Article:

Ellison, N. orcid.org/0000-0001-6198-5470, Potts, J.R. orcid.org/0000-0002-8564-2904, Strickland, B.K. et al. (2 more authors) (2024) Combining animal interactions and habitat selection into models of space use: a case study with white-tailed deer. Wildlife Biology, 2024 (3). e01211. ISSN 1903-220X

https://doi.org/10.1002/wlb3.01211

WILDLIFE BIOLOGY

Research article

Combining animal interactions and habitat selection into models of space use: a case study with white-tailed deer

Natasha Ellison[1,2,3], Jonathan R. Potts[4], Bronson K. Strickland[1], Stephen Demarais[1] and Garrett M. Street[1,2]

[1]Department of Wildlife, Fisheries, and Aquaculture, Mississippi State University, Mississippi State, MS, USA
[2]Quantitative Ecology and Spatial Technologies Laboratory, Mississippi State University, Mississippi State, MS, USA
[3]Geosystems Research Institute, Mississippi State University, Mississippi State, MS, USA
[4]School of Mathematics and Statistics, University of Sheffield, Sheffield, UK

Correspondence: Natasha Ellison (ne235@msstate.edu)

Wildlife Biology
2024: e01211
doi: 10.1002/wlb3.01211
Subject Editor:
Stephanie Kramer-Schadt
Editor-in-Chief: Ilse Storch
Accepted 7 December 2023

Animals determine their daily movement trajectories in response to a network of ecological processes, including interactions with other organisms, their memories of previous events, and the changing environment. These combine to cause the emergent space use patterns observed over longer periods of time, such as a whole season. Understanding which processes cause these patterns to emerge, and how, requires a process-based modelling approach. Individual-based decisions can be described as a system of partial-differential equations (PDEs) to produce a dynamic description of space use built from the underlying movement process. Here we combine PDE-based models with step-selection analysis to investigate the combined effects of three established ecological processes that partially shape movement and space use: 1) a heterogeneous environment; 2) the environmental markings of moving conspecifics; and 3) the memory of direct interactions with conspecifics. We apply this framework to a large GPS-based dataset of white-tailed deer *Odocoileus virginianus* in the southeastern US. We fit models at the population level to provide predictive models, then tailor these to fit individual deer. We specifically incorporate relationships between each possible pair of deer and define each animal's responses to their unique local environments using separate integrated step-selection analyses. We show how individual movements and decisions yield emergent patterns in animal distributions, and we provide a full generalised description of the framework so that it may be applied to any species simultaneously responding to multiple potentially interacting stimuli (e.g. sociality, morphology, etc.). We found that the population of bucks had highly varied preferences for vegetation, but were shaping their space use in response to conspecific interactions, dependent on the individual relationships between two deer. We advocate for increased consideration of individual-based movement rules as determinants of realized animal space use, and particularly how these affect emergent distributions of entire species.

Keywords: movement ecology, movement process, space use, spatial pattern, white-tailed deer

---

Introduction

Animal space use patterns are driven by the underlying movement decisions of individuals (Kernohana et al. 2001, Nathan et al. 2008). Understanding the behavioural mechanisms that guide an individual animal to move across a landscape is therefore an important area of ecological research (Miller and Holloway 2015, Allen and and Singh 2016, Tucker et al. 2018). Discovering the key motivations of an animal's movement choices and their relationship with other interacting processes enables one to model how these behavioural mechanisms affect spatial patterns. This yields predictions of realized space use that can have implications for ecology (Merow et al. 2014). However, in lieu of identifying the processes behind the animal distribution patterns, many tools for studying animal ranges either describe the pattern of locations (e.g. kernel density estimators; Worton 1989) or correlate known locations to habitat features (e.g. resource-selection analysis and species-distribution models; Boyce et al. 2002, Elith and Leathwick 2009, respectively). Although useful ecological inference can be gained from these correlative methods of space use estimation, they neither explicitly account for the underlying movement mechanisms (although step-selection and continuous-time movement models have made progress in this direction; Thurfjell et al. 2014a, Calabrese et al. 2016) nor allow for feedback processes such as conspecific interactions and predator–prey dynamics (Kearney and Porter 2009). Furthermore, accurately predicting the spatial distribution of a group of animals in a changing landscape can positively inform conservation and management strategies, allowing for a better understanding of the habitats most in need of protection (Elith and Leathwick 2009, Franklin and Miller 2010, Zimmermann et al. 2010, Martínez-Minaya et al. 2018).

As animals navigate their available landscape they make movement decisions based on their potential journey ahead and the state of the environment around them (Nathan et al. 2008). The movement of individuals can be modelled by assigning probabilities to possible steps from one location to the next, subsequently producing a time-series of possible decisions. There are a number of tools available for defining probabilities of moving, such as step-selection functions (Thurfjell et al. 2014b) and continuous-time movement models (Calabrese et al. 2016), which essentially involve parameterising individual-based movement models using data. Step-selection analysis (SSA) provides an advantageous way of defining and fitting movement models, as its mathematical form means conditional logistic regression can be used to estimate parameters. Despite this efficient way to parameterise models, current methods of SSA do not easily incorporate feedback processes, such as the fine-scale movements of one animal depending on the whereabouts of another (although Schlägel et al. 2019 and Potts et al. 2022b model feedback with dynamic space use descriptions), this suggests a need for new methodological advancements to streamline the parameterisation process of step-selection models.

However a movement model is constructed, a time series of movement decisions can be simulated to produce a description of space use in the form of a probability density function (Signer et al. 2017, 2023, Potts et al. 2022a), but often at high computational cost. An alternative to simulating stochastic individual-based movement models is to model the mechanisms using a system of partial differential equations (PDEs), which describe the change in the probability density function of animal locations over time (Murray 1993), without the need for thousands of simulations to smooth out stochasticity. In particular, advection-diffusion equations are a type of PDE that can model movement behaviours as advection mechanisms (Moorcroft and Lewis 2013) describing attraction (or repulsion) to parts of the landscape due to these behaviours. These equations can be coupled to other spatio-temporal processes such as conspecific interactions (Moorcroft et al. 2006, Bateman et al. 2015) or cognitive maps (Potts and Lewis 2016a), thereby permitting the inclusion of ecological feedback when estimating space use.

Advection-diffusion equations can be solved numerically to produce an estimate of the probability density of finding the individual animal through time (i.e. the changing space use pattern), based on biases towards or away from spatial features (Moorcroft et al. 2006). However, due to their technical complexity, there are no easy-to-use packages available to input data and output results. Despite this, the predictions and ecological lessons that these models produce can be highly valuable. For example, Moorcroft et al. (2006) used advection-diffusion equations to show that the main drivers of space use of coyotes were responses to the scent marks of nearby packs, Bateman et al. (2015) used similar methods to show that dynamic meerkat home ranges were formed in response to direct and indirect conspecific interactions, and Ellison et al. (2020) used a memory mechanism to show the space use patterns of flocks of birds were due to the interplay of memory and avoidance. Recent advancements have provided methods of quickly moving from a fitted step-selection function to a space use description using PDEs (Potts and Schlägel 2020, Potts and Börger 2023), improving the accessibility of PDE models.

We advance recent studies linking step-selection analysis to advection-diffusion equations by presenting methods to model the space use of a population of interacting animals that move in response to multiple interacting biotic and abiotic conditions. As a case study, we test our approach using a population of 27 male white-tailed deer *Odocoileus virginianus* (hereafter, deer), known to be an important conservation species in the USA and useful here since their ecology and biology are well known (Foster et al. 1997, Strickland and Demarais 2000, McShea 2012). Prior research provides us with some initial hypotheses for how deer use space; for example, whilst searching for females, male deer in the rutting season will leave visual and olfactory marks on trees to display their condition (Moore and Marchinton 1974), to which conspecifics are likely to respond (Gassett et al. 1996). Furthermore, male deer establish dominance directly, by locking antlers and sparring with other males (Michael 1968, Hirth 1977). It is thought that deer in general have complex spatial memory processes influencing their future decisions (Gautestad et al. 2013, Jakopak et al. 2019) and select for different vegetation types (Henderson et al. 2020). Overall, this prior knowledge indicates that male deer are likely to be moving in relation to a variety of landscape layers, the environmental marks of other male deer (indirect interactions), and the memory of aggressive displays (direct interactions) with these conspecifics, likely including a variety of complex feedbacks and interactions. As such, we implement PDE models to investigate the competing and interacting effects of three established ecological processes that can modify movement and space use: 1) a heterogeneous environment (Moorcroft and Barnett 2008), 2) the environmental traces of other moving conspecifics (Moorcroft et al. 2006) and 3) their memory of direct interactions with these conspecifics (Potts and Lewis 2016a).

