Title: Memory drives the formation of animal home ranges: evidence from a reintroduction

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Abstract

Most animals live in a characteristic home range, a space-use pattern thought to emerge from the benefits of memory-based movements; however, a general model for characterizing and predicting their formation in the absence of territoriality has been lacking. Here, we use a mechanistic movement model to quantify the role of memory in the movements of a large mammal reintroduced into a novel environment, and to predict observed patterns of home range emergence. 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 emerging properties of movement and revisits observed in the reintroduced animals. These results provide a quantitative framework for combining memory-based movements, resource preference and the emergence of home ranges in nature.

Introduction

Most animals live in home ranges – areas that are typically much smaller than their movement capabilities would otherwise allow[1]. The spatially-constrained nature of animal space-use has important implications for many ecological processes, including density-dependent regulation of population abundance[2], predator-prey dynamics[3], the spread of infectious diseases[4], as well as for the design of conservation strategies[5]. Home ranges are pervasive throughout the animal kingdom, suggesting that they may provide fitness benefits in a wide range of ecological contexts, and originate from general biological mechanisms[6]. In territorial species, the emergence of a constrained space-use has been successfully characterized by analytical movement models based on conspecific avoidance[3,7–9]. However, a general model for predicting emergent patterns of space-use is still lacking for animals that form home ranges in the absence of territoriality or central place foraging.

In recent years, increasing attention has been devoted to the hypothesis suggesting that home ranges emerge from the foraging benefits of memory[10,11]. Theoretical studies have demonstrated the foraging advantages of memory over proximal mechanisms (e.g., area-restricted search and perception) in spatially-heterogeneous, predictable landscapes[12–14]. In turn, simulations have shown that memory-based movements can lead to the formation of stable home ranges[15,16], and to non-territorial spatial segregation between individuals[17]. However, our understanding of how memory influences animal movement and resulting space-use patterns in nature is still in its infancy.

Optimal foraging experiments have provided evidence for the adaptive value of memory. For example, green-backed fire-crown hummingbirds (*Sephanoides sephaniodes*) can achieve substantial energy gains by adjusting their visit frequency to the renewal dynamics of high-quality resources at memorized locations[18]. At larger spatial scales, mechanistic models based on

telemetry data have shown that animals are capable of memorizing the location and profitability of resources[19,20]. For example, roe deer (*Capreolus capreolus*) rely on memory, and not perception, to track the dynamics of resource availability within their home range[21]. Whether mechanistic movement models parametrized with empirical data can capture the spatial patterns of animal home ranges in nature remains, however, largely unanswered.

Most studies of animal home range movements have been conducted on resident animals whose experience and knowledge of the surrounding environment is already well-developed at the onset of monitoring[19,20,22,23]. This is problematic when studying the effects of memory because animals are utilising knowledge obtained prior to the observation period, which has been proposed as the reason for discrepancies between memory-based movement model predictions and observed space-use patterns[22]. One approach to address this challenge is to examine the process of home range formation (also referred to as emergence) when animals have been introduced into a novel environment[11], where it can be reasonably assumed that the animals have no existing memories of the local environment.

In this study, we elucidate the role of memory in the movements of animals by analysing the process of home range formation of individuals reintroduced into a novel environment. Our results show how the interplay between memory and resource (landscape attributes) preferences gives rise to observed patterns of home ranges. Specifically, we fit an individual-based, spatially explicit movement model to the observed trajectories of European roe deer reintroduced into the Aspromonte National Park (Calabria, Italy), where the species had previously been extirpated. This experimental system is ideally-suited to the study of the biological determinants of home ranging behaviour for three reasons. First, because roe deer were released into a novel environment, as noted above, the theoretical challenge of how to initialize memory at the beginning of the simulation is essentially side-stepped. Second, because roe deer are solitary[24],

73 their movements are expected to be primarily based on individual information rather than group
74 decision making[25]. Third, because roe deer population was being re-established, animal density
75 was low throughout the study, therefore limiting the influence of intraspecific competition on
76 individual movements and space-use.

