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Research article

Social interactions and habitat structure in understanding the dynamic space use of invasive wild pigs

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Untangling the abiotic and biotic feedback mechanisms driving animal movements and ranges is a core question in ecology, yet progress is hampered by inadequate modelling procedures. Here we show how a recently developed process-based modelling approach, combining step-selection functions and individual-based models, enables a flexible method to infer movement drivers and multi-scale emergent space use patterns. As a case study, we examine the movement behaviours of a highly invasive social generalist (wild pigs, *Sus scrofa*) in relation to conspecific space use and multiple land cover types in a complex agricultural landscape, showing that social interactions are predominantly more important to this species than selection for land cover. Thus, animal movement studies should not neglect the effects of sociality when inferring resource driven movements and, crucially, use multi-scale techniques that incorporate movement processes to untangle drivers of animal space use.

Keywords: process-based models, social interactions, space use, spatial patterns, step-selection, *Sus scrofa*

Introduction

Deciphering the patterns created by animals as they navigate the landscape is a key area of ecological research, with results providing evidence for management decisions crucial for the sustainable use of natural resources (Morris 2003, Allen and Singh 2016, Yang et al. 2021). Patterns of animal space use emerge from a complex network of movements driven by multiple dynamic and interlaced abiotic and biotic feedback processes. These mechanisms include spatio-temporal processes such as the movement of other organisms (Fryxell et al. 2007, Macandza et al. 2012, Jeltsch et al. 2013),

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changing landscapes (Riotte-Lambert et al. 2015) and anthropogenic factors (Tabak et al. 2017), which are all challenging processes to model. Spatio-temporal models provide useful tools for studying these processes, though there is a challenge in selecting the most adequate and appropriate modelling approach for the questions being investigated (Murray 1993, Turchin 1998, Moorcroft et al. 2006, Avgar et al. 2016, Potts et al. 2022a). Of particular note, the process-based home range analysis methods of Moorcroft et al. (2006) use differential equations to model the interacting processes that change through time, but are used rarely in the literature due to the complexity of the methods (Ellison et al. 2024a).

Studies analysing animal movement generally fit into two broad categories: correlative or process-based. In the former approach, animal location or population density data are correlated with environmental layers to gain an understanding of which environments are selected for, using species distribution methods such as resource-selection analysis (Boyce et al. 2002). Although such methods have value in interpreting environmental preference, these models do not account for movement processes and biotic feedbacks, possibly missing important aspects that drive space use, such as social or inter-specific interactions (Potts et al. 2022b). Furthermore, when fitting such resource-selection models, the best model can be chosen using a variety of model selection procedures (AIC/BIC, cross-validation, etc.). These resource selection models generally evaluate the pattern of space use rather than evaluating the underlying process that leads to the pattern. However, many different movement processes can lead to very similar space-use patterns (Börger et al. 2011), meaning that untangling the behavioural drivers of space use, simply by correlating space use to environmental covariates, is difficult, if not impossible.

When modelling movement in response to variables that are themselves affected by animal movement, the feedback between movement decisions and the changing variable must be accounted for. For example, sociality is known to be a key driver of animal movement (Port et al. 2011, Carter et al. 2013, Ward and Webster 2016), but is often ignored when modelling space use. The effect of conspecific and heterospecific interactions on movement is not often implemented in animal movement research, most likely due to the requirement of complex modelling techniques. Despite this, studies using process-based differential equation models have shown that territoriality and social interactions in mammals (Moorcroft et al. 2006, Bateman et al. 2015) and birds (Ellison et al. 2020) are key drivers of space use, alongside some basic environmental structures.

Process-based models describe movements or the changing location of an animal through time, rather than just describing the fixed locations. They can also account for dynamics governed by complex interconnected mechanisms, such as interacting animals or changing environments. Yet they can be mathematically challenging, difficult to implement and rely on the ability to identify the key governing mechanisms in the first place. However, a solution is provided by step-selection analysis (SSA, Thurfjell et al. 2014a), a method commonly used by ecologists and wildlife managers to investigate animal habitat selection but without realising its wider potential. Specifically, SSA advances resource-selection analysis by accounting for an animal's ability to move as it makes habitat selection decisions, but furthermore is a process-based model. The model provides both a dynamic model of each animal's spatial probability distribution over time (Potts and Schlägel 2020, Potts and Börger 2023) and an individual-based model of the movements of each animal (Potts et al. 2022a). The recently developed approach by Potts et al. (2022a) provides an advancement to the popular method of integrated SSA (Avgar et al. 2016) to parameterise a simulation model, introducing an accessible way to understand SSA-based movement models.

Here, we expand upon the recent advancements of SSA (Fleming et al. 2015, Potts et al. 2022a, Potts and Börger 2023) and exemplify our approach by studying a highly social species, the invasive wild pig *Sus scrofa* (Keiter et al. 2016). Wild pigs are generalists that are able to use anthopogenically impacted and highly fragmented landscapes such as agroecosystems (Schley et al. 2008, Thurfjell et al. 2009, Oliveira-Santos et al. 2016), leading to extensive alterations to both natural and managed landscapes. In the USA alone, estimated damage to agricultural interests by pigs exceeds US$1.5 billion annually (Pimentel et al. 2005, Lewis et al. 2019). Pig behaviour is dictated at least in part by social interactions, where they show high animal intelligence (Held et al. 2005, Kornum and Knudsen 2011, Bolhuis et al. 2013) and have exceptional spatial memory (Held et al. 2005, Bolhuis et al. 2013, Morelle et al. 2015, Brogi et al. 2022). This allows them to develop large social networks (Gabor et al. 1999, Podgórski et al. 2014), and since they are known to live in sounders of approximately 25 to 40 pigs (Beasley et al. 2018) this should have an influence on realized patterns of space use and habitat-related decisions. Understanding the interplay between social interactions and movement of wild pigs is thus paramount for ongoing management activities (Beasley et al. 2018), mitigating potential disease transmission (Brown and Bevins 2018) and, by extension, improving our understanding of the general drivers of ecosystem function and change.