Our models account for environmental effects using a step-selection analysis and conspecific interactions using a PDE formalism. We begin by defining individual-based movement mechanisms to describe attraction or repulsion to different parts of the environment for each individual, where the attraction or repulsion is quantified using an integrated step-selection analysis (iSSA, Avgar et al. 2016). We then define mechanisms describing the deposit and decay of scent marks (Moorcroft et al. 1999, 2006, Moorcroft and Lewis 2013), and the memory of individuals interacting with other individuals (Potts and Lewis 2016a). From these mechanisms we construct a corresponding system of PDEs and fit these to the population of deer, producing a system of equations that can be used to predict broad-scale space use patterns. The resulting system of PDEs are then used to define a map corresponding to the emergent space use patterns by each individual. This approach to space-use modeling thus incorporates the feedbacks between interacting individuals, while using step-selection analysis to inform decisions on their response to land cover layers.

The biological relevance of our methods is illustrated by generating valuable knowledge about white-tailed deer response to static land cover variables and providing a predictive model for the population within the hunting season. We determine that selection of land cover layers is quite varied between individual deer (Stache et al. 2013, Haus et al. 2020) and show that their response to these layers is not sufficient to describe their movement ranges. Introducing mechanisms to describe the deers' responses to both indirect (e.g. scent) and direct interactions (e.g. defense displays), alongside vegetation preference, model their restricted ranges. Furthermore, we show that by focusing on the individual relationships between pairs of deer, we can fine-tune spatial predictions. Our model selection procedure indicates that adding ecological features of these relationships into the description of interactions does create better fitting models, meaning that the deer are likely basing their movement responses to conspecific interactions and social dynamics (Taillon and Côté 2006).

Material and methods

In our model, each individual moves in response to three movement drivers: 1) various heterogeneous environmental layers, 2) memory of direct interactions with other individuals and 3) indirect interactions with other individuals by sensing their environmental markings. Each of these processes are combined into a system of partial differential equations (PDEs). For computational efficiency, environmental parameters will be initially fitted using step-selection analysis. Then interaction parameters will be inferred by fitting the PDE's steady state space use patterns to locational data, using a similar approach to Moorcroft et al. (2006).

A schematic of this modelling process is shown in Fig. 1. Having constructed a population-level model, we then accommodate individuality into the system in two ways: (a) by including a self attraction mechanism and (b) by varying the direct interaction mechanisms for each individual. We first outline our methods for a general case of interacting animals. We then introduce our deer population and explain how we fine-tune our models for the species and each individual deer.

Step-selection analysis

Locations in space are denoted by $\mathbf{x}=(x_1,x_2)$ and each environmental layer can be described by a function of space and time, $Z(\mathbf{x},t)$. We model the habitat selection of each individual i as a function of p environmental features using the habitat-selection function:

$$\Psi_i(\mathbf{x},t)=\exp\left(\beta_{1,i}Z_1(\mathbf{x},t)+\ldots+\beta_{p,i}Z_p(\mathbf{x},t)\right), \qquad (1)$$

where $Z_1(\mathbf{x},t),\ldots,Z_p(\mathbf{x},t)$ are a set of functions describing p environmental covariates at each location $\mathbf{x}$ at time t. Selection is defined by the parameters controlling each covariate $(\beta_{1,i},\ldots,\beta_{p,i})$ that are to be estimated in the analysis. Movement is modelled using a movement kernel, $\phi_{\tau,i}(\mathbf{x}|\mathbf{y})=\lambda$ exp $(-\lambda|\mathbf{x}-\mathbf{y}|)$ where $\frac{1}{\lambda}$ is the mean step length calculated from the data. The step-selection function that defines the probability of moving from $\mathbf{y}$ at time t to $\mathbf{x}$ at time $t+\tau$ is thus

$$f_i(\mathbf{x},t+\tau\,|\,\mathbf{y},t)=K^{-1}\varphi_{\tau,i}(\mathbf{x}\,|\,\mathbf{y})\Psi_i(\mathbf{x},t+\tau). \qquad (2)$$

Here, $K=\int_\Omega \phi_{\tau,i}(\mathbf{z}\,|\,\mathbf{y})\Psi_i(\mathbf{z},t+\tau)d\mathbf{z}$ ensures f_i is a probability density function, where Ω is the available spatial domain. We use integrated step-selection analysis (iSSA) with lasso penalties implemented by the R package 'clogitL1' to parameterise Eq. 2. Lasso regression uses the bias/variance tradeoff to identify the variables providing the greatest fit of the model to the data, with uninformative variables having their associated model coefficients reduced toward 0 (Tibshirani 1996).

Space use models

We form partial differential equations to estimate the utilisation distribution of individual i in the form of a probability density function, $u_i(\mathbf{x},t)$. The equation that defines $u_i(\mathbf{x},t)$ is comprised of functions that describe the change

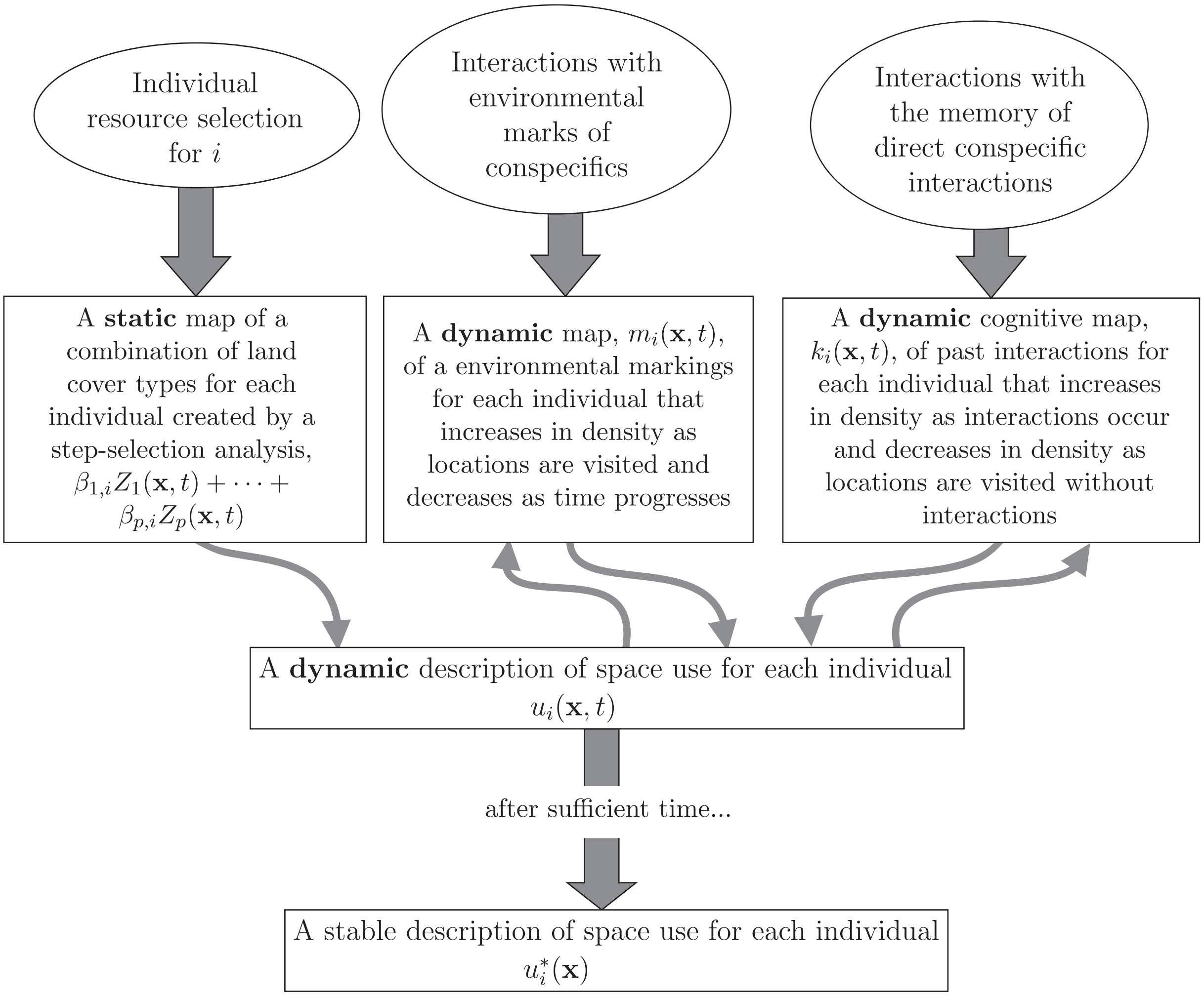


Figure 1. A schematic diagram describing the how the system shown by Eq. 3–7 work to create a space use distribution $u_i(\mathbf{x},t)$ for an individual i. Under the right conditions (e.g. enough avoidance of conspecifics) the space use patterns can stabilise over time to produce a steady-state distribution, $u_i^*(\mathbf{x})$.