77 Roe deer were fitted with GPS telemetry collars and monitored from their release into the
78 study area till the collars ceased functioning (n =17 individuals; see *Methods*). We analysed the
79 biological processes underlying roe deer movements (n = 17,136 six-hour movement steps) using
80 a redistribution kernel[9,20,26]. The model characterizes the probability that a given individual
81 moves from its current position to any location in the landscape as a function of motion capacity,
82 and a weighting function including resource preferences and memory. Building up on earlier
83 work[15–17], memory was represented as a bi-component mechanism: a *reference memory* encoding
84 long-term attraction to previously visited locations, and a *working memory*, which accounts for a
85 short-term avoidance of recently visited locations (for example, due to local resource
86 depletion[15]). The dynamics of both memory components are governed by their respective
87 learning and decay rates, and associated spatial scale.

88 We hypothesized that the interplay between memory and resources was the primary driver
89 underlying roe deer movements (H1). To this end, we fitted two competing movement models: (i)
90 a *resource-only* model (M_{res}) in which roe deer movement was only influenced by resource
91 preferences (which in this case corresponds to landscape attributes such as slope, tree cover and
92 landcover categories; sensu [27]). (ii) a *memory-based* model ($M_{mem:res}$) in which movement was
93 governed by the interplay between memory and resource preference (sensu [26]). Following on our
94 previous work that examined memory dynamics in an experimental setting[21,28], we predicted that
95 the empirical movement data would provide a higher support to the memory-based model than its

resource-only counterpart (P1.1). In addition, we predicted that, overall, roe deer would strongly select for previously visited locations (P1.2).

We further hypothesized that the interplay between memory and resource preferences can lead to formation of home ranges, as observed in the reintroduced roe deer (Cagnacci *et al.* in prep; H2). To this end, we compared the emerging movement and space-use properties of trajectories simulated from the parametrized redistribution kernels with those from the empirical roe deer movements. Accordingly, 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 a high prevalence of acute turning angles (P2.2). In addition, we predicted that memory-based movements would be characterized by a high number of revisitations (also referred to as movement recursions[29]; P2.3). Further details on the mathematical formulations of the redistribution kernel and on the movement simulations can be found in the *Methods* section.

Results

Biological drivers of reintroduced roe deer movements

The movement model that included both memory and resource preferences ($M_{mem:res}$) had overwhelmingly stronger support compared to the resource-only model (M_{res}; Δlog-likelihood = –8684; Δdf = -6; ΔAIC = 17355; p-value < 0.001; Table 1; P1.1 supported). Memory was a key biological process underlying the movements of reintroduced roe deer (most influential variable; Table 1; P1.1 supported). The importance of memory was primarily due to the effects of reference memory (ΔAIC = 1278 when working memory was removed, compared to ΔAIC = 17355 when both working and reference memory were removed; see Table 1). With respect to reference memory, the spatial scale of learning was most influential (ΔAIC = 7444 if learning

119 occurred only on the visited locations i.e., $\lambda_R = \infty$), followed by learning rate (ΔAIC = 3434 if
120 learning was immediate i.e., $l_R = 1$) and decay rate (ΔAIC = 2631 if there was no memory decay
121 i.e., $\delta_R = 0$).
122
123 Roe deer acquired memories of visited locations, with the learning curve reaching half its
124 maximum value (i.e., memory = 0.5) after 7.9 days for reference memory (l_R = 0.0217 $6h^{-1}$; see
125 Fig. 1a for confidence intervals), and after 8.4 days for working memory (l_W = 0.0204 $6h^{-1}$).
126 Spatially, information was gained beyond the visited locations: reference memory learning
127 decayed with distance to half its maximum value at 14.3 m (λ_R = 0.0485 m^{-1}; meaning that at 25
128 m distance, learning was approximately 30 % that of the amount of memory acquired on the
129 visited spatial location). Working memory learning declined to half its maximum value at 8.1 m
130 (λ_W = 0.0855 m^{-1}; meaning that the learning rate at 25 m distance was approximately 12 % that
131 of the visited location). Temporally, reference memory decayed with time since last visit with a
132 half-life ($t_{1/2}$) of 9.5 days (δ_R = 0.0182 $6h^{-1}$) while working memory decay was nearly
133 instantaneous ($t_{1/2}$ < 1 h; δ_W = 0.99 $6h^{-1}$).
134 The combined effect of memory dynamics and of the intrinsic component of resource
135 preference (i.e., the attraction of locations in absence of memory; $\varepsilon = 6.94\times10^{-4}$; Fig. 1b) led to a
136 very strong selection for previously-visited locations (P1.2 supported). Specifically, the first visit
137 of a given location resulted in a 31.6-fold increase in its attraction, and a 10.1-fold increase on the
138 adjacent locations (Fig. 2a).
139 Roe deer movements were also influenced by their resource preferences (Fig. 1b; ΔAIC =
140 304 when resource preferences were null i.e., $\beta_1 : \beta_6 = 0$; Table 1). Roe deer preferred
141 intermediate slopes (Fig. 2b), with peak preference at eight degrees (most influential resource;

