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RESEARCH ARTICLE

Mechanistic home range analysis reveals drivers of space use patterns for a non-territorial passerine

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Abstract

1. Home ranging is a near-ubiquitous phenomenon in the animal kingdom. Understanding the behavioural mechanisms that give rise to observed home range patterns is thus an important general question, and mechanistic home range analysis (MHRA) provides the tools to address it. However, such analysis has hitherto been principally restricted to scent-marking territorial animals, so its potential breadth of application has not been tested.

2. Here, we apply MHRA to a population of long-tailed tits *Aegithalos caudatus*, a non-territorial passerine, in the non-breeding season where there is no clear 'central place' near which birds need to remain. The aim is to uncover the principal movement mechanisms underlying observed home range formation.

3. Our foundational models consist of memory-mediated conspecific avoidance between flocks, combined with attraction to woodland. These are then modified to incorporate the effects of flock size and relatedness (i.e. kinship), to uncover the effect of these on the mechanisms of home range formation.

4. We found that a simple model of spatial avoidance, together with attraction to the central parts of woodland areas, accurately captures long-tailed tit home range patterns. Refining these models further, we show that the magnitude of spatial avoidance by a flock is negatively correlated to both the relative size of the flock (compared to its neighbour) and the relatedness of the flock with its neighbour.

5. Our study applies MHRA beyond the confines of scent-marking, territorial animals, so paves the way for much broader taxonomic application. These could potentially help uncover general properties underlying the emergence of animal space use patterns. This is also the first study to apply MHRA to questions of relatedness and flock size, thus broadening the potential possible applications of this suite of analytic techniques.

KEYWORDS
advection–diffusion, home range, long-tailed tit, mechanistic modelling, partial differential equation, passerine, space use, taxis

1 | INTRODUCTION

Understanding the spatial distributions of animals is a core concern for ecological research, being at the interface of population dynamics, behavioural ecology and conservation concerns (Franklin & Miller, 2010). However, while emergent patterns of space use may be observed broadly across time and space, they are ultimately caused by movement decisions of individual animals (Nathan et al., 2008). These movements can affect the structure of entire ecosystems by altering populations (Morales et al., 2010), influencing environments (Riotte-Lambert & Matthiopoulos, 2019) and modifying population dynamics such as predator–prey (Lewis & Murray, 1993) and competitive (Potts & Petrovskii, 2017) interactions.

Home range formation provides a particular example of animal space use that is prevalent across a wide range of taxa (Börger, Dalziel, & Fryxell, 2008; Jetz, Carbone, Fulford, & Brown, 2004). It occurs whenever animals restrict their movement to an area of the landscape far smaller than they could cover given their locomotive capabilities (Burt, 1943). Many reasons have been put forward for the formation of home ranges, including optimizing foraging benefits (Mitchell & Powell, 2012; Moorter et al., 2009), avoiding costly conflicts with conspecifics (i.e. territoriality, Jetz et al., 2004; Moorcroft & Lewis, 2006) or avoiding predators (Bastille-Rousseau et al., 2015; Coleman & Hill, 2014). This has led to the hypothesis that there may be general mechanisms underlying home range formation that operate across many species (Börger et al., 2008), although the mechanisms involved have proved rather elusive.

Indeed, many home range models do not seek to understand the movement mechanisms (a.k.a. processes) behind home range formation, but simply aim to describe the space use distribution corresponding to a home range (a.k.a. patterns). These include the Minimum Convex Polygon (Harris et al., 1990; Mohr, 1947), which describes the extent of the home range, and kernel density estimators (Worton, 1989) and their extensions (e.g. Fleming et al., 2015), which estimate the utilization distribution of an animal or group. Such descriptive, statistical models of the home range are sufficient for understanding various ecological questions. For example, statistical methods have been used to ascertain the extent to which animals use different habitat types (Mokross, Potts, Rutt, & Stouffer, 2018), the relatedness of neighbouring groups (Gompper, Gittleman, & Wayne, 1998; Mcloughlin, Ferguson, & Messier, 2000) and hierarchies of size and social dominance (Höjesjö, Økland, Sundström, Pettersson, & Johnsson, 2007; Woodward et al., 2005).

However, there are many behavioural questions which cannot be easily answered by traditional, statistical estimators of home range. Principally, those which seek to unveil the movement and interaction processes that give rise to home range pattern formation require a mechanistic modelling approach. In such an approach, the proximate behavioural decisions of an animal (i.e. processes) are modelled explicitly and the home range (i.e. pattern) arises as an emergent property of this model. This mechanistic modelling approach has enabled researchers to understand various ecological phenomena, such as the processes underlying the emergence of prey corridors

between predator home ranges (Hamelin & Lewis, 2010; Lewis & Murray, 1993), the effect of disease spread on movement decisions (Potts, Harris, & Giuggioli, 2013), coyote *Canis latrans* territory rearrangement following the death of an alpha male (Moorcroft, Lewis, & Crabtree, 2006), and fission processes in meerkat *Suricata suricatta* territories (Bateman, Lewis, Gall, Manser, & Clutton-Brock, 2015). All of these examples make use of explicit, mathematical links between movement and interaction mechanisms and the emergent home range patterns, to make important biological inferences.

Despite the insights gained from mechanistic home range analysis (MHRA) in the context of partial differential equations (PDEs), these analytic techniques have hitherto been used almost exclusively on scent-marking animals (but see Potts, Mokross, & Lewis, 2014), with the exception of the earliest and simplest models, where home ranging arose purely from an attraction to a central place (Holgate, 1971). However, many animals advertise their territory through cues other than scent, such as dominance displays, vocalizations and fighting (collectively known as 'ritualized aggression'). Furthermore, not all animals have a clear 'central point' (such as a den or nest site) which pins their home range in a particular place. The model of Potts and Lewis (2016) was designed to extend MHRA for use with such animals in the context of PDEs. While home range formation with neither a central place nor scent-mark avoidance had previously been modelled using simulations of individual-based models (Moorter et al., 2009; Riotte-Lambert, Benhamou, & Chamaillé-Jammes, 2015; Siniff & Jessen, 1969), the extension to the PDE framework offered by Potts and Lewis (2016) enabled rigorous mathematical analysis of the conditions under which home ranges can form. There, the authors showed mathematically that home ranges can form purely from a mechanism of ritualized aggression, coupled with memory of those aggression events.

In this study, we advance the applicability of PDE-based MHRA further still, by showing that MHRA can be used in situations where there is no explicit territorial behaviour, and also no 'central point' around which animals localize their movement. This is the case for our study species, the long-tailed tit *Aegithalos caudatus*, outside the breeding season. At these times of year, they live in flocks, each of which has a distinct home range that only overlaps slightly with those of neighbouring flocks (Gaston, 1973; Hatchwell, 2016; Hatchwell, Anderson, Ross, Fowlie, & Blackwell, 2001). They do not maintain a fixed roosting site, so have no clear localization centre, and have rarely been observed to engage in territorial interactions (Napper, Sharp, McGowan, Simeoni, & Hatchwell, 2013).

Nonetheless, it may be that long-tailed tits avoid areas where they have seen neighbouring flocks foraging. This could be to avoid social interaction with other flocks or to strengthen relationships within flocks. We hypothesize that this behaviour acts as a proxy for territoriality, causing distinct home ranges to form without requiring directly observable, aggressive, territorial behaviour. To test this hypothesis, we formulate a mechanistic model, incorporating such non-aggressive avoidance mechanisms and observe whether this can explain the various home range patterns observed in a long-tailed tit population across a number of seasons.

