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RESEARCH ARTICLE

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An intuitive method to calculate the utilization distribution of an animal from step-selection analysis

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Abstract

1. Step-selection analysis (SSA) is a popular tool for estimating resource/habitat selection conditional on the local availability of conditions as determined by an animal's movement capacity. These models can be subsequently used to parameterize a movement model; however, most SSAs focus instead merely on interpreting the direction and magnitude of model coefficients. This is at least partly due to perceived complexities of generating such models through simulation or Partial Differential Equation (PDE)-based approaches, suggesting a need for alternative methods that are intuitive, approachable, and ideally, already familiar to ecological application.
2. We advocate here for the full predictive functionality of SSA and provide methods to use a fitted step selection function to predict an animal's space use. Specifically, we use fundamental mathematical principles to construct a transition matrix from the step selection movement process. We demonstrate that transition matrices can efficiently produce the emergent spatial pattern from SSA using two different methods (eigen decomposition and iterations). This alleviates the need for thousands of simulations of the underlying model while leveraging a well-established tool in applied ecology.
3. We show how such matrices may be parameterized under competing definitions of the underlying movement kernel and link these back to realistic ecological processes. To emphasize the flexibility of this approach, we apply these transition matrices to field data from two species with markedly different movement capacities and strategies: wild pigs (*Sus scrofa*) and long-tailed tits (*Aegithalos caudatus*). We discuss the caveats in transition matrix parameterization and resulting predictions of space use with respect to the underlying movement process and provide suggestions for application of this procedure to SSA.
4. Our framework represents a powerful tool for space-use prediction from SSA while also highlighting critical gaps in our current knowledge about and tools to describe animal space-use processes. In particular, we discuss higher order Markovian processes and spatiotemporally dynamic variables as particularly important topics for further development.

KEYWORDS
home range, movement ecology, step-selection analysis, utilisation distribution

1 | INTRODUCTION

Accurate predictions of animal space use allow a greater understanding of species and habitat interactions, but they require substantial knowledge of how behaviour and movement processes relate to eventual emergent patterns (Gomez et al., 2025; Kernohana et al., 2001; Patterson et al., 2008). An animal's space use refers to the way that the animal occupies and interacts with their landscape to fulfil their ecological and behavioural needs. Space use can first be defined broadly as their range, which is the geographic area of the animals' whereabouts. Space use can be further characterized as an occurrence distribution which describes the recent space use of an animal, or as a utilization distribution, which represents locations visited and the time spent there (Powell, 2000) and measures the probability of finding an animal at a location at a particular time. Detailed movement data can be encapsulated as a utilization distribution, defining an animal's intensity of space use as a probability density (Fieberg & Börger, 2012). Traditional space use predictions often ignore movement processes in favour of phenomenological descriptions (Elith & Leathwick, 2009; Moorcroft, 2012; Potts, Börger, et al., 2022). For example, animal space-use patterns are commonly analysed by describing the spatial pattern of the recorded locations using non-parametric methods such as kernel density estimation (Seaman & Powell, 1996; Worton, 1989), which estimates occurrence distribution or minimum convex polygons (Nilsen et al., 2008), that estimate a range. These methods can provide useful ecological insight for studies of, for example, range size (Börger et al., 2006), spatial overlap (Winner et al., 2018) and core areas (Vander Wal & Rodgers, 2012). Whilst kernel density estimation describes the occurrence distribution of an animal, range estimates can be unrealistic when data is sparse or movement patterns are irregular (Fleming et al., 2015). Furthermore, these descriptions of space use typically consider only the local density and arrangement of animal relocations while ignoring the movement from one location to the next. Advancements that include autocorrelation between locations in space-use models have proven more robust than descriptive models (Benhamou, 2011; Fleming et al., 2015; Kranstauber et al., 2012), but like their predecessors, these methods do not consider the key ecological mechanisms that are driving the space use patterns without post hoc comparisons of the predicted range and ecological conditions.

In the light of these shortcomings, there has been a growing trend toward incorporating mechanistic approaches directly into space-use predictions (Elith & Leathwick, 2009; Moorcroft, 2012; Potts, Börger, et al., 2022). In particular, step selection analysis (SSA; Thurfjell et al., 2009; Avgar et al., 2016) has emerged as a powerful and flexible tool to analyse and interpret animal trajectories for a variety of movement types, including different spatiotemporal scales (Munden et al., 2020), investigating individual animals or populations (Osipova et al., 2019) and responses to dynamic variables (Potts, Börger, et al., 2022), all using a diverse range of locomotive descriptions (Avgar et al., 2016). Due to efficient parameterization via conditional logistic regression and ready availability of appropriate statistical packages (Reid & Tibshirani, 2014), SSA has become one of the more popular tools for studying animal movement and has been used to test complicated behaviourally driven movement hypotheses such as responses to memory (Oliveira-Santos et al., 2016) and to other moving organisms (Potts, Börger, et al., 2022). The underlying model of SSA, the step selection function (SSF), usually takes a nonlinear form depending on a suite of environmental variables and their corresponding parameters, which are to be estimated (Thurfjell et al., 2014). Furthermore, the SSF inherently provides a predictive movement mechanism capable of simulating stochastic animal trajectories and therefore predicting space use patterns (Potts & Börger, 2023).

Despite this mechanistic capability, most SSA-based studies focus only on interpreting model parameters with respect to preference for corresponding variables (e.g. the response to a particular land-cover class or attraction to a central place; Thurfjell et al., 2014), which may be attributed to implementation concerns or that predictive modelling is not a goal of the study. Predicting emergent space use from an SSF requires quantifying the probability density of moving from one location to another, dependent on given spatiotemporal variables. Iteratively calculating probabilities between consecutive relocations yields an individual-based model for simulating movement, and recent advancements in applications of SSFs to space-use predictions have demonstrated the efficacy of simulation-based approaches for calculating space use (Potts, Börger, et al., 2022). However, simulations can be computationally costly and require moderate to advanced programming proficiency to implement, and so investigations often end at interpreting the estimated parameters (though some less advanced packages are available; Signer et al., 2024).

By contrast, under some conditions, SSFs can be used to parameterize advection–diffusion equations capable of predicting the emergent spatial pattern of a movement process at any point in time (Moorcroft et al., 2006). These equations bypass the need for simulation and can yield easy-to-use functional forms describing space use from different movement strategies under specific assumptions (Ellison, Potts, Strickland, et al., 2024; Potts & Börger, 2023), but require advanced mathematical and computational training to understand. Advection–diffusion equations allow the user to produce space use patterns that are built from complicated behaviours such as territoriality, yet producing the space use patterns requires advanced mathematics, such as pattern formation analyses (Murray, 1993), to ensure parameters that produce realistic patterns. Therefore, using advection–diffusion equations to model space use from a SSF is not always necessary but is useful for modelling interacting processes such as territoriality or predator–prey (Moorcroft & Lewis, 2013).

Altogether, these caveats indicate a need for alternative methods of space-use prediction from SSA that are intuitive, accessible and computationally efficient. Here, we propose methods to move from a fitted SSF to a space use prediction using matrix methods.

We seek to address this need using a tool already familiar to many trained ecologists: transition matrices. Broadly, a transition matrix $\mathbf{A}$ is a square $n \times n$ matrix describing the state-change of a Markov process from time t to $t+1$ (Chung, 1960). These are commonly introduced as population models in ecological curricula, specifically as Leslie (i.e. age-structured; Leslie, 1945) and Lefkovich (i.e. stage-structured; Lefkovitch, 1965) matrices. In these applications, the transition matrix is multiplied by a state-vector $\mathbf{n}_t$ describing the composition of a population at time t to produce the new state-vector at $t+1$ (i.e. $\mathbf{n}_{t+1} = \mathbf{A}\mathbf{n}_t$). Here, we demonstrate that when provided a discrete landscape of cells (e.g. rasters) over which we seek to calculate an emergent utilization distribution from an SSF, this same rationale may be applied such that $\mathbf{n}$ represents the space use of an animal, at some time. Then, $\mathbf{A}$ defines all possible movements across the landscape from all possible starting locations and can be used to efficiently calculate the animal space use pattern from an SSF through time. We calculate this space use pattern using the methods of matrix multiplication (Chung, 1960) and ergodic theory (Perron, 1907), and discuss caveats that complicate calculation of these space use patterns given two previous states (i.e. a second-order Markov process) to accommodate autocorrelation in turning angles. Finally, we apply this approach to predict the space use of two case populations with markedly different movement capacities and strategies: wild pigs (*Sus scrofa*) in Mississippi, USA, and small birds in Sheffield, UK (the long-tailed tit, *Aegithalos caudatus*). The methods we present describe an intuitive approach for predicting spatial patterns from fitted SSFs by (a) representing the function as a matrix of step-to-step possibilities that can be iterated; (b) providing an efficient mathematical tool to predict the pattern through time; and (c) leveraging methodological concepts already familiar to practicing ecologists.

2 | STEP-SELECTION ANALYSIS

Here, we provide methods of using a fitted SSF to predict space use. We assume that readers are already familiar with the strengths and caveats of these models, and we do not seek to revisit these here. We strongly encourage readers unfamiliar with these models to investigate current literature on conducting SSA (e.g. Avgar et al., 2016; Fieberg et al., 2021, 2024; Potts & Börger, 2023) before attempting our methods.