142 ΔAIC = 138 when $\beta_1 = \beta_2 = 0$; Table 1). Roe deer preference for tree cover was characterized
143 by slight qualitative differences between models: preference for intermediate tree cover (a clear
144 peak at 57%) in the resource-only model, and for intermediate and high levels of tree cover (a
145 broad peak at 73%) in the memory-based model (Fig. 2c; ΔAIC = 34 when $\beta_3 = \beta_4 = 0$; Table
146 1). In addition, roe deer strongly preferred reforested areas and avoided agricultural areas (Fig.
147 3c; ΔAIC = 83 when $\beta_6 = 0$ and ΔAIC = 59 when $\beta_5 = 0$, respectively; Table 1). For all
148 evaluated resources, preferences had a lower effect size for the memory-based model than for the
149 resource-only model (Fig. 1b).

150 Roe deer motion capacity greatly differed between the two competing movement models.
151 The resource-only model characterized the movement distances between six-hour relocations as a
152 heavy-tailed Weibull distribution (shape parameter κ_S = 0.79; decay rate parameter λ_S = 0.0078;
153 Fig. 1c), with a corresponding mean step length of 147.0 m. In contrast, the memory-based model
154 indicates a nearly 3-fold larger motion capacity (κ_S = 1.02; λ_S = 0.0024) corresponding to a mean
155 step length = 409.4 m). The value of the shape parameter κ_S being close to one implies that the
156 step length distribution can be simplified to a negative exponential with a relatively small
157 decrease in model accuracy (ΔAIC = 4 if κ_S = 1.00; Table 1). Step length decay rate was,
158 however, a highly influential parameter (ΔAIC = 4945 when compared with a resource-selection
159 type movement kernel which assumes that roe deer spatial locations independently of their
160 proximity i.e., λ_S = 0; Table 1).

161

162 *Emergent space-use and movement properties*

163 Most reintroduced roe deer settled into a constrained space (i.e., formation of a home range) as
164 shown visually by the spatial concentration of their movements (Fig. 3b). The movement

165 simulations from the resource-only model were typical of a random walk (technically, an
166 inhomogeneous random walk due to the effects of resource preferences; Fig. 3a). In contrast, the
167 memory-based model captured the characteristic space-use behaviour observed in released roe
168 deer (Fig. 3c; see Supplementary S1 for additional movement trajectories).

169 The visual differences in patterns of movement behaviour seen in Figure 3 were
170 characterized and quantified by examining the temporal trends in net squared displacement
171 (NSD) with time since release (Fig. 4). The resource-only model did not capture the observed
172 spatially-restricted movements of the released roe deer, with no saturation in the NSDs of
173 individuals (Fig. 4a), and a linear increase of the mean NSD across individuals (compare the solid
174 red line on Fig. 4b with the red line and grey shaded area in Fig. 4a). In contrast, the predictions
175 of the memory-based movement model were consistent with the temporal trends in the observed
176 movements of the released animals as demonstrated by the occurrence of prolonged plateaus in
177 the NSD of individual animals (Fig. 4c; P2.1 supported), and the fact that the observed mean
178 NSD across individuals is within the bounds of the predictions of the memory-based movement
179 model (compare the solid red line on Fig. 4b with the grey area on Fig. 4c).

180 Both the resource-only and memory-based models had step length distributions that
181 closely matched the observations (Fig. 5a,b). The memory-based model more accurately
182 characterized the observed median step length while the resource-only model better captured its
183 mean (median step lengths of 55.9, 75.0 and 50.0 m; means of 141.1, 135.2 and 105.5 m for
184 observed movements, resource-only simulations and memory-based simulations, respectively). In
185 contrast, the two models differed greatly in their ability to reproduce the observed patterns of
186 turning angles: the resource-only model showed a uniform circular distribution of turning angles
187 (Fig. 5c) whereas the memory-based model captured the high density of acute turning angles (in

188 the vicinity of $-\pi$ and $+\pi$), that are characteristic of observed roe deer movements (Fig. 5d; P2.2
189 supported).