Using wild pigs as a case study for our modelling framework, we demonstrate how process-based models of emergent space use may be used to gain new inference regarding the combined effects of conspecifics and vegetation type and structure. We investigate a preference for different areas of desired habitats constructed from a variety of agricultural crop species, alongside social interaction mechanisms to gain a full understanding of pigs' movement choices. This allows us to better describe the spatial patterns emerging from movement processes in response to both environmental variables and conspecific interactions. In particular, we are interested in understanding which factors are of greatest importance in determining pig movements: particular crops (resource availability), conspecific presence (social interactions) or a combination of both.

Within our framework there are two key components determining the space use of animals: the underlying movement process (between two-hourly fixes) and the emergent space use pattern of conspecifics across a longer time window (in our case, one month). We first use step-selection analysis to fit models to wild pig movements (the process) with respect to land cover types and the occurrence distributions of conspecifics. We further assess the eventual estimates of pig ranges (the patterns) using simulations of the step-selection function and choose the best models based on three different comparisons with the empirical data. By evaluating both the process and pattern of spatial dynamics we construct a model that is better fit to the data than evaluating either one alone.

Material and methods

Data

Sixteen adult wild pigs were captured from November 2015 to June 2016 in our study site in the Mississippi Alluvial Valley (approximately 33°31′34.32″N 90°4′38.28″W; Fig. 1). In this highly agricultural area of the Mississippi Delta pigs are known to be widespread and increasing in number (Paolini et al. 2018). In Mississippi, the wild pig population has expanded such that they are present in all counties of the state, but population density estimates are unknown. Each individual was equipped with a GPS collar that recorded locations every 2 h. Pigs were captured opportunistically with landowner approval from November 2015 to May 2016. The pigs were fitted with Iridium Global Positioning System (GPS) collars (LOTEK Engineering Ltd, (n = 3); Vectronic Aerospace GmbH (n = 13)). For this study we focused on the 60 days of data from 5 April 2016 until 3 June 2016, as 5 April 2016 was the first point when all 12 socially interacting individuals had data. From the 16 collared pigs, 12 individuals were chosen for our analysis (six females and six males) as they were determined to be both moving nearby to other pigs and somewhat independent, using correlation analysis (Supporting information). Finding enough sounders for the data collection was challenging, therefore on some occasions two pigs per trapped group were collared; furthermore, this indicates that the potential influence of unmarked sounders within the area was low. We analysed movements with respect to a variety of land cover types using the USDA National Agricultural Statistics Service Cropland Data Layer (2016). More details on data collection and the environmental layers used are included in the Supporting information and in Paolini et al. (2018).

Movement hypotheses

To fulfill their life history needs animals make movement decisions based on a combination of factors based on their physiology and knowledge gained from their previous movements. Prior studies of wild pig behaviour indicate their decisions are due to various land cover types (Paolini et al. 2018), but how are these decisions influenced by the spatial configuration of that land cover and social interactions? We expect pigs may choose their movements based on some configuration of land cover types and where other pigs have chosen to move in the past, with some overuse avoidance.

The predictive modelling framework

To understand habitat selection alongside the influence of social interactions, we used a modelling framework first

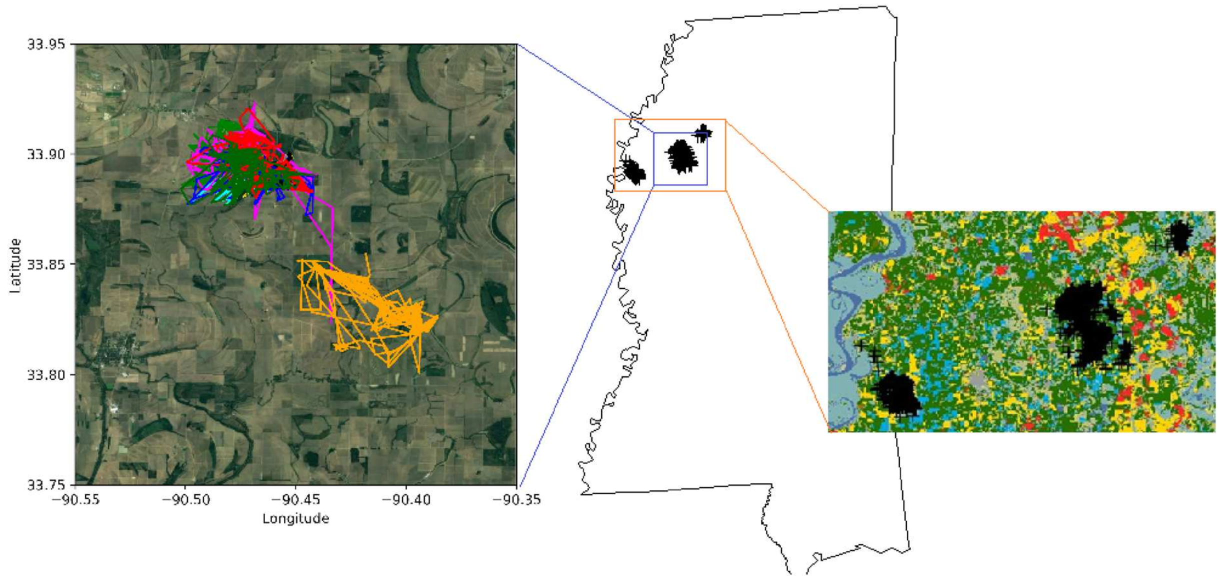

Figure 1. Study site in the Mississippi Alluvial Valley represented on an outline of the state with all pig locations (in black). The movement tracks of 12 pigs used in this study are shown over a satellite image of the study site in the left panel. The right panel shows all pig locations over the USDA CropScape layers.

