

## LETTER

# Memory drives the formation of animal home ranges: Evidence from a reintroduction

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**Editor:** Tim Coulson**Abstract**

Most animals live in home ranges, and memory is thought to be an important process in their formation. However, a general memory-based model for characterising and predicting home range emergence has been lacking. Here, we use a mechanistic movement model to: (1) quantify the role of memory in the movements of a large mammal reintroduced into a novel environment, and (2) predict observed patterns of home range emergence in this experimental setting. We show that an interplay between memory and resource preferences is the primary process influencing the movements of reintroduced roe deer (*Capreolus capreolus*). Our memory-based model fitted with empirical data successfully predicts the formation of home ranges, as well as emergent properties of movement and spatial revisitation observed in the reintroduced animals. These results provide a mechanistic framework for combining memory-based movements, resource preferences, and the formation of home ranges in nature.

**KEYWORDS***Capreolus capreolus*, familiarity, home range emergence, mechanistic movement model, redistribution kernel, resource preferences, roe deer, site fidelity, space-use, spatial memory

## INTRODUCTION

Most animals live in home ranges – areas that are typically much smaller than their movement capabilities would otherwise allow (Burt, 1943). The spatially-constrained nature of animal space-use has important implications for many ecological processes, including: density-dependent regulation of population abundance (Riotte-Lambert et al., 2017), predator-prey dynamics (Lewis & Murray, 1993), the spread of infectious diseases (White et al., 1995), and for the design of conservation strategies (Schofield et al., 2010). Home ranges are pervasive throughout the animal kingdom, suggesting that they provide fitness benefits in a wide range of ecological contexts, and originate from general biological mechanisms (Börger et al., 2008). Constrained space-use by territorial species has been successfully characterised using movement models based on conspecific avoidance

(Bateman et al., 2015; Ellison et al., 2020; Moorcroft et al., 2006); however, analogous models for predicting patterns of space-use by animals that form home ranges in the absence of conspecific avoidance have been lacking.

In recent years, the hypothesis that home ranges emerge from the foraging benefits of memory has gained attention (Fagan et al., 2013; Van Moorter et al., 2009; Riotte-Lambert et al., 2015; Spencer, 2012). Furthermore, there has been accumulating evidence that animals select for familiar locations (Dalziel et al., 2008; Oliveira-Santos et al., 2016; Ranc et al., 2020; Wolf et al., 2009), a process that can be captured using memory decay functions (Avgar et al., 2015; Merkle et al., 2014, 2017; Ranc et al., 2021; Schlägel et al., 2017). Whether such observed memory-based movements are sufficient to explain the formation of animal home ranges in nature remains, however, unanswered.

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In this study, we elucidate the role of memory in the formation of animal home ranges (i.e., home range emergence) by analysing the movements of individuals reintroduced into a novel environment. Specifically, we fit an individual-based, spatially-explicit movement model, which integrates the interplay between memory and resource (landscape attributes) preferences, to the observed trajectories of roe deer reintroduced into the Aspromonte National Park, Italy, where the species had been extirpated. Animal reintroductions are ideal scenarios for studying the role of memory in home range formation for three reasons. First, because roe deer were released into a novel environment, it can be reasonably assumed that the animals have no pre-existing memories of the local environment (Fagan et al., 2013), and thus the theoretical challenge of how to initialise memory is avoided. Previous attempts to uncover the processes underlying home range behaviour have been conducted on animals that are well-acquainted with their local environment (Avgar et al., 2015; Merkle et al., 2014, 2017; Ranc et al., 2021; Schlägel et al., 2017). When studying the effects of memory, this is problematic because animals utilise knowledge obtained prior to the observation period. Second, because roe deer are relatively solitary (Hewison et al., 1998), their movements are expected to be primarily based on individual information rather than group decision making and resulting collective behaviour (Dall et al., 2005; Haydon et al., 2008). Third, because the roe deer population was being re-established, animal density was low throughout the study, therefore limiting the influence of intraspecific competition.

We hypothesised that the interplay between memory and resources was the primary driver underlying roe deer movements (H1). We evaluated two competing movement models: (1) a *resource-only* model ( $M_{res}$ ) in which roe deer movement was only influenced by resource preferences; and (2) a *memory-based* model ( $M_{mem:res}$ ) in which movement was governed by the interplay between memory and resource preferences. Following on our previous work that examined memory dynamics in an experimental setting (Ranc et al., 2021), we predicted that the empirical movement data would provide a higher support to the memory-based model than its resource-only counterpart (P1.1), and that roe deer would strongly select for previously visited locations (P1.2).

We further hypothesised that the interplay between memory and resource preferences can lead to the formation of home ranges, as observed in the reintroduced animals (H2). We evaluated these hypotheses by comparing the emergent movement and space-use properties of trajectories predicted by the parameterised movement models with those from the empirical roe deer movements. We predicted that, in contrast with the resource-only model, the simulations from the memory-based model would lead to spatially-constrained movements (P2.1) with an increased prevalence of acute turning

angles (P2.2), and be characterised by a higher number of revisitations (i.e., movement recursions; Berger-Tal & Bar-David, 2015; P2.3). Our analyses reveal that the interplay between memory and resource preferences is the primary process influencing the movements of reintroduced roe deer, and is sufficient to explain home range formation.

## MATERIAL AND METHODS

### Roe deer reintroduction

After being extirpated in most of its distribution range during the 19th century, roe deer were reintroduced in the Aspromonte National Park (AspNP; Calabria, Italy; Appendix A) between 2008 and 2011. Ninety-two roe deer were captured in Siena county (Tuscany, Italy), a hilly landscape consisting of open fields alternating with patches of dense Mediterranean forest, of which 75 were hard-released at four sites in the south-west portion of the AspNP (47 females and 28 males).

The park covers 640 sq.km and is characterised by rugged mountains (range: 101–1955 m a.s.l.) giving rise to a diverse vegetation cover (Spampinato et al., 2008) including Mediterranean maquis, dry pine and oak forests, and mountain forests. The region includes small-scale agriculture, pastures and small settlements at the margins of the AspNP. The climate is Mediterranean (annual precipitation: 826 mm; temperature:  $-0.8/5.4^{\circ}\text{C}$  in January,  $14.9/23.0^{\circ}\text{C}$  in August; Gambarie, 1300 m a.s.l.). Wolves (*Canis lupus*) are the only natural predators of adult roe deer. Hunting is forbidden within the park.