190 Observed roe deer movement behaviour was characterized by frequent revisits: 33.8% of
191 the utilized locations (spatial scale = 25 x 25 m) were visited twice or more. The simulations
192 from the resource-only model, however, had very few revisits – only 4.5% spatial locations were
193 revisited – leading to a large mismatch with the revisitation patterns of observed trajectories (Fig.
194 6a). In contrast, the memory-based simulations were characterized by many revisits: 35.2% of the
195 locations were revisited (P2.3 supported). The revisitation patterns of the memory-based model
196 were highly similar to those of the observed roe deer movements (Fig. 6b), albeit with a slight
197 tendency to underestimate the number of locations with few revisits (i.e., less than five), and to
198 overestimate those with many revisits (especially above 20). Consistent with these patterns in the
199 number of revisits, the memory-based model also captured the observed patterns of time since
200 last visit more accurately than the resource-only model (compare Figs 6c and 6d, respectively).
201

202 **Discussion**

203 The past two decades have seen remarkable advances in the ability to monitor animal
204 movements[30], and the development of ever more complex and comprehensive mechanistic
205 movement models. However, our understanding of the underlying biological determinants of
206 home ranges – the most prevalent space-use pattern observed in animals – has been relatively
207 limited[6,11,31]. In this study, we evaluated how memory-based movements can predict the
208 formation of home ranges in nature by parametrizing a mechanistic movement model with
209 empirical data from animals reintroduced into a novel environment. We found that an interplay
210 between memory and resource preferences was the primary process influencing reintroduced roe
211 deer movements (Fig. 2; H1), and that it led to the formation of characteristic home ranges, as

212 observed in the released individuals (Figs 3 and 4; H2; see also Cagnacci *et al.* in prep). To our
213 knowledge, this is the first demonstration that a mechanistic movement model parametrized with
214 empirical movement data can capture patterns of home range formation in a non-territorial
215 species.

216 We found that the emergent properties of the memory-based movement model, as
217 opposed to a resource-only movement model, were realistic and similar to the patterns observed
218 in the reintroduced roe deer (Figs 3-5). First and foremost, the memory-based simulations gave
219 rise to spatially-restricted movements, as shown by the saturation of individual net squared
220 displacement with time since release (Fig. 4). In addition, the model successfully reproduced the
221 heterogeneity and complexity of observed movement patterns, including long-distance
222 explorations, multiple areas of concentrated use, and patterns of revisitation (Figs 3 and 6).

223 Two approaches can be used to study the underlying determinants of animal space-use[32]:
224 analyses inferring underlying movement parameters that capture observed space-use patterns i.e.,
225 pattern-oriented[3,8,31,33,34], and analyses of individual movement trajectories to parametrise
226 movement models[20,23,35]. In this study, we used the latter approach: characterizing the biological
227 drivers of fine-scale behavioural decisions through the fitting of a mechanistic movement model
228 to empirical trajectories, and subsequently evaluating resulting predictions of space-use
229 properties. Although challenging, this approach is appealing because the space-use pattern itself
230 is not fitted to data, but rather arises as an emergent property from the underlying movement
231 process[32,35].

232 Previous analyses have shown that memory influences the proximate behavioural
233 decisions of free-ranging animals[19,20,22,23]. Our study extends these analyses in three major ways.
234 First, we show that a movement model operating in a spatially continuous landscape not only
235 accounts for the observed aggregate (population-level) patterns of space-use, but also yields

236 realistic patterns of individual space-use (Figs 3 and 4). Second, our empirical setting of animals
237 reintroduced into a novel environment allowed us to avoid the problematic issue of how to
238 initialize memory-based movement models[19,20,23] that has been invoked to explain the
239 discrepancies between predicted and observed space-use patterns[22]. Third, as we discuss in more
240 detail below, in addition to space-use patterns, the memory-based movement model captured
241 several emergent characteristics of empirical roe deer trajectories (Figs 5 and 6). This provides
242 confidence that the model's realistic predictions of space-use are arising because the model
243 closely approximates the key characteristics of individual movement behaviour that underlie the
244 formation of the home ranges.