Since there is a clear and well-documented effect of habitat type on the space use of long-tailed tits, arising from the structure and composition of woodland (Gaston, 1973), we also incorporate into our study a set of models that are each linked to a distinct hypothesis on the effect of woodland on bird movement. Woodland structure is very complex in our study system, incorporating dozens of genera of trees and shrubs of varying sizes, so we use a simplified approach by viewing woodland as a binary variable: either present or absent. Then our hypotheses all relate to how flocks move with respect to the presence or absence of trees. We use the resulting model to show that the home range patterns of long-tailed tits can be predominantly explained by a combination of conspecific avoidance and attraction towards woodland areas.

From this starting point, we extend our model to test various hypotheses about more subtle drivers of home range patterns. First, we examine how the relative size of a flock (i.e. number of individuals) affects the extent to which it avoids neighbouring flocks. We hypothesize that smaller flocks will tend to have a stronger avoidance mechanism than larger flocks because if there is competition over space use, smaller flocks are likely to be less competitive than large flocks and so are predicted to avoid potential conflict (Adams & Plowes, 2019; Dyble, Houslay, Manser, & Clutton-Brock, 2019; Port, Kappeler, & Johnstone, 2011). Second, given that there is an apparent correlation between spatial proximity and relatedness (Napper & Hatchwell, 2016), we hypothesize that the relatedness of neighbouring flocks will be inversely related to the strength of avoidance mechanism. We show that these subtle effects of flock size and relatedness cannot be observed using kernel density estimators, a popular statistical model describing a flock's home range, but do emerge from a MHRA approach. This demonstrates the usefulness of mechanistic models of home range for uncovering features of movement that cannot easily be detected using descriptive, statistical models.

Overall, our study makes theoretical advances by demonstrating (a) that MHRA is applicable in a much wider range of situations than previously used and (b) that MHRA can uncover behavioural drivers of movement and space use that are not simple to find using traditional, statistical measures of home range. Furthermore, our study makes important advances in avian behavioural ecology by demonstrating (c) that relatedness and flock size can affect between-flock movement responses and (d) that avoidance mechanisms may exist in species that do not display obvious territorial behaviour, explaining the existence of home range segregation in such species.

2 | MATERIALS AND METHODS

2.1 | Study system

The data come from a study on long-tailed tits, a small non-territorial bird found across Europe and Asia. Long-tailed tits weigh only 6–8 g (Glen & Perrins, 1988) and their main life-history goal while not focusing on breeding is to forage for food (Gaston, 1973; Hatchwell, 2016). We studied the behaviour of these birds in the non-breeding season

when they live in home ranging flocks of around 5–25 individuals (Napper & Hatchwell, 2016). One or more fledged broods and their parents and helpers are usually the nucleus of a winter flock, which are then joined by failed breeders who may or may not be related to the brood(s) (Napper & Hatchwell, 2016). Thus, the majority of flock members (60%–70%) are typically related ($r \geq 0.25$, where r is the coefficient of relatedness, Wright, 1922) to at least one other member of the same flock, although those relatives may be drawn from two or more families (Hatchwell et al., 2001). In addition, members of one flock often have relatives in other flocks as a result of dispersal during the non-breeding season (Napper & Hatchwell, 2016). Members of a flock forage together in the day and then sleep together in a communal roost, which often changes location between nights.

The study site is contained within the Rivelin Valley, Sheffield, UK (53°23′N, 1°34′W), covering approximately 3 km^2. The population of long-tailed tits that inhabits this site has been studied since 1994. Here we use data from 2010 to 2013, which were first reported in Napper and Hatchwell (2016), together with data from 2018 to 2019 which has not been previously studied in published work. Data were collected in the Fox Hagg woodland of the Rivelin Valley for the 2011–2012 season, in the Black Brook woodland for the 2010–2011 and 2012–2013 seasons, and for the 2018–2019 dataset we studied both the Fox Hagg and Black Brook woodlands. The approximate home range size for a single flock is 0.15 ± 0.03 km^2 (mean $\pm$ 95% CI; using a 100% minimum convex polygon). As flocks of long-tailed tits move through their environment, they usually stay in each tree for less than a minute before moving on (B. J. Hatchwell, pers. obs.). Consequently, tracking data of the birds consists of GPS locations, recorded at time intervals of 1 min. Locations were recorded on a Garmin Geko 201 GPS with a standard error of 10 m. Observations were made by finding a flock in the study site by recognizing their calls and then identifying ringed individuals. At least 95% of the population are typically ringed by the end of the breeding season (Napper & Hatchwell, 2016). An observation period began when a flock was first encountered and the first location was recorded. The observation period ended when sight of the flock was lost. We recorded one location every minute to give a trajectory for each observation period. There were 19 ± 2 (mean $\pm$ 95% CI) locations per observation period.

For this study, we used location data from six of eight flocks that were followed in the non-breeding season of 2011–2012 in the Fox Hagg woodland. We removed from our analysis two flocks which contained only four and seven locations, collected over one observation period, as we concluded this was not enough data to estimate home ranges. Datasets for the six remaining flocks consisted of 155, 341, 140, 110, 152 and 83 locations, recorded over a range of 5–21 observation periods between May 2011 and February 2012. In addition to the 2011–2012 data, we validated our results using data from the non-breeding seasons of 2010–2011, 2012–2013 and 2018–2019 collected in various parts of the Rivelin Valley study site. We followed a similar procedure to remove from our analysis any flocks that had data collected over only one observation period. In each case, there were at most 18 locations per flock in the removed datasets. The flocks that we ended up using each had >40 recorded locations taken over >1 observation periods.

2.2 | Mathematical models

The trajectories from each observation period are too short to esti-mate covariates of stepwise movement decisions dependent upon the presence of other flocks, and therefore fit a stepwise movement kernel to the data as in, for example, Avgar et al. (2015) and Avgar, Potts, Lewis, and Boyce (2016). Additionally, it would be difficult to infer any inter-flock interaction behaviour since the trajectories of different flocks are not recorded at the same time. Instead, we infer the movement processes of a flock by fitting a mechanistic model of space use to locations collected over the entire non-breeding season (May–February). This method is known as MHRA (Moorcroft & Lewis, 2006). We use a system of advection–diffusion equations, each of which models a flock's utilization distribution, $u_i(\mathbf{x}, t)$, which is the probability density function for the location of flock i, where $i \in \{1, \dots, N\}$ indexes the N flocks. Each equation has the form.

$$\frac{\partial u_i}{\partial t} = \underbrace{D_i \nabla^2 u_i}_{\substack{\text{diffusive} \\ \text{movement} \\ \text{due to} \\ \text{foraging}}} - \underbrace{c_i \nabla \cdot [u_i \mathbf{A}_i]}_{\substack{\text{biased} \\ \text{movement} \\ \text{towards} \\ \text{preferential} \\ \text{areas}}}, \tag{1}$$

where D_i is the diffusion constant and c_i is the magnitude of advection in the direction of vector field $\mathbf{A}_i(\mathbf{x}, t)$ for flock i. This vector field can take various forms depending on the question at hand, and is used to test hypotheses about the drivers of space use; some specific examples are described later. In Equation 1, $\mathbf{x} = (x, y)$, where x and y are Cartesian coordinates and $\nabla = \left(\frac{\partial}{\partial x}, \frac{\partial}{\partial y} \right)$, as is standard. The diffusion term models any behavioural drivers behind movement that are unknown or that are not explicitly tested, for example foraging. To avoid using an unreason-ably large number of parameters in our inference, we initially assume that diffusion is constant and the magnitude of advection is the same for all flocks so that $D_i = D$ and $c_i = c$, for all $i \in \{1, \dots, N\}$.