### Empirical data

The movements of 27 roe deer were monitored after their release using GPS-GSM collars scheduled to acquire relocations at 6-hour intervals (schedule: 00:00, 06:00, 12:00, 18:00 UTC). For the purpose of our analysis, we retained all animals for which we could obtain a trajectory of at least 30 days with a high acquisition success rate ( $>85\%$ ), which led to the exclusion of 10 individuals. Our final sample consisted of 17 roe deer (15 adults: 11 females, 4 males; 2 subadult males), tracked for an average of 281 days ( $\sigma = 167.3$ ; range: 39–624 days; Nicoloso et al., 2021). Acquisition success rate was high (93.6%). Missing relocations were not interpolated.

We analysed the movement behaviour of the reintroduced roe deer within a rectangular area ( $40.8 \times 30$  km; 1,224 sq.km; Appendix A), that encompassed all available GPS locations ( $n = 19,186$ ). Given the average 6-hour movement distance of the animals (140.0 m;  $\sigma = 267.4$ ) and the high landscape heterogeneity of our study area, the landscape was represented at a spatial resolution of 25 m. The resource preference component of

the mechanistic movement model (Equation 5) included both topographic (slope) and landcover variables (tree cover, agriculture and reforested landcover). We selected these variables as they are known predictors of roe deer movement and resource selection (Coulon et al., 2008; De Groeve et al., 2020; Mancinelli et al., 2015; Tufto et al., 1996), and a preliminary step selection analysis SSA (Fortin et al., 2005) ascertained their relevance in our study system (Fenton, 2020).

We obtained the slope (0–90°) and tree cover (0–100%) layers from Copernicus (European Environment Agency 2012b, 2016). We calculated tree cover as a focal average with a spatial grain of 325 m (best supported spatial scale in a multi-grain SSA; Fenton, 2020; McGarigal et al., 2016). We included in the model both linear and quadratic terms for slope and tree cover to allow for hump-shaped responses to these landcover variables because roe deer avoid steep slopes and sometimes avoid flat areas where human disturbances are concentrated (Coulon et al., 2008; Fenton, 2020), and frequently select intermediate levels of forest cover associated with ecotones and small clearings, where browse is abundant (Fenton, 2020; Tufto et al., 1996). In addition, we used a detailed, high spatial resolution vegetation layer (94 categories; 0.05 ha mapping unit; Spampinato et al., 2008) covering AspNP to specify two land cover (LC) types influencing roe deer movements within our study area (Fenton, 2020): (1) areas reforested with deciduous trees ( $LC_{reforested}$  binary variable; study area mean = 0.18%), and (2) areas dominated by agriculture and neighbouring pastures, and anthropogenic areas ( $LC_{agriculture}$  binary variable; mean = 35.72%). For areas outside the AspNP, and in the vicinity of roe deer relocations (<1 km), we used the CORINE LC layer (European Environment Agency 2012a) and visually inspected Google Satellite images for validation.

## Movement model

We characterised the movement of reintroduced roe deer using an individual-based, spatially-explicit *redistribution kernel* combining spatial memory and resource preferences. Specifically, we defined the probability of moving between the relocations  $\mathbf{x}_{t-1}$  and  $\mathbf{x}_t$  (as it is standard:  $\mathbf{x} = (x, y)$ ), as the normalised product of an *information-independent movement kernel*,  $k(\mathbf{x}_t; \mathbf{x}_{t-1}, \theta_1)$ , and a *cognitive weighting function*,  $w(\mathbf{x}_t; t, \theta_2)$  (Rhodes et al., 2005; Moorcroft & Barnett, 2008; Schlägel & Lewis 2014; Avgar et al., 2015):

$$p(\mathbf{x}_t | \mathbf{x}_{t-1}, \theta_1, \theta_2) = \underbrace{k(\mathbf{x}_t; \mathbf{x}_{t-1}, \theta_1)}_{\text{Movement kernel}} \cdot \underbrace{w(\mathbf{x}_t; t, \theta_2)}_{\text{Weighting function}} \cdot \underbrace{\left[ \sum_{\mathbf{u} \in \Omega} k(\mathbf{u}; \mathbf{x}_{t-1}, \theta_1) \cdot w(\mathbf{u}; t, \theta_2) \right]^{-1}}_{\text{Normalisation over the spatial domain } \Omega} \quad (1)$$

with  $\mathbf{u} = (x, y)$  denoting all the locations within the spatial domain  $\Omega$ , and  $\theta_1$  and  $\theta_2$  the ensemble of parameters governing the movement kernel, and the weighting function, respectively.

## Motion capacity – the information-independent movement kernel

The information-independent movement kernel characterises the movement of an animal independently of its cognitive abilities and of the surrounding landscape, and therefore quantifies its motion capacity (Avgar et al., 2015). It is obtained through the product of two probability distributions for step length,  $S(\rho)$  and movement directions,  $D(\phi)$ . Here, we characterised roe deer step length using a truncated Weibull distribution (shape  $\kappa_S > 0$ ; rate  $\lambda_S \geq 0$ ) to account for both a high density of short movements and rare, long movements (i.e., heavy tail; Morales et al., 2004). The resulting step length distribution for any location  $\mathbf{u}$  is given by:

$$S(\rho; \kappa_S, \lambda_S) = \lambda_S \kappa_S (\lambda_S \rho)^{\kappa_S - 1} e^{-(\lambda_S \rho)^{\kappa_S}} \quad (2)$$

where the movement distance  $\rho$  is the distance between location  $\mathbf{u}$  and the individual's position at the previous time step (i.e.,  $\rho = \|\mathbf{u} - \mathbf{x}_{t-1}\|$ ). We represented the underlying distribution of movement directions,  $D(\phi)$ , as a circular uniform distribution:

$$D(\phi) = \frac{1}{2\pi} \quad (3)$$

It follows that the information-independent movement kernel is given by:

$$k(\mathbf{u}; \mathbf{x}_{t-1}, \kappa_S, \lambda_S) = \frac{S(\rho; \kappa_S, \lambda_S)}{2\pi \rho} \quad (4)$$

where  $\rho$  in the denominator is required to translate from the distribution of movement distances and directions specified in terms of polar coordinates ( $\rho, \phi$ ) into a corresponding probability of moving to location  $\mathbf{u}$  from location  $\mathbf{x}_{t-1}$  specified in terms of cartesian (x,y) coordinates (Moorcroft & Lewis, 2006). Given the temporal resolution of the movement data, we omitted serial correlation in movement direction. See details on the calculation of the movement kernel in a discretised landscape in Appendix B.