245 Patterns of animal space-use recorded by GPS-telemetry can be viewed as resulting from
246 a sequence of movement decisions by the animal about how far to move, and in which direction
247 i.e., sequences of movement distances and turning angles[9,36]. Our memory-based model was able
248 to accurately characterize the distributions of both these quantities (Fig. 5). We found that a
249 realistic, heavy-tailed distribution of step lengths emerged from the combination of a large,
250 exponentially-weighted motion capacity (that accounts for rare, long steps), and memory-based
251 attraction (that accounts for the high density of short steps). It has been suggested that
252 characterizing step lengths with heavy-tailed Gamma or Weibull distributions could improve the
253 predictive performance of empirically-parametrized movement models[20]. Here we show that
254 accounting for memory makes this unnecessary. Furthermore, incorporating the effects of
255 memory also gave rise to frequent reversals in movement directions (i.e., sharp turning angles)
256 that closely matched the movement behaviour of released roe deer, even though the underlying
257 redistribution kernel did not include any form of autocorrelation in movement directions.

258 Similarly, home ranges are thought to emerge from the revisitation of specific geographic
259 locations (also referred to as movement recursions[29]), considered to be the visible manifestations

of the influence of memory on movements[11,29]. 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 (Fig. 6). The memory-based model predicted well the overall distribution of time since last visits, although it tended to underestimate both short (a day or less) and very long time since last visits (especially above 100 days) i.e., smaller variance that the observed pattern. The high density of short-term revisits in observed roe deer trajectories could be the result of daily, local movements such as an alternation between a foraging ground and a neighbouring area used for shelter[37]. The discrepancy observed for long-term revisits could instead be due to an artefact of the data collection (time since last visit can be overestimated in empirical data if visits occur between two successive GPS relocations), or could reflect biological factors that are not characterized in the model formulation (e.g., particular environmental conditions may be exploited through proximal mechanisms such as perception; see Avgar *et al.*[20] for a cognitive model including perception and memory).

Similar to previous studies[15–17], we hypothesized that home ranges emerge from the influence of a bi-component memory process in which reference memory captures the long-term attraction to previously-visited locations, while working memory accounts for a short-term repulsion (e.g., to adjust to resource dynamics). However, we found that it was not necessary to include a bi-component memory to give rise to home ranges. This result contrasts with the patch-to-patch transition model of Van Moorter *et al.*[15], where absence of working memory leads to repeated utilization of a sole resource patch. In the memory-based movement formulation used here, an intrinsic component of resource preference ensures that all locations, including those that

283 have not been visited, or that have been forgotten (i.e., whose reference memory is zero), have a
284 non-zero probability of being visited at each time step.

285 When fitting the movement model to empirical data, reference memory was the most
286 influential driver of roe deer movement (Table 1). The learning associated to the initial visit of
287 any given location led to a 31.6-fold increase in its attraction (Fig. 2a), and hence to a substantial
288 increase in its probability of being revisited in the future. We found that the influence of memory
289 on movements was very strong despite the learning rate of reference memory being low.
290 Although, learning was modelled as an exponentially saturating function of experience[38,39], the
291 low value of learning rate effectively meant that learning never approached its asymptote, and
292 was essentially a quasi-linear function of number of visits. In this aspect, our findings provide
293 support for the simple memory enhanced random walk formulation proposed by Tan *et al.*[40].
294 However, in contrast to Tan *et al.*[40], our formulation also includes a spatial scale of learning
295 parameter, which was strongly supported (Table 1), and implies that roe deer are likely to return
296 not only to their previously visited locations but also to adjacent areas (Fig 2a).

297 Reference memory decayed relatively rapidly (half-life of 9.5 days) with time since last
298 visit. This estimate is relatively consistent with the decay rate reported in a recent experimental
299 study of roe deer foraging behaviour (half-life of 3.4 days)[21], but contrasts markedly with the
300 negligible decay of spatial memory over several months reported for bison (*Bison bison*)[19] and
301 woodland caribou (*Rangifer tarandus caribou*)[20]. Comparative studies may shed light on whether
302 the factors underlying the differences in estimated memory decay rates are biological (e.g.,
303 variation in revisitation patterns linked to differences in movement rates and home range sizes),
304 or methodological (e.g., between-model differences in the formulations of the cognitive
305 processes).