in the probability density with respect to a static resource layer, $\Psi_i(\mathbf{x},t)$ (characterised by a step-selection analysis, Eq. 2), a cognitive map of past direct interactions, $k_i(\mathbf{x},t)$ and maps of environmental markings left by other individuals, $m_j(\mathbf{x},t)$. Here we note that the spatio-temporal density maps $k_i(\mathbf{x},t)$ and $m_j(\mathbf{x},t)$ can be derived rigorously from an individual-level description of interactions, as explained in Potts and Lewis (2016a, b) and the Supporting information. Furthermore, we include a self attraction mechanism to model some attraction for each individual to their utilisation distribution $u_i(\mathbf{x},t)$, which represents a tendency to return to places it has been before, controlled by the parameter s. The utilisation distribution for individual i is modelled using the a system of PDEs. The first PDE is an advection-diffusion equation for which the advection terms represent attraction towards or away from markings left by other individuals, the memory of past interactions, the resource layers and their space use, represented within the square brackets in the following system:

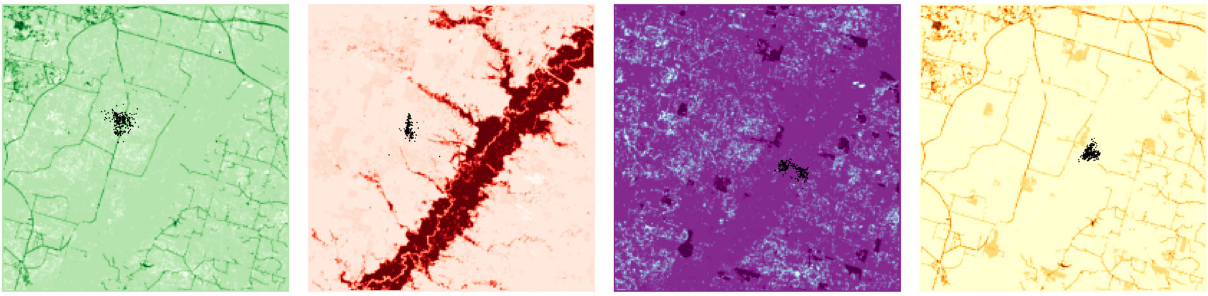
$$\frac{\partial u_i}{\partial t} = \nabla^2 u_i + 2\nabla \cdot \left(u_i \nabla \left[a\sum_{j\neq i} \overline{m}_j^{\delta} + b\overline{k}_i^{\delta} - c\beta_{1,i}Z_1 - \ldots - c\beta_{p,i}Z_p - su_i) \right] \right), \tag{3}$$

$$\frac{dm_i}{dt} = \rho_M u_i - \mu_M m_i, \tag{4}$$

$$\frac{dk_i}{dt} = \rho_K u_i \sum_{j\neq i} u_j \left(1-k_i\right) - \alpha k_i u_i, \tag{5}$$

$$\int_\Omega u_i \, d\mathbf{x} = 1, \tag{6}$$

where



deer 1 deer 5 deer 10 deer 23

Figure 2. Examples of the space use predicted by the step-selection analysis for four deer, chosen to be displayed for their attraction to a variety of resources (Table 1). The panels show the results of modelling space use without interactions, by including only crop layer preference as a movement driver. Colours in the online version are used only to differentiate the four deer and darker areas indicate a higher probability density of use. Here we note that although the utilisation distributions of these four individuals are close in space, they show different preferences for the land cover layers. Furthermore, modelling movement in response to the land cover layers does not fully describe the restricted ranges shown by the data in black.

$$\begin{aligned}\bar{k}_i^{\delta}(\mathbf{x},t)&=\frac{1}{\pi\delta^2}\int_{B_\delta(\mathbf{x})}k_i(\mathbf{x},t)\mathrm{d}\mathbf{x},\\ \bar{m}_i^{\delta}(\mathbf{x},t)&=\frac{1}{\pi\delta^2}\int_{B_\delta(\mathbf{x})}m_i(\mathbf{x},t)\mathrm{d}\mathbf{x},\end{aligned}\tag{7}$$

and $\nabla=\left(\frac{\partial}{\partial x},\frac{\partial}{\partial y}\right)$. The factor of two included in the advection term of Eq. 3 comes from the mathematical approximation of Eq. 2 into a PDE, see Potts and Schlägel (2020). Equation 3–7 have been re-parameterised from the individual-based formulations to reduce the amount of parameters, with the re-definitions shown in the Supporting information. Parameter *a* controls the avoidance of the scent marks of other individuals, *b* controls the avoidance of the cognitive interaction map, and *c* controls the attraction to the heterogeneous resource map. Parameter ρ_M describes the increase in scent mark density and μ_M describes the decay of the scent mark density. The parameter ρ_K describes the increase in density of the cognitive map and α describes the decay in density due to no interactions occurring. Lastly, δ describes the perceptive radius of each individual, that is the distance which individual *i* is able to detect any other individual, whether by sight, smell or sound.

It is important to explain that the magnitude of parameters *a* and *b* describe the strength of attraction (if negative) or repulsion (if positive) to the scent marks and memory of interactions of conspecifics respectively. The functions $m_i(\mathbf{x},t)$ and $k_i(\mathbf{x},t)$ are functions that are changing through space and time and $u_i(\mathbf{x},t)$ is a description of the animals location in terms of probabilities. For example, if *b* were positive (and a, $c=0$), spatial areas of $k_i(\mathbf{x},t)$ that are represented by high values would indicate that the animal would be less likely to be found in those areas, and more likely to be found in lower density areas of $k_i(\mathbf{x},t)$. Equation 5 means that $k_i(\mathbf{x},t)$ increases in density in places where interactions happen and decreases in density as time goes on (memory decay). As interactions happen, they are less likely to occur again in the same general area (if the parameter *b* is positive) but can still happen, particularly with memory decay.

The parameters *a*, *b*, *c*, ρ_M, μ_M, ρ_K, α, δ and *s* are estimated by maximising a likelihood function using a Nelder–Mead algorithm. The likelihood function has the following form:

$$L(D\mid a,b,c,\rho_M,\mu_M,\rho_K,\alpha,\delta,s)=\prod_i\prod_{\mathbf{z}\in\text{data}}u_i^*(\mathbf{z}),\tag{8}$$

where $D=\{d_1,\ldots,d_N\}$ consists of the N known locations for allindividuals and $u_i^*(\mathbf{x})$ is the steady state distribution, which represents the utilization distribution of individual *i*. Note that $\beta_{i,1},\ldots,\beta_{i,p}$ are already fixed from the maximisation procedure of Eq. 2; Figure 1 shows a schematic diagram of how the equations work to estimate the utilisation distribution for individual *i*. To aid computational efficiency, initial parameter values for the Nelder–Mead algorithm are found by combining a linear pattern formation analysis (Supporting information) with some initial testing runs. Alongside finite-difference approximations, we use array vectorisation and bespoke smoothing algorithms in Python 3.9 to ensure that the code is running as fast as possible in this language, on an average machine. The numerical scheme that solves Eq. 3–7 to produce space use is detailed in the Supporting information. We use a sequential approach to first model environmental effects (using a SSA) and then introduce conspecific effects. We acknowledge this as a limitation of our methods and recognise that ideally all parameters would be estimated at the same time. However, jointly estimating the parameters for 35 land cover variables for the 27 deer within a similar maximum likelihood procedure (Eq. 8) would likely take years of computational time. Therefore, we instead use the sequential two-step parameterisation process to allow for more efficiency.

A case study

White tailed deer *O. virginianus* are capable of living in a variety of vegetation types and changing their behaviour to be more aggressive towards conspecifics in the rutting season each year. We study a population in the breeding season, where the male deer become more aggressive and engage in behaviours such as heavily marking the environment and directly interacting with each other (Michael 1968), providing a well matched case study for the system (Eq. 3–7). The dynamics of $m_i(\mathbf{x},t)$, shown by Eq. 4, represent the deer marking the landscape as they move around their habitat and the function $k_i(\mathbf{x},t)$ (Eq. 5) models each deer's spatial memory of directly interacting with other male deer.

For this study we use data collected in central Mississippi (Madison County), USA, from 30 September 2017 to 30 January 2018. We use data from 27 collared males which have consistent 15-minute relocation intervals throughout the season and whose overlapping ranges (based on visual inspection of standard 95% KDE home ranges) suggest the opportunity for both direct interactions and scent marking. To estimate the preferred habitat of these deer we use the 2017 USDA CropScape data layer (USDA 2017), which in our study site yields 35 distinct landcover types (Supporting information). Previous studies of this deer population (Henderson et al. 2020) suggest that canopy coverage of thicket- producing, herbaceous, live woody, and dead woody plants are all drivers of the deer movement, and we include similar vegetation types in this analysis, outlined in the Supporting information.