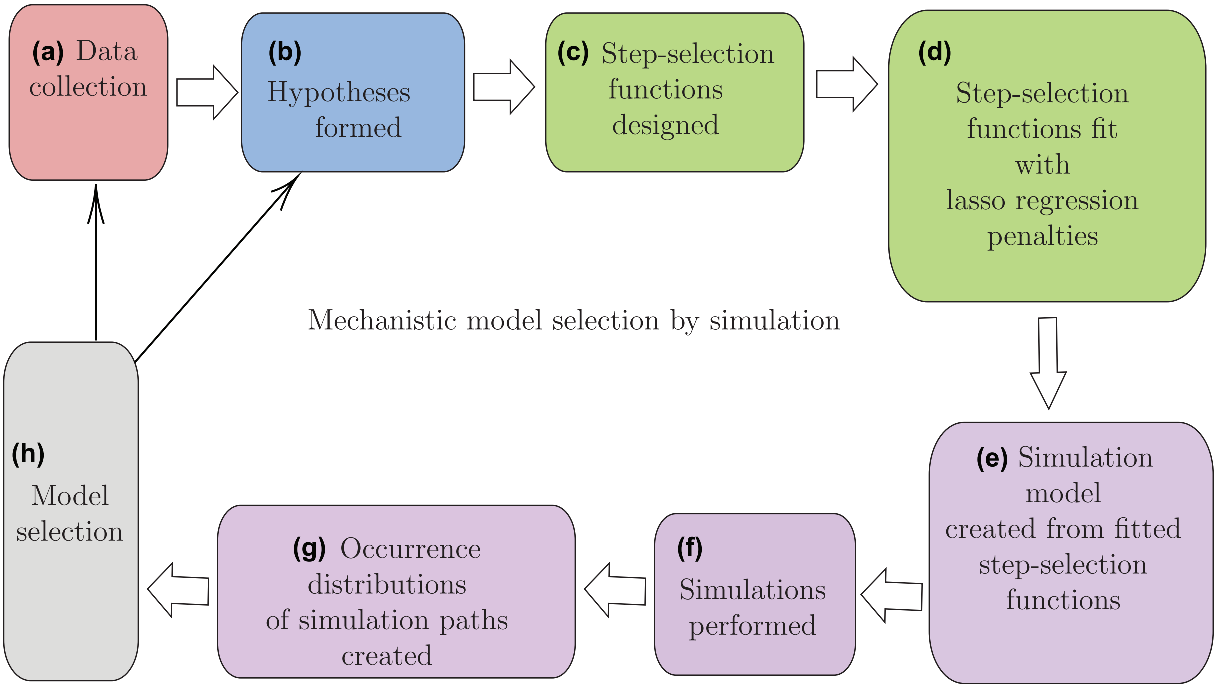

Figure 2. A schematic of the steps performed to create predictive models iteratively using both a step-selection analysis and movement simulations. The framework follows that introduced by Potts et al. (2022a) where we adapt the model parametrisation in step (d) to choose variables using lasso penalties (Tibshirani 1996) and adapt the model selection procedure in step (h) to include comparing simulated and empirical movement paths using autocorrelated kernel density estimation (AKDE, Fleming et al. 2015).

introduced by Potts et al. (2022a), which is adapted here to include different methods of variable selection and model comparison (Fig. 2).

Step-selection analysis and lasso regression

Step-selection analysis (SSA) quantifies movement choices by comparing movements in the data to alternative possible movements, while controlling for the confounding effects of preference for environmental conditions. We begin at step (c) in Fig. 2, as we have already detailed the data collection and outlined hypotheses (steps a–b). We parametrise a movement kernel describing the probability density of movement using SSA for each individual i from one location, $\mathbf{y}$, at time $t-\tau$ to another, $\mathbf{x}$, at time t, where τ is the time step. The movement kernel used here has the following form (Eq. 1):

$$f_{i,\tau}(\mathbf{x},t\,|\,\mathbf{y},t-\tau) = \frac{\exp\left(\beta_0|\,\mathbf{x}-\mathbf{y}\,|+\beta_1 Z_1(\mathbf{x},t)+\ldots+\beta_n Z_n(\mathbf{x},t)\right)}{K_i(\mathbf{x},t)}, \tag{1}$$

where movement is modelled by a step length distribution such that $|\mathbf{x}-\mathbf{y}|$ is the distance (step length) from $\mathbf{y}$ to $\mathbf{x}$ and β_0 is the corresponding parameter to be estimated. In general, movement in step-selection analyses is defined using a combination of steps and turning angles with a variety of functions. We aim to keep our models simple and therefore use an exponential distribution of step lengths to define movement, resulting in the form of Eq. 1, detailed further in Supporting information. The exponential distribution is preferable to the discrete distribution of step lengths as it has an analytical form that relies on only one parameter. Turning angles are assumed to be described by a uniform distribution as this fits our data better than the well-used von Mises distribution (Avgar et al. 2016, Supporting information). The variables hypothesised to influence movement decisions are given by $Z_1(\mathbf{x},t),\ldots,Z_n(\mathbf{x},t)$ and the corresponding parameters to be estimated are $\beta_1,\ldots,\beta_n$. The functions $Z_1(\mathbf{x},t),\ldots,Z_n(\mathbf{x},t)$ represent either an environmental layer or the occurrence distribution of another animal that changes through time (Potts et al. 2022a). The denominator $K_i(\mathbf{x},t)$ is a function which normalises $f_i(\mathbf{x}|\mathbf{y})$, ensuring the output is a probability density function, and has the form

$$K_i(\mathbf{x},t) = \int_\Omega \exp\left(\beta_0|\,\mathbf{x}-\mathbf{z}\,|)+\beta_1 Z_1(\mathbf{z},t)+\ldots+\beta_n Z_n(\mathbf{z},t)\right)d\mathbf{z}\,.$$

We use integrated step-selection analyses (iSSA, Avgar et al. 2016) to estimate parameters, as these methods parametrise movement capabilities simultaneously with habitat choice.