306 Our results were, in contrast, much less sensitive to working memory. Working memory
307 primarily influenced the duration that roe deer spent at visited locations (i.e., residence time).
308 Because of its nearly instantaneous decay, the repulsion effect of working memory ceased as
309 soon as the individual left a visited location. As a result, working memory did not influence the
310 timing of revisits, which contrasts with predictions derived from theoretical movement
311 simulations[15–17]. The probability that roe deer returned to previously visited locations decreased
312 monotonically with time since their last visit (Fig. 5d), suggesting that a single memory
313 component (reference memory, in our case) could capture roe deer revisitation patterns.
314 Altogether, our results did not support the existence of characteristic multi-day revisitation
315 periodicities, which would be expected if roe deer relied on working memory to optimally adjust
316 their visits to underlying resource renewal dynamics. Because roe deer are very selective
317 browsers, able to switch feeding between an important diversity of plant species[41,42], it is indeed
318 unlikely that their foraging behaviour is influenced by short-term dynamics of resource renewal.
319 In contrast, a bi-component memory process may be more suited to model the foraging behaviour
320 of species whose resources are concentrated within distinct, continuously-renewing patches such
321 as grazing lawns in bison[43] or geese[44].
322
323 In our study, the estimated memory parameters gave rise to a strong attraction to familiar
324 locations, consistent with published literature in roe deer[21,28], and other ungulates[19,45]. Two main
325 hypotheses have been formulated for the fitness benefits associated with site familiarity: (i)
326 improved resource acquisition through the memorization of resource locations and attributes[10,15],
327 and (ii) predator avoidance through the knowledge of fine-scale variations in predation risk and
328 of escape routes[46]. Previous work has shown that in roe deer, individuals rely on memory to
329 efficiently track the spatio-temporal changes in food availability within their familiar

environment[21] but are also prone to elevated predation risk from Eurasian lynx (*Lynx lynx*) when outside of their familiar space[47]. These two benefits of site familiarity are difficult to disentangle in nature; in our study, both factors may likely have driven the revisitation patterns that contributed to the emergence of roe deer home ranges.

Our analysis also revealed the resource preferences of roe deer in our study area. First, roe deer exhibited strong preference for intermediate slope steepness (Fig. 2b). Their avoidance of flat areas is likely explained by the fact that, in the rugged landscape of Aspromonte National Park, anthropogenic disturbances such as roads and logging activities[48] were concentrated along valley bottoms, as well as high plateaus. In other ecological systems, these topographic features have also been associated with elevated predation risk from wolves[49]. Their avoidance of steep slopes is consistent with roe deer natural history (long limbs, and short and narrow hoofs not adapted to climbing), and its unsuitability supported by the occurrence of two mortality cases linked to falls during the reintroduction project (*S. Nicoloso pers. comm.*). Second, roe deer preferred areas of intermediate-to-high tree cover (Fig. 2c), a finding that is consistent with published literature on roe deer resource selection[50–52]. Intermediate cover values may indicate heterogenous environments rich in ecotones, which provide abundant browsing resources[53]. Third, we found that roe deer strongly preferred reforested areas with young deciduous trees (Fig. 2d), which is likely because these areas provide both cover and abundant browse[42]. Fourth, roe deer avoided agricultural areas (and associated pastures and settlements; Fig. 2d) in agreement with existing literature[50,51].

Despite qualitative similarities between the resource-only and memory-based model formulations, the effect sizes of resource preference parameters were consistently smaller for the memory-based model than for the resource-only model (Fig. 1; Fig. 2b-d). In absence of memory, the relative attraction (and hence probability of use) of equally-distant locations solely depends

354 on their respective resource attributes. In contrast, when memory processes operate the relative
355 attraction is partitioned between two interacting components: resource attributes (i.e., resource
356 effect), and memory (i.e., site familiarity effect) – thereby reducing the influence of resources *per*
357 *se*. Because animal home ranges ultimately emerge as the revisitation of familiar, beneficial
358 resources[10,15], disentangling the influence of resources from that of site familiarity is challenging
359 in nature. In particular, where important resource drivers are omitted – either because they are
360 unknown or because they are not measured – the attraction for familiar areas can be confounded
361 with attraction for unaccounted resources (i.e., a spurious familiarity effect[54]). Further progress to
362 characterize the interplay between memory and resource preferences will be contingent on the
363 ability to identify and quantify underlying spatio-temporal variation in resource patterns. In this
364 context, combining mechanistic movement models with *in situ* experimental resource
365 manipulations appears a promising way to disentangle the effects of memory from the effects of
366 resources[21,28].
367
368 Connecting animal movement behaviour to space-use patterns and, ultimately, population
369 dynamics is a long-term challenge that promises to provide a unifying theory for animal
370 ecology[55]. In this study, we demonstrated that the interplay between memory and resource
371 preferences is sufficient to explain the formation of animal home ranges following reintroduction
372 to a novel environment, and thus contributing to our understanding of the space-use implications
373 of movement behaviour. The approach utilised here could be expanded to model the
374 interconnections between movement behaviour and energy acquisition and consumption[56],
375 providing a framework to quantitatively characterize the fitness, and demographic consequences
376 of animal movement patterns, and space-use[57].
377