We begin by introducing a movement model in the form of a SSF (Avgar et al., 2016; Thurfjell et al., 2014). This function describes the probability of an individual moving to location $\mathbf{x}$ at time $t+\delta t$, given it was previously at location $\mathbf{y}$ at time t and $\mathbf{z}$ at time $t-\delta t$ on a continuous landscape Ω. An animal's available landscape can be determined by observing their recorded locations and having some knowledge of their landscape (including obstructions such as large water bodies). We suggest creating an area much greater than the observed locations to determine availability. The SSF we use here is the product of three functions: two that describe the movement capabilities of an animal (a distance kernel, $\phi(\mathbf{x},\mathbf{y})$, and a turning angle kernel, $\theta(\mathbf{x},\mathbf{y},\mathbf{z})$) and one that describes a map of environmental variables (a weighting function, $\Psi(\mathbf{x},t)$). The SSF is thus defined as:

$$p_{\mathbf{xyz}}(\mathbf{x}, t+\delta t|\mathbf{y},\mathbf{z}) = \frac{\phi(\mathbf{x},\mathbf{y})\theta(\mathbf{x},\mathbf{y},\mathbf{z})\Psi(\mathbf{x},t)}{K}, \quad (1)$$

where K normalizes the function and is equal to $\int_\Omega \phi(\mathbf{x}',\mathbf{y})\theta(\mathbf{x}',\mathbf{y},\mathbf{z})\Psi(\mathbf{x}',t)d\mathbf{x}'$. The functions ϕ, θ and Ψ can each assume a variety of mathematical representations; below we choose specific forms to investigate our methods.

2.1 | An example of a SSF

The kernel $\phi(\mathbf{x},\mathbf{y})$ is a function of the distance from $\mathbf{y}$ to $\mathbf{x}$. As is common in SSF, we define this as an exponential distribution (Avgar et al., 2016):

$$\phi(\mathbf{x},\mathbf{y}) = \lambda \exp(-\lambda|\mathbf{y}-\mathbf{x}), \quad (2)$$

where λ is the reciprocal of the mean distance travelled from t to $t+\delta t$. The kernel $\theta(\mathbf{x},\mathbf{y},\mathbf{z})$ is a function of the angle turned through when facing the direction from $\mathbf{z}$ to $\mathbf{y}$ to move to $\mathbf{x}$, denoted as $\alpha_{\mathbf{yx}}$, and calculated using the `atan2` function. The product of ϕ and θ produces a movement kernel from which theoretical movements of particular step lengths and turning angles may be generated.

We investigate two options for the turning angle distribution, which yield two presumed movement processes. The first uses a uniform turning angle kernel such that every angle has an equal chance of being chosen in the movement process. This simplifies Equation (1) such that the probability of movement to $\mathbf{x}$ depends only on the current location $\mathbf{y}$, creating a Markov process:

$$p_{\mathbf{xy}}(\mathbf{x}|\mathbf{y}) = \frac{\phi(\mathbf{x},\mathbf{y})\Psi(\mathbf{x},t)}{K}. \quad (3)$$

The second form of the turning angle distribution is a non-uniform distribution such that some angles are more likely to be chosen by the moving individual. This takes into account the previous location $\mathbf{z}$; as such, the process is no longer Markovian (technically a second-order Markov process) and slightly more complicated to model. For consistency with common applications of SSF, we use a Von-Mises distribution to reflect a tendency to select steps with an average turning angle of μ (commonly $\mu = 0$, i.e. directional persistence; Avgar et al., 2016). The Von-Mises distribution for turning angles of $\alpha_{\mathbf{yx}}$ has the form:

$$\theta(\mathbf{x},\mathbf{y},\mathbf{z}) = \frac{\exp\left(\kappa\cos\left(\alpha_{\mathbf{yx}}-\mu\right)\right)}{2\pi I_0(\kappa)}, \quad (4)$$

where κ defines the magnitude of the tendency to choose angles close to μ, and $I_0(\kappa)$ is the modified Bessel function of the first kind of order 0.

Equations (1) and (3) contain a weighting function, $\Psi(\mathbf{x},t)$, describing attraction to specific environmental conditions at location $\mathbf{x}$ at time t. Generally, these functions are composed of several environmental features and take a log-linear form:

$$\Psi(\mathbf{x},t)=\exp\left(\beta_1 Z_1(\mathbf{x},t)+\ \dots\ +\beta_n Z_n(\mathbf{x},t)\right), \quad (5)$$

where $Z_1(\mathbf{x},t),\ \dots\ ,Z_n(\mathbf{x},t)$ are functions of the available environment and $\beta_1,\ \dots\ ,\beta_n$ are parameters to be estimated. When fitting Equations (1) and (3) to animal movement data, the parameters within $\phi(\mathbf{x},\mathbf{y})$, $\theta(\mathbf{x},\mathbf{y},\mathbf{z})$, and $\Psi(\mathbf{x},t)$ (i.e. λ; μ and κ; and $\beta_1,\ \dots\ ,\beta_n$, respectively) are commonly estimated using conditional logistic regression (Avgar et al., 2016; see Section 4).

2.2 | Example from step selection

Provided the functions described by Equations (2), (4) and (5) are determined, the SSF (Equations 1 or 3) may then be used to simulate steps combining inherent movement capacities with environmental preferences using the probabilities defined by the equation. This section is provided as a pedagogical description of how SSFs can be used to simulate movement. To demonstrate, we first simulate an environment using Equation (1), with a Gaussian random field to represent a variable $Z(\mathbf{x})$, and set the weighting function as $\Psi(\mathbf{x})=\exp(\beta Z(\mathbf{x}))$ (Figure 1, top panel). Next, we define $\lambda=1/10$ to represent a mean distance of 10 units, and $\mu=0$ to represent a tendency to continue in the same direction. We set the attraction parameters as $\kappa=2.5$ and $\beta=5$. For a two dimensional landscape on the positive Cartesian plane, we simulate a path starting at location $\mathbf{y}=(20,35)$ with a previous location $\mathbf{z}=(5,5)$. The results of this simulation are shown in Figure 1, where each column shows a different step. The resulting probability density function for the next step (Figure 1, bottom panels) is calculated from the SSF in Equation (1). Space use estimates can be calculated by simulating the steps thousands of times until the probability density function reaches some stable state (if one exists). To reduce the stochasticity of these space use predictions, the simulations must also be repeated thousands of times, requiring substantial computational power and processing time. In this example, the environment that attracts the simulated animal is unchanging, therefore, given a sufficiently large amount of steps and averaging over multiple simulations, the eventual space use distribution of the animal would always be the same, regardless of starting position. This stable description of space use, where adding more simulations to average would no longer change the outcome, is the *mathematical* steady state. We note here that when we refer to the steady-state throughout, we do not mean the *ecological* steady-state; which can be thought of as the space use pattern created by an animal that is reasonably stable for a period of time (such as a home range in a season), but the mathematical steady-state that is decided by the form of the SSF. In further sections, we propose using a mathematical equivalence that would alleviate the need to perform computationally costly simulations to reach the steady state.

3 | PREDICTING SPACE USE USING TRANSITION MATRICES

Although movement trajectories are usually recorded on an almost continuous spatial area, landscape features are often recorded on a much coarser grid, partly due to the heavy fieldwork required to sample a landscape (Parsons et al., 2022). Therefore, space use predictions are commonly calculated on a grid that matches the sample grid, and here we describe that landscape grid in the form of a matrix, where each entry in the matrix represents a discrete cell on the landscape. In the following section, we describe how to use these landscape matrices to form transition matrices that describe the movements to all possible **x** cells, given all possible previous movements from **y** (and **z**).

3.1 | From a continuous to a discrete landscape

The movement processes defined by Equations (1–5) are defined in discrete time (time steps of τ) and across a continuous landscape Ω. We now consider the movement process in discrete space so that the continuous landscape is converted to a $n\times n$ matrix consisting of square cells of length l, where the matrix represents a grid, similar to the concept of a raster. We have used a square matrix with square cells for simplicity here, but we note that a rectangle or other polygon may be a more realistic choice when later applying to data. Previously we denoted movements on the continuous landscape as movements through locations **z** to **y** to **x**; here we define those movements across the grid as k to j to i respectively to account for the change from continuous space (x,y,z) to cells on a discrete grid (i,j,k).

3.2 | From a space use estimate to a state vector

SSFs (Equations 1 and 3), in our discrete space, define the probability of moving to cell i at time $\tau+1$, given the animal was previously in cell j at time τ. Therefore to calculate the probability of movement, some initial space use would need to be specified. The space use matrix that provides the probability of an animal being in cell i at time τ is denoted here as $\mathbf{U}_i^\tau$ (hereafter termed the *state matrix*), which has the same size and shape as the landscape Ω. This state matrix may be a discrete version of the result of a SSF (Equations 1 and 3) calculation (see the bottom panels of Figure 1) or could be defined from some other knowledge of an animals whereabouts. The state matrix, $\mathbf{U}_i^\tau$, is normalized such that, $\sum_i \mathbf{U}_i^\tau=1$, to represent that all the probabilities of the cells sum to 1. Furthermore, to later form our matrix equation, we vectorize the state matrix to become a *state vector*, where vectorize is meant in the mathematical sense in which a matrix is flattened to become a vector. As $\mathbf{U}_i^\tau$ is a matrix of n^2 cells, we denote the vectorized version of the matrix $\mathbf{U}_i^\tau$ as the *state vector* $\mathbf{F}_i^\tau$, which is a $n^2\times 1$ matrix (or vector of length n^2).