To solve (1) numerically, we must pick a domain, Ω, and enforce boundary conditions on the boundary $\partial\Omega$. A biologically reasonable condition is to assume zero flux across the boundary, meaning that the number of birds exiting the domain at a boundary point is, on average, the same as the number entering at that point. In Equation 1, the flux is $-D\nabla u_i + cu_i\mathbf{A}_i$, so a zero flux boundary condition means that

$$\left| \mathbf{n_x} \cdot [D\nabla u_i - cu_i \mathbf{A}_i] \right|_{\mathbf{x} \in \partial\Omega} = 0, \tag{2}$$

where $\mathbf{n_x}$ is a vector normal to the boundary at $\mathbf{x}$. Because $u_i(\mathbf{x}, t)$ is a probability density function defined on Ω, we must also impose the following condition

$$\int_\Omega u_i \, d\mathbf{x} = 1. \tag{3}$$

Having set up the general modelling framework in Equations 1–3, we now describe specific choices of the vector field $\mathbf{A}_i(\mathbf{x}, t)$, that corre-spond to different hypotheses about the movement and interaction mechanisms behind observed home range patterns. First, note that each flock tends to reside in a slightly different part of space with only minimal overlap (Figure 2a), suggesting that flocks may be delib-erately avoiding areas that they know to be used by other flocks. In the decades that this population has been studied, interactions be-tween flocks occur regularly, but aggression is very rarely involved in these encounters (Napper & Hatchwell, 2016), meaning that this avoidance mechanism is highly unlikely to be a result of aggressive defence. Another hypothesized reason for spatial segregation of an-imal populations was given by Riotte-Lambert et al. (2015), and in-volves depletion and renewal of resources. However, for long-tailed tits, resources are abundant and deplete only minimally as the birds forage (B. J. Hatchwell, pers. obs.).

Therefore, instead of these previously used mechanisms, we use a memory-based approach, assuming that a flock has some knowledge of other flocks' space use, due to previous meetings which they remember. This knowledge causes a flock to avoid areas where they believe other flocks may reside. The precise details of interactions between adjacent flocks are not import-ant for the model, but could include one flock seeing another, or hearing their calls. As long as some interaction has occurred be-tween flocks and there is some avoidance mechanism (of places where past interactions have happened) in place, then our model is appropriate.

To model the avoidance mechanism, we introduce the concept of an interaction zone (IZ) for each flock. The IZ of a flock models a cognitive map of places where the flock remembers having previ-ously interacted with other flocks. We assume that individuals within a flock share information, and so have a common IZ. The probability that a location, $\mathbf{x}$, is in the IZ for flock i at time t is denoted by $k_i(\mathbf{x}, t)$. The probability k_i increases in places where other flocks have a high probability of using that space and decreases as other flocks become less likely to use the space. Thus, the dynamics of $k_i(\mathbf{x}, t)$ are de-scribed by the following equation:

$$\frac{\partial k_i}{\partial t} = \underbrace{\rho_i u_i \Sigma_{i \neq j} u_j (1 - k_i)}_{\text{interactions}} - \underbrace{\beta_i k_i u_i}_{\substack{\text{decay of} \\ \text{memory}}}, \tag{4}$$

where ρ_i is the rate at which the IZ is reinforced when two flocks of long-tailed tits are at the same location and β_i is the rate of decay of the IZ due to revisiting parts of space without encountering other flocks. Mathematically, the IZ is equivalent to the concept of a 'conflict zone' introduced by Potts and Lewis (2016). For simplicity, and to avoid an unreasonably large number of parameters, we start by assuming that $\rho_i = \rho$ and $\beta_i = \beta$ for all i so that they are the same for all flocks. However, in Section 2.4, we relax this assumption.

When making movement decisions, it is not realistic to assume a flock will examine the infinitesimally precise location where it cur-rently happens to be. Rather, it is better to assume the flock will ex-amine a small area around that location. We model this area as a disc with radius δ. This can be thought of as the flock's perceptual radius for which it makes its movement decisions. This idea corresponds, mathematically, to averaging the value of $k_i(\mathbf{x}, t)$ over this disc.

We thus define $\bar{k}_i(\mathbf{x}, t|\delta)$ to be a spatial average over all $k_i(\mathbf{x}, t)$ within a radius δ of $\mathbf{x}$, so thats

$$\bar{k}_i(\mathbf{x}, t|\delta) = \frac{1}{\pi\delta^2}\int_{B_\delta(\mathbf{x})} k_i(\mathbf{x}, t)\mathrm{d}\mathbf{x}, \tag{5}$$

where $B_\delta(\mathbf{x})$ is a disc of radius δ, centred at $\mathbf{x}$. A similar local averaging was also used by Potts and Lewis (2016) to model territories formed by ritualized aggression, where they showed that it is necessary to use $\bar{k}_i$ instead of k_i, to ensure the system is mathematically well-behaved.

Long-tailed tits are known to forage predominantly in woodland habitats (Gaston, 1973; Hatchwell, 2016) and our location data suggest that the flocks are almost always inside woodland. We therefore incorporate into our modelling framework a tendency for flocks to move in areas with tree coverage, alongside the tendency to move away from the IZ. This leads to the following definition of $\mathbf{A}_i$ from Equation 1.

$$\mathbf{A}_{i,M} = -c_1\nabla\bar{k}_i + c_2\mathbf{v}_M. \tag{6}$$

Here, c_1 and c_2 describe the relative magnitude of advection away from the IZ and towards woodland, respectively, and M indexes different models of attraction to woodland, which we now describe. We first discretise the landscape and define any cell with more than half tree coverage to be in a woodland area. Each woodland area is defined visually using a procedure detailed in Appendix S4. We define six models as follows:

- ($M = 0$) no attraction to woodland ($c_2 = 0$),
- ($M = 1$) advection acts solely on the woodland edges, to draw flocks in (Figure 1b),
- ($M = 2$) advection acts both on the edges and within the woodland to draw flocks towards the centre of a woodland area (Figure 1c),
- ($M = 3$) advection acts on the woodland edges and all space outside of the woodland areas to draw the flocks towards the woodland (Figure 1d),

- ($M = 4$) inside the woodland the flocks are drawn towards the centre of the woodland area and outside they are drawn in (Figure 1e).
- ($M = 5$) no advection away from the IZ ($c_2 = 0$) and $\mathbf{v}_M$ corresponds to the best-fitting model from Models 0–4.

The vector fields, $\mathbf{v}_M(\mathbf{x}|\omega_M)$, for the Fox Hagg and Black Brook woodlands (see Figure 1a) are shown in Figure 1b–e and defined precisely in Appendix S1. Each $\mathbf{v}_M$ depends upon a parameter ω_M, which controls how much the birds are attracted to woodland.