## Interplay between memory and resource preferences – the cognitive weighting function

The interaction between the landscape and the animal cognitive abilities was represented via the weighting function  $w$ . The attraction of location  $\mathbf{u}$  at time  $t$ ,  $w(\mathbf{u};t) \geq 0$ , was assumed to vary as a function of memory,  $m(\mathbf{u};t) \geq 0$ , and resource preferences,  $Q(\mathbf{u}) \geq 0$ :

$$w(\mathbf{u};t) = \left[ \underbrace{m(\mathbf{u};t) + 1}_{\text{Memory}} \right] \underbrace{Q(\mathbf{u})}_{\text{Resource preferences}} \quad (5)$$

The weighting function quantifies the attraction due to the interaction between memory and resources relative to that of resources alone. It assumes that, in absence of memory, animals may visit locations in proportion to their underlying resource preferences – an assumption widely made in optimal foraging (Charnov, 1976; McNamara & Houston, 1987) and resource selection models (Avgar et al., 2016; Boyce & McDonald, 1999; Fortin et al., 2005; Manly et al., 2002). In absence of any spatial variation in memory, Equation 5 reduces to a classic resource selection analysis (Boyce & McDonald, 1999; Manly et al., 2002), and the model as a whole to an integrated step selection analysis (Avgar et al., 2016). We also explored an alternative cognitive weighting function, whereby, in absence of memory, the probability of moving to a given location is solely driven by the information-independent movement kernel (i.e., independent of resources; Appendix C).

We modelled the preference for location  $\mathbf{u}$ ,  $Q(\mathbf{u})$ , using an exponential resource selection function (Manly et al., 2002):

$$Q(\mathbf{u}) = e^{(\beta_1 \text{slope} + \beta_2 \text{slope}^2 + \beta_3 \text{cover} + \beta_4 \text{cover}^2 + \beta_5 LC_{\text{reforested}} + \beta_6 LC_{\text{agriculture}})} \quad (6)$$

where  $\beta_i$  ( $i = 1..6$ ) are the resource selection coefficients for the six landscape explanatory covariates included in the model.

Evidence suggests that animals also commonly select for previously visited locations (i.e., site familiarity; Avgar et al., 2015; Dalziel et al., 2008; Gehr et al., 2020; Merkle et al., 2014, 2017; Oliveira-Santos et al., 2016; Ranc et al., 2020, 2021; Wolf et al., 2009). Spatial memory,  $m(\mathbf{u};t)$ , was represented as the long-term attractive effect of previously visited locations. For simplicity and generality, the proposed memory formulation does not distinguish between behaviour-specific elements of memory (e.g., foraging, rumination, bedding). Memory dynamics were governed by learning (acquisition of information) and decay (loss of information). Specifically, memory was assumed to increase linearly with previous experience (Tan et al., 2002) at rate,  $l_m \geq 0$  per unit time

the animal remains at the location. An associated spatial scale of learning,  $\lambda_m \geq 0$ , specifies how memory was acquired over a proximal area surrounding each visited location to account for sensory perception and uncertainty in the GPS position. Finally, memory was expected to decay with time since last visit, at rate  $0 \leq \delta_m \leq 1$ . Both the spatial attenuation of acquisition, and the temporal decay of memory were characterised using negative exponential functions. This functional form, widely used in movement models (Avgar et al., 2015; Bracis et al., 2015; Ranc et al., 2021), is supported both theoretically and by empirical evidence (Avgar et al., 2013; White, 2001, 2013; Ziegler & Wehner, 1997).

Together, this yields the following equations for the dynamics of memory across space  $\mathbf{u}$ , given the animal's current position  $\mathbf{x}_t$ :

$$m(\mathbf{u};t, \mathbf{x}_t) = m(\mathbf{u};t-1) + \underbrace{\alpha(\mathbf{u};\mathbf{x}_t, \lambda_m) \cdot l_m}_{\text{Learning}} - \underbrace{(1 - \alpha(\mathbf{u};\mathbf{x}_t, \lambda_m)) \cdot m(\mathbf{u};t-1) \cdot \delta_m}_{\text{Decay}} \quad (7)$$

$$\alpha(\mathbf{u};\mathbf{x}_t, \lambda_m) = e^{-\lambda_m \cdot \|\mathbf{u} - \mathbf{x}_t\|} \quad (8)$$

where the function  $\alpha(\mathbf{u};\mathbf{x}_t, \lambda_m)$  describes how the rate of memory acquisition attenuates as a function of distance from  $\mathbf{x}_t$ . For missing relocations, no learning was assumed to occur.

We also explored an alternative distance attenuation function  $\alpha$  in which learning attenuates with the square of distance (i.e., a Gaussian function with a shoulder; Appendix D). In addition, we considered a more complex, bi-component memory formulation (Bracis et al., 2015; Van Moorter et al., 2009; Riotte-Lambert et al., 2015) in which animals display a temporary aversion to recently visited locations (Appendix E). See all model parameters and their biological interpretations in Appendix F.

## Model fitting

We fitted two models representing competing hypotheses pertaining to the biological processes influencing the movements of reintroduced roe deer: resource-only ( $M_{\text{res}}$ ), and interplay between memory and resources ( $M_{\text{mem:res}}$ ). For  $M_{\text{res}}$ , no memory learning took place (i.e.,  $l_m = 0$ ). We estimated the model parameters through maximum-likelihood (Appendix G). We then evaluated the contribution of each variable to the model support by calculating the delta Akaike Information Criterion of the reduced model (i.e., excluding the variable of interest) relative to the full model (Appendix H).

## Movement simulations and emergent properties

We evaluated whether the two parameterised movement models ( $M_{\text{res}}$  and  $M_{\text{mem:res}}$ ) could characterise the spatial behaviour of reintroduced roe deer by conducting movement simulations with the parameterised models. For each animal, we ran 100 simulations initiated on its first GPS relocation and matching the duration of the observed trajectory.

We compared the observed and simulated trajectories by evaluating a suite of their emergent properties. First, to evaluate the emergence of spatially restricted movements, we compared the temporal trend in net squared displacement (NSD), calculated as the squared distance between the individual position at time  $t$ ,  $\mathbf{x}_t$ , and the trajectory start position,  $\mathbf{x}_0$ . We further computed the mean NSD for the 17 released roe deer as a 1-day running mean to remove short-term variability in displacement distances. For the simulations, we calculated the 5% and 95% confidence bounds around the mean NSD via bootstrapping (1000 random samples of 17 simulated trajectories). Second, we evaluated whether the fitted movement models captured the observed distributions of step lengths and turning angles. Third, we evaluated their ability to capture observed patterns of revisitations: for each visited cell along the trajectory, we computed the number of revisits, and associated times since last visit. We evaluated the difference between observed and simulated distributions using the Wasserstein Distance (Dobrushin, 1970).

