A lattice and random intermediate point sampling design for animal movement

Elizabeth Eisenhauer | Ephraim Hanks

Department of Statistics, The Pennsylvania State University, State College, Pennsylvania

Correspondence
Elizabeth Eisenhauer, Department of Statistics, The Pennsylvania State University, State College, PA 16802.
Email: eisenhauer@psu.edu

Funding information
NSF EEID, Grant/Award Number: 1414296; NIH, Grant/Award Number: GM116927-01

Abstract
Animal movement studies have become ubiquitous in animal ecology for the estimation of space use and the analysis of movement behavior. In these studies, animal movement data are primarily collected at regular time intervals. We propose an irregular sampling design that could lead to greater efficiency and information gain in animal movement studies. Our novel sampling design, called lattice and random intermediate point (LARI), combines samples at regular and random time intervals. We compare the LARI sampling design to regular sampling designs in an example with common black carpenter ant location data, an example with guppy location data, and a simulation study of movement with a point of attraction. We modify a general stochastic differential equation model to allow for irregular time intervals and use this framework to compare sampling designs. When parameters are estimated reasonably well, regular sampling results in greater precision and accuracy in prediction of missing data. However, in each of the data and simulation examples explored in this paper, LARI sampling results in more accurate and precise parameter estimation and, thus, better prediction of missing data as well. This result suggests that researchers might gain greater insight into underlying animal movement processes by choosing LARI sampling over regular sampling.

KEYWORDS
animal movement, animal tracking, ecology, sampling design, spatial statistics, stochastic differential equations

1 | INTRODUCTION

Animal movement studies advance scientific knowledge of animal behavior in space and time. Insight from animal movement models helps researchers understand how animals interact with human and environmental factors. For example, researchers have conducted analyses of wildlife telemetry data to predict the effect of climate change on species range (Schloss, Nuñez, & Lawler, 2012) and to assess the impact of roadways on gene flow in terrestrial vertebrate populations (Shepard, Kuhns, Dreslik, & Phillips, 2008). Furthermore, understanding the relationships between animals and their surroundings can benefit conservation efforts (Berger, 2004; Chester, 2012; Festa-Bianchet & Apollonio, 2003) and provide insight into disease dynamics (Conner & Miller, 2004; Wijeyakulasuriya, Hanks, Shaby, & Cross, 2019).

Researchers often record wildlife telemetry data at regular intervals (Forester et al., 2007; Kareiva & Shigesada, 1983; McDuie et al., 2019; Parlin, Nardone, Dougherty, Rebein, & Safi, 2018; Roeleke, Teige, Hoffmeister, Klingler, & Voigt, 2018; Weimerskirch et al., 2002) and occasionally at higher frequencies at times when finer movement behavior is of interest.
In a given animal movement study, assume data collection is set to begin at time $0$ and end at time $T$. Assume resources are limited and only $n$ samples will be collected in this time frame for a single individual. Sampling the animal's position at regular time intervals of length $h = \frac{T}{n-1}$ results in the data matrix

$$D_{\text{Regular}} = \begin{bmatrix} r_0 & r_h & r_{2h} & \ldots & r_{T-h} & r_T \end{bmatrix}'$$


(1)

There is evidence that increasing the frequency of regular samples greatly improves estimates of movement distance and territory size (Mills, Patterson, & Murray, 2006), but resource limitations often lead to difficulties in consistently obtaining samples at high frequencies without reducing the overall length of the study. In this work, we show that the use of sampling designs other than regular sampling can lead to better inference on parameters in animal movement models without requiring additional samples or reducing study duration. While Millspaugh and Marzluff (2001) mention the application of a range of sampling designs with stochastic components for wildlife telemetry studies, these designs have not been thoroughly compared in context and are rarely implemented.

There is a widely accepted view in geostatistics that samples at regular intervals in space lead to better interpolation of data, whereas clustered samples lead to better estimation of spatial covariance parameters (Zimmerman, 2006). To compromise between parameter estimation and prediction at unobserved locations, Zimmerman (2006) suggests the inclusion of samples with regular spacing as well as groups or pairs of points that are close together. One example of this is a “lattice plus close pairs” approach, in which at least half of the locations form a regular lattice in two-dimensional space, and the remaining points are randomly assigned within a disc centered at randomly selected lattice locations (Diggle & Lophaven, 2006). Diggle and Lophaven (2006) found that a “lattice plus close pairs” design performed better than a lattice alone or a lattice and infill approach in regard to spatial prediction.

Theoretical support for sampling at different scales is lacking in the geostatistical literature. On the contrary, systematic or regular sampling has been shown to be optimal within some subclasses of two-dimensional sampling designs in regard to minimizing variance of the sample mean (Bellhouse, 1977). However, few problems remain in animal movement modeling, in which the only goal is precise estimation of a population mean. Instead, we look to the experimental literature that evidences the superiority of irregular sampling for the detection of spatial patterns (Fortin, Drapeau, & Legendre, 1990; Oliver & Webster, 1986).

In this paper, we propose a sampling scheme for animal telemetry data inspired by the “lattice plus close pairs” geostatistical design. Our proposed approach, which we call the lattice and random intermediate point (LARI) design, requires data collection at regular time intervals coupled with one randomly selected time point in between each adjacent pair of regular samples. We conjecture that the regular time intervals will result in suitable temporal coverage, whereas the random intermediate points will capture behavior at short time lags. We suspect that capturing behavior at different time scales will correspond with improved estimation of movement parameters.

This LARI sampling design was motivated by a problem that arose in the collection of wood-nesting carpenter ant (Camponotus pennsylvanicus) movement data at The Pennsylvania State University. Members of the David Hughes Lab captured video footage of ants in a wooden nest over a 4-hr time frame and recorded coordinate locations of the ants at 1-s intervals (Modlmeier et al., 2019). The data collection procedure was manually expensive, requiring the recruitment, training, and labor of 17 undergraduate students (Modlmeier et al., 2019). As a new experiment was planned involving a large number of nests over a longer time frame, it became apparent that the data collection strategy previously employed would not be feasible at the necessary scale. Thus, we set out to develop a sampling design that would result in similar model inference while reducing the manual cost. Of course, this motivation is not limited to the ant example. Restrictions on data collection frequency and magnitude are commonplace in animal movement studies, especially those that employ tracking devices (Tomkiewicz, Fuller, Kie, & Bates, 2010).