To accurately model deer movement and the overall space use of each individual we reproject latitude/longitude coordinates into coordinates on a square landscape of −12000 to 12000 m in both the horizontal and vertical directions. When fitting parameters to the step-selection model, all movements at time intervals of 15 min are used. However, when fitting the PDE system we aim to maximise the likelihood function (Eq. 8) and this requires data to be independent, therefore we subsample the data using the procedure described in Benhamou et al. (2014) and Ellison et al. (2020). This results in subsampling one point every 12 h (Supporting information).

Integrated step-selection analyses are performed for each of the 27 deer, where their recorded movements are analysed in response to the 35 environment layers listed in the Supporting information, we use lasso regression penalties to indicate which of the resources were influencing the movement of each deer and choose to use the model with the least number of parameters within one standard error of the best fitting model. We choose this to reduce the number of environments being used within our model. However we recognise that for some studies it could be suitable to choose variables based on initial ecological knowledge rather than a statistical procedure. The results of the analysis are used to create an environment map for each of the deer, which is equivalent to a normalised version of Eq. 1 where the relevant β parameters are estimated in the analysis and multiplied by two (as in Moorcroft and Barnett 2008 and Potts and Schlägel 2020).

Individually varying model parameters

Individuality is known to be a factor in deer resource selection (Haus et al. 2020) and we include this in the models by fitting the step-selection functions separately for each deer. Furthermore, since male deer are known to respond to a variety of stimuli of other male deer in the rutting season (Michael 1968) there is likely individuality in the conspecific interaction processes as well. The models shown in the system (Eq. 3–7) are fitted by estimating a set of parameters (Eq. 8) for the entire population of 27 deer, where some individuality is included by estimating the parameters $\beta_1,\ldots,\beta_p$ for each deer i. Since the computational time to parameterise these systems of two-dimensional PDEs is long we do not estimate a different set of parameters for each deer. Instead we estimate the main set of parameters, that is a, b, c, ρ_M, μ_M, ρ_K, α, δ and s at a population level.

We extend the models using two separate subsets of four deer, chosen to be adjacent in space. Fitting the same models to these subsets allows for more efficient parameterisation, thereby improving the viability of including new parameters. This also allows us to investigate a finer landscape because we focus the numerical grid on a smaller area of the true landscape. We expand the model to include two further mechanisms of individuality, which we investigate separately: 1) a different avoidance strength of the interaction landscape, $k_i(\mathbf{x},t)$, for each deer and 2) a different interaction parameter for each pair of deer. Deer are known to show individual behaviour within social networks that varies in relation to vigilance (Lashley et al. 2014), relatedness (Hawkins and Klimstra 1970), previous interactions and difference in body mass (Taillon and Côté 2006), all suggesting that conspecific avoidance likely depends on the individual deer. Since the parameters estimated in the system (Eq. 3–7) were estimated at a population level, we extend the system to allow for individual personality to affect each deer's response to direct conspecific interactions.

In Eq. 3, the avoidance of the interaction landscape is controlled by the parameter b, and we vary this parameter for each deer i to model a different avoidance of previous interactions, we replace b with b_i in Eq. 3. This means that the system of equations for n deer includes n − 1 more parameters. To parameterise models in this situation, we fix all parameters in the best fitting model and vary the interaction parameter b_i, which is found using a maximum likelihood procedure. Avoidance may depend on the relationship between deer i and any other deer j. Therefore we also consider varying avoidance between each pair of deer and introduce an alternative parameter w_{ij}. Here we resort back to keeping b fixed for the population and include variation inside the mechanism that described the interaction landscape k_i. As such, Eq. 5 becomes:

$$\frac{dk_i}{dt} = \rho_K u_i \sum_{j\neq i} w_{ij} u_j \left(1-k_i\right) - \alpha k_i u_i, \tag{9}$$

Introducing w_{ij} as a parameter to be fit increases the number of parameters by a factor of n − 1 for n individuals. As an alternative to estimating each w_{ij} using a maximum likelihood procedure, we use the individual characteristics of the deer to inform the w_{ij} parameters. For our case study, we define w_{ij} to be a function of the body mass, Mass_i, of deer *i* and the body mass $Mass_j$ of deer *j*, which is known to be related to the reproductive success of rutting deer (Foley et al. 2018) and social dynamics (Taillon and Côté 2006):

$$w_{ij} = \exp\left(w_v \frac{\text{Mass}_i}{\text{Mass}_j}\right). \tag{10}$$

This leaves only one parameter, w_v, to be estimated. The form given in Eq. 10 means that when $w_v < 0$, w_{ij} gets smaller as $\frac{\text{Mass}_i}{\text{Mass}_j}$ gets larger and when $w_v > 0$, w_{ij} gets larger as $\frac{\text{Mass}_i}{\text{Mass}_j}$ gets larger. For example, a negative w_v would decrease the interaction density map in places where interactions are likely to occur, and that decrease would increase in magnitude as the relative mass of deer *i* and *j* increased. Assuming that the deer are attracted away from their interaction zone, a negative w_v would describe a situation where deer are less likely to avoid interactions with deer that have a smaller relative mass. The relative mass matrix of the 27 deer is included in the Supporting information.

To investigate individual variation, we took two separate subsets of four of the deer. We refit Eq. 3–6 with the self attraction mechanism. We included individuality into the models by varying the interaction parameter (*b* in Eq. 3), first by varying the avoidance of the interaction map and second by varying the parameter based on the relative mass of each pair of deer. We used Eq. 9 to vary the avoidance of the interaction map for subsets of four deer and Eq. 10 to estimate the variation of avoidance as a function of the relative body mass of the pair (Taillon and Côté 2006, Foley et al. 2018) for both the full population and the subsets of deer.

Results

Step-selection analyses

Results of the analyses are shown in Table 1 for deer which lasso penalties indicated that one or more of the environments were important (10 deer are not shown). We note some similarities with the findings of Henderson et al. (2020); many of our animals move in response to deciduous and evergreen forests and away from areas of grass or pasture and woody wetlands. However, the population showed substantial variability in responses to these tested environment layers, indicating that individuality is key when modelling deer movements in response to environment layers. Furthermore, to exemplify that selection for the environmental resources is not sufficient to describe the bucks movement, we show example space use distributions (Fig. 2) created from the fitted step-selection models (Eq. 2).

Table 1. Step-selection results for the deer (0–25, shown as columns) in response to land cover layers (1–195, shown as rows), defined in the Supporting information. Each cell shows the estimated value for the β coefficient (Eq. 1) that corresponds to the variable represented by a land cover layer. The non-zero values are estimated using lasso penalties where we have chosen to use the model with the lowest number of non-zero parameters within one standard error of the best fitting model. The 17/27 deer shown in the table are indicated to be driven by the presence of at least one environment layer. The deer numbered 2, 7, 9, 11–13, 17, 19, 21 and 26 are not shown as the lasso regression indicated no significant resource based movement drivers.

	Deer number																
	0	1	3	4	5	6	8	10	14	15	16	18	20	22	23	24	25
1	0	0	−1.02	3.55	2.98	0	0	0	0	0	0	0	−0.68	0	0	0	0
2	0	0	0	4.10	0	0	0.20	0.13	0	0	−0.01	0.17	0	−0.14	0	0	0
5	0	0	−0.82	−1.38	0	0	0	0.25	0	0	0.53	0	−0.22	0	0.22	0	0
24	0	0	0	−2.37	0	0	0	0	0	0	0	0	11.33	0	0	0	0
37	−0.95	0	0.79	−0.11	−0.85	8.00	0	0	0	0	0	0	0	0	0	0	0
61	0	0	0	0.03	−0.13	0	0	−0.73	0	0	0	0	−0.73	0	0.04	0	0
74	0	0	0	0	0	0	0	0	0	0	0	0	−4.09	0	0	0	0
111	0	0	0	−0.47	0	0	0	0	0	0	0.06	0	−0.31	0	0	0	0
121	0	0.94	0	−1.54	0	0	0	0	−1.62	0	0	0	0.08	0	0	0.51	0
131	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	−1.46	0
141	0.09	0.32	−0.13	0	0	0	0	0	0	0.41	0.22	0	0.62	0.58	0.79	0.34	0.83
142	−0.23	0	0.33	0.04	1.48	0	0	−0.42	0.96	0	−0.10	0	−0.03	0	0	0.16	0
143	0	0	0	0	0	0	0	0	−5.58	0	0	0	−3.12	0	0	0	0
152	0.61	0	0	0.28	0.39	0	0	0	2.21	0	0	0	−0.18	0.19	0	0.72	0
176	0	−0.05	0.68	0.28	0.95	−0.05	0	0.49	0	0.54	−0.24	0	−0.02	−0.84	0	0	−0.34
190	0	−0.20	0.67	0.69	−0.06	0.09	−0.02	−1.79	3.06	0	0	0	−1.92	0.14	−0.09	−0.47	0
195	0	0	0	−7.06	0	0	0	0	0	0	0	0	0	0	0	0	0

Table 2. Results for fitting the system Eq. 3–7 and Eq. 9–10 to the set of 27 deer and the subsets of four deer, denoted as 4a–b. Table 2A shows the results for fitting the model to the 27 deer with and without the self-attraction mechanism (top row) and with the self attraction mechanism (bottom row). The ΔBIC column shows the difference in BIC between the models, here we see that including some self-attraction is a significantly better fit than not including it. Table 2B shows the results of fitting the system (Eq. 3–6) with self-attraction to two different subsets of four deer. Table 2C shows the results of fixing the parameters from the second table and estimating the parameters b_i for $i = 1,\ldots,4$. Table 2D–E show the results of fitting the parameter w_{ij} (Eq. 9–10) such that corresponds to the relative mass of deer i and j. The ΔBIC column in Table 2C–E shows the difference in BIC values with the corresponding models where b does not vary (Table 2B) and all show an improvement of fit.

