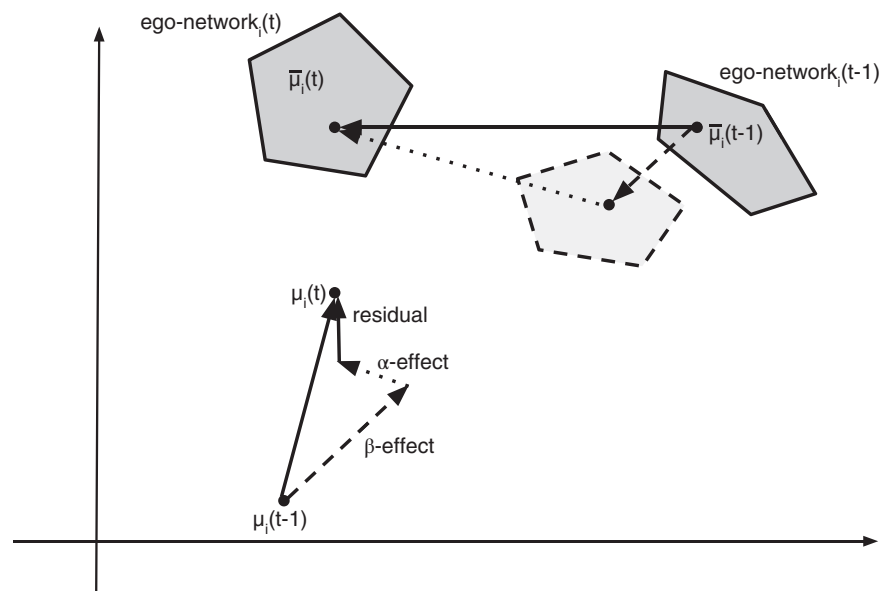
Models have also been developed that may be used to estimate both the link between behavior and pairwise relationships, and the latent network itself simultaneously. Scharf et al. (2016) proposed a discrete-time model in which a dynamic, binary network summarizes relationships among a population of seven killer whales. Two unknown parameters define the degree to which individuals are attracted/repulsed toward/away from each other, and the degree to which individuals align/anti-align their trajectories. Thus, in principle, this model could be used for both positively and negatively interacting species.

Figure 6 reproduced from Scharf et al. (2016) provides a schematic representation of the two channels of attraction (repulsion) and alignment (anti-alignment) through which the dynamic social network influences movement. The points in the bottom left of the figure show a hypothetical increment in the position process of individual i, and the solid-edged polygons represent the collective increment in position of all individuals that share a connection with i (its "ego-network"). The points in the middle of the polygons represent the average locations of the ego-network. The dashed line and polygon represent the effect of attraction alone, (β-effect) on individual i and its ego-network. The dotted lines represent the effect of positive alignment (α-effect), and the residual vector represents variability in movement not attributable to either effect. A strong attractive effect would manifest itself in observed telemetry data as a coming together of individual i and its ego-network. A strong aligning effect would manifest itself as a tendency for connected individuals to move along parallel trajectories (similar to Calabrese et al., 2018).

4 | CONCLUSIONS

Animal movement modeling has been a vibrant and growing field of research for decades. More recently, ecologists and statisticians have increasingly focused attention on the development of methods applicable to the study of multiple, dependent individuals. Advances in practical, implementable statistical models have required creativity and collaboration on the part of researchers to address considerable challenges. We briefly discuss a selection of the most pressing open problems in the field that continue to propel methodological reach.

4.1 | Indirect dependence

Although we discussed a number of ways to account for indirect dependence exhibited by individuals, many of these methods have rarely been implemented due to an absence of user-friendly software and computational limitations. However, there have been a number of recent software developments, such as advances in the "momentuHMM" package (McClintock & Michelot, 2018) for the R statistical programming environment that implements random effects within a HMM, the "TwoStepCLogit" R package (Craiu et al., 2016) that fits the two-stage algorithm for conditional logistic regression models, the work by Muff et al. (2019) on an efficient formulation of the same, and the "amt" R package (Signer, Fieberg, & Avgar, 2019) package for iSSA that facilitates fitting specific formulations of hierarchical movement models. More generally, the increasing number of platforms and decreasing computational burden for implementing Bayesian models has been a boon for hierarchical animal movement modeling (e.g., Bachl, Lindgren, Borchers, & Illian, 2019; NIMBLE Development Team, 2019; Plummer, 2018; Stan Development Team, 2019). As methods become more accessible to ecologists, we expect to see an increase in the use of the more rigorous methods for describing emergent behavior across individuals within a population.

Historically, ecologists have been forced by technological constraints to choose between monitoring a few individuals frequently, or many individuals rarely. As tools for monitoring many individuals at fine temporal scales become both less invasive and less costly, the constraints that guide study designs will need to include the computational challenges of analyzing so-called big data. Utilizing the entirety of high resolution movement data for several individuals over long periods of time directly may be unfeasible. Thus, researchers will need to carefully consider the relevant temporal and spatial scales of their research questions, and choose or potentially develop new methods that appropriately cohere. For example, Buderman, Hooten, Alldredge, et al. (2018) used the computationally demanding method proposed in Hanks et al. (2015) to model fine-scale cougar behavior across 1 month for two reasons: first, cougars in this system were expected to traverse their home-range within 1 month, and second, extending this model to a longer span of time was computationally unfeasible.

4.2 | Direct dependence

Several important challenges remain to be addressed in the study of directly dependent animal trajectories. For one, "negative" interactions, such as those arising in territorial settings, are equally if not more challenging to study from a methodological point of view, but have not yet received as much attention in the literature. Positive pairwise interactions are intuitively summarized by simple to compute quantities such as the amount of time two individuals spend within a

prespecified distance of one another. In contrast, summary statistics that distinguish negatively interacting pairs from independent ones are not as immediate. Thus, the lack of methodological development for negatively interacting individuals probably more accurately attributed to a scarcity of useful statistical models than to scientific disinterest.

Another set of challenges that hinder implementation of the existing methods for unknown networks are computational. Even with dimension-reducing latent-space approaches, the number of parameters to be estimated can grow rapidly with the number of individuals in the study population. Many models for joint movement are specified as instances of dependent Gaussian processes, which implies likelihood functions with dense, potentially massive covariance matrices that must be inverted. The development of alternative models admitting more easily calculated likelihoods, and/or approximate inference procedures would increase the size of analyzable data sets from dozens of individuals to hundreds or thousands.

Finally, both Scharf et al. (2018) and Hooten et al. (2018) demonstrated that accounting for positive dependence among multiple trajectories has the potential to drastically reduce uncertainty in estimates of the true locations of individuals. In essence, it is sometimes possible to use precise information about the location of one animal to infer the location of a connected individual for which fewer observations are available. This result has implication for the optimal design of future data collection efforts which are often constrained by the battery life available in radio tracking devices.

CONFLICT OF INTEREST
The authors have declared no conflicts of interest for this article.

AUTHOR CONTRIBUTIONS
Henry Scharf: Conceptualization; methodology; writing-original draft; writing-review and editing. **Frances Buderman:** Conceptualization; methodology; writing-original draft; writing-review and editing.

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