We describe the LARI sampling scheme in detail in Section 2. In Section 3, we outline a stochastic differential equation (SDE) model for movement similar to that of Russell, Hanks, Haran, and Hughes (2018). In Section 4, we compare parameter estimation and prediction accuracy between sampling designs via a simulated example. In Section 5, we compare parameter estimates between sampling designs using subsamples of guppy movement data. In Section 6, we present a novel numerical estimation procedure, which we apply to the high-resolution carpenter ant movement data and implement to compare sampling designs.

### 2 A LARI SAMPLING SCHEME

In a given animal movement study, assume data collection is set to begin at time 0 and end at time $T$. Assume resources are limited and only $n$ samples will be collected in this time frame for a single individual. Sampling the animal's position at regular time intervals of length $h = \frac{T}{n-1}$ results in the data matrix

$$D_{\text{Regular}} = \begin{bmatrix} 0 & h & 2h & \ldots & T-h & T \end{bmatrix}'$$


(1)
where \( \mathbf{r}_t \equiv [x_t, y_t]' \) is the x- and y-coordinate vector of the animal’s position at time \( t \in \{0, h, 2h, \ldots, T-h, T\} \). While regular sampling minimizes the maximum time between observations, movement behavior occurring at finer time scales than those sampled is not captured in the observed data.

We propose a LARI sampling scheme, which produces the data matrix

\[
\mathbf{D}_{\text{LARI}} \equiv \begin{bmatrix}
0 & t_0^* & 2h & t_1^* & 4h & \ldots & T-2h & t_n^* & T \\
\mathbf{r}_0 & \mathbf{r}_n^* & \mathbf{r}_{2h} & \mathbf{r}_1^* & \mathbf{r}_{4h} & \ldots & \mathbf{r}_{T-2h} & \mathbf{r}_T^* & \mathbf{r}_T
\end{bmatrix}^\top,
\]

where

\[
t_i^* \sim \text{Uniform}(2hi, 2h(i+1)), \quad i \in \{0, 1, 2, \ldots, n\}.
\]

In practice, it may be more realistic to choose \( t_i^* \) from a discrete uniform distribution depending on the sampling resolution.

Both data matrices \( \mathbf{D}_{\text{Regular}} \) and \( \mathbf{D}_{\text{LARI}} \) contain \( n \) observations for a single individual. To collect data for multiple individuals over multiple time frames, repeat this procedure as necessary.

### 3 | SDE MODEL FOR ANIMAL MOVEMENT

We follow the works of Russell et al. (2018) and Hanks, Johnson, and Hooten (2017) and consider a flexible SDE model for an animal’s position \( \mathbf{r}_t \) at time \( t \), that is,

\[
d\mathbf{r}_t = \mathbf{v}_t dt
\]

\[
d\mathbf{v}_t = -\beta(\mathbf{v}_t - \mu(\mathbf{r}_t))dt + c(\mathbf{r}_t)I d\mathbf{w}_t,
\]

where \( \mathbf{v}_t \) is the velocity of the animal at time \( t \); \( \beta \) is the coefficient of friction (Nelson, 1967), which controls autocorrelation in movement; \( \mu(\mathbf{r}_t) \) is the mean drift in the direction of movement; \( c(\mathbf{r}_t) \) is a scalar that controls the variance in the stochastic term; \( I \) is a \( 2 \times 2 \) identity matrix; and \( d\mathbf{w}_t \) is independent Brownian motion in \( \mathbb{R}^2 \). This SDE framework is attractive because of the wide range of movement behaviors that can be modeled. For example, the right-hand side of (4) can be viewed as the sum of forces acting on the animal at time \( t \) and position \( \mathbf{r}_t \). For instance, there could be a force toward the center of the animal’s home range, toward the nearest food source, toward breeding grounds, toward higher or lower elevation, away from the nearest predator, or away from cooler temperatures. Depending on the time frame and study species, these forces could vary over time or space.

Brillinger, Preisler, Ager, and Kie (2012) used a similar SDE framework and adopted potential functions from particle and planetary movement models to model elk movement by setting \( \mu(\mathbf{r}_t) = -\nabla p(\mathbf{r}_t) \), the negative gradient of a potential surface \( p(\mathbf{r}_t) \). The potential surface is a continuous surface or grid with the highest values on the surface at repulsive locations, lowest values at attractive locations, and relatively central values in areas where the force is neutral. Under this model, the average animal in a population moves around a space avoiding those points of repulsion or areas with high potential and moving toward points of attraction or areas with low potential. A simple example of a potential surface is the quadratic function \( k(x^2 + y^2) \), which will be used in a simulation example in Section 4. This quadratic potential surface has a single point of attraction at the origin, as shown in Figure 1 with the parameter \( k = 1 \). The white arrows displayed in Figure 1 point down the gradient of the potential surface, in the direction of mean drift. One might utilize this potential surface in a model for movement of a central place forager, with movement centered around \( [0, 0]' \) and \( k \) controlling the strength of attraction to this central location. Potential surfaces can be much more complex than this example, as we will see in Section 6. For further details on the use of potential surfaces to model animal movement, see the work of Preisler, Ager, and Wisdom (2013).

The works of Russell, Hanks, Modlmeier, and Hughes (2017) and Russell et al. (2018) expanded the SDE framework of Brillinger et al. (2012) to include motility surfaces, which describe the overall speed independent of direction as a function of location. The motility surface is a surface or grid of values assigned on the space inhabited by the animal. High motility values are indicative of fast movement or high speed in the corresponding location. Low motility is indicative of slow movement.

The SDE model we define in this section is similar to that of Russell et al. (2018), with zero measurement error and assuming the motility surface is smooth. As in the work of Russell et al. (2018), we define the mean drift and magnitude of stochasticity with spatially varying motility and potential surfaces. The potential surface \( p(\mathbf{r}_t) \) captures spatially varying
directional bias (drift) through \(-\nabla p(r_t)\), whereas the motility surface \(m(r_t)\) models spatial variation in speed without directional bias by compressing and dilating time. The mean drift \(\mu(r_t)\) and magnitude of stochasticity \(c(r_t)\) are defined as

\[
\mu(r_t) \equiv m(r_t)[-\nabla p(r_t)] \quad \text{(5)}
\]
\[
c(r_t) \equiv \sigma m(r_t). \quad \text{(6)}
\]

where \(\sigma\) controls the magnitude of the random forces acting on the animal. We chose to ignore measurement error because the measurement error in our ant data is negligible. As sophisticated technology allows for greater accuracy in animal tracking, we expect the need for measurement error specification for animal location to diminish. When movement error is not negligible, state-space models can be used, with the SDE models (3)–(6) being a model for the true, but latent, animal position over time.