For our analysis, we use a square domain, $\Omega = [0, L] \times [0, L]$, to represent the landscapes shown in Figure 1a. We non-dimensionalize the system in Equations 1–6 as follows

$$\tilde{x} = \frac{x}{L}, \quad \tilde{y} = \frac{y}{L}, \quad \tilde{\delta} = \frac{\delta}{L}, \quad \tilde{u}_i = Lu_i, \quad \tilde{k}_i = k_i, \quad \tilde{\mathbf{v}}_M = L\mathbf{v}_M, \quad \tilde{t} = \frac{Dt}{L^2},$$
$$a = \frac{D}{\rho}, \quad b = \frac{\beta L}{\rho}, \quad \gamma = c\frac{c_1}{D}, \quad \zeta = c\frac{c_2}{D}, \quad \tilde{\Omega} = \frac{\Omega}{L^2}. \tag{7}$$

Immediately dropping the tildes for notational convenience, we arrive at the following dimensionless version of Equations 1–6:
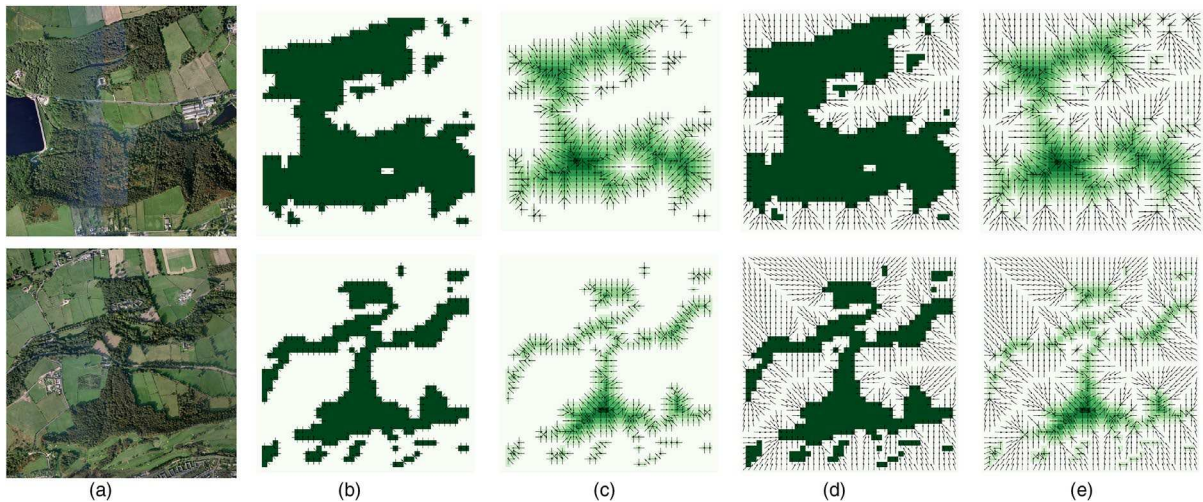
$$\frac{\partial u_i}{\partial t} = \nabla^2 u_i + \nabla \cdot [\gamma u_i \nabla \bar{k}_i - \zeta u_i \mathbf{v}_M], \tag{8}$$

$$a\frac{\partial k_i}{\partial t} = u_i \Sigma_{i \neq j} u_j (1 - k_i) - bk_i u_i, \tag{9}$$

$$\left| \mathbf{n}_\mathbf{x} \cdot [\nabla u_i + \gamma u_i \nabla \bar{k}_i - \zeta u_i \mathbf{v}_M] \right|_{\partial\Omega} = 0, \tag{10}$$

$$\int_\Omega u_i \, \mathrm{d}\mathbf{x} = 1. \tag{11}$$

We summarize all the notation used in Table 1.

FIGURE 1 Panel (a) shows the real landscape taken from satellite images for the Fox Hagg (top) and Black Brook (bottom) woodlands, which are the study sites for the datasets 2011–2012 and 2012–2013, respectively. Panels (b–e) show the vector fields $\mathbf{v}_M$ for the Models 1–4, respectively, corresponding to the woodland images (a) on their respective row. Each of these models represents an attraction into a woodland area, following the vector fields

TABLE 1 Glossary of variables and constants

Symbol	Interpretation
IZ	The interaction zone, which is a cognitive map of the places a flock has had interactions with another flock
$\mathbf{x}$ and t	Space and time, respectively
$u_i(\mathbf{x}, t)$	The probability density function of flock i at time t
$k_i(\mathbf{x}, t)$	The probability of location $\mathbf{x}$ being in the IZ of flock i at time t
$\mathbf{v}_M(\mathbf{x})$	A vector field of unit vectors directing towards woodland, different for each model M, visualized in Figure 1
$\bar{k}_i(\mathbf{x}, t\|\delta)$	An average of $k_i(\mathbf{x}, t)$ over the circular area within a radius, δ and centre $\mathbf{x}$
ρ	The rate at which an interaction happens when two flocks meet
β	The rate of decay of the IZ due to i visiting without encountering other flocks
c_1	The magnitude of advective tendency away from the IZ
c_2	The magnitude of advective tendency towards woodland
ω_M	A parameter related to the rate of attraction towards larger woodland areas (see Appendix S1)
δ	The perceptual radius of a flock
Ω	The domain to be solved over, where $\Omega = [0, L] \times [0, L]$
$\partial\Omega$	The boundary of the domain to be solved over

2.3 | Model fitting and comparison

We solve Equations 8–11 for u_i and k_i numerically using a finite-difference approximation (Smith, 1986), detailed in Appendix S3. To fit the steady-state of Equations 8–11 to a dataset, we find the set of parameters b, γ, δ, ζ and ω_M which maximize the following likelihood function

$$L(b, \gamma, \delta, \zeta, \omega_M | X) = \prod_{i=1}^{N} \prod_{n=1}^{N_i} u_i^*(\mathbf{x}_{i,n}), \qquad (12)$$

where $\mathbf{x}_{i,n}$ is the nth location of flock i, $X = \{\mathbf{x}_{i,n}\}_{i,n}$ is the set of all locations, u_i^* is the numerical steady-state solution of u_i, N is the number of flocks and N_i is the number of locations in the dataset for flock i. Equation 12 assumes the locations are independent, which we justify in Appendix S2 using a method by Benhamou, Valeix, Chamaillé-Jammes, Macdonald, and Loveridge (2014). To maximize Equation 12, we use the Nelder–Mead maximization algorithm (Nelder & Mead, 1965) and select the best model based on their Bayesian information criterion (BIC) scores (Schwarz, 1978).

2.4 | Testing for other behavioural effects of movement

As well as testing hypotheses regarding inter-flock interactions and effects of woodland, we also use our modelling approach to test effects

TABLE 2 The number of kin-connections between flocks and the size of flocks for the second dataset in 2018–2019 shown in Figure 3d. There is a kin-connection if two birds are related by either being siblings, parents or offspring. The size of the flocks is the number of birds in a flock, if a bird has been seen in different flocks it is given a value of 0.5 in both (no birds here were seen in more than two of the flocks)

Kin-connections	A	B	C	D	E
A	—	11	7	0	1
B	11	—	6	0	1
C	7	6	—	2	4
D	0	0	2	—	1
E	1	1	4	1	—
Size of flock	29.5	39.5	12	9.5	8.5

on movement of (a) flock size and (b) inter-flock relatedness. For the data collected in 2018–2019, we have a record of the individual birds seen in each flock, so we can estimate the size of the flocks. Additionally, from social pedigrees, we know the identity of close kin (parents, offspring and siblings) for 108 of the 192 birds. Table 2 shows the size of each flock and the number of kin-connections between them.