A

Set	a	b	c	μ_m	ρ_m	ρ_k	α	δ	s	BIC	ΔBIC
27	0.179	9.97	1.038	79.4	0.89	6.11	287	0.054	NA	121208	266
27	0.171	9.95	0.901	102	1.208	6.13	289	0.053	1.1×10^{-4}	120942	0

B

Set	a	b	c	μ_m	ρ_m	ρ_k	α	δ	S	**BIC**
4a	0.936	4.74	0.086	98.8	1.26	15.2	32.9	0.044	8.8×10^{-5}	15278
4b	0.901	3.3	1.98	9.091	1.72	21.3	46.6	0.055	8.9×10^{-5}	18582

C

Set	$b_{v,1}$	$b_{v,2}$	$b_{v,3}$	$b_{v,4}$	**BIC**	**ΔBIC**
4a	0.456	0.124	0.132	−0.182	15184	94
4b	0.4	0.095	−0.212	− 0.411	18390	192

D

Set	b_v	**BIC**	**ΔBIC**
4a	0.063	15273	5
4b	0.219	18545	36

E

	b_v	**BIC**	**ΔBIC**
27	−0.00101	120905	37

F

Set	a	b	c	μ_m	ρ_m	ρ_k	α	δ	s	*edge*	b_v	**BIC**
4b	1.10	2.89	1.79	23.2	3.33	19.4	29.8	0.0368	0.000105	0.0599	0.00391	17799

Direct and indirect conspecific interactions

Results for the model fitted to all 27 deer and certain subsets of four deer are shown in Table 2A. Including individuality in the form of self-attraction improved fit, provides evidence that each deer is attracted towards places it has been before. Visualising each of the space use models (Fig. 3) revealed that for some individuals, models did not fit well (Fig. 3c, for example), reinforcing that individual variation should be considered in later models.

Results for fitting models with individual variation are shown in Fig. 3–4 and Table 2. Including the variation of the parameter b showed that the model was a significantly better fit (ΔBIC = 94; group a, ΔBIC = 192; group b), where the b parameter varied from around 2.9–5, still indicating that deer were avoiding areas where interactions could happen.

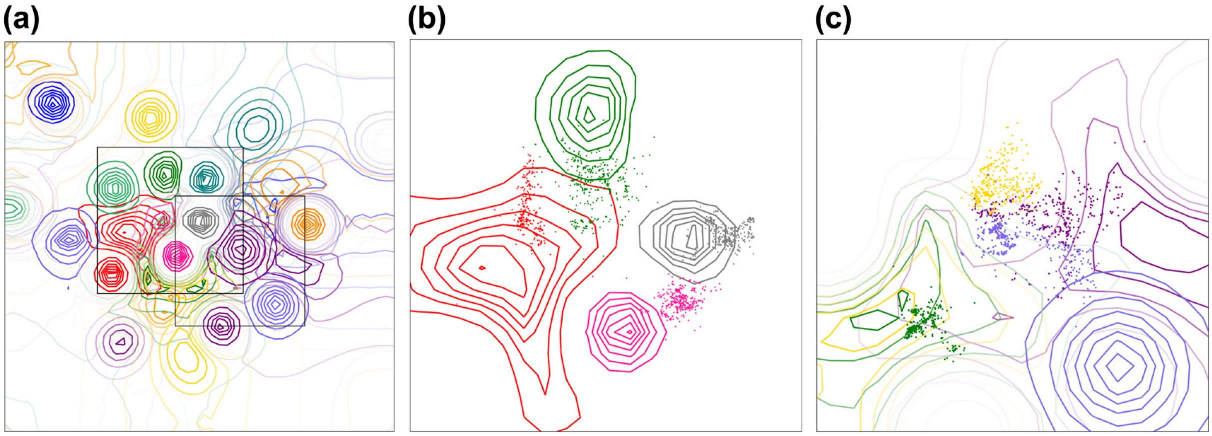


Figure 3. Space use estimates created by fitting the Eq. 3–7 to the data for 27 deer are shown as contour plots. (a) shows the results for the home range estimations of the 27 deer, where the boxes indicate the areas of (b) and (c). (b) shows a smaller section of the first panel with only the home ranges for deer 1, 5, 9 and 16 and their data shown. (c) shows another smaller section of the first panel with only the home ranges for deer 8, 10, 14 and 23 and their data shown. Here we see that the utilisation distributions in (b) fit the data slightly better than those in (c). We show these subsets of the 27 deer as we focus on these to model the individually-varying interaction mechanisms, shown in Fig. 4 and Table 2.

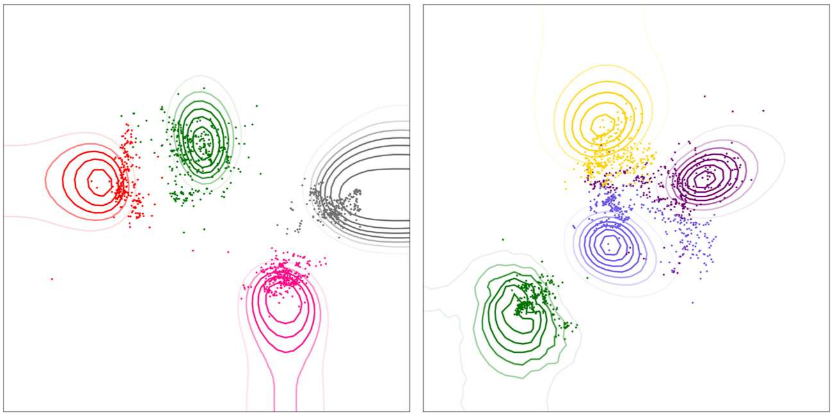
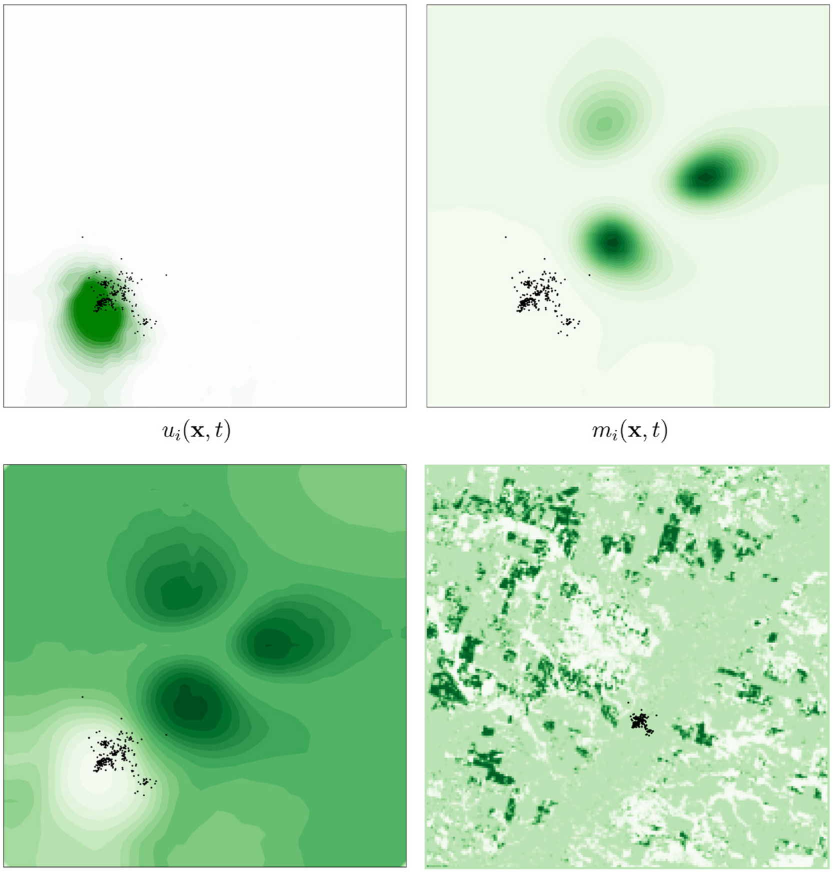


Figure 4. Space use estimates for two subsets of four deer where parameter values and details of model fit are shown in Table 2C. The left panel shows the subset of deer 1, 5, 9 and 16 and the right panel shows deer 8, 10, 14 and 23.