In Section 3.3, we focus on the movement process described by Equation (3), which describes movement to **x** that depends only on the current location **y** (in matrix terms, j to i). Since the SSF defines an available landscape, which movement is allowed on, movement across the landscape is fully described by the transition matrix and movement outside of the landscape has a probability of zero. All

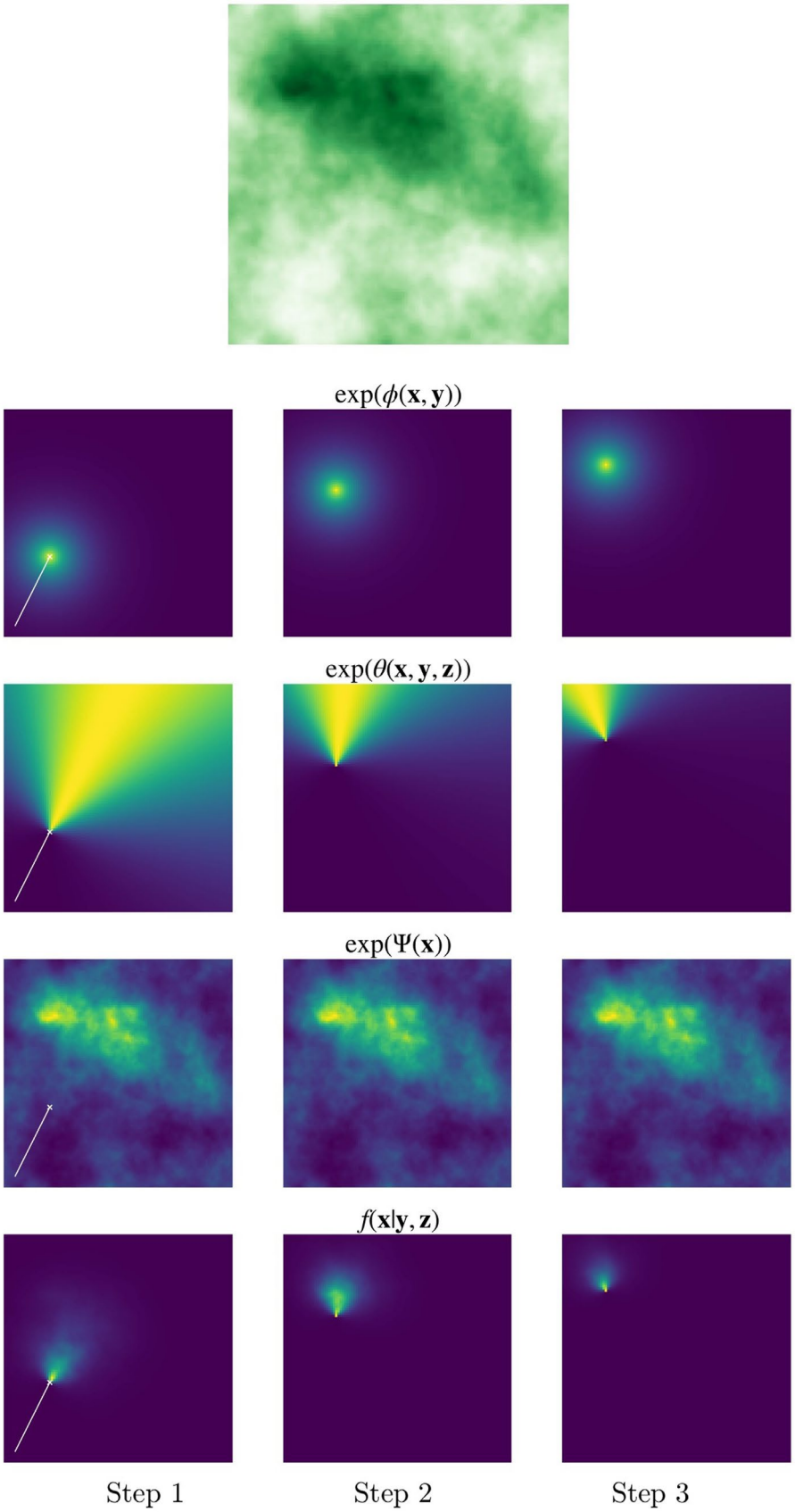


FIGURE 1 A simulated step selection function (SSF; Equation 1) for three steps represented on a grid of 100 by 100 cells. The bottom panel in each column shows the step selection function, $p_{xyz}(\mathbf{x}, t + \delta t|\mathbf{y}, \mathbf{z})$ which describes the probability density of the next location, given the previous two locations. We also show the distance kernel, $\phi(\mathbf{x}, \mathbf{y})$ (Equation 2), the turning angle kernel, $\theta(\mathbf{x}, \mathbf{y}, \mathbf{z})$ (Equation 4) and the weighting function, $\Psi(\mathbf{x}, t)$ (Equation 5) all contribute to the form of the SSF. The top panel shows a simulated environment $Z(\mathbf{x})$ (Equation 5).

transitions are confined to be within the defined spatial domain; therefore, the process has zero-flux boundary conditions.

3.3 | A transition matrix for a SSF with uniform turning angles: A Markov process

Since the movement from j to i depends on only the location j (and not k), this process is Markovian and may be defined using a transition matrix. The transition matrix provides the probability of moving to any location i from any location j, by calculating a different $\mathbf{F}_i^\tau$ for every possible j we obtain the values for the columns of the transition matrix, where each column is $\mathbf{F}_i^\tau$ for a different j. Given the shape of the state vector, $\mathbf{F}_i^\tau$, the transition matrix is therefore a $n^2 \times n^2$ matrix (which we denote as $\mathbf{A}_{ji}$) where each column sums to 1. The transition matrix defines the probability of moving from an origin cell to any possible target cell and can describe the transition from one step to the possible next step as:

$$\mathbf{F}_i^{\tau+\delta t} = \mathbf{A}_{ji}\mathbf{F}_j^\tau. \tag{6}$$

When starting with an initial state vector $\mathbf{F}_i^0$, we may calculate $\mathbf{U}_i^\tau$ for the next step in an iterative fashion. Specifically, if we are interested in $\mathbf{U}_i^\tau$ as $\tau \to \infty$, we can use matrix multiplication a large number of times, which essentially leads to calculating $\left(\mathbf{A}_{ji}\right)^\tau$ for large τ. Since the state matrix is a representation of the space use pattern of an animal, calculating it for large τ means we are able to predict a *stationary* space use pattern, if one exists for the movement process (Moorcroft et al., 2006). This is particularly useful when predicting the space use of animals that are living in restricted ranges, as these ranges are often stable over some period of time (e.g. a breeding season; Burt, 1943; Giuggioli et al., 2011; Bateman et al., 2015). We denote the stationary space use pattern as $\mathbf{U}_i^*$ where $\mathbf{F}_i^* = \left(\mathbf{A}_{ji}\right)^\tau \mathbf{F}_i^0$ as $\tau \to \infty$.

Calculating the stationary distribution $\mathbf{U}_i^*$ by matrix multiplication can be computationally costly. However, since all columns of $\mathbf{A}_{ji}$ sum to 1, and all entries are positive for $\left(\mathbf{A}_{ji}\right)^\tau$ for all τ (as they represent a probability density), the matrix is *ergodic* (Meyer, 2000; Perron, 1907). Ergodic matrices have the property that there exists a stationary distribution $\mathbf{F}_i^* = \lim_{t\to\infty}\mathbf{F}_i^\tau$ such that:

$$\mathbf{F}_i^* = \mathbf{A}_{ji}\mathbf{F}_i^*. \tag{7}$$

Since Equation (7) takes the form of an eigenvector equation, we may use an eigen decomposition to find the possible forms for $\mathbf{F}_i^*$ (as there can be infinite forms for Equation (7) to be true). The Perron Frobinius theorem (Perron, 1907) states that given a regular square transition matrix in which the columns sum to 1, the largest eigenvalue of that matrix is equal to 1 and the corresponding family of eigenvectors provides a stationary distribution, which does exist under these conditions. Therefore, to find the stationary matrix we can find the eigenvalue which is equal to 1, and the corresponding eigenvector that is normalized to 1 is equal to the stationary distribution $\mathbf{F}_i^*$, which corresponds to the stationary space use estimate $\mathbf{U}_i^*$, a $n \times n$ matrix, the same size and shape as the available landscape Ω.

We investigate using both the method of matrix multiplication (Equation 6) and eigen decomposition (Equation 7) to find the stationary distribution for the simulated SSF shown in Section 2.1 (Figure 2). Using matrix multiplication, we observe that τ must be sufficiently large to produce the same stationary distribution as the eigen decomposition. We record the computational cost of both methods by calculating the stationary distribution for varying landscapes of $n \times n$ cells, where n ranges from 10 to 200. All calculations were performed using `numpy` and `scipy` functions in Python 3.9 (see Section SI:2 for more information). Lastly, we compare our method to simulating the SSF (Equation 3) and methods described in Potts and Börger (2023). We report these results in Figure SI:1, where we show that, although the same spatial patterns arise from all methods, the transition matrix approach is both computationally easier than simulating, and similarly efficient to that of Potts and Börger (2023).