For this part of the investigation, our null model is the best-fit model out of Models 0–5. We then modify this model by assuming that the IZ of each flock develops at a different rate for interactions with each of the other flocks, dependent on either its kin-connections or relative size. More precisely, we change Equation 9 to

$$a\frac{\partial k_i}{\partial t} = u_i \Sigma_{i \neq j} \alpha_{ij} u_j \left(1 - k_i\right) - bk_i u_i, \qquad (13)$$

where the various α_{ij} take different values depending on the kin-connections between two flocks or their relative flock size (in Section 2.2–2.3, $\alpha_{ij} = 1$ for all flocks i and j). A larger α_{ij} means that flock i is less likely to visit places that it has previously interacted with flock j than if it were to have a smaller α_{ij}. We then set α_{ij} to be a function of either the relative size of flock j compared to flock i and/or the number of kin-connections between i and j, denoted κ_{ij}. For this, we use three functional forms

$$\alpha_{ij}^{(1)} = 1 + \sigma_1 \frac{s_j}{s_i}, \qquad (14)$$

$$\alpha_{ij}^{(2)} = \frac{\sigma_2}{\kappa_{ij}^{\sigma_3}}, \qquad (15)$$

$$\alpha_{ij}^{(3)} = \alpha_{ij}^{(1)} \alpha_{ij}^{(2)}, \qquad (16)$$

where s_i (resp. s_j) is the size of flock i (resp. j).

Equation 14 gives a higher value for $\alpha_{ij}^{(1)}$ when $s_j > s_i$ than when $s_j < s_i$, meaning the probability that a location will be considered to be in the IZ of flock i will be higher if flock j is larger. This tests the hypothesis that a flock is less likely to consider a location safe if they have observed it being used by a larger flock than if the same location were observed being used by a smaller flock. Equation 15 gives

a smaller value for $\alpha_{ij}^{(2)}$ if there are more kin-connections between flock i and j. This means a flock would be less likely to consider a location part of its IZ if it had observed a highly related flock there than if it had observed a less related flock in the same location. Equation 16 combines the two hypotheses. We fit the parameters σ_1, σ_2 and σ_3 using the functions 14–16. We use BIC both to select between the three models, and examine whether they are an improvement on the null model ($\alpha_{ij} = 1$ for all i, j).

2.5 | The effect of the landscape on kinesis

We have so far considered the effects of woodland and the IZ on advection. However, it is also possible for such landscape features to have an effect on kinesis (i.e. the diffusion coefficient in Equation 1) as well. To test this, we change Equation 8 to

$$\frac{\partial u_i}{\partial t} = \nabla^2[\Phi_i u_i] + \nabla \cdot [\gamma u_i \nabla \bar{k}_i - \zeta u_i \mathbf{v}_M], \qquad (17)$$

where $\Phi_i(\mathbf{x}, t)$ is a function of space, and depends upon the presence of woodland and/or the IZ. We choose $\mathbf{v}_M$ to be the function from the best-fit model out of Models 0–5, and perform model selection (via BIC as in Section 2.3) using the following three functional forms for Φ_i

$$\Phi_i^{(1)}(\mathbf{x}) = \exp(\mu w(\mathbf{x})), \qquad (18)$$

$$\Phi_i^{(2)}(\mathbf{x}, t) = \exp(\psi \bar{k}_i(\mathbf{x}, t)), \qquad (19)$$

$$\Phi_i^{(3)}(\mathbf{x}, t) = \exp(\mu w(\mathbf{x}) + \psi \bar{k}_i(\mathbf{x}, t)), \qquad (20)$$

where $w(\mathbf{x})$ is the density value of the woodland, defined as follows. When extending Model 1 or 3 to incorporate Equations 18–20, we use $w(\mathbf{x}) = 1$ for $\mathbf{x}$ in woodland and $w(\mathbf{x}) = 0$ for $\mathbf{x}$ outside woodland. When extending Model 2 or 4, we use $w(\mathbf{x}) = D(\mathbf{x})^{\omega_M}$ for $\mathbf{x}$ in woodland, where $D(\mathbf{x})$ is the distance from $\mathbf{x}$ to the woodland edge, and $w(\mathbf{x}) = 0$ outside woodland. Here, Equation 18 models a situation where the presence of woodland alone has an effect on kinesis. In Equation 19, only the IZ has an effect on kinesis. Equation 20 incorporates both effects. We investigate this effect on kinesis both with and without the taxis term in Equation 17.

3 | RESULTS

For home range observations from the non-breeding season of 2011–2012 (Figure 2a), we found that Model 4, which contains movement away from areas of past interaction with other flocks and movement towards woodland, captured the home ranges best (Figure 2b).

FIGURE 2 Utilization distributions informed by fitting the steady-state of Equations 8–11 to data from the non-breeding season of 2011–2012. Flock locations are shown on top of a photograph of the landscape in panel (a) where each color represents a different flock. Panels (b–d) show the steady-state solution of Equations 8–11 together with observed locations (dots), here darker contour lines mean a higher probability density. Panel (b) shows the corresponding utilization distribution for the best-fit model ($M = 4$). Panel (c) shows the utilization distribution for Model 0, where there is no attraction to woodland. Panel (d) shows the utilization distribution for Model 5, where there is no directed movement away from other flocks. Here the contour lines coincide since there are no interactions. We see that both movement in response to the environment and in response to other flocks are necessary to create home range patterns which represent the data
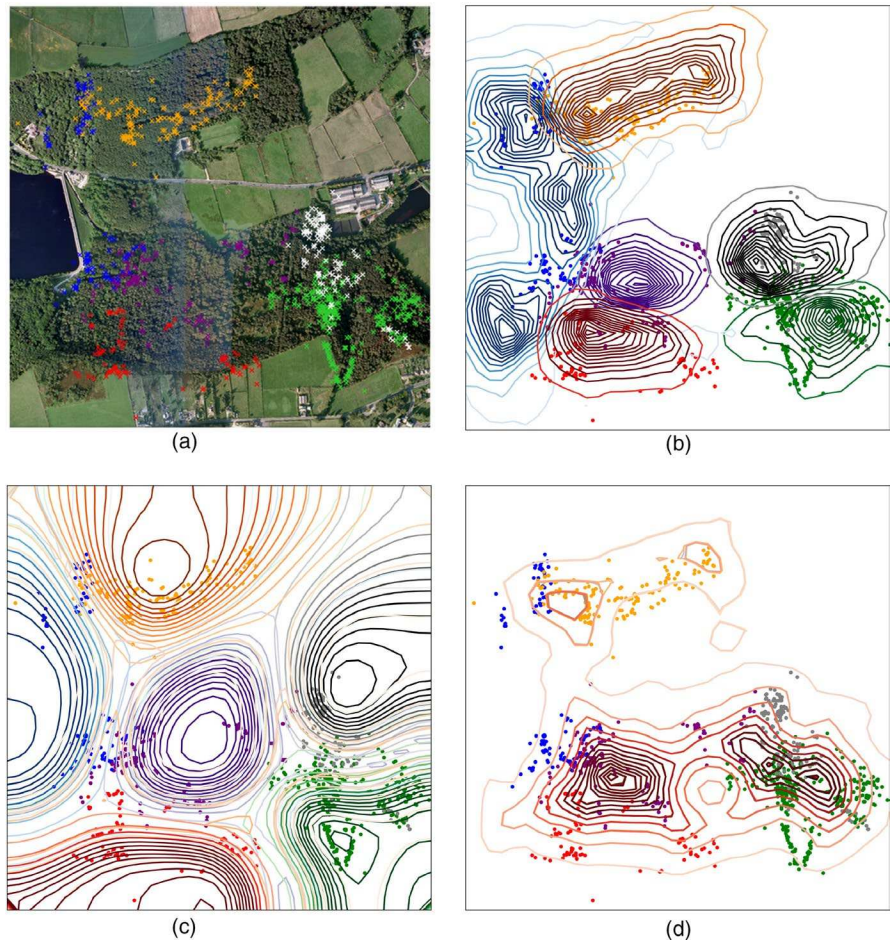
This contrasts with the relatively poor fit of the base models that included inter-flock interactions only (Model 0; Figure 2c) or with attraction to woodland only (Model 5; Figure 2d), which can be considered as null models for the purpose of illustrating the value of Model 4 in capturing the home range patterns. These results indicate that two aspects of movement, responses to habitat and conspecifics, combine to give the key ingredients in the formation of long-tailed tit home ranges.