Wild pigs are thought to show quite different preferences for environmental features (Brogi et al. 2022), therefore we fit the step-selection models separately for each individual. The parameters estimated from fitting the above model give an indication of which land cover and social interaction variables are important to each individual. For each wild pig we fit parameters associated with 35 land cover classes and interactions with the other 11 pigs, producing a large amount of potential predictors in any regression which may lead to overfitting. We thus use least absolute shrinkage and selection operator (lasso) regression (Tibshirani 1996) to estimate the important variables that lead to feral pig space use (step d, Fig. 2). These methods combine variable selection with overfitting prevention (i.e. regularization) to produce a fitted model that maximizes predictive accuracy by purposefully biasing uninformative model covariates toward 0. We implement the lasso in a conditional logistic regression framework (Breslow and Day 1980), a commonly used method used to fit step-selection models that is easily implemented using the R package '`clogitL1`' (Reid and Tibshirani 2014). Conditional logistic regression with lasso regularization adds a penalty term to traditional conditional logistic regression which, in short, encourages simpler models with less parameters by highlighting the most important variables. In general lasso regression is extremely efficient when compared to other regression methods, particularly when elastic-net penalties are incorporated, as in the '`clogitL1`' package (Hastie et al. 2009, Reid and Tibshirani 2014). Throughout this study we use lasso regression to fit the parameters of Eq. 1, which in turn indicates the variables that are important to each pig.

Model selection by simulation

To select between different models, corresponding to different formulations of the movement kernel (Eq. 1), we simulate space use patterns using the movement kernel and compare these to the data (step (e), Fig. 2). Rather than simulating the movement kernel directly, we use a lattice-based version of the model, following the methods of Potts et al. (2022a). This enables simulation of a continuous path though the landscape, rather than 'jumping' between successive locations each time step of length τ. The continuous path is important when modelling response to conspecifics, as in reality the pigs could have detected conspecifics at any point on their path, not just the locations recorded in the data. Simulations are performed on a grid of 400 × 400 square cells, where each cell represents 100 × 100 m, over 14 400 timesteps, where each timestep represents 3 min. Thus each simulation represents 30 days of actual time. Mathematical details of how the individual-based model is constructed from movement are given in Potts et al. (2022a) and Supporting information.

To compare models to the data we simulate movements of the 12 wild pigs over 30 days (steps f, g, Fig. 2) and compare the simulation patterns to occurrence distributions (ODs) that are calculated from the movement tracks in the relocation data. Comparisons are calculated in three ways: by comparing (1) ODs created by the simulated and empirical tracks, (2) comparing the average OD over all 1000 simulated tracks to the empirical OD and (3) comparing autocorrelated kernel density estimations (AKDE, Fleming et al. 2015) for the simulated and empirical tracks (step h, Fig. 2). Comparisons (1) and (2) create ODs from the simulated tracks by counting the times each cell was visited in the simulated landscape and normalizing to create a discrete probability distribution, with the latter case using the average of all 1000 simulated ODs. For (3), we calculate AKDEs using the '`ctmm`' package in R to estimate the space use of an animal from a stochastic movement track. Each of the three comparison methods are evaluated for similarity using Bhattacharyya's affinity index (BA, Bhattacharyya 1946), which assumes values between 0 and 1, where a value of 1 would indicate that both distributions are exactly the same. We use the first two comparison methods as they are both easy to calculate when performing the simulations and additionally use AKDEs as they are more accurate estimates of space use. However, we recognise that calculating AKDEs is computationally expensive, so we later compare results to determine whether using AKDEs is worthwhile when investigating model fit.

Interactions with the environment

To examine which combination of land cover types are selected for by the wild pigs, we first reduce the amount of variables with an initial lasso regression. We remove any land cover types that do not seem important to any of the pigs (the β parameter was estimated as 0) and combine similar environments (detailed in Supporting information), leaving 12 land cover maps (Supporting information). For each of the 12 binary land cover maps we create two density maps. First, the binary land cover layer is smoothed using a Gaussian function (detailed in Supporting information) to create environments that have a lower density of a specific resource at the edges and higher density at the centre, which produces a gradient of resources. This smoothing allows one to model the gradual attraction gradient towards an environment by removing the abrupt edges defined by the cells of the land cover map. A second new map is created for each land cover type by squaring the values of the smoothed map; we will hereafter refer to the new maps as the linear and quadratic land cover maps.

The reason for using these two land cover maps is that it enables us to create a map of intermediate resources, that in some cases can be interpreted as using an environmental edge. Suppose $Z(\mathbf{x},t)$ denotes a the smoothed land cover map, then both $Z(\mathbf{x},t)$ and $Z(\mathbf{x},t)^2$ will be variables in the step selection analysis. Let β_Z and β_{Z^2} be the respective selection strengths for the variables defined by each map, which can be estimated using step-selection analysis. In the case that $\beta_Z > 0$ and $\beta_{Z^2} < 0$ (i.e. realized selection for intermediate values of the resource), then the quantity $Z_{\text{int}}(\mathbf{x},t) = \beta_Z Z(\mathbf{x},t) + \beta_{Z^2} Z(\mathbf{x},t)^2$ produces a map where the largest magnitude values are areas of intermediate resource abundance, calibrated so this intermediate abundance tends to be selected over areas of lower or higher abundance. Because our landscape is characterized by wide expanses of common land cover types (e.g. large corn fields and wildlife reserves; Fig. 1), $Z_{\text{int}}(\mathbf{x},t)$ tends to have larger values at boundaries between land cover types – that is, land cover edges. We provide visual examples of this in the Supporting information.

Hence, by including both linear and quadratic versions of the variables we are testing whether the pigs' functional response to each land cover type is linear or quadratic, which in turn tests whether the pigs were attracted to intermediate values of each land cover type. We define three models to compare against a null model, each including the 12 environmental variables (Supporting information). These models describe movement with respect to: M_1, the binary environments; M_2, the smoothed environments; or M_3, the smoothed environments and their quadratic functions. Model M_3 is defined to understand whether pigs select for intermediate values of resource abundance, which for certain environment structures and parameter magnitudes can be considered as a preference for the edges of crops, as described above.