## RESULTS

### Biological drivers of reintroduced roe deer movements

The movement model that included both memory and resource preferences ( $M_{\text{mem:res}}$ ; log-likelihood  $L = -83745$ ) had overwhelmingly stronger support compared to the resource-only model ( $M_{\text{res}}$ ;  $L = -92792$ ;  $\Delta\text{AIC} = 16088$ ;  $p$ -value  $< 0.001$ ). Memory was a key biological process underlying the movements of the reintroduced animals (see Table 1 for variable contributions; P1.1 supported).

Roe deer strongly selected for previously-visited locations ( $l_m = 27.53$ ; see Appendix I for parameter estimate values and confidence intervals; P1.2 supported). Specifically, the first visit of a given location resulted in a 28.5-fold increase in its attraction, and a 10.8-fold increase on the adjacent locations (Figure 1a). Learning decayed to half its maximum value at 16.8 m ( $\lambda_m = 0.0413 \text{ m}^{-1}$ ), meaning that at 25 m distance, learning was 36% that of the amount of learning on the visited location. The alternate Gaussian formulation for spatial decay of memory was less supported by the observations compared to the negative exponential form ( $\Delta\text{AIC} = 180$ ;

**TABLE 1** Variable contributions to the memory-based model ( $M_{\text{mem:res}}$ )

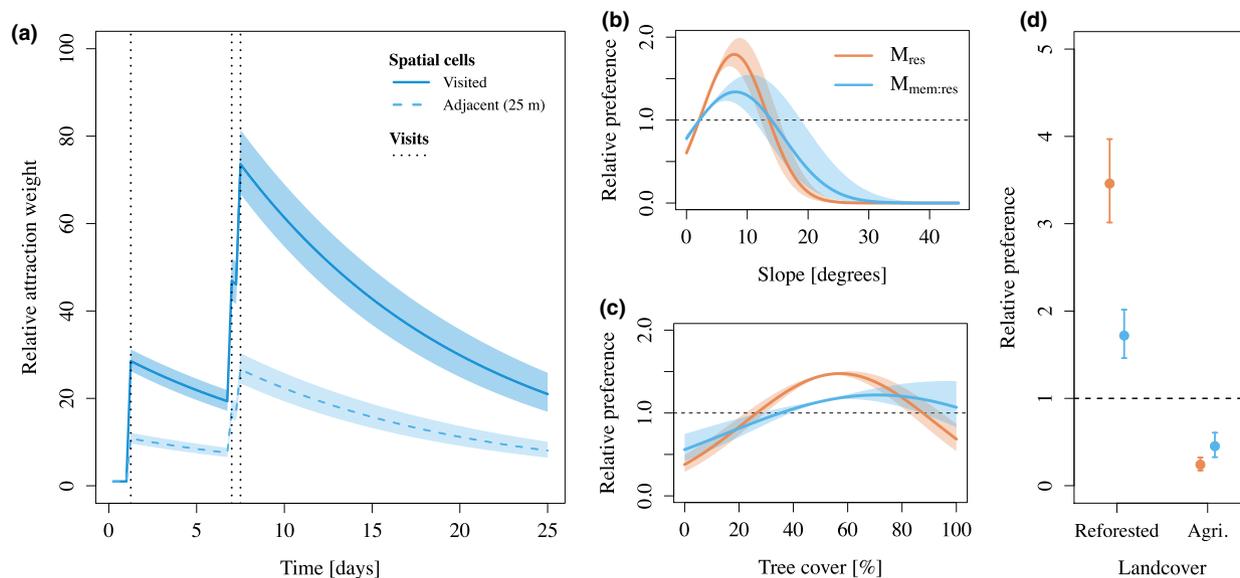
| Variable(s) removed from the full model | Equation(s) | $\Delta\text{AIC}$ |
|---|-------------|--------------------|
| Memory (i.e., $M_{\text{res}}$ )        | 7           | 16,088             |
| Memory spatial scale                    | 8           | 9037               |
| Step length decay                       | 2           | 4363               |
| Memory decay                            | 7           | 2686               |
| Step length rate                        | 2           | 403                |
| All resources                           | 6           | 350                |
| Slope + Slope <sup>2</sup>              | 6           | 161                |
| Landcover – reforested                  | 6           | 105                |
| Landcover – agriculture                 | 6           | 62                 |
| Cover + Cover <sup>2</sup>              | 6           | 39                 |

Variable importance is calculated as the delta AIC of the reduced model (i.e., excluding the variable of interest) relative to the full model. Equations refer to the numbered formulations in the *Material and methods* section.

Appendix D). Temporally, memory decayed with time since last visit with a half-life ( $t_{1/2}$ ) of 9.5 days ( $\delta_m = 0.0730 \text{ day}^{-1}$ ). Both the spatial scale of learning ( $\Delta\text{AIC} = 9037$  if learning occurs only on the precise location visited), and memory decay rate ( $\Delta\text{AIC} = 2686$  if no memory decay occurs) were crucial to capturing memory dynamics.

Roe deer movements were also influenced by resource preferences ( $\Delta\text{AIC} = 350$  when no resource preferences were included). They preferred intermediate slopes (Figure 1b; the most influential landscape attribute;  $\Delta\text{AIC} = 161$ ), and intermediate-to-high tree cover (Figure 1c;  $\Delta\text{AIC} = 39$ ). In addition, roe deer strongly preferred reforested areas and avoided agricultural areas (Figure 1d;  $\Delta\text{AIC} = 105$  and  $\Delta\text{AIC} = 62$ , respectively). For all evaluated resources, preferences had a lower effect size for the memory-based model than for the resource-only model (Appendix I: Figure S6b). The alternate formulation of the weighting function, in which animals redistribute themselves independently of resources in absence of memory (rather than according to resource preferences) was less supported by our data ( $\Delta\text{AIC} = 140$ ; Appendix C).

Roe deer motion capacity greatly differed between the two competing movement models. The resource-only model characterised the movement distances between 6-hour relocations as a heavy-tailed Weibull distribution (shape parameter  $\kappa_S = 0.79$ ; decay rate parameter  $\lambda_S = 0.0078$ ), with a corresponding mean step length of 148.6 m. In contrast, the memory-based model indicates a nearly three-fold larger motion capacity ( $\kappa_S = 1.14$ ;  $\lambda_S = 0.0022$ ) corresponding to a mean step length of 438.9 m. Both step length shape ( $\Delta\text{AIC} = 403$  when compared to a negative exponential distribution,  $\kappa_S = 1.00$ ), and decay rate ( $\Delta\text{AIC} = 4363$  when compared with a movement kernel which assumes selection of spatial locations independently of their proximity), were highly influential parameters.