Similar findings hold across four other non-breeding seasons from 2010 to 2018 and different parts of the study site (Figure 3). By comparing BIC values, we see that for three of the other datasets, the best-fitting model is confirmed to be Model 4, and for one it is

Model 2 (Table 3). This gives further indication that the birds prefer to move away from the woodland edge, as these models are the only two which describe this movement (Figure 1). The datasets and their corresponding utilization distributions are shown in Figure 3 and Appendix S6.

Using data collected in 2018–2019, we extended the model selection procedure to test for an effect of flock size and relatedness between flocks on home range utilization. In the absence of this additional mechanism, Model 4 was the best-fitting model (Table 3; Figure 4a), and Model 2 was the next best-fit, both indicating avoidance of other flocks and movement towards the centre of woodland. When Model 4 was extended to incorporate flock size and
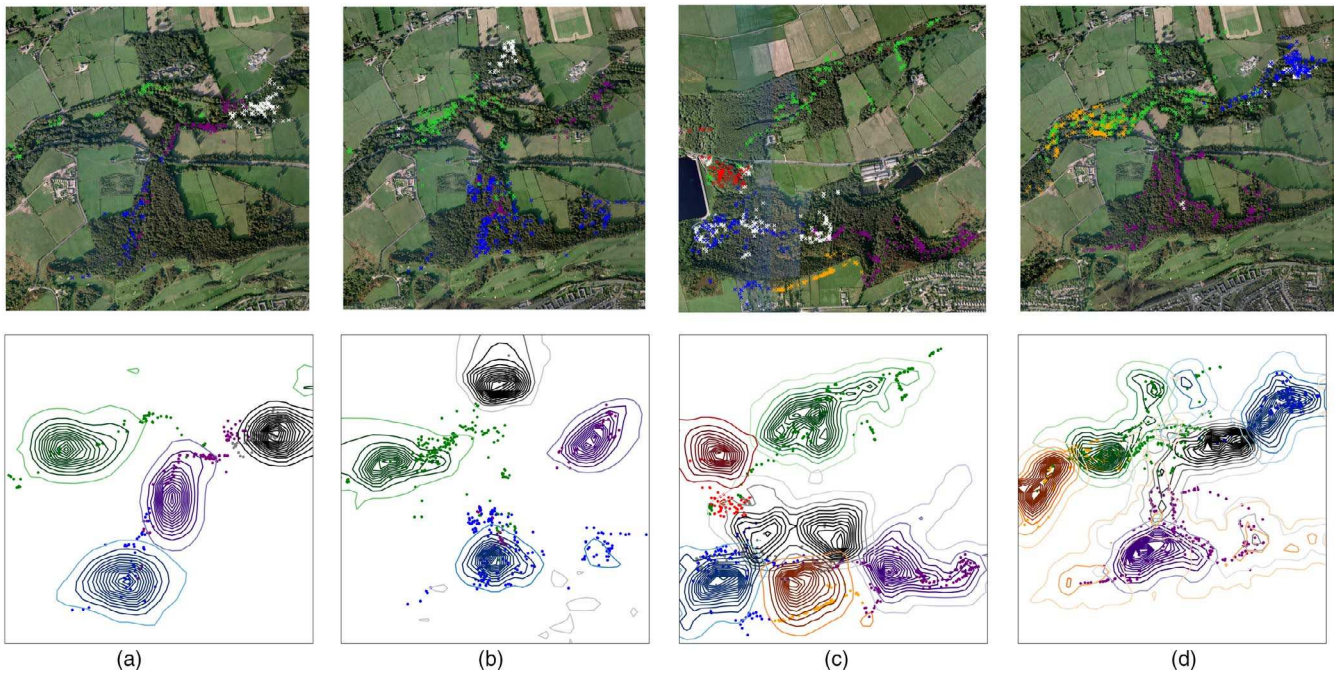
FIGURE 3 Results for the best-fit model for Equations 8–11. The data for the non-breeding season of 2010–2011 are shown in (a) and the non-breeding season of 2012–2013 is shown in (b) with the corresponding utilization distributions for the best-fitting models shown underneath. Panels (c) and (d) show the utilization distributions for the best-fit models for the data collected in the non-breeding season of 2018–2019, in different spatial areas with their corresponding datasets shown above. All datasets apart from (b) give Model 4 as the best-fitting model, where (b) gives Model 2. These two best-fitting models are the only models that direct movement into woodland and away from the woodland edges

TABLE 3 Best-fitting models, their parameter values and their Bayesian information criterion (BIC) scores for all of the datasets. The BIC values from each dataset can be compared with the other models which were tested using the last column in the table. The subscripts on the 2018–2019 datasets refer to the two datasets collected that season. We do not report a as its value does not affect the steady-state distribution $u_i^*(\mathbf{x})$

Dataset	Best-fit Model	Number of flocks	b	γ	δ	ζ	ω	BIC	Difference in BIC from next best-fitting model
2010–2011	4	4	1.14	8.0	0.054	12.9	2.1	3,411	227
2011–2012	4	6	13.3	9.6	0.072	18.1	0.51	11,089	29
2012–2013	2	4	2.9	10.0	0.074	19.9	0.74	6,399	258
2018–2019$_1$	4	6	9.2	9.7	0.096	23.5	0.64	10,905	151
2018–2019$_2$	4	5	11.7	7.7	0.047	25.9	1.1	14,297	283

(a)   (b)   (c)   (d)
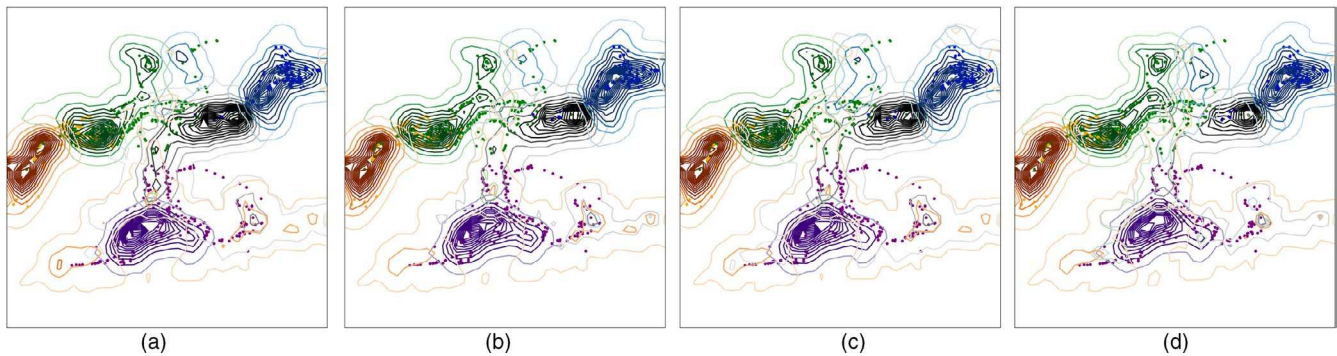
FIGURE 4 Panel (a) shows the best-fitting model (Model 4) for the second 2018–2019 dataset (Figure 3d). Panels (b–d) show Model 4 with α_{ij} defined in Equations 14–16, respectively. Although we see little change visually from the previous best-fitting model where $\alpha_{ij} = 1$ (Panel [a]) there is a reasonable improvement in the Bayesian information criterion values (Table 4)