Methods

Roe deer reintroduction

After being extirpated in most of its southern distribution range during the 19th century, a roe deer reintroduction project was undertaken by the Aspromonte National Park (AspNP; Calabria, Italy; Supplementary S2: Fig. S1) between 2008 and 2011. Ninety-two roe deer were captured in Sienna County (Tuscany, Italy), of which seventy-five were hard-released at four sites in the south-west portion of the AspNP (47 females and 28 males). The remaining seventeen either died during translocation or were not genotyped as *Capreolus capreolus italicus*, the roe deer subspecies native to the Italian peninsula.

The AspNP is 640 sq.km and is characterized by the rugged Aspromonte mountain range peaking at 1955 m a.s.l, and alternating gorges and torrent river valleys. The climate is Mediterranean with precipitations concentrated in winter, leading to irregular snow cover above 1000 m a.s.l, and dry and warm summers (annual precipitation: 826 mm; temperature: -0.8/5.4°C in January, 14.9/23.0°C in August; Gambarie, 1300 m a.s.l). The significant topography within the region gives rise to a diverse vegetation cover[58] ranging from temperate mountain forests (e.g., European beech *Fagus sylvatica*, silver fir *Abies alba* and alder *Alnus sp.*) to dry pine and oak forests (e.g., Calabrese black pine *Pinus laricio*, Mediterranean oaks *Quercus ilex* and *Quercus suber*), and high Mediterranean maquis (e.g., strawberry tree *Arbutus unedo*, heather *Erica arborea* and myrtle thickets *Myrto-Pistacietum lentisci*). The region also includes small-scale, mixed agriculture, orchards and plantations (e.g., chestnut *Castanea sativa*, and olive groves), pastures at high elevation, as well as small settlements at the margins of the park. Wild boar (*Sus scrofa*) is the dominant wild ungulate in the study area (red deer, *Cervus elaphus* are locally extinct). Wolves (*Canis lupus*) are the only natural predators of adult roe deer, although red fox (*Vulpes vulpes*) may predate upon fawns. Hunting is forbidden within the national park.

Empirical data

The movements of twenty-seven individual roe deer were monitored after their release via telemetry. Roe deer were fitted with GPS-GSM collars scheduled to acquire one relocation every 30 min during the first month after release, and at six-hour intervals thereafter (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%). This choice led to the exclusion of ten individuals – seven died in the first month after release and three had malfunctioning collars. Our final sample consisted of 17 roe deer (15 adults: 11 females, 4 males; 2 subadult males), tracked for an average of 281.82 days (σ = 167.37, minimum = 39, maximum = 624; Supplementary S3: Table S1).

We regularized the trajectories to a homogeneous relocation interval of six hour and did not interpolate the missing relocations. The final dataset consisted of 19,186 GPS relocations (acquisition success rate = 93.61%). Roe deer step length averaged 140.04 m between two successive relocations (σ = 267.37, maximum = 6254.68 m).

We analysed the movement behaviour of the reintroduced roe deer within a rectangular area (40.8 x 30 km; 1,224 sq.km; Supplementary S2: Fig. S1), that encompassed all available roe deer GPS locations and a buffer of 7 km (more than the longest observed step length). Given the average movement distance of the reintroduced roe deer, and the high landscape heterogeneity of our study area, the landscape was represented at a spatial resolution of 25 x 25 m.

The resource preference component of the mechanistic movement model included both topographic (slope) and landcover variables (tree cover, agriculture and reforested landcover). We selected these variables a priori as they are known predictors of roe deer movement and

426 resource selection[42,48,51,52], and a preliminary step selection analysis (SSA[59]; results not shown)
427 ascertained their relevance in our study system.