**FIGURE 1** Predictor effects. The response curves for the resource-only ( $M_{res}$ ; orange) and the memory-based ( $M_{mem:res}$ ; blue) models are plotted with the corresponding 95% marginal confidence intervals. Panel (a) shows the attraction of a visited spatial cell (continuous line) and an adjacent cell (25 m away; dashed line) relative to a cell that has never been visited (attraction = 1) resulting from the fitted memory-based model. Illustrative example shows visits (at  $t = 1.25, 7.00$  and  $7.50$  days) are shown in dotted vertical lines. Panel (b) and (c) illustrate the relative preferences for slope and tree cover, respectively; panel (d) shows the relative preference for reforested and agriculture landcover types.

## Emergent space-use and movement properties

As shown visually by the spatial concentration of their movements (Figure 2, central column), most of the reintroduced roe deer settled into a constrained pattern of space-use (i.e., formed a home range). The movement simulations from the resource-only movement model were typical of an inhomogeneous random walk (Figure 2, left column). In contrast, the memory-based movement model captured the characteristic pattern of space-use behaviour observed in released animals (Figure 2, right column and Appendix J).

The visual differences in patterns of movement behaviour seen in Figure 2 were quantified by the trends in net squared displacement (NSD) with time since release (Figure 3). The resource-only model did not capture the observed spatially-restricted movements of the released roe deer, with no saturation in the NSDs of individuals, and a linear increase of the mean NSD across individuals (Figure 3a). In contrast, the predictions of the memory-based movement model were consistent with the temporal trends of the released roe deer as demonstrated by the occurrence of prolonged plateaus in the NSDs of individuals (Figure 3c; P2.1 supported), and the fact that the observed mean NSD across animals lie within the bounds of the predictions of the memory-based movement model (Figure 3b, c).

Both the resource-only and memory-based models had step length distributions that closely matched the observations (Figure 4a, b). However, they differed markedly in their ability to reproduce the observed patterns of turning angles: the resource-only model showed a uniform circular distribution (Figure 4c), whereas the

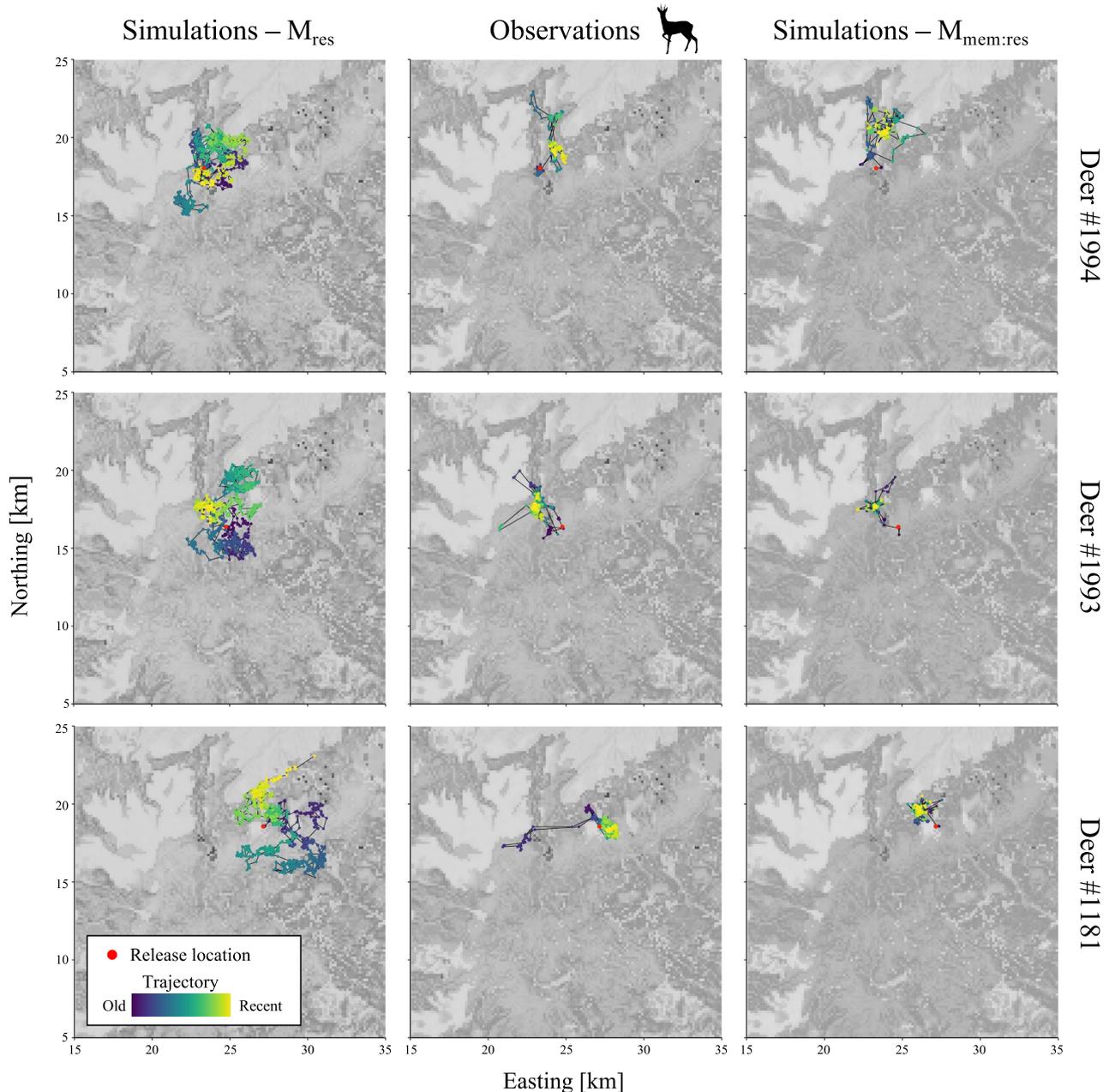
memory-based model captured the observed high density of acute turning angles (in the vicinity of  $-\pi$  and  $+\pi$ ), that are characteristic of observed movements (Figure 4d; P2.2 supported).

Observed roe deer movement behaviour was characterised by frequent revisits: 33.8% of the utilised locations (spatial scale =  $25 \times 25$  m) were revisited, far more than in the resource-only simulations (2.8%), but comparable to the memory-based simulations (32.8%; P2.3 supported). The memory-based model captured the observed patterns of revisitation (Figure 5b), and times since last visit (Figure 5d) in contrast with the resource-only model (Figure 5a and 5c).