Social interactions

The space use of the 12 pigs visualised in Fig. 1 is restricted to one area and therefore unlikely to be fully described by the land cover types that are distributed across the entire landscape. Social interactions are known to affect wild pigs' movement behaviour (Spitz and Janeau 1995) and therefore their overall space use (Potts et al. 2022a). To understand each pig's movement choices in response to the 11 other pigs, we create occurrence distributions (ODs) for each pig that reflect their probable space use over time (Cozzi et al. 2018). Over a 30-day moving window the OD for each pig ($U_i(\mathbf{x},t)$ for $i=1,\ldots,12$) is calculated each day using the R package '`ctmm`', using movements over the previous 30 days (Potts et al. 2022a). The knowledge each pig holds of the other 11 pigs' space use may be formed from either direct and/or indirect social interactions, possibly mediated by memory (Potts and Lewis 2019). Direct social interactions occur when the pigs overlap in both space and time, and indirect interactions could, for example, be marks on the environment such as scent marking or rooting.

In addition to evaluating each pig's movement in response to the other pigs' ODs, we consider the possibility that wild pigs are avoiding too many social interactions with the same individuals by analysing their movement in response to the quadratic values of the other pigs' ODs. We note here that including both the linear and quadratic versions of each pig's ODs can model the situation where pigs are attracted to other pigs' ODs but not to the high density areas, therefore modelling an overuse avoidance. This is similar to the linear and quadratic land cover maps showing intermediate values of resources, whereas for ODs it models intermediately used areas.

We define two models for conspecific interactions (without environmental parameters): M_4 and M_5, which both estimate parameters for each of the 12 pigs' ODs, but M_5 has 12 additional β parameters that describe movement with respect to the quadratic values of the ODs. We include the quadratic variable for each pig's own OD in model M_4 and M_5 to describe an overuse avoidance of previously visited locations, shown to be important in Potts et al. (2022a).

Social and environmental interactions

We combine the social and environmental models detailed above and develop further models that reflect pigs making movement decisions based on a combination of the 11 other pigs ODs and the 12 environmental conditions. Models M_6–M_8 define movement based on social interactions alongside the binary environments (model M_1 and interactions), the smoothed environments (model M_2 and interactions) and the smoothed environments with their quadratic versions (model M_3 and interactions), respectively.

The modelling framework we follow (Fig. 2) uses an iterative process that redefines models based on the results of the previous steps. Therefore, after fitting and simulating models M_0–M_8, we further created models that consist of a subset of environmental variables that reflect the most influential variables on space use and use those within simulations, named models M_9 onward. All models and their structures are reported in Table 1.

Results

Interactions with the environment

Before introducing social interactions into the models we first consider only interactions with the 12 environmental factors. The purpose of this is to see what inference we observe in the absence of controlling for social interactions. Later on, we will report our more complete results, where we account for social interactions and give a comparison. This comparison will help highlight the importance of controlling for social interactions. The results for these models (M_1 and M_2) indicate that generally wild pigs are selecting for corn, cotton, open water and woodland environments, while avoiding rice, soybean, fallow and open spaces (Table 2). However, this story unfolds further when movement is evaluated in respect to the quadratic version of these land cover maps (Table 3). Here we see that, overall, pigs are selecting for corn, soybean, water and woodland, yet the positive parameters for linear variables and the negative parameters for quadratic variables suggest pigs are selecting for the intermediate values of these land cover types, suggesting that there may be some optimum land cover structure. Only by including quadratic variables do we find the attraction to open water is specific to intermediate densities of water. Similarly, we note that pigs are attracted to intermediate values of soybean land cover, whereas the prior analysis (M_2) indicted pigs did not select for soybean fields. We note here that many of these variables are not selected by the lasso analysis when social variables are included. Despite this, it is possible that some social selection could actually be selection for land cover variables and vice versa (some land cover selection could be social selection) and this is hard to disentangle. Therefore, we report these land cover selection lessons tentatively.

Table 1. Simulation results for models using social interactions, binary environments and Gaussian smoothed environments ($\sigma=25$, Supporting information). Variables that describes conspecific overuse avoidance and self overuse avoidance are denoted as OA and SOA, respectively (these appear as quadratic terms in the movement kernel). For models containing environmental variables (e.g. Binary env, Gaussian env), if the quadratic variables for these environments were included then this this is denoted as 'QuadEnv' in the table. Full descriptions of the models are shown in the Supporting information alongside the results for the models including Gaussian smoothing for both $\sigma=50$ and $\sigma=75$. Similarity between each model and the empirical movement tracks is evaluated using Bhattacharyya's affinity index (BA, Bhattacharyya 1946) averaged over all simulations and all pigs, where bold values indicate the highest BA. Comparisons are calculated in three ways, by (1) comparing the OD of the empirical and simulated movements for each track and taking the overall average BA, (2) calculating the average OD for all simulations and comparing to the empirical OD and (3) calculating an autocorrelated kernel density estimation (AKDE) of each of the empirical and simulated movements for each track and taking the overall average BA.

Model	Variables in model	(1) Simulation BA	(2) Ave BA	(3) AKDE BA
M_0	Null model	0.118 ± 0.0033	0.254	0.459 ± 0.0053
M_1	Binary Env	0.132 ± 0.0034	0.266	0.48 ± 0.0054
M_2	Gaussian Env	0.129 ± 0.0033	0.261	0.508 ± 0.0058
M_3	Gaussian Env + QuadEnv	0.145 ± 0.0035	0.280	0.576 ± 0.0056
M_4	Social + SOA	**0.218 ± 0.0055**	**0.414**	0.58 ± 0.0066
M_5	Social + OA	0.12 ± 0.0033	0.249	0.408 ± 0.0092
M_6	Social + SOA + Binary Env	0.215 ± 0.0054	0.413	0.58 ± 0.0072
M_7	Social + SOA + Gaussian Env	0.199 ± 0.0054	0.393	0.577 ± 0.0077
M_8	Social + SOA + Gaussian Env + QuadEnv	0.192 ± 0.0051	0.395	0.582 ± 0.0079
M_9	Social + SOA + Fallow Gaussian Env	0.211 ± 0.0054	0.396	**0.596 ± 0.0065**
M_{10}	Social + SOA + Woodland Gaussian Env	0.216 ± 0.0054	0.402	0.579 ± 0.0074
M_{11}	Social + SOA + Fallow and Woodland Gaussian Env	0.21 ± 0.0054	0.402	0.572 ± 0.0073
M_{12}	Social + SOA + Fallow Gaussian Env + QuadEnv	0.207 ± 0.0053	0.395	0.584 ± 0.0073
M_{13}	Social + SOA + Woodland Gaussian Env + QuadEnv	0.211 ± 0.0054	0.393	0.575 ± 0.0077
M_{14}	Social + SOA + Fallow and Woodland Gaussian Env + QuadEnv	0.202 ± 0.0052	0.395	0.566 ± 0.0077