### 3.1 Numerical approximations

A closed-form solution to (3)–(6) only exists for very simple choices of \(m(\cdot)\) and \(p(\cdot)\). There is no closed-form solution whenever spatial constraints are present (e.g., Hanks et al., 2017; Russell et al., 2018). In this section, we present a general numerical approximation to the SDE, which is applicable in a broad range of settings including those where there is no closed-form solution.

The works of Hanks et al. (2017) and Russell et al. (2018, 2017) describe numerical approximations using samples at regular time intervals and do not consider irregular time lags between samples. Our discrete-time approximation approach is similar to that of Russell et al. (2018), but we extend their framework to the case where the intervals between observation times can vary. Developing numerical methods for irregular time intervals will make inference more straightforward when data are missing or irregularly sampled. To simplify the notation for irregular samples, we now change the subscript in equations from continuous time \(t\) to ordered observation number \(\tau\). Henceforth, \(r_\tau\) is the vector of elements in column \(\tau\), row 2 of a data matrix of the form (1) or (2).

Euler–Maruyama approximations are derived from Taylor series expansions (Kloeden & Platen, 2013) and are commonly used to numerically approximate SDE models because they are easy to calculate. The Euler–Maruyama method approximates (3) and (4) by

\[
r_{\tau+1} = r_\tau + v_\tau h_\tau \quad \text{(7)}
\]
\[
v_{\tau+1} = v_\tau - \beta(v_\tau - \mu(r_\tau)h_\tau) + c(r_\tau) w_\tau, \quad \text{(8)}
\]

where \(h_\tau\) is the change in time from observation \(\tau\) to observation \(\tau + 1\). Here, our approach differs from the SDE model of Russell et al. (2018), where \(h_\tau\) was constant with respect to \(\tau\). Substituting (7) into (8) following the work of Hanks et al. (2017) results in

\[
\frac{r_{\tau+2} - r_{\tau+1}}{h_{\tau+1}} - \frac{r_{\tau+1} - r_{\tau}}{h_\tau} = \beta h_\tau \left( \mu(r_\tau) - \frac{r_{\tau+1} - r_\tau}{h_\tau} \right) + c(r_\tau) h_\tau^{1/2} \epsilon_\tau, \quad \text{(9)}
\]

where \(\epsilon_\tau \sim \text{iid } N(0, I)\) and \(0\) is the zero vector in \(\mathbb{R}^2\). This can be reexpressed as

\[
r_{\tau+2} = r_{\tau+1} + h_{\tau+1} \frac{r_{\tau+1} - r_\tau}{h_\tau} + \beta h_\tau h_{\tau+1} \left( \mu(r_\tau) - \frac{r_{\tau+1} - r_\tau}{h_\tau} \right) + c(r_\tau) h_\tau^{1/2} h_{\tau+1} \epsilon_\tau, \quad \text{(10)}
\]
an equation in which the ant’s position is a function of the two previous observed positions.

In Supplemental Material A, we provide examples of potential and motility surfaces, which we simulate from using (10). These examples illustrate how changing the motility and potential surfaces affects the movement behavior described by the model.

4 | SIMULATION EXAMPLE

4.1 | Simulation from an SDE model with quadratic potential function

We conducted a simulation example to compare the sampling schemes in (1) and (2). We simulated data at a fine temporal scale from an SDE model with a quadratic potential function and constant motility surface. The quadratic function biases movement toward a single attraction point at \([0, 0]'\). This approximates real movement behavior exhibited by central place foragers such as the white-tailed deer (Tierson, Mattfeld, Sage, & Behrend, 1985). In this example, we have

\[
m(r_t) \equiv 1 \\
p(r_t) \equiv kr_t, 
\]

where \(k \in \mathbb{R}\) controls the strength of attraction to the central location \([0, 0]'\). Consequently,

\[
\mu(r_t) = -\nabla p(r_t) = -2kr_t \\
c(r_t) = \sigma.
\]

The set of SDEs (3) and (4) becomes

\[
dr_t = v_t dt \\
dv_t = -\beta[v_t - (-2kr_t)] dt + \sigma I d\mathbf{w}_t,
\]

and numerical approximation (9) becomes

\[
\frac{r_{t+2} - r_{t+1}}{h_{t+1}} - \frac{r_{t+1} - r_t}{h_t} = \beta h_t \left(-2kr_t - \frac{r_{t+1} - r_t}{h_t}\right) + h_t^{1/2} \sigma \epsilon_t.
\]

Since the simulated data are generated at regular time steps, we set \(h_t = h\) for all observations \(t\) and solve for \(r_{t+2}\) to get

\[
r_{t+2} = r_{t+1}(2 - \beta h) + r_t(\beta h - 1 - 2\beta kh^2) + h^{3/2} \sigma \epsilon_t,
\]

which is an autoregressive model of order 2.

We simulated movement data for one individual over \(n = 500\) time points with time step \(h = 1\) and model parameters \(\beta = 0.4, \alpha \equiv k\beta = 0.08,\) and \(\sigma = 0.5.\) Since the simulation of observation \(t\) requires observations \(t - 1\) and \(t - 2\) as input, we fixed the positions at the first two time points near the point of attraction \([0, 0]'\). Specifically, \(r_1 = r_2 = [1, 1]'\).

The next 498 time points were simulated recursively from (14). Figure 2 depicts one path simulated with this procedure. We will simulate 150 paths and consider each path separately. We will compare regular and LARI sampling schemes by subsampling each simulated path using (1) and (2) with \(h = 5\) and comparing subsamples.

We refer to the full simulation containing all \(x-\) and \(y\)-coordinates by \([r]\). The general notation for the positions included in the LARI or regular subsample is \([r]_\text{obs},\) and the positions removed by the subsampling procedure are \([r]_\text{unobs}\). Thus, the subsampling procedure is represented by

\[
[r]_\text{obs} = [r] \setminus [r]_\text{unobs}.
\]

4.2 | Parameter identifiability

In the work of Kloeden and Platen (2013), the authors derive vector and matrix ordinary differential equations for the vector mean and second moment of a general vector linear SDE. In this section, we will interpret this derivation in the
FIGURE 2  (a) Simulated data for an individual with gray lines connecting those data points that are adjacent in time. The single attraction point is displayed as a red “+.” (b) The quadratic potential surface with simulated positions for a single individual depicted in white.

context of (11) and (12). For simplicity, we describe this result in the x-direction only, where \( r_x(t) \) is the x component of the coordinate vector \( r_t \), \( v_x(t) \) is the x component of the coordinate vector \( v_t \), and \( w_x(t) \) is independent Brownian motion in \( \mathbb{R}^1 \).