There was significant statistical support for a bi-component memory model ( $\Delta AIC = -1255$  when compared to a single-component memory map). However, this more complex memory formulation had limited impacts on the emergent movement properties (Appendix E): it results in smaller deviations between observed and predicted patterns of time since last visit, but slightly larger deviations in NSD and visitation patterns.

## DISCUSSION

The understanding of the underlying biological determinants of home ranges – the most prevalent space-use pattern observed in animals – has thus far been limited (Börger et al., 2008; Fagan et al., 2013; Nabe-Nielsen et al., 2013). In this study, we evaluated whether memory-based movement can capture patterns of home range formation observed when animals are reintroduced into a novel environment. We show that an interplay between

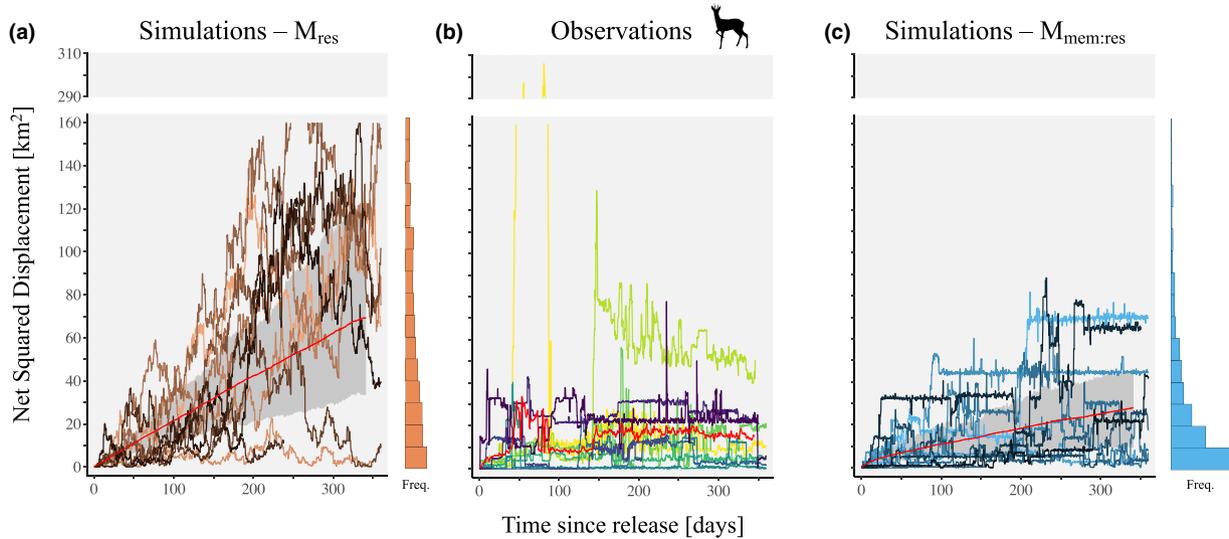


**FIGURE 2** Movement trajectories. Observed roe deer movements (central column) and corresponding simulations for the resource-only model ( $M_{res}$ ; left column) and the memory-based model ( $M_{mem:res}$ ; right column) are shown for three individual roe deer. For each individual and model type, we present the simulation whose NSD was closest to the observed temporal trend in NSD. The release location is shown as a red dot and the time since release illustrated as a colour gradient (blue = old, yellow = recent). The movement trajectories of the remaining individuals can be found in Appendix J.

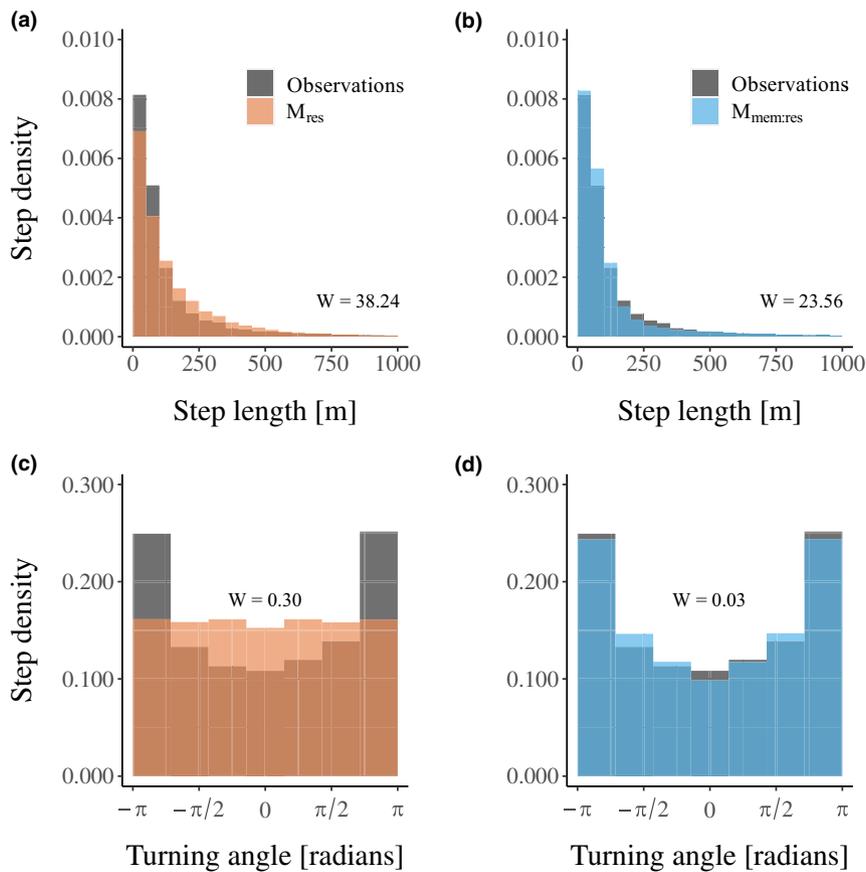
memory and resource preferences was the primary process influencing reintroduced roe deer movements (Figure 1; H1), and that it led to the formation of home ranges, as observed in the released individuals (Figures 2 and 3; H2). To our knowledge, this is the first empirical demonstration that memory is a key determinant of home range formation in the absence of conspecific avoidance (e.g., Bateman et al., 2015; Ellison et al., 2020; Moorcroft et al., 2006).