Social interactions

The effect of conspecific interactions on wild pig movement indicated that almost all pigs are either attracted to the occurrence distributions of the other pigs ($\beta_i > 0$) or not affected by them ($\beta_i = 0$); however, there are eight occurrences of pigs avoiding other pigs, and nearly all pigs are repelled away from areas they and other pigs had used often (Supporting information). When including an overuse avoidance we find that all non-zero parameters were positive for the linear variables and almost all negative for the quadratic variables. These parameter estimations suggest that pigs are selecting for locations known to be used by other individuals but avoiding those areas which are overused.

Social and environmental interactions

Combining both the parameters for environmental and conspecific interactions provide step-selection models that reflect pig movements based on both sociality and habitat choice. We find that social interactions between pigs are predominantly more important to their movement choices than the environmental layers (Supporting information). The model coefficients reduce to 0 for almost all environmental layers, apart from fallow areas and woodlands. An attraction towards woodland areas and away from fallow areas is indicated for all pigs; and, when including quadratic terms, attraction to intermediate areas is indicated where for larger areas of soybean and woodland is likely to be edge habitat.

Table 2. The results of performing fitting the parameters $\beta_1,\ldots,\beta_n$ for a step-selection model (Eq. 1) for model M_2 with the smoothed environmental variables shown in the header. The parameters are fitted using conditional logistic regression with lasso penalties. The columns for pecans, developed low/med intensity and other crops were removed, as the corresponding parameters were all reduced to zero and were unimportant for pig movement.

Pig/Layer	Corn	Cotton	Rice	Soybeans	Fallow	Water	Open space	Wetland	Woodland
1	0	2.564	−0.224	0	−1.275	1.132	−0.93	3.887	0.561
2	0.171	0	−1.434	−0.364	0	0	0	0	0.65
3	0	0	0	0	−1.155	1.347	0	0	0.421
4	0.808	0	0	−0.346	−0.151	1.311	0	0	0
5	0.112	0	−0.277	−0.037	0	1.179	−0.854	0	0.749
6	0	1.764	−0.793	0	−1.585	0.967	−1.07	0	0.408
7	1.709	0	−0.332	0	0.439	0	−0.525	0	1.389
8	0	1.949	−0.359	0	−1.222	0.927	−0.881	0	0.346
9	0	2.265	−0.318	0	−1.416	1.29	−0.494	1.16	0.516
10	1.724	0	−0.355	0	−0.185	1.966	0	0	0
11	0	0	0	0	−0.628	0	0	0	0.783
12	0.809	0	0	−0.088	0	0	−0.443	0	0.125

Table 3. The results of performing fitting the parameters $\beta_1,\ldots,\beta_n$ for a step-selection model (Eq. 1) for model M_3 with the smoothed environmental variables shown in the headers. The parameters fitted are using conditional logistic regression with lasso penalties. The columns for developed low/med intensity and other crops were removed as they were all reduced to zero. This model can be compared with the model in Table 2 as it includes the quadratic values of each variable. A positive value for a parameter in the linear variable and a negative value in the quadratic variable would indicate that the pig is attracted to only the edge areas of the corresponding environment (Supporting information). Superscript '2' refers to the quadratic version of the variable.

Pig/Layer	Corn	Cotton	Rice	Soybeans	Fallow	Pecans	Water	Open space	Wetland	Woodland
1	0	1.189	0	0.685	−1.83	−3.115	3.618	−2.684	2.863	0
2	3.515	0	−1.596	0.093	0	0	0	0	0	2.845
3	0	0	0	0	0	0	2.352	0	0	0.774
4	0	0	0	−0.418	0.042	0	0.304	−2.044	0	0.459
5	0	0	−1.112	0.584	0.	0	1.317	−2.102	0	1.061
6	0	2.098	0	0	−0.311	−2.341	0.507	−2.169	1.152	0.142
7	0.54	0	0	0.262	0	0	−0.274	−3.208	0	0.77
8	0	0.623	0	1.259	−2.519	−4.711	3.659	−2.649	0.452	−0.765
9	0	0.48	0	0.278	−2.349	−2.481	2.268	−2.367	0.009	0
10	3.255	2.364	−2.684	0	−0.787	0	2.743	−0.393	0	0
11	0.94	0	0	1.621	0	0	1.948	−1.008	0	−0.074
12	0.106	0	−1.555	0.313	0.134	0	0	−2.517	0	−0.141
Pig/Layer	Corn^2	Cotton^2	Rice^2	Soybeans^2	Fallow^2	Pecans^2	Water^2	Open space^2	Wetland^2	Woodland^2
1	0	0	−1.848	−2.6	−1.307	0	−7.607	0	0	−0.655
2	−3.384	0	0	−0.404	0	0	0	0	0	−2.124
3	0	0	0	−0.145	−1.502	0	0	0	0	0
4	0	0	−1.361	−1.283	−1.78	0	0	0	0	−1.767
5	−0.143	0	0	−1.29	−0.549	0	0	0	0	−0.734
6	0	0	−1.599	−0.713	−2.633	0	0	0	0	−0.234
7	0	0	−2.019	−1.89	−1.19	0	−1.942	0	0	−0.798
8	0	0.403	−2.067	−3.264	0	0	−6.991	0	0	0
9	0	0	−1.937	−2.312	−1.043	0	−4.597	0	0	−0.909
10	−1.47	0	0	−0.094	0.581	0	0	0	0	0
11	−0.419	0	−1.869	−1.636	−0.894	0	−3.078	0	0	1.091
12	0	0	0	−1.578	−1.104	0	0	0	0	−0.496

Model selection by simulation

Simulations were used to understand whether a combination of both sociality and environmental layers create the best movement models for the wild pigs (Fig. 3). When including both social interactions and the 12 environmental layers, the SSA results indicated that both an attraction toward woodland areas and away from fallow land is important to the majority of individuals, and we defined models M_9–M_{14} to reflect these behaviours. Table 1 shows each model with the BA indices averaged over all pigs. Overall, comparing the AKDE of both the empirical and simulated movement tracks provides the most similarity between simulations and data. However, all comparisons show the same pattern of best-fitting models.