We are interested in determining whether the parameters we intend to estimate (\( \beta \), \( \sigma \), and \( \alpha \)) are identifiable as we approach the stationary distribution (i.e., as \( t \to \infty \)). By combining (11) and (12), we obtain the vector SDE

\[
d \begin{bmatrix} r_x(t) \\ v_x(t) \end{bmatrix} = \begin{bmatrix} 0 & 1 \\ -2\alpha & -\beta \end{bmatrix} \begin{bmatrix} r_x(t) \\ v_x(t) \end{bmatrix} dt + \begin{bmatrix} 0 \\ \sigma \end{bmatrix} dw_x(t),
\]

which allows us to derive the vector mean

\[
\mathbf{n}(t) = E \left( \begin{bmatrix} r_x(t) \\ v_x(t) \end{bmatrix} \right) = \begin{bmatrix} 0 & 1 \\ -2\alpha & -\beta \end{bmatrix}^{-1} \frac{dn(t)}{dt}.
\]

As we approach the stationary distribution and \( \frac{dn(t)}{dt} = 0 \), the mean vector

\[
\mathbf{n}(t) = 0.
\]

Therefore, the second moment of the stationary distribution

\[
S(t) = E \left( \begin{bmatrix} r_x(t) \\ v_x(t) \end{bmatrix} \right) ^T = \text{Var} \left( \begin{bmatrix} r_x(t) \\ v_x(t) \end{bmatrix} \right)
\]

is found by solving the system of equations

\[
\frac{dS(t)}{dt} = \begin{bmatrix} 0 & 1 \\ -2\alpha & -\beta \end{bmatrix} S(t) + S(t) \begin{bmatrix} 0 & 1 \\ -2\alpha & -\beta \end{bmatrix} + \begin{bmatrix} 0 \\ \sigma \end{bmatrix} \begin{bmatrix} 0 \\ \sigma \end{bmatrix} ^T.
\]

The stationarity of the distribution implies \( \frac{dS(t)}{dt} = 0 \), which, along with (18), yields

\[
S(t) = \begin{bmatrix} \frac{\sigma^2}{2\beta} & 0 \\ \frac{\sigma^2}{4\beta\alpha} & \frac{\sigma^2}{4\beta\alpha} \end{bmatrix}.
\]

Thus, we have two equations and three unknowns, rendering \( \sigma \), \( \beta \), and \( \alpha \) unidentifiable.

This result highlights the value of having samples at short time lags. When telemetry data are sampled regularly at large time lags, the transient distribution will be well approximated by the stationary distribution, and parameters in the model may become unidentifiable or only weakly identifiable. Thus, we expect that the regular subsample will lead to unidentifiability in parameter estimation. In Section 4.3, we outline the model fitting procedure applied to the LARI and regular subsamples.
4.3 | Estimation of model parameters and missing values

Initially, we attempted a posterior approximation of the model parameters, ignoring the missing data. However, this approach led to poor parameter inference (see Supplemental Material B), which could be due to the large reduction in movement variability that occurs when data are subsampled. These results led to our decision to estimate the positions at unobserved time points, thus reintroducing an appropriate amount of variability into the movement paths.

To estimate $\beta$, $\alpha$, $\sigma$, and $\{r\}_{\text{unobs}}$, we took a Bayesian approach and constructed a Markov chain Monte Carlo (MCMC) algorithm to sample from the joint posterior $\pi(\alpha, \beta, \sigma, \{r\}_{\text{unobs}}|\{r\}_{\text{obs}})$. For details on the posterior distribution and the MCMC sampler, see Supplemental Material C.

4.4 | Simulation example results

We simulated 150 paths, subsampled the paths using both a LARI and a regular design, and individually fit each subsample using the estimation approach described in Section 4.3. We assessed the convergence of the MCMC algorithm in each case using Geweke’s convergence diagnostic (Geweke, 1991). Geweke’s convergence diagnostic quantifies the dissimilarity of the means of the first 10% and the last 50% of the Markov chain iterations. In Geweke’s convergence diagnostic, the test statistic for variable $\eta$ is a $z$-score, that is,

$$z = \frac{\bar{\eta}_{\text{first 10%}} - \bar{\eta}_{\text{last 50%}}}{SE},$$

where $\bar{\eta}_{\text{first 10%}}$ is the sample mean of the first 10% of the Markov chain, $\bar{\eta}_{\text{last 50%}}$ is the sample mean of the last 50% of the chain, and $SE$ is the asymptotic standard error of the difference, computed using spectral density estimates for the two sections of the chain.

For each subsample and each simulated path, Geweke’s convergence diagnostic was computed for the three parameters $\alpha$, $\beta$, and $\sigma$. We labeled a subsample “converged” if the absolute values of Geweke’s convergence diagnostics for all three chains were less than 3. By this definition, of the 300 subsamples, 76.3% converged. Specifically, 84% of the LARI subsamples and 68.7% of the regular subsamples converged. We removed all simulations where at least one subsample (regular or LARI) did not converge, leaving 87 of the 150 simulations for analysis.

Moreover, 95% equal-tailed credible intervals for the model parameters are shown for the 174 remaining subsamples in Figure 3. As depicted in Figure 3, many of the regular subsamples result in poor estimation of the model parameters. Only 46.6% of the 87 regular subsamples resulted in credible intervals containing all three true parameter values, compared to 78.4% of the 87 LARI subsamples. This result is consistent with the theoretical justification in Section 4.2, which suggests unidentifiability when we use a regular subsample at large enough time steps.

Although we have already obtained evidence in favor of LARI sampling for parameter estimation, we are also interested in the “best case” scenario where both subsamples capture the true parameter values in their 95% credible intervals. There are 34 remaining simulations in this “best case” subset. The model parameter 95% credible intervals for the “best case” subsamples are shown in Figure 4.

We are now limited to two subsets: the subsamples that led to convergence by our definition and the “best case” subsamples. For each of these subsets, we will compare parameter estimation and prediction of missing values between the LARI and regular sampling designs with eight metrics. We define these metrics in the following passages and display our results in Figures 5 and 6.

![FIGURE 3 95% equal-tailed credible intervals for each subsample. LARI = lattice and random intermediate point](image-url)
FIGURE 4 95% equal-tailed credible intervals for the “best case” subset.
LARI = lattice and random intermediate point.

FIGURE 5  Stacked histograms using all converged simulations (the absolute values of Geweke Z-scores for \( \alpha \), \( \beta \), and \( \sigma^2 \) were all less than 3). The dotted line delineates the mean of the lattice and random intermediate point (LARI) subsamples, and the solid line portrays the mean of the regular subsamples. CI = credible interval; MSPE = mean squared prediction error; PMSE = posterior mean squared error.