In this study, we characterised the biological drivers of fine-scale behavioural decisions through the fitting of

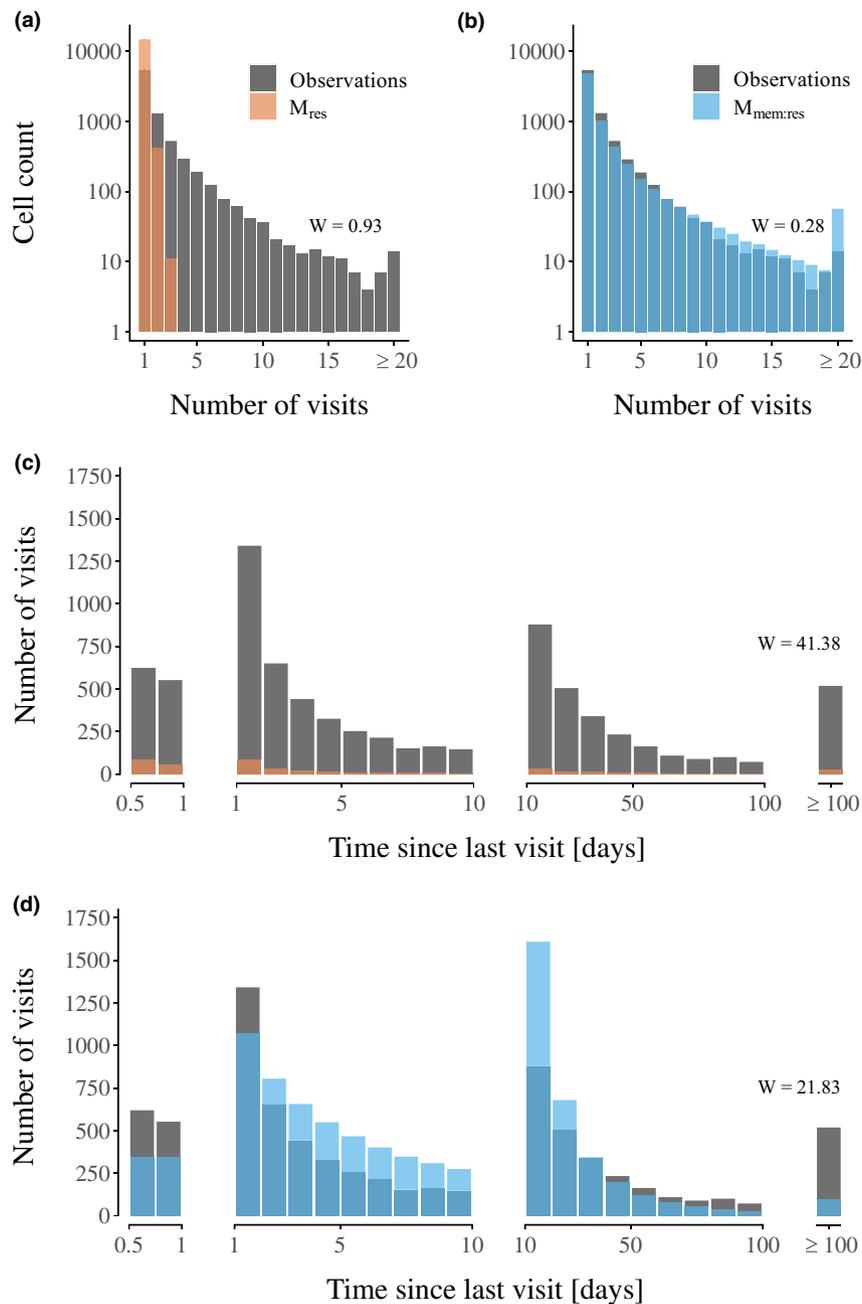
a mechanistic movement model to empirical trajectories, and evaluated resulting predictions of space-use patterns. Although challenging, this approach is appealing because the space-use pattern itself is not fitted to data, but rather arises as an emergent property from the underlying movement process (Potts & Lewis, 2014). Previous analyses have shown that memory influences the proximate behavioural decisions of free-ranging animals (Avgar et al., 2015; Merkle et al., 2014, 2017; Ranc et al., 2021; Schlägel et al., 2017). Our study extends these analyses in three major ways. First, our empirical setting of



**FIGURE 3** Trends in net squared displacement (NSD) with time since release. Panel (a): resource-only simulations ( $M_{res}$ ). Panel (b): observed roe deer movements. Panel (c): memory-based simulations ( $M_{mem:res}$ ). For the sake of clarity, only the individuals with more than 230 days of monitoring are shown ( $n = 10$ ). For the simulations, one run for each of the selected individuals was randomly chosen. The trends in one-day rolling mean NSD across individuals are plotted as solid red lines (grey ribbons indicate the 5% and 95% bootstrapped quantiles for the simulations; panels a and c). The vertical histograms show the frequency of final NSD (i.e., evaluated at the end of the trajectories) for the simulations; panels a and c).



**FIGURE 4** Emergent movement properties. The distributions of step length (panels a and b) and turning angle (panels c and d) are shown for observed roe deer movements (grey), the simulated trajectories from the resource-only model ( $M_{res}$ ; orange), and the simulated trajectories from the memory-based model ( $M_{mem:res}$ ; blue). The Wasserstein Distance ( $W$ ) measures the difference between the observed and simulated distributions.



**FIGURE 5** Emergent revisitation properties. The distributions of revisits (panels a and b) and time since last visit (panels c and d) are shown for observed roe deer movements (grey), the simulated trajectories from the resource-only model ( $M_{res}$ ; orange) and the simulated trajectories from the memory-based model ( $M_{mem:res}$ ; blue). The Wasserstein Distance (W) measures the difference between the observed and simulated distributions.

animals reintroduced into a novel environment allowed us to avoid the problematic issue of how to initialise memory-based movement models (Avgar et al., 2015; Merkle et al., 2014; Schlägel et al., 2017) that has been invoked to explain the discrepancies between predicted and observed space-use patterns (Merkle et al., 2017). Second, we show that a memory-based movement model not only accounts for the observed aggregate (population-level) patterns of space-use, but also yields realistic patterns of individual space-use, as evidenced by spatially restricted movements (Figure 2) and the saturation of net squared

displacement with time since release (Figure 3). Third, as we discuss in more detail below, the memory-based movement model, as opposed to a resource-only movement model, captured several emergent characteristics of empirical roe deer trajectories (Figures 4 and 5). This provides confidence that the model's realistic predictions of space-use are arising because it closely approximates the key characteristics of individual movement behaviour that underlie the formation of home ranges.

Patterns of animal space-use recorded by GPS-telemetry can be viewed as resulting from a sequence

of movement decisions by the animal about how far to move, and in which direction that is, sequences of movement distances and turning angles (Turchin, 1998). Our memory-based model was able to accurately characterise the distributions of both these quantities (Figure 4). In particular, incorporating the effects of memory gave rise to frequent reversals in movement directions (acute turning angles) that closely matched the movement behaviour of released roe deer, even though the underlying redistribution kernel did not include any directional autocorrelation.