Including either a combination of environmental variables or social interactions improves the null model, but those that include social interactions generally fit best. Moreover, the model that consists of social interactions (model M_4) is not improved when environment layers are added (models M_6–M_{14}); this is indicated by comparisons (1) and (2) and is only improved slightly using comparison (3). Overall these findings suggest that social interactions could be more important for pig movement decisions than the environmental variables.

We note that the null models do have a reasonably high level of overlap with the empirical data, particularly when comparing using AKDE. This may be due to some simulation paths of the models hitting the edge of the simulated landscape, and these were particularly noticeable for the null model where 168/1000 simulations came within the edges of the landscape. In the Supporting information we report the number of simulations that hit the edge of the landscape for each model, where we see that the better fitting models (those that include social interactions) go within two cells of the boundaries for an average of 35 ± 8 simulations out of 1000 (around 3.5% of the simulations).

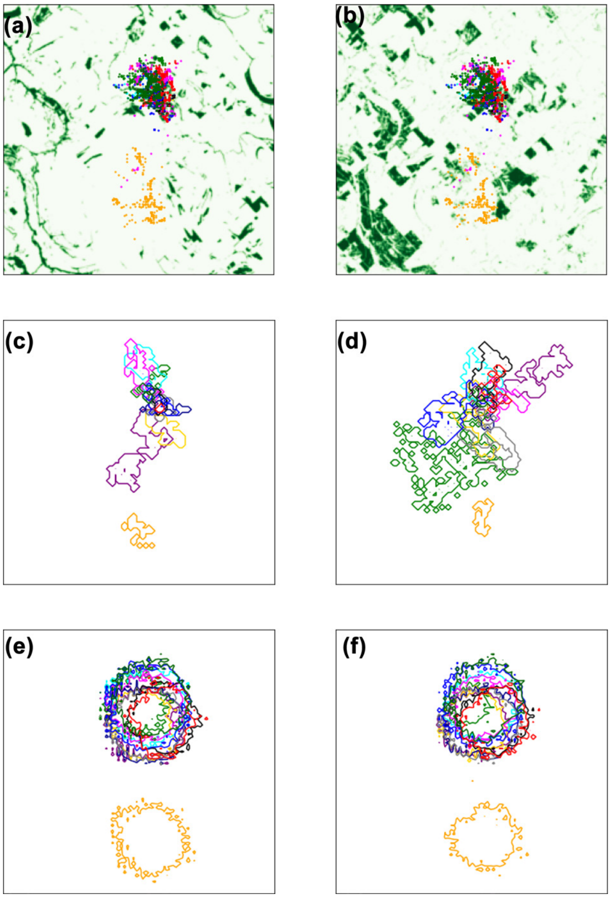

Figure 3. Examples of simulated space use using the simulation rules shown in the Supporting information. Each panel represents a 22.5 km^2 area and simulations are performed over 30 days. Panels (a) and (b) show the GPS locations from Fig. 1 projected to the computational landscape with the smoothed fallow and woodland land covers respectively. Panels (c) and (d) show example ODs calculated from simulated paths for models M_9 and model M_{10} respectively. Lastly panels (e) and (f) show the average ODs calculated over 1000 simulations for models M_9 and model M_{10} respectively.

Discussion

Estimating animal space use at both individual and population levels focuses predominantly on analysing and predicting space use patterns based on interactions with static environments (Hoffmeister et al. 2005). In reality, animal space use is a result of movements in response to changing processes, and including these dynamics into spatial models can reveal behaviours that are unable to be discovered with correlative methods (Moorcroft et al. 2006). Our study reinforces the importance of including changing processes by demonstrating that movements and realized space use of wild pigs are influenced by the movements of other wild pigs, and that this selection is potentially stronger than the influence of various land cover types.

Step-selection models can be thought of as extending resource-selection models to include movement mechanisms, allowing one to infer habitat selection with the knowledge of an animal's location through time, now widely used in ecological studies (Thurfjell et al. 2014b). Our modelling process extends step-selection analysis to infer variable selection using lasso regression, rarely seen in the step-selection literature (Street et al. 2016). Furthermore, we extend a recently developed model selection process (Potts et al. 2022a) that selects models by comparing the estimated space use of simulated step-selection tracks with empirical tracks using AKDE (Fleming et al. 2015). Estimating space use with AKDE can provide a more realistic pattern than traditional kernel density estimates by taking the autocorrelation of movements into account, providing a useful nonparametric way of comparing simulated tracks to data. However, estimations using AKDE come at high computational cost, and when combined with 1000 simulations of the movement model, it may be more efficient to consider faster measures such as classical fixed-kernel methods. Overall, we use methods of combining model selection via spatial patterns with SSA, providing ecological inference of both the movement process and the resulting space use pattern.

By modelling movement in response to social interactions without the environment layers we found that, although pigs are often attracted to areas used by conspecifics, this attraction only holds up to a point. Specifically, the attraction turns into repulsion if the areas are used a very large amount by other pigs (the negative quadratic terms in the Supporting information). This conspecific avoidance structure could be due to a number of factors; wild pigs are known to damage native habitats dramatically (Schley et al. 2008), meaning avoidance could be due to hindering resource depletion for the population (Held et al. 2005). Alternatively, the level of attraction towards or away from other individuals could depend on relatedness or social rank, which is a known driver of pig behaviour (Delcroix et al. 1990, Giersing et al. 2000).