Including both the current location and the previous location into the movement process allows one to model a tendency to choose new locations based on directional persistence between steps, where movement is defined by Equation (1). However, this introduces a new level of complexity to the Markov chain process that drives our transition matrix theory. It is not currently clear how the transition matrix approach should best be modified to accommodate directional persistence. We believe that this represents a critical next step in the development of these methods since current wisdom regarding SSFs is that incorporation of non-random movements (i.e. a second-order Markov process) is both more ecologically realistic and better separates estimated habitat-selection trends that covary with directed movements (Avgar et al., 2016; Fieberg et al., 2024; Potts & Börger, 2023).

4 | APPLICATIONS TO ECOLOGICAL DATA

Our methods are designed to predict the space use patterns of wild animals for which movement tracks have been collected and SSAs have been performed. In this section, we share results of an integrated step selection analysis (iSSA; Avgar et al., 2016) for two different species: the wild pig and the long-tailed tit. Due to the computational time required to include turning angles into the SSF formulation, we focus only on movement processes that are Markovian and do not consider non-uniform turning angles. We show that this is reasonable for these data as the turning angles fit a uniform distribution as well as a Von Mises distribution (by comparing BIC values; Appendix SI:3.1; Ellison, 2021).

4.1 | Wild pigs

Wild pigs are a well-studied invasive species throughout the United States and are known to damage a variety of farmland crops (Beasley et al., 2018; Carlisle et al., 2020; Risch et al., 2021). Given previously identified preferences for crop types (Paolini et al., 2018, 2019), we used the CropScape Data Layer (USDA, 2016) as environmental inputs for our iSSA. Twelve pigs were captured

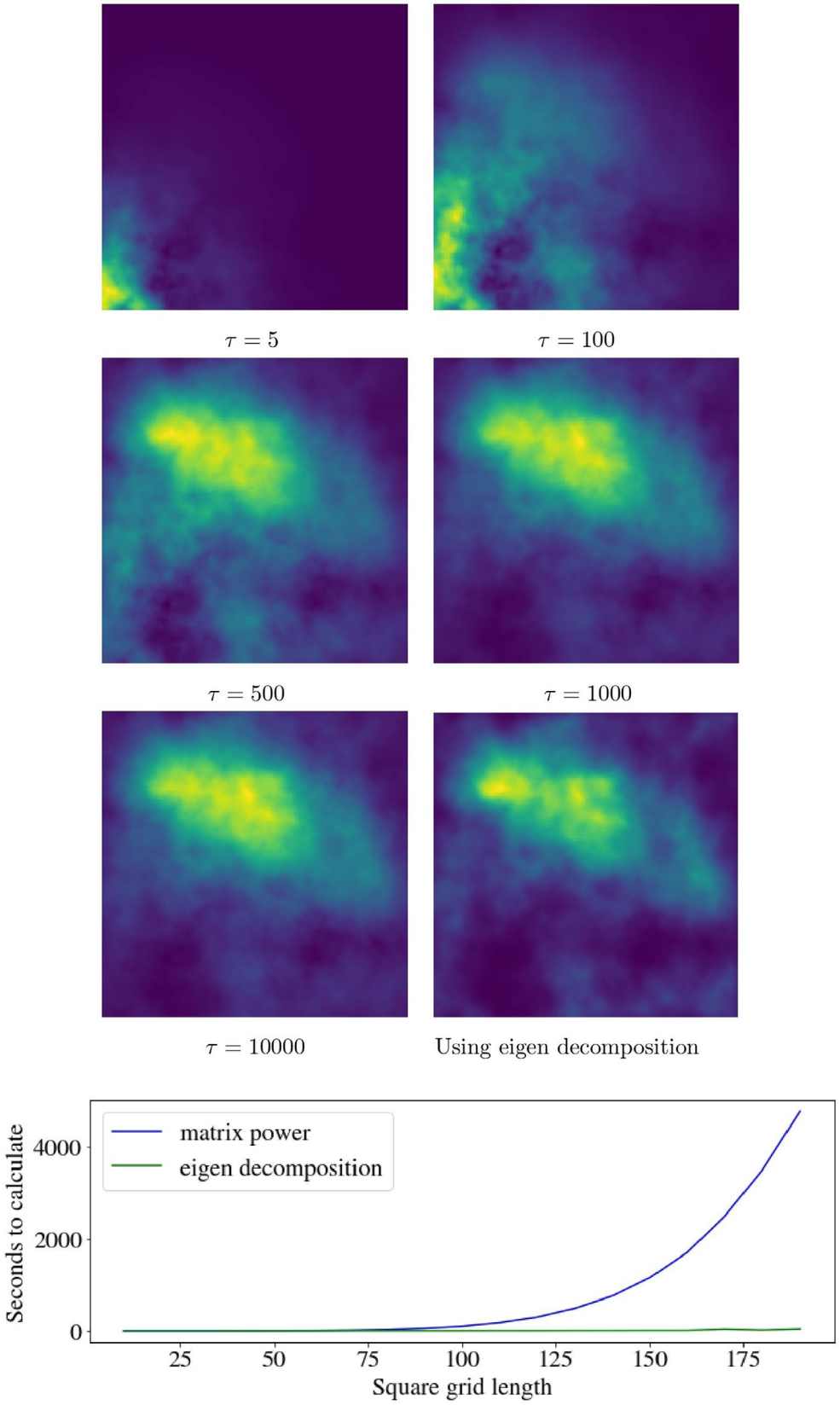
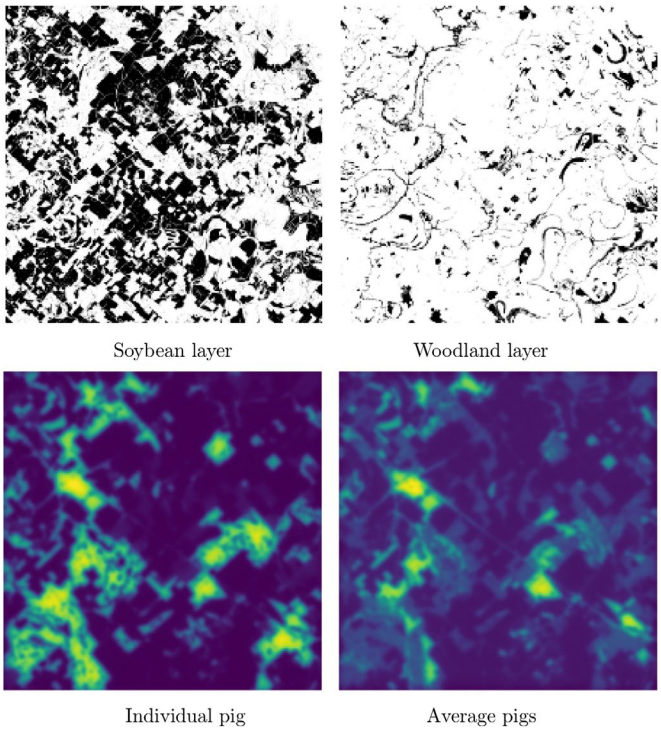


FIGURE 2 Examples of calculating the stationary distribution, $\mathbf{U}_i^*$, using (1) the methods of matrix multiplication (calculating $\mathbf{A}_{ij}^{\tau}$ for various τ) and (2) by eigen decomposition, that is, finding the eigenvector that corresponds to an eigenvalue of 1. We show method (1) for different values of τ and compare this to method (2) in the final square panel. The calculation time for both methods is shown in the bottom panel for increasing grid sizes, where we note that eigen decomposition is consistently computationally efficient when compared with using matrix multiplication.

in Mississippi, USA, and fitted with GPS devices recording animal relocations every 2 h. Animal capture and handling was approved by the Mississippi State University Institutional Animal Care & Use Committee (protocol #14-100; see Paolini et al., 2018 for a complete description of the data, capture protocols, and animal characteristics). The pigs' locations were taken over almost an entire year from March 2016 to January 2017, and therefore, we assumed to be catching their entire landscape preferences. However, our iSSA does not contain any restrictive behaviours of the pigs, such as sociality (Ellison, Potts, Boudreau, et al., 2024); therefore, this is a home range prediction that represents of landscape utilization, only within the timeframe of the study. We performed iSSA with Least Absolute Shrinkage and Selection Operator (LASSO) penalties on each individual in the population in response to 12 different types of crop layers (see Appendix SI:3.2). LASSO penalties are a regulization method for performing feature selection and can be considered an alternative way to parameterise a SSF here. As an alternative to choosing significant variables using low p-values, LASSO regulization shrinks insignificant parameters to zero. The fitted step selection model has the same form as Equation (3), where the function $\Psi(\mathbf{x})$ takes the same form as Equation (5). Each Z function is a crop layer (Figure 3) and each β parameter is estimated using iSSA with lasso penalties (Tibshirani, 1996).