To assess parameter estimation accuracy, we found the posterior mean squared error (PMSE) for each of the model parameters \( \alpha \), \( \beta \), and \( \sigma^2 \). The PMSE of variable \( \eta \) is the mean squared difference between the MCMC draws \( \eta^{(i)} \) and the true parameter value \( \eta_{\text{true}} \), that is,

\[
\text{PMSE}(\eta) = \int (\eta - \eta_{\text{true}})^2 \pi(\eta | \{r\}_\text{obs}) d\eta \\
\approx \frac{1}{100,000} \sum_{i=1}^{100,000} (\eta^{(i)} - \eta_{\text{true}})^2.
\]

We constructed 95% equal-tailed credible intervals for \( \alpha \), \( \beta \), and \( \sigma^2 \) and recorded credible interval width to assess parameter estimation precision.

To assess prediction accuracy for missing time points, mean squared prediction errors (MSPEs) were found for each subsample, where

\[
\text{MSPE}(\{r\}_\text{unobs}) = \sum_{k \in \{r \in \{r\}_\text{unobs} \}} \left[ \hat{r}_k^{(i)} - r_k \right] \left[ \hat{r}_k^{(i)} - r_k \right],
\]

where \( \hat{r}_k^{(i)} \) is the MCMC draw at time point \( k \) for the \( i \)-th subsample.
We found the mean width of 95% equal-tailed credible intervals for missing values \( \{\mathbf{r}\}_{\text{unobs}} \) to assess precision of the predictions.

Figure 5 depicts the statistics for all converged simulations (that is, all with Geweke Z-scores for \( \alpha, \beta, \) and \( \sigma^2 \) less than 3), and Figure 6 looks at a further subset, the “best case” simulations (those that included the true values of \( \alpha, \beta, \) and \( \sigma^2 \) in their equal-tailed 95% credible intervals). The results displayed in Figure 5 indicate that the LARI subsamples outperform the regular subsamples with respect to 95% credible interval width and PMSE for \( \alpha, \beta, \) and \( \sigma^2 \). The LARI subsamples also outperform the regular subsamples on average when we compare them based on the metrics for predicting missing data. However, in the “best case” subset where LARI and regular subsamples both estimate the parameters well, the regular subsamples more accurately predict missing data. The missing data MSPEs from all but one of the LARI subsamples are lower than all MSPEs from the regular subsamples.

Thus, for the simulations that converged, the LARI sampling design led to better estimation of the model parameters \( \alpha, \beta, \) and \( \sigma \) as well as better prediction of missing locations; however, when both LARI and regular subsamples estimated the parameters well, the regular sampling design led to greater accuracy and precision in the prediction of missing data points. This result is consistent with the hypothesis that the variability in time intervals between observations in the LARI design leads to a better understanding of movement behavior through greater accuracy in model parameter estimation.

To better understand the missing data prediction results, we explore one of the “best case” simulations. In Figure 7, we plot the true \( x \)- and \( y \)-coordinates for the first 50 time points with corresponding 95% credible intervals. As shown in Figure 7, sampling at regular intervals often results in smaller credible intervals for unobserved values. We suspect this is because the LARI design includes larger time gaps than regular sampling, which disproportionately affects the mean of credible interval widths.

5 | GUPPY DATA EXAMPLE

In our first data example, we will use movement data from a captive population of guppies (Poecilia reticulata). The group of guppies was released in the bottom-right corner of a flat-bottomed square tank and swam toward a sheltered area in the opposite corner of the tank. The data consist of 360 observations recorded at 0.1-s intervals for each of 10 guppies. For more information regarding data collection, see the work of Bode et al. (2012). After fitting an SDE to the full data, we will compare the sampling schemes in (1) and (2) by subsampling the data and comparing the resulting model fits.
5.1 SDE model

As in the simulation example, we can represent the movement of individual guppies with a set of SDEs. In this example, we define motility and potential surfaces

\[ m(r_t) \equiv 1 \]
\[ p(r_t) \equiv k |r_t - a|, \]

where \( k \in \mathbb{R} \) controls the strength of the drift toward a known point of attraction \( a = [281 \ 434]' \) in the sheltered corner of the tank. The potential surface is defined in this way to elicit a constant force toward the point of attraction. This specification of potential and motility surfaces results in mean drift and magnitude of stochasticity

\[ \mu(r_t) = -\nabla p(r_t) = -k \times \text{sign}(r_t - a) \]
\[ c(r_t) = \sigma. \]

The set of SDEs (3) and (4) becomes

\[ dr_t = v_t dt \]
\[ d\dot{v}_t = -\beta [v_t - (-k \times \text{sign}(r_t - a))] dt + \sigma d\omega_t, \]

and numerical approximation (9) becomes

\[ \frac{r_{t+1} - r_t}{h_t} - \frac{r_{t+1} - r_t}{h_t} = \beta h_t \left( -k \times \text{sign}(r_t - a) - \frac{r_{t+1} - r_t}{h_t} \right) + h_t^{1/2} \sigma \epsilon_t. \]

Linear regression was implemented to estimate \( k, \beta, \) and \( \sigma^2. \)

5.2 Results

We implemented a data subsampling procedure that resulted in three regular subsamples and 300 LARI subsamples. The regular subsamples were recorded at 0.3-s intervals beginning at each of the first three time points. For each of the regular subsamples, 100 corresponding LARI subsamples were collected, which consisted of every other sample from the regular data (i.e., regular samples at 0.6-s intervals) coupled with a random time point selected from the observations in each subinterval. This resulted in three groups of subsamples, each consisting of one regular subsample and 100 corresponding LARI subsamples.

The potential surface estimated with the full data is shown in Figure 8, with observations depicted in white. The potential surfaces estimated with subsampled data are similar in appearance, so we analyze them by comparing estimates.
of $k$, $\beta$, and $\sigma^2$. The three groups of subsamples resulted in identical conclusions, so we chose a random group to plot in Figure 9. In Figure 9, we display the parameter estimation results for $k$, $\beta$, and $\sigma^2$. While all subsamples led to an underestimation of the model parameters compared to the full data, the LARI subsamples are closer to the full data. In particular, when estimating $\sigma^2$, the LARI subsamples always outperform the regular subsample.