Home ranges are thought to emerge from the revisitation of specific geographic locations (i.e., movement recursions) considered to be the visible manifestations of memory-based movements (Berger-Tal & Bar-David, 2015; Fagan et al., 2013). Our results are consistent with this interpretation. The resource-only model led to very few revisits, while a revisitation behaviour similar to that observed in reintroduced roe deer emerged from the memory-based movement simulations (Figure 5). The memory-based model predicted the overall distribution of time since last visits relatively well, although it tended to underestimate both short (a day or less) and very long time since last visits. These discrepancies are likely explained by the relatively simple nature of the proposed memory formulation, which does not distinguish memories associated with specific behaviours (e.g., bedding, foraging, rumination) and assumes no temporal variation in the influence of a given level of memory on movement (e.g., seasonal or circadian): the memory parameters describe an average response across different components of memory. As we have shown, this is sufficient to characterise the formation of home ranges in roe deer; however, it does not capture the full complexity of their revisitation patterns that occur at multiple temporal scales (e.g., locations used for shelter over long temporal scales as well as during circadian alternations between habitat types; De Groeve et al., 2020). In addition, the discrepancy observed for long-term revisits may have been caused by individuals directly perceiving environmental conditions, although roe deer have been shown to rely primarily on memory over perception (Ranc et al., 2021). In this context, more complex cognitive models – incorporating both perception and memory processes (Avgar et al., 2015), behaviour-specific memories (Merkle et al., 2014; Ranc et al., 2021), episodic effects of memory on movement, and decay in information value, accuracy and precision – have the potential to characterise the complex patterns of revisitation observed in animal movements (Lewis et al., 2021).

When fitting the movement model to empirical data, memory was the most influential driver of roe deer movement (Table 1). Our findings provide support for simple memory-enhanced random walk formulations (e.g., Tan et al., 2002), but with an explicit spatial scale of learning, implying that roe deer are likely to return not only

to their previously visited locations, but also to adjacent areas (Figure 1a). Memory decayed fairly rapidly with time since last visit (a half-life of 9.5 days). This value is relatively consistent with a recent experimental study of roe deer foraging behaviour (half-life of 5.6 days) (Ranc et al., 2021); however, it contrasts with the negligible decay of spatial memory over several months reported for bison (*Bison bison*) (Merkle et al., 2014) and woodland caribou (*Rangifer tarandus caribou*) (Avgar et al., 2015). Comparative studies may shed light on whether the factors underlying the differences in estimated memory decay rates are biological (e.g., variation in revisitation patterns linked to differences in movement rates and home range sizes) or methodological (e.g., differences in the formulations of the cognitive processes; Lewis et al., 2021).

In our study, the estimated memory parameters gave rise to a strong attraction to familiar locations: the learning associated to the initial visit of any given location led to a 28.5-fold increase in its attraction (Figure 1a). This finding is consistent with published literature in roe deer (Ranc et al., 2020, 2021), and other ungulates (Dalziel et al., 2008; Merkle et al., 2014; Wolf et al., 2009). Roe deer can use memory to efficiently track the spatio-temporal changes in food availability within their familiar environment (Ranc et al., 2021), and are prone to elevated predation risk outside of their familiar space (Gehr et al., 2020). These two benefits of site familiarity are difficult to disentangle in nature; in our study, both factors likely influence revisitation patterns and contribute to the emergence of roe deer home ranges.

Our analysis also revealed the resource preferences of these animals in our study area. First, roe deer exhibited strong preference for intermediate slope steepness (Figure 1b). Their avoidance of flat areas is likely explained by the fact that, in the rugged landscape of AspNP, anthropogenic activities were concentrated along valley bottoms, as well as high plateaus (Coulon et al., 2008). Second, roe deer preferred areas of intermediate-to-high tree cover (Figure 1c), a finding that is consistent with published literature on their resource use (De Groeve et al., 2020; Tufto et al., 1996). Third, we found that roe deer strongly preferred reforested areas with young deciduous trees (Figure 1d), likely because they provide both cover and abundant browse (Mancinelli et al., 2015). Fourth, roe deer avoided agricultural areas (Figure 1d) in agreement with existing literature (Tufto et al., 1996). In our model, we considered macro-categories describing key aspects of roe deer ecology that are relevant and available in both the origin and translocated areas. In this context, we considered resource preferences as static (temporally-invariant) effects. However, finer-grained habitat conditions not shared between the source area and the translocation area would likely require temporally dynamic learning by the released individuals. This could be accommodated in the proposed model by allowing for time-dependent selection coefficients (Picardi et al., 2021) and would be an interesting avenue for future analyses.

Despite qualitative similarities, the effect sizes of resource preference parameters were consistently smaller for the memory-based model than for the resource-only model (Figure 1b–d; Appendix I). In the absence of memory, the relative attractions of equally distant locations solely depend on their respective resource attributes. In contrast, when memory processes operate, the attraction is partitioned between two interacting components – resource attributes (resource effect), and memory (site familiarity effect) – thereby reducing the influence of resources *per se*. Further progress to characterise the interplay between memory and resource preferences will be contingent on the ability to identify and quantify underlying spatio-temporal variation in resource patterns. In this context, combining mechanistic movement models with *in situ* experimental resource manipulations appears a promising way to disentangle the effects of memory and resources (Ranc et al., 2020, 2021).

Connecting animal movement behaviour to space-use patterns and, ultimately, population dynamics is a long-term challenge that promises to provide a unifying theory for animal ecology (Morales et al., 2010). In this study, we demonstrated that the interplay between memory and resource preferences is sufficient to explain the formation of animal home ranges following reintroduction to a novel environment, and thus contributing to our understanding of the space-use implications of movement behaviour. The approach utilised here could be expanded to model the interconnections between movement behaviour and energy acquisition and consumption, providing a framework to quantitatively characterise the fitness, and demographic consequences of animal movement patterns and space-use (Gaillard et al., 2010).

## COMPETING INTEREST

The authors declare no competing interests.

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## AUTHORSHIP

NR, FC and PM conceived the ideas and designed the methodology; NR developed the model and analysed the data with support from PM and FC; NR led the writing of the manuscript, together with PM and FC. All authors contributed critically to the drafts, and gave final approval for publication.

## DATA AVAILABILITY STATEMENT

Data and code are available from the Zenodo Digital Repository (<https://doi.org/10.5281/zenodo.5189835> and <https://doi.org/10.5281/zenodo.5208215>, repository).

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## SUPPORTING INFORMATION

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