4.2 | Long-tailed tits

Long-tailed tits are a small passerine bird found throughout Europe and known to forage in a variety of different tree and shrub types (Burt, 2014; Hatchwell, 2016). In the nesting season, the birds have a tendency to move in pairs whilst foraging around their nest site, with pairs being easier to follow at this time of year due to their fidelity to the nest (Halliwell et al., 2023). Data were collected for 18 breeding pairs by finding nest sites, following pairs of birds on foot, and recording any movements more than 10 m away. Pairs of birds moved together and can be considered one entity. Because birds were not directly manipulated research approvals were not required. The tree species were recorded across a 25-m-resolution grid across the known ranges of the birds (for more information, see Ellison, 2021). The locations of the birds were recorded at the times that they moved a significant distance (>10 m), so we altered the movement kernel shown by Equation (2) to also include the time between steps. We included the distance to the nest from location $\mathbf{x}$ for pair i as $N_i(\mathbf{x}, \mathbf{n}_i)$ and the percentage cover of n tree types as the variables $Z_1(\mathbf{x}, t)$, … , $Z_n(\mathbf{x}, t)$. Therefore, we use both tree types and nest locations to analyse the recorded movements of the pairs of birds. The SSF used to model the movements of pair i, nesting at location $\mathbf{n}_i$ for timestep δt, is:



	λ	corn	cotton	rice	s.beans	fallow	water	open
Ind	0.352	0.703	0	0	0.580	0	-0.007	-3.162
Ave	0.228	1.208	1.246	-1.743	0.699	-0.944	1.535	-1.938
	wetland	wood	s.beans (Q)	fallow (Q)	pecans (Q)	open (Q)	other (Q)	
Ind	-0.519	1.040	-1.893	-2.093	-1.119	-2.492	-1.001	
Ave	0.413	0.386	-1.367	-1.573	-1.168	-2.979	-0.457	

FIGURE 3 Examples of predicting space use using transition matrices and eigen decomposition for the movement data of wild pigs. Space use predictions and the results of an integrated step selection analysis for an individual pig and the average of all pigs are shown (bottom panels) alongside two examples of the crop layers (top panels). Analyses were performed on a population of 12 pigs and here we include the results for one pig and an average result, calculated from averaging each parameter over all of the pigs. More yellow areas in the space use predictions (colour version) indicate areas that are more likely to be used by pigs. The table shows the results of the integrated step selection analysis (iSSA) where 12 crop layers are included alongside their quadratic values. The quadratic values were included to model a possible preference for intermediate values of crops. Open water is denoted as 'water', open developed areas are denoted as 'open', 's.beans' is soybean, 'wood' is woodland and (Q) denotes the quadratic layer.

$$g_i(\mathbf{x}|\mathbf{y},t)=\frac{\exp\left(\lambda_1\delta t+\lambda_2|\mathbf{y}-\mathbf{x}|/\delta t+\beta_0 N_i(\mathbf{x},\mathbf{n}_i)+\beta_1 Z_1(\mathbf{x},t)+\ \ldots\ +\beta_n Z_n(\mathbf{x},t)\right)}{K} \tag{8}$$

where $K=\int_\Omega \exp\left(\lambda_1\delta t+\lambda_2|\mathbf{y}-\mathbf{x}'|/\delta t+\beta_0 N_i(\mathbf{x}',\mathbf{n}_i)+\beta_1 Z_1(\mathbf{x}',t)+\ldots+\beta_n Z_n(\mathbf{x}',t)\right)d\mathbf{x}'$. The functions $\lambda_1\delta t$ and $\lambda_{21}/\delta t$ arise from an exponential movement kernel that depends on both step length and step time, allowing for variable step times (Ellison, 2021; Munden et al., 2020). For the transition matrix, we set δt equal to the mean step time before using eigen decomposition.

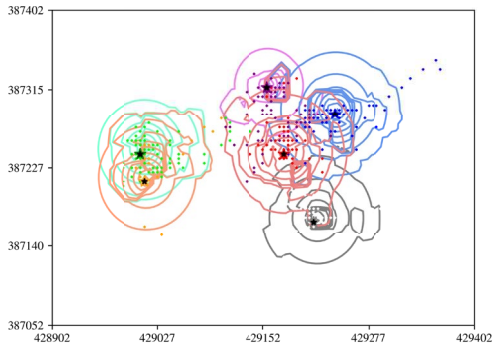
4.3 | Species results

Both species show a preference for a variety of environmental variables, resulting in substantial spatial variation in emergent space use (Figures 3 and 4). The iSSA for the wild pigs indicated that many crop layers were favoured as they foraged (Figure 3). We averaged the beta coefficients over all pigs to infer landscape use at a population level and report the results of the average and one individual pig (Figure 3). Particularly notable results for all pigs were their attraction to intermediate areas of open water (potentially as a source of thermoregulatory facilitation; VerCauteren et al., 2020), and intermediate soybean (Paolini et al., 2018, 2019), yet away from fallow and open developed areas. Pig behaviours were represented across their spatial landscape using the eigen decomposition method (Figure 3). Our approach quickly and efficiently generated predictions of pig space use from the SSF (Figure 3, Average pigs), thereby providing a simple tool for managing this invasive species (and others) and mitigating billions of dollars in associated damages to crops and natural landscapes (VerCauteren et al., 2020).

The iSSA for the population of long-tailed tits indicated that they foraged in response to a large number of trees and shrubs (Figure 4, bottom table). We observed both positive and negative responses to the vegetation species, and the population-level analysis provides a model for predicting the space use of any pair of birds with a known nest location. For our study population, we modelled the predicted space use of six pairs of birds using eigen decomposition (Figure 4), which indicates the space use of the small population across the forest. Each year, approximately 95% of this population's nests are located within the study site, but the pairs of birds are difficult to track due to their size (Hatchwell et al., 2014). Our approach allows us to easily predict emergent space use from the SSF and approximate the home range of future pairs of birds to provide a general idea of their potential location and places for management. Furthermore, we provide a method of estimating space use from irregularly sampled data; our central place approach generalizes well to unobserved individuals, and we summarized the space use using contours rather than a raster (Figure 4).

5 | DISCUSSION

SSFs are inherently a mathematical description of the probability density function of an animal moving to any location in their available landscape, given its current location (and sometimes its previous location). The probability density of an animal moving to each location on the landscape described by an SSF can be represented as a heat map that changes for all possible given steps (e.g. Figure 1) and represents the animal's space use. Simulations of the SSF can be performed thousands of times to estimate spatial patterns in the form of a probability density function, but this is an underused method in the literature. Our approach advances step selection theory by providing a method to efficiently predict spatial patterns from the analyses in lieu of using computationally costly simulations. Our method begins by forming a transition matrix that describes every possible movement from one place on an animal's available landscape to the next, using an already fitted SSF. We show that the corresponding transition matrix for a SSF can be (a) easily calculated following parameterization of the SSF; (b) used to iteratively produce



λ_1	λ_2	β_0	sycamore	oak	holly	hawthorn	birch	brambles	alder
0.0049	0.362	-0.0243	0.00713	0.00859	-0.000619	0.00410	0.00423	0.0354	0.0191
ash	lime	beech	willow	hazel	elder	cherry	chestnut	cypress	elm
-0.00167	0.00687	0.00262	0.00605	0.0167	0.015	0.0018	0.0905	0.0384	0.0129
gorse	larch	rowan	norway spruce	sitka spruce					
0.00416	0.0121	0.0104	-0.000418	-0.016					

FIGURE 4 Examples of predicting space use using transition matrices and eigen decomposition for GPS data collected by observing long-tailed tits. The space use predictions for a population of nesting birds are shown as a contour map, where each colour represents the range for a pair of birds. Here, the integrated step selection analysis (iSSA) was conducted at a population level so that the model can be used to predict foraging around the nests of future pairs of long-tailed tits.

animal space use distributions at each point in time (analogous to simulations of the changing distribution through time); and (c) used to output the eventual space use distribution of the step selection model in one matrix calculation (eigen decomposition). We believe that our method of predicting or estimating space use patterns is pedagogically advantageous for advancing movement ecology due to the accessibility of the method to a wide ecological audience. Transition matrices and eigenvectors are already commonly implemented in ecology, e.g. as the right and left eigenvectors from a Leslie matrix in population dynamics (Leslie, 1945), and so are conceptually accessible. As such, these methods can be used to efficiently expand the inference obtained from step selection applications, which represents an important expansion of a number of already high impact studies that parameterise SSFs but do not use them to predict space use (e.g. Duchesne et al., 2010; Prokopenko et al., 2017; Thurfjell et al., 2014).

Our study provides an extension of SSA (Avgar et al., 2016; Thurfjell et al., 2014) that allows the user to efficiently estimate space use from a fitted SSF. The question that the space use prediction answers is therefore within the formulation of the SSF. Should the user be modelling central place foraging, with a SSF that quantifies sufficient attraction to a central place then the prediction from using eigen decomposition would be a home range. Whereas a SSF that was fitted to evaluate attraction to different types of environment may be a space use prediction that is only valid within the temporal window of the data collection. Therefore, data that leads to an ecological steady state is not necessary for using our methods, but care should be taken when describing the space use outcome produced by ergodic theory. For example, with a nomadic species, we may construct a sufficiently large landscape grid that defines all possible areas the animals may travel to, and with a SSF that describes their main movement processes, a mathematical steady state may be reached using our methods (yet this would be computationally expensive with a large landscape). The user would then need to decide whether this is an appropriate model to describe the space use of the animal, given it is nomadic. We advocate for users of our methods to first ensure they are appropriately using SSF concepts, using the extensive available literature (Avgar et al., 2016; Potts, Börger, et al., 2022), before applying our process of defining space use from the SSF.