6 CARPENTER ANT EXAMPLE

We now turn to the data set introduced in Section 1, which consists of the positions of 78 ants at 1-s intervals over a 4-hr time frame (14,401 total observations per ant). Researchers observed the ants in a 200 × 65 × 6 mm wooden nest, shown in Figure 10 along with the positions of all ants at all time points. The ants could enter or exit the nest at any time to utilize a separate foraging area. The data collection procedure is described in further detail by Modlmeier et al. (2019). In Figure 11, we illustrate movement observed for one individual who stayed inside the nest throughout the 4-hr time frame.

From these data, we obtained four data sets for comparison, one of which is the full data (1-s intervals). The three additional data sets are subsamples from the full data; we produced one with the regular sampling design using $h = 3$ s, one data set with the LARI sampling design using $h = 5$ s, and one with the regular sampling design using $h = 5$ s. Ants display “stop and start” behavior, but the SDE model alone cannot handle state switching. Thus, we removed observations where the ants were stationary within each data set. After the removal of stationary observations, a total of 232,571 observations...
remained in the full data set, the largest of the four data sets. Similar to the work of Russell et al. (2018), we only consider modeling ant movement when ants are in motion.

### 6.1 Ant movement model

In this example, we apply the framework from (9) to model ant movement behavior. We represent the surface of the ant nest using $J = 9,998$ grid cells ($1 \times 1$ mm). Following the work of Russell et al. (2018), we specify spatially varying motility and potential surfaces to capture spatial heterogeneity in ant movement. The zeroth-order spline representations of the potential and motility surfaces evaluated at position $r_\tau$ are

$$ p(r_\tau) \equiv \sum_{j=1}^{J} p_j s_j(r_\tau), $$

$$ m(r_\tau) \equiv \sum_{j=1}^{J} m_j s_j(r_\tau), $$

where

$$ s_j(r_\tau) \equiv \begin{cases} 1, & r_\tau \text{ in } j\text{th grid cell} \\ 0, & \text{otherwise} \end{cases} $$

and $p_j$ and $m_j$ are the potential and motility surfaces, respectively, evaluated in grid cell $j$. Of course, there are other basis functions we could use to build potential and motility surfaces, such as thin plate splines. However, thin plate splines and other bases are more difficult to work with in the constrained geometry of the ant nest.

Model Equation (9) has infinitely many solutions if constraints are not imposed. To obtain identifiability, we fix $\sigma = 1$ as in the work of Russell et al. (2018). Russell et al. (2018) took a Bayesian approach to parameter estimation with a similar model. However, our novel approximation in (10) allows for a direct evaluation of the likelihood of animal locations observed at irregular time intervals. We propose an algorithm for the estimation of model parameters based on maximizing the likelihood (10) while penalizing the roughness of the potential and motility surfaces. Modlmeier et al. (2019) used a related algorithm, but only allowing for regularly sampled data. Modlmeier et al. (2019) also do not provide full mathematical details of the algorithm, which we provide in summary here and in detail in Supplemental Material D.

We estimate $p \equiv [p_1 \ldots p_J]'$ and $m \equiv [m_1 \ldots m_J]'$ with an iterative procedure beginning with model Equation (9). Rewriting (9), we have

$$ \frac{r_{r+2} - r_{r+1}}{h_{r+1}} - \frac{r_{r+1} - r_r}{h_r} \sim N \left( \beta h_r \left( \mu(r_r) - \frac{r_{r+1} - r_r}{h_r} \right), \text{diag} \left( c^2(r_r)h_r \right) \right), $$

where $\mu(r_r) = m(r_r)[ -\nabla p(r_r)]$ is estimated as a function of $m$ and $p$ and $c(r_r) = m(r_r)$ is estimated as a function of $m$. Thus, we refer to $p$ as a mean parameter, and $m$ could be considered both a mean and a variance parameter. However, we will estimate $m$ using the variance, and thus, we refer to it as a variance parameter.
We hold out 20% of the data to use when choosing the tuning parameter $\lambda$, which controls the smoothness of the surfaces, later in the procedure. The remaining 80% of the data are fit simultaneously for all ants, assuming ants move independently and there is no correlation in the $x$ and $y$ components of movement. The procedure is similar to restricted maximum likelihood approaches common in mixed models, as we use residuals to estimate covariance parameters, which are then used to estimate mean parameters. Our proposed approach is as follows.

1. Obtain a preliminary estimate of mean parameters ($\beta$ and $p$) assuming the motility surface is constant (model errors are independent and identically distributed).
2. Estimate variance parameters ($m$) using residuals from Step 1.
3. Estimate mean parameters ($\beta$ and $p$) conditioned on the variance estimates from Step 2.

For details about the estimation approach, refer to Supplemental Material D.

### 6.2 Results

Section 6.1 describes a computationally efficient method of fitting spatially varying coefficients in SDE movement models. We completed the three-step procedure for 17 values of the tuning parameter using the full data (232,571 total observations) in less than 25 min. We completed the procedure in the programming language R (Version 3.5.2) on a MacBook Pro with a 2.9-GHz Intel Core i5 processor and 8 GB of 2133-MHz LPDDR3 RAM.

We estimated motility and potential surfaces for four samples: the full data with observations at 1-s intervals, a subsample with observations every 3 s, a subsample with observations every 5 s, and a LARI subsample with regular samples every 10 s coupled with a random point in between each pair of regular samples. The “10 s” LARI sample and the “every 5 s” regular sample have an equal number of observations; hence, a comparison of the results from these two data sets amounts to a direct comparison of the LARI sampling scheme to the regular sampling scheme for these data.

For each of the four samples, we chose the optimal value of $\lambda$ separately based on prediction accuracy on the holdout set. We chose $\log(\lambda) = 0$ for the full data, $\log(\lambda) = 2$ for the “every 3 s” sample, $\log(\lambda) = 3$ for the “every 5 s” sample, and $\log(\lambda) = 4$ for the “10 s” LARI sample.

Figure 12 displays the estimated log motility surfaces for the four data sets. Since high motility indicates high activity, it is evident from the plots that the ants moved more quickly in the center chambers (Modlmeier et al., 2019). Assuming the motility surface generated with the full data is closest to the truth, we found mean squared errors (MSEs) of the log motility surfaces in Figure 12b–d by summing up squared differences between those surfaces and the surface in Figure 12a over all grid cells. As shown in the text in Figure 12, the MSE for the “10 s” LARI sampling scheme is smaller than that for the “every 5 s” sampling scheme, which suggests that the motility surface was better estimated with the LARI subsample than with the regular subsample of the same size. Each of the three subsamples underestimated the motility surface compared to the full data, a sign that, regardless of sampling design, we lost information about the motility surface by subsampling (see Figure 13).