Social dynamics of wild pigs have been shown to affect growth rate and feed intake (Bergsma et al. 2008), boar hormone balances (Giersing et al. 2000) and foraging time (Focardi et al. 2015). Furthermore, a link between social interactions, movement and hunting has been indicated in previous studies; the social structures of wild pig populations in Europe (Janeau et al. 1995, Rosell et al. 2004) are affected by mortality, which inevitably leads to unstable space use patterns (Scillitani et al. 2010) and avoidance of hunting areas (Amici et al. 2012). Alongside this study, the effect of social dynamics on the movements of these invasive animals prompts control measures to be more focused on understanding group dynamics and predicting the areas that surviving populations might spread to, given an eradication attempt. African swine fever (Dixon et al. 2019) is a considerable risk to the US swine industry (Brown and Bevins 2018) and is affecting wild populations in Europe (Sauter-Louis et al. 2021). A full understanding of how social dynamics influences pig movement would be extremely important for this potential disease transmission (Nunn et al. 2008, Craft 2015).

It is important to note that there may be a feature of the environment we have not analysed that manifests in the results as social preferences. Animals may be selecting for resources we have not identified, and by modelling selection for where other animals occur we may be indirectly capturing this unidentified effect via its role in shaping emergent movement trajectories. It is also interesting that when including some environments into the social model (extensions of M_4 in Table 1), the fit to the data is actually worse, despite the modelling processes indicating that these land cover layers are important. However, these differences in fit are small (less than 0.02 difference in the BA index) and may be due to the parameter estimations from iSSA and simulated movements being calculated over slightly different landscapes. Despite this, simulating this social process allows one to ensure some useful predictive capability, even when we are not able to fully capture the hypothetical mechanism behind the small population's movements. Note, however, that a full understanding would require knowledge of most or all pigs' movement, whereas here we were only able to sample 12 from a much larger population.

Edge and overuse effects of pig movements were analysed by smoothing the USDA CropScape data layers that are formed of binary cells (values of either 0 or 1). Since social interactions have such a large effect on the pigs' movement we ran a separate step-selection analysis with only environmental layers (no social interactions), which showed most pigs are attracted to soybean fields, open water and woodland, yet away from fallow lands, rice fields and open space. We concluded this population of wild pigs generally select for intermediate values of land cover, which in some of the studied layers may represent the edges of habitats, a finding that is strengthened by previous studies. For example, soil disturbance by invasive wild pigs in both Malaysia (Fujinuma and Harrison 2012) and Sweden (Thurfjell et al. 2009) declines with distance from the forest cover. The attraction to the intermediate values of open water and soybean are particularly interesting, since including only the linear variables for these environment layers in the analysis indicated a different conclusion: pigs are attracted to open water and away from soybean fields. Our results demonstrate that is meaningful to understand not only which types of environment animals select for, but also how movement decisions are affected by specific land cover configurations as agricultural landscapes, something that is particularly necessary with increasing habitat fragmentation (Haddad et al. 2015). Effects of edges are well known to be present in animal responses to vegetation types (Malcolm 1994, Murcia 1995), and modelling attraction or repulsion to edges has been investigated in a number of studies by calculating the 'distance to edge', for example Holl and Lulow (1997), Thurfjell et al. (2009), Roever et al. (2010), Vales et al. (2022). However combinations of using 'distance to edge' variables alongside habitat structure variables can result in collinearity issues (Ruffell and Didham 2016). Rather than using the 'distance to edge' variable here, we chose to investigate intermediate values of the land cover layers which was more suited to varied landscape structures of the Cropscape layers (Supporting information) that varied from consisting of small patches where edges were unclear to very large patches where the intermediate values indicated edges (Supporting information).

Although we conclude here that the importance of social interactions potentially outweighs that of resource selection there is a possibility that there is a scale-dependent functional response that our modelling process does not sufficiently account for. For example, there may be a hierarchical selection process such that an abundance of resources means the main limiting factor of space use falls upon the social network. A mechanistic link between second and third order selection has already been suggested for this population (Paolini et al. 2019). Thus, to understand this mechanistic link further, we would suggest a study similar to Rettie et al. (2000), where home ranges of sounders could be estimated using social interactions (second order), whilst environmental layers within home ranges (third order) could then be analysed to determine resource selection, or vice versa. In general, some level of hierarchical spatial selection has been indicated in a vast range of animal species from warblers (Chandler and King 2011) to wolves (McLoughlin et al. 2004) to rattlesnakes

(Harvey and Weatherhead 2006). Despite a large number of studies considering only one scale of selection, omitting the idea of either investigating hierarchically or modelling space use as a hierarchical process in resource selection may lead to analyses missing key limiting factors (Beasley et al. 2007, McGarigal et al. 2016). On the other hand, including hierarchical selection could maximise the inference gained from location data, reduce anthropocentric bias and determine the relative significance of space use drivers (Rettie et al. 2000, Lipsey et al. 2017).

Our finding that movement decisions of wild pigs are influenced by social dynamics and selection for habitat edges is an important step towards controlling this invasive species. We suggest that, when designing control methods, the social dynamics of targeted groups are considered to maximise eradication attempts. Furthermore, we advocate for field-based methods to approximate population densities to begin determining target areas. Overall, our results highlight the importance of considering dynamic processes as drivers of movement which ultimately determine space use; an appeal also supported in the recent ecological literature (Hoffmeister et al. 2005, Börger et al. 2008, Kearney and Porter 2009, Potts and Lewis 2019, Potts and Börger 2023).

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Data availability statement

Data are available from the Figshare Digital Repository: https://figshare.com/s/c79fcfa7ae2739807793 (Ellison et al. 2024b). The Cropland Data Layer is available on https://nassgeodata.gmu.edu/CropScape/.

Supporting information

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

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