Calculating transition matrices for a SSF representing animal movement requires expressing the animal's available landscape as a grid. Animal locations that can be used to predict space use are often recorded using GPS devices where GPS error is generally 10–15 m (Hegarty & Kaplan, 2017). For a home ranging animal, if the 100 × 100 cell grid we tested models on represented 30 m × 30 m cells, this would equate to a square home range of 9 km^2, sufficient for many mammalian home ranges (Tucker et al., 2014), and could be expanded for little computational cost (Figure 2). In general, animal movement occurs on multiple spatial and temporal scales and these should be accounted for when using SSA. Temporally, the behaviour of some animals changes over seasons and throughout the day, such as with the crepuscular, and annually territorial, white-tailed deer (*Odocoileus virginianus*; Ellison, Potts, Strickland, et al., 2024). Animal movement also changes over spatial scales, which are linked to the temporal scales (Benhamou et al., 2014), such as selecting their range over a long period such as a year (second-order selection), selecting places to go within a range, which may occur over a day or a week (third-order selection), and selecting places within certain habitats within the range, potentially occurring over very small time steps such as sub-minute (fourth-order selection; Johnson, 1980). Acknowledging the correct scale, and accounting for it, is essential for forming a realistic SSF and creating a utilization distribution using a transition matrix and eigen decomposition.

We showed that our approach of predicting space use patterns from SSFs describing a Markovian process is highly applicable to ecological problems using the results of an iSSA for two different species. For an invasive population of wild pigs, we used the results of individual iSSAs to calculate a space use map for an average pig in our population, which could potentially be used to inform management of the area (an important priority of the USDA; Beasley et al., 2018). Similarly, we analysed movements of long-tailed tits in response to a number of known plant species alongside the known nest location for each pair. Since this data set was smaller than that of the pigs, we performed iSSA at the population level and produced a predictive foraging model for any pair of these birds, which we then used to calculate space use. Predicting the space use of pairs of birds can predict home ranges, which can potentially help monitoring efforts, which may be important for this species since they have such a high level of nest predation (Hatchwell, 2016). Overall, the outcome of efficiently predicting the spatial pattern using transition matrices was useful for both species, but in different ways. For the pigs, we predicted the most used areas of a given landscape, and for the birds, we predicted their foraging ranges, given a known nest location. In both of our real-world examples, space use is defined on the area of the landscape we chose to be representative of the animals' available landscape, and this should be considered carefully depending on the purpose of the study. For the long-tailed tits, we wanted to visualize their nesting home ranges, so it was important to extend the landscape to cover these.

When developing step selection models, ecologists often consider the influence of two types of movement measures: (1) the distance required to move to a location (step length); and (2) the autocorrelation or directional change (turning angle) from the previous movement step. Including turning angles in our methods (via a second order Markovian process) is a natural next step in expanding our methods. However, the inclusion of non-uniform turning angles may not be necessary at long temporal scales (e.g. a season) for animals that live in small stable ranges and the Markovian movement process may be sufficient for modelling step selection patterns for variables that are not changing in time. However, for animals that do not live in stable ranges (e.g. under nomadism or resource-tracking across broad gradients such as the 'green wave'; Rivrud et al., 2016), a second-order Markov process may be required to understand how an animal's distribution changes through time. Analysing an animal's movement tracks allows one to determine whether such autocorrelation along trajectories is important when modelling movement, and

again this often depends on the spatiotemporal scale of the recorded trajectories. For example, dispersing elk (*Cervus elaphus*) exhibit directional persistence only at long distances (Killeen et al., 2014), but for possums (*Trichosurus vulpecula*) turning angle distributions become more uniform as the time interval between steps increases (Postlethwaite & Dennis, 2013). Regardless, although animal tracks may indicate directional persistence when visualizing the distribution of turning angles, such persistence may be irrelevant in terms of model fit (Appendix SI:3.1). Furthermore, when including turning angles into models it is important to note that SSFs and their corresponding step lengths and turning angles are likely dependent on behavioural state (Klappstein et al., 2023; Pasquaretta et al., 2021), adding another layer of complexity to the form of the transition matrix model. Recent advancements on predicting space use from SSFs show tremendous promise for improving computational efficiency, neural network models (Forrest et al., 2025) show greatly improved predictive accuracy by allowing a non-specific form for the movement and habitat kernels, and graphical outcomes of simulated SSFs (Fieberg et al., 2024) can be used to improve goodness of fit, both providing alternative methods to predicting SSFs.

Our methods provide an efficient way of calculating the space use prediction from parameterised SSFs given heterogeneous environments that are not changing over time. We analysed movement in response to features of the potential future locations (the end of the step), which is common in step selection applications (Thurfjell et al., 2014); however, we may also wish to consider features of the landscape at the location (the start of the step). Predicting space use at $t + 1$, given behaviours at both t and $t - 1$ would mean the transition matrix is a function of variables that change through time. As an example, some foraging animals may choose to move only when resources are depleted below an energetically beneficial level, so modelling the variation of a characteristic of the current location and the future location could be an important modelling technique. We showed that although using iterations of the transition matrix is viable, and potentially interesting for visualizing interacting processes, the method of finding the stable spatial pattern is dramatically improved, in terms of computational speed, when using ergodic theory. Using eigen decomposition to find the eventual space use distribution means a steady state must exist. The question of whether using eigen decomposition from ergodic theory is suitable therefore lies within the form of the SSF, and whether or not it will reach a mathematical steady-state. To check a steady state exists, the associated Markov chain must be ergodic (Norris, 1997; Perron, 1907), which can be checked using numerical software (Section 3.3). However, should the transition matrix depend on other matrices that change through time, for example, mechanisms describing territoriality (Giuggioli & Kenkre, 2014), one may perform matrix multiplication to check for convergence. Recently, more complicated drivers of movement have been proposed in SSFs such as sociality (Potts, Giunta, & Lewis, 2022) and memory (Ranc et al., 2022), that may require such computational checks for reaching a steady-state. Mechanisms of territoriality (Moorcroft, 2012; Moorcroft et al., 2006) and memory (Ellison et al., 2020; Oliveira-Santos et al., 2016) have been shown to produce stable spatial patterns using alternative models, which implies that including these behaviours in SSFs can still result in patterns that are stable through time. However, Figure 2 implies that care must be taken when performing matrix multiplication for animals that live in large ranges compared to the landscape scale due to potentially long computational times (e.g. Figure 2). These potential extensions of the SSF shown by Equation (1) are outlined in Avgar et al. (2016), and would also benefit from an increase in computational power so that second-order Markovian methods can be used. Furthermore, our approach could incorporate different behavioural states by assigning a different transition matrix to each behaviour with some probability of switching, as in Michelot et al. (2016) and Klappstein et al. (2023). As with spatiotemporally changing variables, this approach would take advantage of the iterative transition matrix process, whilst selecting different behavioural states using probabilities, but could also be encapsulated in one large transition matrix that represented all possible movements for all possible behaviours.

We believe that our approach of using transition matrices to predict or estimate emergent space-use patterns from SSFs is an important advancement of step selection theory that is understandable to a wide ecological audience, due to its methodological comparability with well-established modelling tools. However, we also recognize that our work is only the first step in developing this application, where we have outlined the approach and given examples of how it can be applied to understand ecological problems. We hope that future work can focus on more efficient calculations of the second-order Markovian matrix methods and implementation of an accessible R package. Our proposed methods only touch the surface of using transition matrices to describe SSFs and their predictive capability, and we hope this research serves as a basis for the inclusion of more bespoke and realistic mechanisms for predicting animal movement.

AUTHOR CONTRIBUTIONS

Garrett M. Street, Natasha Ellison-Neary and Seth Oppenheimer conceived the ideas, designed the study and led the formal mathematics. Natasha Ellison-Neary formulated the equations, numerical procedures and code. Natasha Ellison-Neary and Garrett M. Street led the writing of the manuscript, with all authors contributing to revisions and providing final approval of the manuscript. Garrett M. Street, Tobit Dehnen and Ben J. Hatchwell provided data.

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CONFLICT OF INTEREST STATEMENT

Garrett M. Street is an Associate Editor at *Methods in Ecology & Evolution*, but he played no role in the handling or reviewing of this paper. The authors declare no other conflict of interest.

PEER REVIEW

The peer review history for this article is available at https://www.webofscience.com/api/gateway/wos/peer-review/10.1111/2041-210x.70316.

DATA AVAILABILITY STATEMENT

All data used in this study are publicly available. The Cropland Data Layer is available from the US Department of Agriculture National Agricultural Statistics Service (https://nassgeodata.gmu.edu/CropScape/index.jsp, last accessed Tuesday, 14 April 2026; USDA, 2016). The pig relocation data is available from FigShare (https://figshare.com/s/c79fcfa7ae2739807793; Paolini et al., 2018; Ellison, Potts, Boudreau, et al., 2024). Long-tailed tit relocation data are available from Dryad (https://datadryad.org/dataset/doi:10.5061/dryad.fqz612jqj; Ellison, 2021).