In Figure 14, we show the estimated potential surfaces and gradient vectors. The gradient vectors depict the negative gradient of the potential surface scaled by 5 to improve visibility. We chose to plot the gradient vectors in every third...
FIGURE 13  Differences between the estimated log motility surfaces from each of the subsamples and the full data (calculated by grid cell). Negative values indicate underestimation of the motility surface. LARI = lattice and random intermediate point. (a) Every 3 s - Every 1 s; (b) Every 5 s - Every 1 s; (c) 10 s LARI - Every 1 s

FIGURE 14  Potential surfaces estimated with the four samples. The same potential surfaces are plotted in three dimensions on the left (using the rayshader R package) and in two dimensions on the right with gradient vectors pointing down the gradient of the potential surface. LARI = lattice and random intermediate point; MSD = mean squared distance. (a) Full Data; (b) Every 3 s, MSD = 18.1455; (c) Every 5 s, MSD = 21.2761; (d) 10 s LARI, MSD = 14.8337

grid cell for visual clarity. Since the potential surface is identifiable only up to an additive constant, we subtracted the mean from each potential surface to view them on roughly the same scale. We carried out comparisons between potential surfaces through mean squared distance (MSD) between the ends of the gradient vectors generated from the full data and those generated from the subsample. Of the three subsamples, the potential surface estimated with the “10 s” LARI subsample had the smallest MSD (see Table 1). We then decomposed the MSD into two additional metrics: mean error in magnitude and angle of the gradient vectors. The “10 s” LARI design resulted in a smaller error in the angle of the gradient vectors compared to the “every 5 s” design, but the “every 5 s” design resulted in a smaller mean error in gradient vector magnitude (see Table 1). On average, all three potential surfaces estimated with subsamples of the data are too smooth, that is, the gradient vectors are biased toward zero (see Table 1).
TABLE 1  Potential surface error statistics for the three subsamples

|                        | Every 3 s | Every 5 s | 10 s LARI |
|------------------------|-----------|-----------|-----------|
| Mean error in gradient vector magnitude | −0.2216  | −0.5045  | −1.624    |
| Mean error in gradient vector angle       | −0.0317  | 0.0565    | 0.0164    |
| MSD between gradient vectors              | 18.1455  | 21.2761   | 14.8337   |

Note. LARI = lattice and random intermediate point; MSD = mean squared distance.

FIGURE 15  Statistics calculated for the motility and potential surfaces fit using 50 different “10 s” lattice and random intermediate point subsamples (orange) are compared to statistics from the “every 5 s” subsample (blue). MSD = mean squared distance; MSE = mean squared error. (a) Potential Surface MSD; (b) Log Motility Surface MSE; (c) Mean Error in Potential Gradient Vector Magnitude; (d) Mean Error in Potential Gradient Vector Angle

Since the LARI sampling scheme requires random samples in each 10-s time interval, there are 91,439 possible “10 s” LARI subsamples. To evaluate the variability attributed to this random component, we took 50 different “10 s” LARI subsamples and fit each subsample separately. We found that the “10 s” LARI subsample consistently outperformed the “every 5 s” subsample in regard to all the metrics we looked at except magnitude of potential surface gradient vectors (see Figure 15).

7 | DISCUSSION

The simulation, guppy data, and ant data examples describe vastly different systems, but the sampling procedures laid out in Section 2 and the general model framework described in Section 3 were applicable in all three cases. We chose to highlight these three examples to emphasize the generalizability of the SDE framework and our proposed sampling approach. In all of the examples, the LARI sampling design led to greater accuracy in parameter estimation compared to samples at regular time intervals. As shown in the simulation example in Section 4, the LARI subsample also resulted in better prediction of missing values compared to the regular subsample. We conclude that when conducting animal movement research on data similar to that examined in this paper, a LARI sample is preferable to a regular sample of the same sample size and duration.

We determined that predicting finer scale movement (infill) was greatly useful for parameter estimation in the simulation example (see Supplemental Material B for details). This result implies that imputation of missing data at a finer scale might improve parameter estimation in the guppy and ant data examples as well. In the ant example, we found that the motility surfaces were underestimated using both regular and LARI sampling schemes. Augmenting observations with additional latent infill points in the ant example would introduce more variation in the movement paths, potentially reducing the underestimation of the motility surface. In the guppy example, all three parameters were underestimated when the data were subsampled, suggesting that augmenting observations might be useful here as well. However, in the simulation example, predicting missing data with the Metropolis-within-Gibbs algorithm was computationally intensive. We needed 90 hr of computational time on a high-performance computing cluster to simulate, subsample, and fit the 150 data sets.

While computational complexity was an issue in the simulation example, the multistep model fitting procedure in the ant example was extremely computationally efficient. For each sample, less than 25 min on a laptop computer was...
required to fit the model with a range of 17 different tuning parameter values. The scalability and computational feasibility of adding components to this model are huge assets.

In this paper, we have presented a general SDE modeling framework along with three model fitting procedures. The SDE framework has a wide range of possible extensions, including the addition of known seasonal variation, asynchronous movement across individuals, and state switching. The model framework as presented here assumes the animals are in constant motion throughout the study period, allowing us to describe movement behavior while an individual is in motion but not when the individual is stationary. In the ant example, we met this restriction by removing all data points where the ants were not moving. The addition of state switching would allow us to capture the “start and stop” behavior in the ant data and could be used to predict finer scale movement.

In this paper, we have compared two sampling designs in the context of animal movement. Thus, we have barely scraped the surface of a research area that is largely unexplored: optimal sampling for animal movement. As of present, there is no comprehensive guide to sampling design for animal movement. A thorough examination of sampling design for animal movement would allow researchers to allocate resources more efficiently and discover details of animal movement behavior that might otherwise be lost.

DATA AVAILABILITY

The raw carpenter ant data are available through Dryad (DOI: 10.5061/dryad.sh4m4s6), as are the guppy data (DOI: 10.5061/dryad.kt3109v7).