Individually varying the b parameter such that the avoidance of prior interactions is dependent on the relative mass of the deer (Table 2D–E) produced a better fitting model. For the subsets of four deer, we found that since $w_{ij} > 0$ (Eq.10), larger deer are avoiding smaller deer. However when considering the whole population we found $w_{ij} < 0$ indicating that



$u_i(\mathbf{x}, t)$ $m_i(\mathbf{x}, t)$

$k_i(\mathbf{x}, t)$ $\Psi_i(\mathbf{x}, t)$

Figure 5. Here we show a solution of Eq. 3 and the components that define the solution. The space use estimate for deer 14 (as estimated by varying the interaction parameter) is shown in the top left panel alongside the environmental marking distributions of the other deer included in the subset (top right panel) and the cognitive interaction map (bottom left panel). The resource-selection map as estimated by a step-selection analysis is shown in the bottom right panel and all panels show the recorded locations of deer 14, subsampled every 12 h. Darker shades indicate a higher density, for example the dark area in the top left panel indicates the space use of the deer, which is confined to one area.

in general, smaller deer avoid larger deer. The result of larger deer avoiding smaller deer in the small population is likely an effect of additional relationships between the deer that potentially outweigh the avoidance effects of relative body mass for these individuals, such as kinship.

We show an example of the space use estimate of one deer alongside the estimates of the three mechanisms driving the space use pattern in Fig. 5 (i.e. that is the conspecifics scent mark distribution the deer's cognitive map and the deer's environment from the step-selection analysis). The panels representing the indirect interactions ($m_i(\mathbf{x},t)$, top right) and direct interactions ($k_i(\mathbf{x},t)$, bottom left) show 'hot spots' of density that coincide with the space use of the other three deer. The hotspots are places that the deer are likely to avoid due to the potential interactions. Since the space use ($u_i(\mathbf{x},t)$, top left) is a description of the probability density of an animal's location, we are modelling potential interactions that could have occurred.

Lastly, we note that using a subset of a deer population to estimate space use of interacting individuals mean the boundaries of the space use estimates are unrealistic (Fig. 4). This is because in reality, each individual is likely to be surrounded by other male deer that were not included in the subset or possibly the data set. In the Supporting information we show an improved solution where we introduce a conjectured population, representing an unobserved but hypothetically present population, surrounding the four deer shown in Fig. 4. We note that including the hypothetical shapes the four distributions to be more distinct, but still does not fully capture the range overlaps.

Discussion

The movement of animals is driven by a complex network of behaviours that depend on multiple interacting biotic and abiotic factors, but these processes are often overlooked in favour of more simple models of space use (Moorcroft 2012, Miller and Holloway 2015). Our objective was to describe a general system for a population of moving animals that are interacting with each other and their environment. We have shown how to parametrise our model, using a combination of step-selection analysis and techniques modified from mechanistic home range analysis. We tested our methods using a case species, white-tailed deer, for which we constructed a model of space use for a specific population. We showed that common hypotheses of deer movements and space use are not mutually exclusive, but interacting and indeed sometimes reinforcing. We introduced individuality into the equations for the deer population and showed that weaving biological traits of the deer into the system is not only possible but teaches ecological lessons, for example, here we showed that body mass affects the memory of conspecific interactions. We highlight in particular that interconnected processes in a population of animals, such as a response to environmental marks and the memory of conspecific interactions, heavily influence each animal's space use pattern and these mechanisms should have a stronger presence in models of animal and species movement.

Our model focuses on three drivers of space use: a heterogeneous environment, a cognitive map of interactions and the scent marks of other individuals. Movement in response to the memory of direct interactions is modelled by the use of a cognitive map that relies on animals having some capacity for spatial memory. However, the episodic memory capacity of animals is widely unstudied for many species. Furthermore, the mechanisms that define memory processes are generally quite difficult to model (Clayton et al. 2001, Dere et al. 2006), despite evidance that animals use memory to forage efficiently (Fagan et al. 2013, Bracis et al. 2015, Riotte-Lambert et al. 2015). We include a memory process into our spatial models by modelling movement in response to a dynamic cognitive map, which changes as animals remember places where interactions with other animals may have occurred. In our system, the amount that animals avoid (or are attracted to) places where previous interactions may have happened is indicated by the parameter b. For our population of deer, b is estimated to be positive ($b \approx 10$; 27 individuals and $b \approx 4$; four individuals) in all fitted models, indicating that deer are avoiding places where previous interactions occurred.

Our results show that fitting individual models to the deer is important, as each deer has unique preferences for land cover layers and varying responses to previous interactions. One explanation for the groups of four deer having an opposite result to the population could be that there is less tendency to avoid each other due to the deer choosing to be close to each other in space. Overall, there are likely many further drivers of individual avoidance than relative body mass, but we used mass, not as a robust method of inferring deer behaviour, but as a way to introduce biological features into these interaction models. Aggressive behaviour of deer is driven by hormone levels competition for food and mating opportunities (Michael 1968, Grovenburg et al. 2009, Donohue et al. 2013), and with sufficient data these hypotheses could be tested with our models. Group size and kinship were previously included into a similar model structure for small birds (Ellison et al. 2020) and could be investigated here with genetic knowledge of the deer.

To further incorporate individuality into the modelling framework we included a 'self attraction' mechanism into the estimates of space use (Eq. 3), which resulted in better fitting models overall. By providing some attraction to places that the deer have already visited, the mechanism accounts for the lack of complete knowledge of environmental preference. Furthermore, we included movement in response to a heterogeneous environment in the system by creating individual environment maps using a step-selection analysis. In general, there was a large variation in the resource-selection parameter estimates across the 27 deer with few clear patterns but some population level response to forested areas and grassland. Since understanding the resource-selection of deer is not the aim of this research, we do not investigate these patterns here but leave them for further studies and note the large range of individuality, which aligns with some prior white-tailed deer studies (Chamrad and Box 1968, Spalinger et al. 1997, Mosbacher and Williams 2009) but not others (Dostaler et al. 2011), suggesting a possible social impact (Spalinger et al. 1997) and the need for incorporating specific forage species as in Author et al. (1991).

Applying our models to subsets of the population provided better fitting models than the full population, but still does not quite capture the overlaps of the deer's utilisation distributions. Introducing a theoretical population of deer at the boundary both improves fit by creating more distinct utilisation distributions, but still appears to be missing a feature that affects the overlaps. One suggestion for an extension to the models would be to investigate the response to conspecifics at different spatial scales, for example, investigating whether deer are likely to be repulsed by each other at short distances and attracted at long-distances, as with many scent marking territorial species (Campos et al. 2017). Introducing the theoretical population of deer does advance the capabilities of the model; as long as we can assume that the density of a species is well estimated surrounding the modelled population, this technique can be used to estimate spatial patterns of the known interacting individuals, when deer density is well-known (McShea 2012).

Partial differential equation models of animal space use estimate the probability distribution of arbitrarily many simulations of animals moving in one numerical process (Moorcroft and Lewis 2013), but without requiring multiple simulations for each set of parameters. However the computational time to fit parameters is still a problem, especially as we increase the number of parameters and individuals, or solve over more detailed landscapes. There are two ways in which these numerical methods can be advanced: first, by more accurately predicting the initial values for the parameterisation process; and second, by using computational processes that iterate the numerical equations faster, as discussed in Mazumder (2015). Here we use a maximum-likelihood procedure to fit the parameters based on the steady state space use pattern, where the number of iterations needed can be reduced greatly by informing the first set of parameters. We use linear stability analysis (Supporting information) to find sets of parameters that produce patterns, but this could be further improved by using biological knowledge of the system being investigated. The next natural development of these methods could be to estimate the parameters in the functions $m_i(\mathbf{x},t)$ and $k_i(\mathbf{x},t)$ using linear stability analysis and to subsequently fit the a and b parameters using step-selection analysis (Supporting information), which takes advantage of conditional logistic regression. Furthermore, numerical differential equations are a continuously evolving field of research, particularly with the advancement of super computing. Here we used a well-known finite-difference algorithm to solve the equations but recognise that with the use of parallelisation methods we may be able to decrease the computational cost (Mazumder 2015).

Increasing the computational speed of solving this system would allow for the equations to have a finer landscape, more individuals and individual level parameters. However, the system and numerical scheme are still useful for estimating the interactions between small groups of animals, whether they be interacting individuals or populations. For example, the spatial dynamics of populations of predators and their main prey at small timescales could be investigated using this system, where instead of estimating the probability density of finding individual i we may consider the probability of finding the population. Many models of species distribution estimate patterns by correlating known locations with static environment layers without considering the behaviours driving the movement processes (Manly 1985, Fleming et al. 2015). When scaling up to a species level, the methods we have outlined here provide a natural next step for estimating species distributions based on both habitat preference and interactions with other species.