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REFERENCES

Avgar, T., Potts, J. R., Lewis, M. A., & Boyce, M. S. (2016). Integrated step selection analysis: Bridging the gap between resource selection and animal movement. *Methods in Ecology and Evolution*, *7*, 619–630. https://doi.org/10.1111/2041-210X.12528

Bateman, A. W., Lewis, M. A., Gall, G., Manser, M. B., & Clutton-Brock, T. H. (2015). Territoriality and home-range dynamics in meerkats, *Suricata suricatta*: A mechanistic modelling approach. *Journal of Animal Ecology*, *84*, 260–271. https://doi.org/10.1111/1365-2656.12267

Beasley, J., Ditchkoff, S. S., Mayer, J. J., Smith, M. D., & Vercauteren, K. C. (2018). *Research priorities for managing invasive wild pigs in North America*. USDA Wildlife Services - Staff Publications.

Benhamou, S. (2011). Dynamic approach to space and habitat use based on biased random bridges. *PLoS One*, *6*, e14592. https://doi.org/10.1371/journal.pone.0014592

Benhamou, S., Valeix, M., Chamaillé-Jammes, S., Macdonald, D. W., & Loveridge, A. J. (2014). Movement-based analysis of interactions in African lions. *Animal Behaviour*, *90*, 171–180. https://doi.org/10.1016/j.anbehav.2014.01.030

Börger, L., Franconi, N., Ferretti, F., Meschi, F., de Michele, G., Gantz, A., & Coulson, T. (2006). An integrated approach to identify spatiotemporal and individual-level determinants of animal home range size. *American Naturalist*, *168*, 471–485. https://doi.org/10.1086/507883

Burt, W. H. (1943). Territoriality and home range concepts as applied to mammals. *Journal of Mammalogy*, *24*, 346. https://doi.org/10.2307/1374834

Burt, W. H. (2014). The ecology and behaviour of the long-tailed tit. *Ecology*, *7*, E73–E82. https://doi.org/10.1890/04-0953

Carlisle, K. M., Harper, E. E., & Shwiff, S. A. (2020). An examination of ethical attitudes towards wild pig (*Sus scrofa*) toxicants in the United States. *International Journal of Pest Management*, *68*, 1–8. https://doi.org/10.1080/09670874.2020.1791372

Chung, K. L. (1960). *Markov chains with stationary transition probabilities*. Springer. https://doi.org/10.1007/978-3-642-49686-8

Duchesne, T., Fortin, D., & Courbin, N. (2010). Mixed conditional logistic regression for habitat selection studies. *Journal of Animal Ecology*, *79*, 548–555. https://doi.org/10.1111/J.1365-2656.2010.01670.X

Elith, J., & Leathwick, J. R. (2009). Species distribution models: Ecological explanation and prediction across space and time. *Annual Review of Ecology, Evolution, and Systematics*, *40*, 677–697. https://doi.org/10.1146/ANNUREV.ECOLSYS.110308.120159

Ellison, N. (2021). *Revealing the drivers of space use patterns in a bird population using mechanistic modelling*.

Ellison, N., Hatchwell, B. J., Biddiscombe, S. J., Napper, C. J., & Potts, J. R. (2020). Mechanistic home range analysis reveals drivers of space use patterns for a non-territorial passerine. *Journal of Animal Ecology*, *89*, 2763–2776. https://doi.org/10.1111/1365-2656.13292

Ellison, N., Potts, J. R., Boudreau, M. R., Börger, L., Strickland, B. K., & Street, G. M. (2024). Social interactions and habitat structure in understanding the dynamic space use of invasive wild pigs. *Wildlife Biology*, *2024*, e01247. https://doi.org/10.1002/WLB3.01247

Ellison, N., Potts, J. R., Strickland, B. K., Demarais, S., & Street, G. M. (2024). Combining animal interactions and habitat selection into models of space use: A case study with white-tailed deer. *Wildlife Biology*, *2024*, e01211. https://doi.org/10.1002/WLB3.01211

Fieberg, J., & Börger, L. (2012). Could you please phrase "home range" as a question? *Journal of Mammalogy*, *93*, 890–902. https://doi.org/10.1644/11-mamm-s-172.1

Fieberg, J., Freeman, S., & Signer, J. (2024). Using lineups to evaluate goodness of fit of animal movement models. *Methods in Ecology and Evolution*, *15*, 1048–1059. https://doi.org/10.1111/2041-210X.14336

Fieberg, J., Signer, J., Smith, B., & Avgar, T. (2021). A 'how to' guide for interpreting parameters in habitat-selection analyses. *Journal of Animal Ecology*, *90*(5), 1027–1043.

Fleming, C. H., Fagan, W. F., Mueller, T., Olson, K. A., Leimgruber, P., & Calabrese, J. M. (2015). Rigorous home range estimation with movement data: A new autocorrelated kernel density estimator. *Ecology*, *96*, 1182–1188. https://doi.org/10.1890/14-2010.1

Forrest, S. W., Pagendam, D., Hassan, C., Potts, J. R., Drovandi, C., Bode, M., & Hoskins, A. J. (2025). Predicting animal movement with deepSSF: A deep learning step selection framework. *Methods in Ecology and Evolution*, *17*, 371–391. https://doi.org/10.1111/2041-210X.70136

Giuggioli, L., & Kenkre, V. M. (2014). Consequences of animal interactions on their dynamics: Emergence of home ranges and territoriality. *Movement Ecology*, *2*, 20.

Giuggioli, L., Potts, J. R., & Harris, S. (2011). Animal interactions and the emergence of territoriality. *PLoS Computational Biology*, *7*, e1002008. https://doi.org/10.1371/journal.pcbi.1002008

Gomez, S., English, H. M., Bejarano Alegre, V., Blackwell, P. G., Bracken, A. M., Bray, E., Evans, L. C., Gan, J. L., Grecian, W. J., Gutmann Roberts, C., Harju, S. M., Hejcmanová, P., Lelotte, L., Marshall, B. M., Matthiopoulos, J., Mnenge, A. M. J., Niebuhr, B. B., Ortega, Z., Pollock, C. J., … Börger, L. (2025). Understanding and predicting animal movements and distributions in the Anthropocene. *Journal of Animal Ecology*, *94*, 1146–1164. https://doi.org/10.1111/1365-2656.70040

Halliwell, C., Beckerman, A. P., Biddiscombe, S. J., Germain, M., & Hatchwell, B. J. (2023). Coordination of care is facilitated by delayed feeding and collective arrivals in the long-tailed tit. *Animal Behaviour*, *201*, 23–44. https://doi.org/10.1016/J.ANBEHAV.2023.04.005

Hatchwell, B. (2016). Chapter 3: Long-tailed tits: Ecological causes and fitness consequences of redirected helping. In *Cooperative breeding in vertebrates*. Cambridge University Press. https://doi.org/10.1017/CBO9781107338357

Hatchwell, B. J., Gullett, P. R., & Adams, M. J. (2014). Helping in cooperatively breeding long-tailed tits: A test of references. *Philosophical Transactions of the Royal Society, B: Biological Sciences*, *369*, 20130565. https://doi.org/10.1098/rstb.2013.0565

Hegarty, C. J., & Kaplan, E. D. (2017). *Understanding GPS/GNSS* (p. 993). IEEE.

Johnson, D. H. (1980). The comparison of usage and availability measurements for evaluating resource preference. *Ecology*, *61*, 65–71. https://doi.org/10.2307/1937156

Kernohana, B. J., Gitzen, R. A., & Millspaugh, J. J. (2001). Analysis of animal space use and movements. In *Radio tracking and animal populations*. Academic Press. https://doi.org/10.1016/B978-012497781-5/50006-2

Killeen, J., Thurfjell, H., Ciuti, S., Paton, D., Musiani, M., & Boyce, M. S. (2014). Habitat selection during ungulate dispersal and exploratory movement at broad and fine scale with implications for conservation management. *Movement Ecology*, *2*, 1–13. https://doi.org/10.1186/S40462-014-0015-4/FIGURES/5

Klappstein, N. J., Thomas, L., & Michelot, T. (2023). Flexible hidden Markov models for behaviour-dependent habitat selection. *Movement Ecology*, *11*, 1–13. https://doi.org/10.1186/S40462-023-00392-3

Kranstauber, B., Kays, R., LaPoint, S. D., Wikelski, M., & Safi, K. (2012). A dynamic Brownian bridge movement model to estimate utilization distributions for heterogeneous animal movement. *Journal of Animal Ecology*, *81*, 738–746. https://doi.org/10.1111/J.1365-2656.2012.01955.X

Lefkovitch, L. P. (1965). The study of population growth in organisms grouped by stages. *Biometrics*, *21*, 1. https://doi.org/10.2307/2528348

Leslie, P. H. (1945). On the use of matrices in certain population mathematics. *Biometrika*, *33*, 183–212. https://doi.org/10.1093/BIOMET/33.3.183

Meyer, C. D. (2000). *Matrix analysis and linear algebra*. SIAM.

Michelot, T., Langrock, R., & Patterson, T. A. (2016). Movehmm: An r package for the statistical modelling of animal movement data using hidden Markov models. *Methods in Ecology and Evolution*, *7*, 1308–1315. https://doi.org/10.1111/2041-210X.12578

Moorcroft, P. R. (2012). Mechanistic approaches to understanding and predicting mammalian space use: Recent advances, future directions. *Journal of Mammalogy*, *93*, 903–916. https://doi.org/10.1644/11-mamm-s-254.1

Moorcroft, P. R., & Lewis, M. A. (2013). *Mechanistic home range analysis*. Princeton University Press.