ORCID

Elizabeth Eisenhauer https://orcid.org/0000-0001-6887-4386

REFERENCES

Bellhouse, D. R. (1977). Some optimal designs for sampling in two dimensions. Biometrika, 64(3), 605–611.
Berger, J. (2004). The last mile: How to sustain long-distance migration in mammals. Conservation Biology, 18(2), 320–331.
Bode, N. W. F., Franks, D. W., Wood, A. J., Piercy, J. J. B., Croft, D. P., & Codling, E. A. (2012). Distinguishing social from nonsocial navigation in moving animal groups. The American Naturalist, 179(5), 621–632.
Brillinger, D. R., Preisler, H. K., Ager, A. A., & Kie, J. G. (2012). The use of potential functions in modelling animal movement. In Selected works of David Brillinger. (pp. 385–409). New York, NY: Springer.
Chester, C. C. (2012). Conservation across borders: Biodiversity in an interdependent world. Washington, DC: Island Press.
Conner, M. M., & Miller, M. W. (2004). Movement patterns and spatial epidemiology of a prion disease in mule deer population units. Ecological Applications, 14(6), 1870–1881.
Diggle, P., & Lophaven, S. (2006). Bayesian geostatistical design. Scandinavian Journal of Statistics, 33(1), 53–64.
Festa-Bianchet, M., & Appolonio, M. (2003). Animal behavior and wildlife conservation. Washington, DC: Island Press.
Forester, J. D., Ives, A. R., Turner, M. G., Anderson, D. P., Fortin, D., Beyer, H. L., … Boyce, M. S. (2007). State-space models link elk movement patterns to landscape characteristics in Yellowstone National Park. Ecological Monographs, 77(2), 285–299.
Fortin, M.-J., Drapeau, P., & Legendre, P. (1990). Spatial autocorrelation and sampling design in plant ecology. In Progress in theoretical vegetation science. (pp. 209–222). Dordrecht, The Netherlands: Springer.
Geweke, J. F. (1991). Evaluating the accuracy of sampling-based approaches to the calculation of posterior moments. Staff Report 148. Minneapolis, MN: Federal Reserve Bank of Minneapolis.
Hanks, E. M., Johnson, D. S., & Hooten, M. B. (2017). Reflected stochastic differential equation models for constrained animal movement. Journal of Agricultural, Biological, and Environmental Statistics, 22(3), 353–372.
Kareiva, P. M., & Shigesada, N. (1983). Analyzing insect movement as a correlated random walk. Oecologia, 56(2–3), 234–238.
Kloeden, P. E., & Platen, E. (2013). Stochastic Modelling and Applied Probability (Vol. 23). Numerical solution of stochastic differential equations. Berlin, Germany: Springer Science & Business Media.
McDuie, F., Casaza, M. L., Overton, C. T., Herzog, M. P., Hartman, C. A., Peterson, S. H., … Ackerman, J. T. (2019). GPS tracking data reveals daily spatio-temporal movement patterns of waterfowl. Movement Ecology, 7(1). Article No. 6.
Mills, K. J., Patterson, B. R., & Murray, D. L. (2006). Effects of variable sampling frequencies on GPS transmitter efficiency and estimated wolf home range size and movement distance. Wildlife Society Bulletin, 34(5), 1463–1469.
Millspaugh, J., & Marzluff, J. M. (2001). Radio tracking and animal populations. San Diego, CA: Academic Press.
Modlmeier, A. P., Colman, E., Hanks, E. M., Bringenberg, R., Bansal, S., & Hughes, D. P. (2019). Ant colonies maintain social homeostasis in the face of decreased density. eLife, 8, e38473.
Nelson, E. (1967). The Ornstein-Uhlenbeck theory of Brownian motion. In Dynamical theories of Brownian motion. (pp. 45–52). Princeton, NJ: Princeton University Press.
Oliver, M. A., & Webster, R. (1986). Combining nested and linear sampling for determining the scale and form of spatial variation of regionalized variables. Geographical Analysis, 18(3), 227–242.

Parlin, A. F., Nardone, J. A., Dougherty, J. K., Rebein, M., Safi, K., & Schaeffer, P. J. (2018). Activity and movement of free-living box turtles are largely independent of ambient and thermal conditions. Movement Ecology, 6. Article No. 12.

Preisler, H. K., Ager, A. A., & Wisdom, M. J. (2013). Analyzing animal movement patterns using potential functions. Ecosphere, 4(3), 1–13.

Richardson, P. L., Wakefield, E. D., & Phillips, R. A. (2018). Flight speed and performance of the wandering albatross with respect to wind. Movement Ecology, 6(1). Article No. 3.

Roeleke, M., Teige, T., Hoffmeister, U., Klingler, F., & Voigt, C. C. (2018). Aerial-hawking bats adjust their use of space to the lunar cycle. Movement Ecology, 6(1). Article No. 11.

Russell, J. C., Hanks, E. M., Haran, M., & Hughes, D. (2018). A spatially varying stochastic differential equation model for animal movement. The Annals of Applied Statistics, 12(2), 1312–1331.

Russell, J. C., Hanks, E. M., Modlmeier, A. P., & Hughes, D. P. (2017). Modeling collective animal movement through interactions in behavioral states. Journal of Agricultural, Biological and Environmental Statistics, 22(3), 313–334.

Schloss, C. A., Nuñez, T. A., & Lawler, J. J. (2012). Dispersal will limit ability of mammals to track climate change in the Western Hemisphere. Proceedings of the National Academy of Sciences, 109(22), 8606–8611.

Shepard, D. B., Kuhns, A. R., Dreslik, M. J., & Phillips, C. A. (2008). Roads as barriers to animal movement in fragmented landscapes. Animal Conservation, 11(4), 288–296.

Terson, W. C., Mattfeld, G. F., Sage, R. W., & Behrend, D. F. (1985). Seasonal movements and home ranges of white-tailed deer in the Adirondacks. The Journal of Wildlife Management, 49(3), 760–769.

Tomkiewicz, S. M., Fuller, M. R., Kie, J. G., & Bates, K. K. (2010). Global positioning system and associated technologies in animal behaviour and ecological research. Philosophical Transactions of the Royal Society B: Biological Sciences, 365(1550), 2163–2176.

Weimerskirch, H., Bonadonna, F., Bailleul, F., Mabile, G., Dell’Omo, G., & Lipp, H.-P. (2002). GPS tracking of foraging albatrosses. Science, 295(5558), 1259.

Wijeyakulasuriya, D. A., Hanks, E. M., Shaby, B. A., & Cross, P. C. (2019). Extreme value-based methods for modeling elk yearly movements. Journal of Agricultural, Biological and Environmental Statistics, 24(1), 73–91.

Zimmerman, D. L. (2006). Optimal network design for spatial prediction, covariance parameter estimation, and empirical prediction. Environmetrics, 17(6), 635–652.

SUPPORTING INFORMATION
Additional supporting information may be found online in the Supporting Information section at the end of the article.

How to cite this article: Eisenhauer E, Hanks E. A lattice and random intermediate point sampling design for animal movement. Environmetrics. 2020;31:e2618. https://doi.org/10.1002/env.2618