TABLE 4 The extended version of Model 4, using Equations 14–16, with the second 2018–2019 dataset, their parameter values and their Bayesian information criterion (BIC) scores corresponding to Figure 4. The BIC values can be compared with the previous Model 4 (BIC = 14,297) using the last column in the table

Model	b	γ	δ	ζ	ω_M	σ_1	σ_2	σ_3	BIC	Difference in BIC from Model 4
α_{ij}^1	14.4	7.8	0.050	25.8	1.9	0.068	—	—	14,233	64
α_{ij}^2	11.8	7.8	0.048	25.9	1.2	—	0.088	1	14,248	48
α_{ij}^3	11.6	8.9	0.047	25.9	1.2	0.087	0.99	0.058	14,230	67

TABLE 5 The version of Model 4 with kinesis, using Equations 18–20, with the 2011–2012 dataset, their parameter values and their Bayesian information criterion (BIC). The BIC values can be compared with the previous Model 4 (BIC = 11,089) using the last column in the table

Model	b	γ	δ	ζ	ω_M	μ	ψ	BIC	Difference in BIC from Model 4
$\Phi_i^{(1)}$	13.2	9.6	0.072	18.2	0.51	−0.00011	—	11,096	7
$\Phi_i^{(2)}$	13.2	9.6	0.071	18.4	0.50	—	0.027	11,095	6
$\Phi_i^{(3)}$	13.3	9.6	0.071	18.2	0.51	−0.000004	0.025	11,103	14

relatedness, although visually there was not a dramatic improvement in the fit between predicted and observed ranges (Figure 4b–d), the extended model resulted in a reasonable improvement in BIC values (Table 4). More specifically, the results showed that smaller flocks avoided large flocks and large flocks were less likely to avoid small flocks while avoidance decreased as inter-flock relatedness increased (Table 4). It should also be noted that these effects of kinship and flock size on avoidance behaviour were not found when home ranges were analysed using KDE, a relatively simple statistical model (Worton, 1989; Appendix S7).

Finally, when considering the effect of a landscape-varying kinesis mechanism on the space use of the flocks, we find no improvement in the model fit: indeed, the BIC values are larger when we include the effect of landscape on kinesis into the best-fit models from the study without such a kinesis effect (Table 5; Appendix S8). Furthermore, when fitting models where landscape only affects kinesis and not advection, the fit is very poor compared with models with landscape-driven advection (Appendix S8).

4 | DISCUSSION

We have used MHRA (Moorcroft & Lewis, 2006) to show that memory of past conspecific interactions and movement towards woodland combine to model home range patterns of long-tailed tits with good accuracy (Figure 2). This study has extended the application of MHRA to non-breeding, non-territorial passerines, thereby showing that an understanding of space use patterns can be gained from this approach in the absence of either territorial scent-marking or advection towards a central place (Potts & Lewis, 2014).

Past research on the foraging behaviours of long-tailed tits suggests that they are attracted to woodland (Gaston, 1973). This idea agrees visually with the location data shown in Figures 2a and 3. Our best-fit model, Model 4, also suggests that the flocks have a tendency to move from the edges of woodland towards the central parts of the woodland area. There are various possible reasons for this. One hypothesis is that core areas of woodland are better than edge habitats for avoidance of predators, as reported in several

taxa (e.g. Angkaew, Sankamethawee, Pierce, Savini, & Gale, 2019; Hansen, Sato, Michael, Lindenmayer, & Driscoll, 2019; Valentine, Apol, & Proppe, 2019). Conversely, other studies have reported the reverse pattern, with lower predation risk in edge habitats relative to core sites (e.g. Newmark & Stanley, 2011; Šálek, Kreisinger, Sedláček, & Albrecht, 2010) and a meta-analysis suggests little consistency across habitat types and landscapes (Vetter, Rücker, & Storch, 2013). We are currently investigating the effects of habitat types on nest predation rate, although their impact on survival of juveniles and adults is much harder to quantify because of long-tailed tits' extensive ranges that typically encompass both core and edge habitats. Alternatively, core areas of woodland may differ from peripheral areas in their food availability (e.g. Rosli, Zakaria, & Rajpar, 2018; Terraube et al., 2016), thereby influencing forager movements. This possibility is also hard to test in long-tailed tits because of the difficulty of sampling food availability for a canopy-feeding generalist insectivore. Teasing apart these hypotheses would require new field studies, particularly tailored to this question. Thus, our results demonstrate the role of mechanistic modelling in determining potentially fruitful ideas for future empirical research.

Our model also suggests that flocks avoid places they remember interacting with other flocks in the past. These interactions could be visual or vocal, and therefore may take place at a distance (incorporated in the averaging kernel, Equation 5). The memory capacity of small passerines is hard to test biologically as little is known about the cognitive abilities of small birds in general, regardless of species (Emery, 2006). However, the avoidance behaviour observed here would be very hard to explain without assuming some capacity for memory: to have an understanding of the spatial extent of the home range of a neighbouring flock (or even just the dividing boundary), birds would need to remember observations of past positions where they have detected the neighbouring flock, either through sight or sound. Without memory, birds would only be able to respond to the current location of a neighbouring flock, which is insufficient for explaining the observed spatial segregation. Mechanistic modelling, as exemplified in this work, can give a way of indirectly inferring the extent to which animals use memory, and such indirect inference is not without precedent (Avgar et al., 2015; Fagan et al., 2013; Merkle, Fortin, & Morales, 2014; Merkle, Potts, & Fortin, 2017).

Although woodland and memory of past interactions affected advective movement, we found no measurable effect on diffusive movement (i.e. kinesis). This is in contrast with MHRA studies on coyote home ranges (Moorcroft & Lewis, 2006) where the diffusive aspect of movement was found to be highly dependent on prey density.

Although the central aim of our study was to select between models, it is also worth commenting briefly on the parameter values of the best-fit models, as they can give some additional insight. Looking at Table 3, the first thing to notice is that, of the four datasets where Model 4 is the best-fit model, there is not a great amount of variation between seasons in γ (7.7–10) which controls the advection away from the IZ, ζ (12.9–25.9) which controls the advection

towards central woodland, or δ (0.047–0.096) which is the birds perceptual radius. However, there is a large variation in b (1.14–13.3), the parameter controlling the decrease in the IZ due to safe visits, across seasons. The outlier is the 2010–2011 season ($b = 1.14$). Here, there were fewer flocks than in other seasons, so we hypothesize this might have affected the best-fit value of b. The reason for this is that the first term on the right-hand side of Equation 9 is a sum that increases with the number of flocks. Thus, one would expect the best-fit value of b to increase with the number of flocks in the study. While this is unlikely to account for all of the variation, it perhaps gives a partial explanation for this anomaly. It is also interesting to note that the mean value of δ, when converted into metres is 81 m. This means that our models suggest birds are, on average, considering an area with a radius of 81 m around their present location when making movement decisions. Here, for simplicity, we have assumed that perception is a binary quantity: perceived within the δ-disc and not perceived outside this disc. However, it would also be possible to consider other non-local formalisms, such as exponential decay (Avgar et al., 2015).