Moorcroft, P. R., Lewis, M. A., & Crabtree, R. L. (2006). Mechanistic home range models capture spatial patterns and dynamics of coyote territories in Yellowstone. *Proceedings of the Royal Society B: Biological Sciences*, *273*, 1651–1659. https://doi.org/10.1098/RSPB.2005.3439

Munden, R., Börger, L., Wilson, R., Redcliffe, J., Brown, M. R., Garel, M., & Potts, J. R. (2020). Why did the animal turn? Time-varying step selection analysis for inference between observed turning points in high frequency data. *bioRxiv*. https://doi.org/10.1101/2020.08.13.249151

Murray, J. D. (1993). *Mathematical biology / 2, spatial models and biomedical applications*. Springer.

Nilsen, E. B., Pedersen, S., & Linnell, J. D. (2008). Can minimum convex polygon home ranges be used to draw biologically meaningful conclusions? *Ecological Research*, *23*, 635–639. https://doi.org/10.1007/S11284-007-0421-9/TABLES/2

Norris, J. R. (1997). *Markov chains*. Cambridge University Press. https://doi.org/10.1017/CBO9780511810633

Oliveira-Santos, L. G. R., Forester, J. D., Piovezan, U., Tomas, W. M., & Fernandez, F. A. S. (2016). Incorporating animal spatial memory in step selection functions. *Journal of Animal Ecology*, *85*, 516–524. https://doi.org/10.1111/1365-2656.12485

Osipova, L., Okello, M. M., Njumbi, S. J., Ngene, S., Western, D., Hayward, M. W., & Balkenhol, N. (2019). Using step-selection functions to model landscape connectivity for African elephants: Accounting for variability across individuals and seasons. *Animal Conservation*, *22*, 35–48. https://doi.org/10.1111/acv.12432

Paolini, K. E., Strickland, B. K., Tegt, J. L., VerCauteren, K. C., & Street, G. M. (2018). Seasonal variation in preference dictates space use in an invasive generalist. *PLoS One*, *13*, e0199078. https://doi.org/10.1371/JOURNAL.PONE.0199078

Paolini, K. E., Strickland, B. K., Tegt, J. L., VerCauteren, K. C., & Street, G. M. (2019). The habitat functional response links seasonal third-order selection to second-order landscape characteristics. *Ecology and Evolution*, *9*, 4683–4691. https://doi.org/10.1002/ECE3.5072

Parsons, I. L., Boudreau, M. R., Karisch, B. B., Stone, A. E., Norman, D. A., Webb, S. L., Evans, K. O., & Street, G. M. (2022). Aiming for the optimum: Examining complex relationships among sampling regime, sampling density and landscape complexity to accurately model resource availability. *Landscape Ecology*, *37*, 2743–2756. https://doi.org/10.1007/S10980-022-01523-8

Pasquaretta, C., Dubois, T., Gomez-Moracho, T., Delepoulle, V. P., le Loc'h, G., Heeb, P., & Lihoreau, M. (2021). Analysis of temporal patterns in animal movement networks. *Methods in Ecology and Evolution*, *12*, 101–113. https://doi.org/10.1111/2041-210X.13364

Patterson, T. A., Thomas, L., Wilcox, C., Ovaskainen, O., & Matthiopoulos, J. (2008). State-space models of individual animal movement. *Trends in Ecology & Evolution*, *23*, 87–94. https://doi.org/10.1016/j.tree.2007.10.009

Perron, O. (1907). Zur theorie der matrices. *Mathematische Annalen*, *64*, 248–263. https://doi.org/10.1007/BF01449896

Postlethwaite, C. M., & Dennis, T. E. (2013). Effects of temporal resolution on an inferential model of animal movement. *PLoS One*, *8*, e57640. https://doi.org/10.1371/JOURNAL.PONE.0057640

Potts, J. R., & Börger, L. (2023). How to scale up from animal movement decisions to spatiotemporal patterns: An approach via step selection. *Journal of Animal Ecology*, *92*, 16–29. https://doi.org/10.1111/1365-2656.13832

Potts, J. R., Börger, L., Strickland, B. K., & Street, G. M. (2022). Assessing the predictive power of step selection functions: How social and environmental interactions affect animal space use. *Methods in Ecology and Evolution*, *13*, 1805–1818. https://doi.org/10.1111/2041-210X.13904

Potts, J. R., Giunta, V., & Lewis, M. A. (2022). Beyond resource selection: Emergent spatio–temporal distributions from animal movements and stigmergent interactions. *Oikos*, *2022*, e09188. https://doi.org/10.1111/OIK.09188

Powell, R. (2000). *Animal home ranges and territories and the estimation of population densities* (pp. 65–110). Columbia University Press.

Prokopenko, C. M., Boyce, M. S., & Avgar, T. (2017). Characterizing wildlife behavioural responses to roads using integrated step selection analysis. *Journal of Applied Ecology*, *54*, 470–479. https://doi.org/10.1111/1365-2664.12768

Ranc, N., Cagnacci, F., & Moorcroft, P. R. (2022). Memory drives the formation of animal home ranges: Evidence from a reintroduction. *Ecology Letters*, *25*, 716–728. https://doi.org/10.1111/ELE.13869

Reid, S., & Tibshirani, R. (2014). Regularization paths for conditional logistic regression: The clogitl1 package. *Journal of Statistical Software*, *58*, 1–23. https://doi.org/10.18637/JSS.V058.I12

Risch, D. R., Ringma, J., & Price, M. R. (2021). The global impact of wild pigs (*Sus scrofa*) on terrestrial biodiversity. *Scientific Reports*, *11*, 1–10. https://doi.org/10.1038/s41598-021-92691-1

Rivrud, I. M., Heurich, M., Krupczynski, P., Müller, J., & Mysterud, A. (2016). Green wave tracking by large herbivores: An experimental approach. *Ecology*, *97*, 3547–3553. https://doi.org/10.1002/ECY.1596

Seaman, D. E., & Powell, R. A. (1996). An evaluation of the accuracy of kernel density estimators for home range analysis. *Ecology*, *77*, 2075–2085. https://doi.org/10.2307/2265701

Signer, J., Fieberg, J., Reineking, B., Schlägel, U., Smith, B., Balkenhol, N., & Avgar, T. (2024). Simulating animal space use from fitted integrated step-selection functions (iSSF). *Methods in Ecology and Evolution*, *15*, 43–50. https://doi.org/10.1111/2041-210X.14263

Thurfjell, H., Ball, J. P., Åhlén, P.-A., Kornacher, P., Dettki, H., & Sjöberg, K. (2009). Habitat use and spatial patterns of wild boar *Sus scrofa* (L.): Agricultural fields and edges. *European Journal of Wildlife Research*, *55*, 517–523. https://doi.org/10.1007/S10344-009-0268-1

Thurfjell, H., Ciuti, S., & Boyce, M. S. (2014). Applications of step-selection functions in ecology and conservation. *Movement Ecology*, *2*, 4. https://doi.org/10.1186/2051-3933-2-4

Tibshirani, R. (1996). Regression shrinkage and selection via the lasso. *Journal of the Royal Statistical Society. Series B, Statistical Methodology*, *58*, 267–288.

Tucker, M. A., Ord, T. J., & Rogers, T. L. (2014). Evolutionary predictors of mammalian home range size: Body mass, diet and the environment. *Global Ecology and Biogeography*, *23*, 1105–1114. https://doi.org/10.1111/GEB.12194

USDA. (2016). *USDA National Agricultural Statistics Service cropland data layer*.

Vander Wal, E., & Rodgers, A. R. (2012). An individual-based quantitative approach for delineating core areas of animal space use. *Ecological Modelling*, *224*, 48–53. https://doi.org/10.1016/J.ECOLMODEL.2011.10.006

VerCauteren, K. C., Beasley, J. C., Ditchkoff, S. S., Mayer, J. J., Roloff, G. J., & Strickland, B. K. (2020). *Invasive wild pigs in North America: Ecology, impacts and management*. Routledge. https://doi.org/10.13140/RG.2.2.35765.50401

Winner, K., Noonan, M. J., Fleming, C. H., Olson, K. A., Mueller, T., Sheldon, D., & Calabrese, J. M. (2018). Statistical inference for home range overlap. *Methods in Ecology and Evolution*, *9*, 1679–1691. https://doi.org/10.1111/2041-210X.13027

Worton, B. J. (1989). Kernel methods for estimating the utilization distribution in home-range studies. *Ecology*, *70*, 164–168. https://doi.org/10.2307/1938423

SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Figure S1. Comparisons of the eigen decomposition method (Figure 2) with simulations of the step-selection function (Equation 3) and Equations (SI:2.2) and (SI:2.3).

Figure S2. An example of the turning angle distribution for pig 19206, where we show the fitted uniform distribution (red) and Von Mises distribution (yellow) that inform the BIC values in Table SI:1.

Table S1. A table that shows the BIC values for fitting a uniform and von mises probability density function to the distribution of turning angles for each pig.

Table S2. Environmental variables used for the iSSA on wild pig movements, where variables that are important to each pig were indicated using conditional logistic regression with lasso penalties.

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