The process-based models of space use outlined in this research provide models which could be used to predict the space use of animal populations in the future. For example, the model we developed for the deer population could be generalised by averaging over the step-selection parameters to gain a population level environmental layer and then solved to predict space use, as in Potts and Börger (2023). Alternatively, space use could be estimated by performing a step-selection analysis for new deer and then using the interaction mechanisms fitted here. Using these models to predict deer space use in the rutting season could have direct impacts on the management of both public and private land deer harvest strategies by understanding how they use the landscape and interact in the hunting season (Foster et al. 1997, McShea 2012). Land managers and hunters often use trail cameras and bait sites to identify target individuals (Kilpatrick and Stober 1973, Belant et al. 2007, Soria-Díaz and Monroy-Vilchis 2015), producing a few known locations of each deer but where some characteristics and body traits can be estimated (Jacobson et al. 1997). Our parameterised models can use these low effort and non invasive methods of data collection to estimate each deer's utilisation distribution within the rutting season, essentially providing the stakeholders with a way of maximising their encounters. Although we do not provide specific management advice for our results for this particular species, we advocate for more models with predictive capability to be used to inform management.

Overall, we have developed a model to estimate the space use distributions of a group of animals that interact with each other and their environment. We have shown that process-based spatial models can provide a platform to test more complex biological theories of movement, as exemplified here by including multiple stimuli and morphological characteristics in our model of deer space use. Following this research we advocate for deeper consideration for how the myriad ecological and biological processes of movement determine emergent patterns animal space use and the eventual distribution of a population and species.

Acknowledgements – We would like to thank Colby Henderson and Ashley Chance for collecting the deer movement data.

Funding – This publication is a contribution of the Forest and Wildlife Research Center, Mississippi State University supported by the Mississippi Department of Wildlife, Fisheries, and Parks and US Fish and Wildlife Service (Pittman-Robertson) Federal Aid in Wildlife Restoration funding. This study was also funded by the USDA Agricultural Research Service (USDA-ARS) grant: Advancing Agricultural Research through High Performance Computing (Sponsor Award no. 58-0200-0-002).

Permits – All capture methods were approved by the Mississippi State University Institutional Animal Care and Use Committee (Protocol no. 16-621).

Author contributions

Natasha Ellison: Conceptualization (equal); Formal analysis (lead); Investigation (lead); Methodology (equal); Writing – original draft (lead); Writing – review and editing (equal). **Jonathan R. Potts**: Conceptualization (equal); Methodology (equal); Writing – review and editing (equal). **Bronson K. Strickland**: Data curation (equal); Writing – review and editing (equal). **Stephen Demarais**: Data curation (equal); Writing – review and editing (equal). **Garrett M. Street**: Conceptualization (equal); Methodology (equal); Data curation (equal); Writing – review and editing (equal).

Transparent peer review

The peer review history for this article is available at https://publons.com/publon/10.1002/wlb3.01211.

Data availability statement

Data are available from the Figshare Digital Repository: https://figshare.com/articles/dataset/Datasets_and_Code_zip/11910831 (Ellison et al. 2024).

Supporting information

The Supporting information associated with this article is available with the online version.

References

Allen, A. M. and Singh, N. J. 2016. Linking movement ecology with wildlife management and conservation. – Front. Ecol. Evol. 3: 155.

Author, Y., Brown, D. T., and Doucet, G. J. 1991. Temporal changes in winter diet selection by white-tailed deer in a northern deer yard. – J. Wildl. Manage. 55: 361–376.

Avgar, T., Potts, J. R., Lewis, M. A. and Boyce, M. S. 2016. Integrated step selection analysis: bridging the gap between resource selection and animal movement. – Methods Ecol. Evol. 7: 619–630.

Bateman, A. W., Lewis, M. A., Gall, G., Manser, M. B. and Clutton-Brock, T. H. 2015. Territoriality and home-range dynamics in meerkats, *Suricata suricatta*: a mechanistic modelling approach. – J. Anim. Ecol. 84: 260–271.

Belant, J. L., Seamans, T. W. and Paetkau, D. 2007. Genetic tagging free-ranging white-tailed deer using hair snares. – Ohio J. Sci. 107: 50–56.

Benhamou, S., Valeix, M., Chamaillé-Jammes, S., Macdonald, D. W. and Loveridge, A. J. 2014. Movement-based analysis of interactions in African lions. – Anim. Behav. 90: 171–180.

Boyce, M. S., Vernier, P. R., Nielsen, S. E. and Schmiegelow, F. K. A. 2002. Evaluating resource selection functions. – Ecol. Modell. 157: 281–300.

Bracis, C., Gurarie, E., Van Moorter, B. and Goodwin, R. A. 2015. Memory effects on movement behavior in animal foraging. – PLoS One 10: e0136057.

Calabrese, J. M., Fleming, C. H. and Gurarie, E. 2016. ctmm: an R package for analyzing animal relocation data as a continuous-time stochastic process. – Methods Ecol. Evol. 7: 1124–1132.

Campos, S. M., Strauss, C. and Martins, E. P. 2017. In space and time: territorial animals are attracted to conspecific chemical cues. – Ethology 123: 136–144.

Chamrad, A. D. and Box, T. W. 1968. Food habits of white-tailed deer in south texas. – J. Range Manage. 21: 158.

Clayton, N. S., Griffiths, D. P., Emery, N. J. and Dickinson, A. 2001. Elements of episodiclike memory in animals. – Phil. Trans. R. Soc. B 356: 1483–1491.

Dere, E., Kart-Teke, E., Huston, J. P. and De Souza Silva, M. A. 2006. The case for episodic memory in animals. – Neurosci. Biobehav. Rev. 30: 1206–1224.

Donohue, R. N., Hewitt, D. G., Fulbright, T. E., Deyoung, C. A., Litt, A. R. and Draeger, D. A. 2013. Aggressive behavior of white-tailed deer at concentrated food sites as affected by population density. – J. Wildl. Manage. 77: 1401–1408.

Dostaler, S., Ouellet, J., Therrien, J. and Côté, S. D. 2011. Are feeding preferences of white-tailed deer related to plant constituents? – J. Wildl. Manage. 75: 913–918.

Elith, J. and Leathwick, J. R. 2009. Species distribution models: ecological explanation and prediction across space and time. – Annu. Rev. Ecol. Evol. Syst. 40: 677–697.

Ellison, N., Hatchwell, B. J., Biddiscombe, S. J., Napper, C. J. and Potts, J. R. 2020. Mechanistic home range analysis reveals drivers of space use patterns for a non-territorial passerine. – J. Anim. Ecol. 89: 2763–2776.

Ellison, N., Potts, J. R., Strickland, Demarais, S. and Street, G. M. 2024. Data from: Combining animal interactions and habitat selection into models of space use: a case study with white-tailed deer. – Figshare Digital Repository, https://figshare.com/articles/dataset/Datasets_and_Code_zip/11910831.

Fagan, W. F., Lewis, M. A., Auger-Méthé, M., Avgar, T., Benhamou, S., Breed, G., LaDage, L., Schlägel, U. E., Tang, W. W., Papastamatiou, Y. P., Forester, J. and Mueller, T. 2013. Spatial memory and animal movement. – Ecol. Lett. 16: 1316–1329.

Fleming, C. H., Fagan, W. F., Mueller, T., Olson, K. A., Leimgruber, P. and Calabrese, J. M. 2015. Rigorous home range estimation with movement data: a new autocorrelated kernel density estimator. – Ecology 96: 1182–1188.

Foley, A. M., Hewitt, D. G., DeYoung, R. W., Schnupp, M. J., Hellickson, M. W. and Lockwood, M. A. 2018. Reproductive effort and success of males in scramble-competition polygyny: evidence for tradeoffs between foraging and mate search. – J. Anim. Ecol. 87: 1600–1614.

Foster, J. R., Roseberry, J. L. and Woolf, A. 1997. Factors influencing efficiency of white-tailed deer harvest in Illinois. – J. Wildl. Manage. 61: 1091.

Franklin, J. and Miller, J. A. 2010. Mapping species distributions: spatial inference and prediction. – Cambridge Univ. Press.

Gassett, J. W., Wiesler, D. P., Baker, A. G., Osborn, D. A., Miller, K. V., Marchinton, R. L. and Novotny, M. 1996. Volatile compounds from interdigital gland of male white-tailed deer (*Odocoileus virginianus*). – J. Chem. Ecol. 22: 1689–1696.

Gautestad, A. O., Loe, L. E. and Mysterud, A. 2013. Inferring spatial memory and spatiotemporal scaling from gps data: comparing red deer *Cervus elaphus movements* with simulation models. – J. Anim. Ecol. 82: 572–586.

Grovenburg, T. W., Jenks, J. A., Jacques, C. N., Klaver, R. W. and Swanson, C. C. 2009. Aggressive defensive behavior by free-ranging white-tailed deer. – J. Mammal. 90: 1218–1223.