Aside from avoidance of other flocks and attraction to woodland, we have also shown that movement decisions in response to adjacent flocks depend on the relatedness between the two flocks. We saw a negative relationship between avoidance mechanisms and flocks with more kin-connections. Other things being equal, one would expect this to cause a positive relationship between home range overlap and kinship, a phenomenon observed in long-tailed tits (Hatchwell et al., 2001), as well as in several other taxa, including mammals (Sera & Gaines, 1994; Støen et al., 2005; Walker, Taylor, & Sunnucks, 2008), lizards (While, Uller, & Wapstra, 2009) and fish (Griffiths & Armstrong, 2002). Our study thus reveals plausible mechanisms behind such observations.

Our results also suggest that the relative size of each flock has an effect on their movement away from other flocks. Specifically, smaller flocks were less likely to move to places where they had interacted with larger flocks in the past and larger flocks were less likely to avoid places where they had encountered smaller flocks, suggesting greater avoidance of larger flocks. This effect of group size on the use or avoidance of overlapping ranges of adjacent social groups appears to be very unusual among social vertebrates and we are not aware of any equivalent findings, presumably because social species typically defend exclusive territories. However, this situation is captured in the theoretical models of 'battle dynamics' between social insect colonies, where the outcome of conflicts over space may be determined by relative colony size (Adams & Plowes, 2019; Adler, Quinonez, Plowes, & Adams, 2018). Testing avoidance of larger flocks directly would require analysis of synchronous observations of many flocks, which is a difficult task for field work. MHRA provides a way of making such inferences with much less data, providing there is sufficient data to capture the home range.

The question of why flocks may benefit from avoiding one another remains open. One possibility is that it is related to avoidance of antagonistic social interactions (Sharp, McGowan, Wood, & Hatchwell, 2005). Although long-tailed tits do not defend territories

and escalated conflicts are observed very rarely, simulated intrusions of individuals into flocks using playback experiments result in brief bouts of aggression that could deter interactions (Napper & Hatchwell, 2016). This would be consistent with the extended version of Model 4, which found that small flocks were more likely to avoid large flocks and large flocks were less likely to avoid small flocks. A second hypothesis is that separation into flocks with segregated space use is an anti-predator tactic, with flocks avoiding each other to prevent total flock size exceeding some optimum at which the benefits of group-living are maximized (Pulliam & Caraco, 1984). A final explanation concerns the social benefit of flocking with a consistent set of conspecifics. Long-tailed tits are cooperative breeders in which helping behaviour is kin-selected (Hatchwell, Gullett, & Adams, 2014), with helpers exhibiting a strong kin preference in their helping behaviour (Leedale, Sharp, Simeoni, Robinson, & Hatchwell, 2018; Russell & Hatchwell, 2001). Kin recognition is achieved through association using learned vocal cues (Sharp et al., 2005) and helping decisions are also influenced by association during the non-breeding season (Napper & Hatchwell, 2016). Therefore, there are substantial fitness benefits to be gained by maintaining contacts with relatives during the winter, and perhaps also by avoiding dilution of those associations by frequent interaction with non-kin in other flocks. The effect of inter-flock relatedness on movement decisions revealed by the extension of Model 4 using 2018–2019 data is consistent with this explanation.

Further ecological factors which limit the population densities of long-tailed tits are yet to be conclusively understood. Weather effects are known to influence the survival of the birds (Gullett, Evans, Robinson, & Hatchwell, 2014), with a stronger effect in the breeding season where wetter and colder weather reduces annual survival, indicating that the birds benefit from the warming climate. Moreover, a demographic study on several passerines, including this population of long-tailed tits, indicates that at population densities close to the carrying capacity there is density dependence in mortality and that at lower densities the population equilibrium is more influenced by stochastic environmental variation driving recruitment (Sæther et al., 2016).

A key advantage of MHRA for studying home range patterns is that it allows users to reveal the behavioural decisions that can lead to the observed space use patterns. This is in contrast with statistical models, such as MCP or KDE, that only give descriptors of the home range. More recent efforts have sought to incorporate some aspects of movement into home range analysis. For example, the Brownian bridge (Horne, Garton, Krone, & Lewis, 2007), which interpolates between successive locations by assuming Brownian movement. This has been extended in various ways, such as the biased Brownian bridge (Benhamou, 2011), which incorporates advective movement into the Brownian motion. Since the MHRA models studied here are based on an advection–diffusion equation, which describes the probability distribution of a biased Brownian motion, it would be natural to incorporate mechanistic modelling into the biased Brownian bridge formalism. This would enable researchers to incorporate behaviourally informed interpolations of space use between successive location fixes into biased Brownian bridges, leading to more accurate estimations of space use.

Here, we have demonstrated how MHRA can reveal specific behaviours that affect movement decisions and space use patterns in long-tailed tits. However, the method is quite flexible, and various hypotheses on the drivers of space use can be tested, in principle, by altering the advection term in the model (Equation 1). For example, if individuals do not use space exclusively, such as in polar bears *Ursus maritimus* (Ferguson, Taylor, Born, Rosing-Asvid, & Messier, 1999) and vultures (Coleman & Fraser, 1989), one would alter the advection term to include movement drivers which do not describe avoidance of other individuals of the same species, instead incorporating advection towards prey or desirable environment. Vultures use a central place which depends upon age so this would mean the advection term would include an attraction towards the central place, with the attraction parameter dependent on age. That said, some species have a similar correlation between relatedness and home range structure to long-tailed tits, despite being of rather different taxonomies, for example, bottlenose dolphins *Tursiops truncatus* (Frère et al., 2010) and giraffes *Giraffa camelopardalis* (Carter, Seddon, Frère, Carter, & Goldizen, 2013). Therefore, the models one might use in those cases may be very similar to the ones used here.

In summary, our finding that kinship influences space use is consistent with previous statistical home range analysis of our long-tailed tit population (Hatchwell et al., 2001; Napper & Hatchwell, 2016), but here we have provided new insight into the avoidance mechanism from which these space use patterns emerge. Our study has also uncovered further drivers of space use, showing that (a) the distance from the woodland edge influences movement, (b) there is a memory-based avoidance mechanism between flocks and (c) flock size influences inter-flock movement decisions. More broadly, MHRA has potential to provide a wealth of understanding of drivers of movement and home range use of animal species. This study extends the usage of MHRA beyond scent-marking, central-place foragers and paves the way to understand the behaviours of a whole new range of taxa.

AUTHORS' CONTRIBUTIONS

J.R.P. and B.J.H. conceived and designed the research; N.E. performed the research; B.J.H., S.J.B. and C.J.N. provided the data; N.E. led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

DATA AVAILABILITY STATEMENT

The datasets supporting this article are available from the Dryad Digital Repository https://doi.org/10.5061/dryad.fqz612jqj (Ellison, Hatchwell, Biddiscombe, Napper, & Potts, 2020).

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