Haus, J. M., Webb, S. L., Strickland, B. K., McCarthy, K. P., Rogerson, J. E. and Bowman, J. L. 2020. Individual heterogeneity in resource selection has implications for mortality risk in white-tailed deer. – Ecosphere 11: e03064.

Hawkins, R. E. and Klimstra, W. D. 1970. A preliminary study of the social organization of white-tailed deer. – J. Wildl. Manage. 34: 407–419.

Henderson, C. B., Demarais, S., Street, G. M., Strickland, B. K. and McKinley, W. T. 2020. Fine-scale vegetation use by white-tailed deer in a forested landscape during hunting season. – J. For. Res. 25: 439–443.

Hirth, D. H. 1977. Social behavior of white-tailed deer in relation to habitat. – Wildl. Monogr. 53: 3-55.

Jacobson, H. A. 1997. Infrared-triggered cameras for censusing white-tailed deer. – Wildl. Soc. Bull. 25: 547–556.

Jakopak, R. P., LaSharr, T. N., Dwinnell, S. P. H., Fralick, G. L. and Monteith, K. L. 2019. Rapid acquisition of memory in a complex landscape by a mule deer. – Ecology 100: e02854.

Kearney, M. and Porter, W. 2009. Mechanistic niche modelling: combining physiological and spatial data to predict species' ranges. – Ecol. Lett. 12: 334–350.

Kernohana, B. J., Gitzen, R. A. and Millspaugh, J. J. 2001. Analysis of animal space use and movements. – In: Millspaugh, J. J. and Marzluff, J. M. (eds), Radio tracking and animal populations. Academic Press, pp. 125–166.

Kilpatrick, H. J. and Stober, W. A. 1973. Effects of temporary bait sites on movements of suburban white-tailed deer. – Wildl. Soc. Bull. 30: 760–766.

Lashley, M. A., Chitwood, M. C., Biggerstaff, M. T., Morina, D. L., Moorman, C. E. and DePerno, C. S. 2014. White-tailed deer vigilance: the influence of social and environmental factors. – PLoS One 9: e90652.

Manly, B. 1985. The statistics of natural selection on animal populations. – Springer Netherlands.

Martínez-Minaya, J., Cameletti, M., Conesa, D. and Pennino, M. 2018. Species distribution modeling: a statistical review with focus in spatio-temporal issues. – Stoch. Environ. Res. Risk Assess. 32: 3227–3244.

Mazumder, S. 2015. Numerical methods for partial differential equations: finite difference and finite volume methods. – Elsevier.

McShea, W. J. 2012. Ecology and management of white-tailed deer in a changing world. – Ann. N. Y. Acad. Sci. 1249: 45–56.

Merow, C., Smith, M. J., Edwards, T. C., Guisan, A., McMahon, S. M., Normand, S., Thuiller, W., Wüest, R. O., Zimmermann, N. E. and Elith, J. 2014. What do we gain from simplicity versus complexity in species distribution models? – Ecography 37: 1267–1281.

Michael, E. D. 1968. Aggressive behavior of white-tailed deer. – Southwest. Nat. 13: 411–420.

Miller, J. A. and Holloway, P. 2015. Incorporating movement in species distribution models. – Prog. Phys. Geogr. Earth Environ. 39: 837–849.

Moorcroft, P. R. 2012. Mechanistic approaches to understanding and predicting mammalian space use: recent advances, future directions. – J. Mammal. 93: 903–916.

Moorcroft, P. R. and Barnett, A. 2008. Mechanistic home range models and resource selection analysis: a reconciliation and unification. – Ecology 89: 1112–1119.

Moorcroft, P. R. and Lewis, M. A. 2013. Mechanistic home range analysis. – Princeton Univ. Press.

Moorcroft, P. R., Lewis, M. A. and Crabtree, R. L. 1999. Home range analysis using a mechanistic home range model. – Ecology 80: 1656–1665.

Moorcroft, P. R., Lewis, M. A. and Crabtree, R. L. 2006. Mechanistic home range models capture spatial patterns and dynamics of coyote territories in Yellowstone. – Proc. R. Soc. B 273: 1651–1659.

Moore, W. G. and Marchinton, R. L. 1974. Marking behavior and its social function in white-tailed deer. – The behaviour of ungulates and its relation to management. 1974: 447–456.

Mosbacher, E. V. and Williams, C. E. 2009. Browse preference and browsing intensity of white-tailed deer (*Odocoileus virginianus*) in allegheny high plateau riparian forests, USA. – Wildl. Biol. Prac. 273: 1651–1659.

Murray, J. D. 1993. Mathematical biology / 2, Spatial models and biomedical applications. – Springer.

Nathan, R., Getz, W. M., Revilla, E., Holyoak, M., Kadmon, R., Saltz, D. and Smouse, P. E. 2008. A movement ecology paradigm for unifying organismal movement research. – Proc. Natl Acad. Sci. USA 105: 19052–19059.

Potts, J. R. and Lewis, M. A. 2016a. How memory of direct animal interactions can lead to territorial pattern formation. – J. R. Soc. Interface 13: 20160059.

Potts, J. R. and Lewis, M. A. 2016b. Territorial pattern formation in the absence of an attractive potential. – J. Math. Biol. 72: 25–46.

Potts, J. R. and Schlägel, U. E. 2020. Parametrizing diffusion-taxis equations from animal movement trajectories using step selection analysis. – Methods Ecol. Evol. 11: 1092–1105.

Potts, J. R. and Börger, L. 2023. How to scale up from animal movement decisions to spatiotemporal patterns: an approach via step selection. – J. Anim. Ecol. 92: 16–29.

Potts, J. R., Börger, L., Strickland, B. K. and Street, G. M. 2022a. Assessing the predictive power of step selection functions: how social and environmental interactions affect animal space use. – Methods Ecol. Evol. 13: 1805–1818.

Potts, J. R., Giunta, V. and Lewis, M. A. 2022b. Beyond resource selection: emergent spatio–temporal distributions from animal movements and stigmergent interactions. – Oikos 2022: e09188.

Riotte-Lambert, L., Benhamou, S. and Chamaillé-Jammes, S. 2015. How memory-based movement leads to nonterritorial spatial segregation. – Am. Nat. 185: E103–E116.

Schlägel, U. E., Signer, J., Herde, A., Eden, S., Jeltsch, F., Eccard, J. A. and Dammhahn, M. 2019. Estimating interactions between individuals from concurrent animal movements. – Methods Ecol. Evol. 10: 1234–1245.

Signer, J., Fieberg, J. and Avgar, T. 2017. Estimating utilization distributions from fitted step-selection functions. – Ecosphere 8: e01771.

Signer, J., Fieberg, J., Reineking, B., Schlägel, U., Smith, B., Balkenhol, N. and Avgar, T. 2023. Simulating animal space use from fitted integrated step-selection functions (issf). – Methods Ecol. Evol. 15: 43–50.

Soria-Díaz, L. and Monroy-Vilchis, O. 2015. Monitoring population density and activity pattern of white-tailed deer (*Odocoileus virginianus*) in central Mexico, using camera trapping. – Mammalia 79: 43–50.

Spalinger, D. E., Cooper, S. M., Martin, D. J. and Shipley, L. A. 1997. Is social learning an important influence on foraging behavior in white-tailed deer? – J. Wildl. Manage. 61: 611–621.

Stache, A., Heller, E., Hothorn, T. and Heurich, M. 2013. Activity patterns of European roe deer (*Capreolus capreolus*) are strongly influenced by individual behaviour. – Folia Zool. 62: 67–75.

Strickland, B. K. and Demarais, S. 2000. Age and regional differences in antlers and mass of white-tailed deer. – J. Wildl. Manage. 64: 903–911.

Taillon, J. and Côté, S. D. 2006. The role of previous social encounters and body mass in determining social rank: an experiment with white-tailed deer. – Anim. Behav. 72: 1103–1110.

Thurfjell, H., Ciuti, S. and Boyce, M. S. 2014. Applications of step-selection functions in ecology and conservation. – Mov. Ecol. 2: 4.

Tibshirani, R. 1996. Regression shrinkage and selection via the lasso. – J. R. Stat. Soc. B 58: 267–288.

Tucker, M. A. et al. 2018. Moving in the Anthropocene: global reductions in terrestrial mammalian movements. – Science 359: 466–469.

USDA 2017. USDA national agricultural statistics service cropland data layer. (2016) published crop-specific data layer. – https://nassgeodata.gmu.edu/cropscape.

Worton, B. J. 1989. Kernel methods for estimating the utilization distribution in home- range studies. – Ecology 70: 164–168.

Zimmermann, N. E., Edwards, T. C., Graham, C. H., Pearman, P. B. and Svenning, J. 2010. New trends in species distribution modelling. – Ecography 33: 985–989.