428 We obtained the slope layer from the European Union Digital Elevation Model EU-DEM
429 v1.0[60]. Slope ranges from 0 to 90°, and was available at a 25 m spatial resolution. We obtained an
430 estimate of tree cover from Copernicus pan-European, high-resolution layers[61], 2012 reference
431 year. Tree cover ranges from 0 to 100%, and was resampled at 25 m from a native spatial
432 resolution of 20 m. Following preliminary SSA explorations, we (1) calculated tree cover at a
433 grain of 325 m (i.e., each squared cell of 25 m averaged tree cover within a larger 325 x 325 m
434 area) and (2) included in the model both linear and quadratic terms for slope and tree cover.

435 Two landcover data sources were available for our study area – a botanical map of high
436 biological detail and fine spatial resolution (94 categories; 0.05 ha mapping unit) for the
437 Aspromonte National Park[58], and the coarser CORINE landcover classification (45 categories; 25
438 ha mapping unit) for the entire study area[62], 2012 reference year. Preliminary SSA conducted
439 within the park boundaries suggested that roe deer selected for areas reforested with deciduous
440 trees (*Alnus cordata*, *Juglans regia* and *Prunus avium*; hereafter referenced to as *Reforested*), and
441 avoided spatially-dominant agriculture areas (olive groves, cultivated fields, mixed agriculture),
442 and more localized pastures and anthropized areas (hereafter referenced to as *Agriculture*).
443 Outside the park, we assumed that there were no *Reforested* areas, and used CORINE to map
444 *Agriculture* – choices that we validated by visually inspecting the satellite images in the vicinity
445 (< 1 km) of the roe deer relocations outside of the park.
446
447 *Modelling approach*
448 We modelled the movement of reintroduced roe deer using an individual-based, spatially explicit
449 *redistribution kernel* combining spatial memory and resource preferences. Specifically, we

defined the probability of moving between the relocation $\mathbf{x}_{t-1}$ and the relocation $\mathbf{x}_t$ (as it is standard: $\mathbf{x} = (x, y)$), as the normalized product of an *information-independent movement kernel*[27], $k(\mathbf{x}_t; \mathbf{x}_{t-1}, \theta_1)$, and a *cognitive weighting function*, $w(\mathbf{x}_t; t, \theta_2)$[20,26]:

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

with $\boldsymbol{u} = (x, y)$ denoting all the locations within the within the spatial domain Ω, and θ_1 and θ_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 characterizes the movement of an animal independently of its cognitive abilities and of the surrounding landscape, and therefore quantifies its motion capacity[20]. It is obtained through the product of two probability distributions: step length, S, and movement direction, Φ. Here, we modelled roe deer step length using a truncated Weibull distribution. The Weibull distribution is governed by two parameters – the shape ($\kappa_S > 0$) and the rate ($\lambda_S \geq 0$), and can account for both a high density of short movements and rare, long movements (i.e., heavy tail), typical of empirical data of animal movement[63]. To reduce the computational power required for model fitting, we assumed that roe deer movement probability was zero beyond 7 km (maximum observed step length = 6.25 km). The resulting step length distribution for any location $\boldsymbol{u}$ is given by:

$$S(\|\boldsymbol{u}-\mathbf{x}_{t-1}\|;\kappa_S,\lambda_S)$$

$$= \begin{cases} \lambda_S\kappa_S(\lambda_S\|\boldsymbol{u}-\mathbf{x}_{t-1}\|)^{\kappa_S-1}e^{-(\lambda_S\|\boldsymbol{u}-\mathbf{x}_{t-1}\|)^{\kappa_S}}, & \|\boldsymbol{u}-\mathbf{x}_{t-1}\| \le 7\ km \\ 0, & otherwise \end{cases} \qquad Eq.2$$

We modelled roe deer movement directions as a circular normal distribution such that:

$$\Phi = \frac{1}{2\pi} \qquad Eq.3$$

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

$$k(\boldsymbol{u};\mathbf{x}_{t-1},\kappa_S,\lambda_S) = \frac{S(\|\boldsymbol{u}-\mathbf{x}_{t-1}\|;\kappa_S,\lambda_S)\Phi}{\|\boldsymbol{u}-\mathbf{x}_{t-1}\|} \qquad Eq.4$$

where the denominator $\|\boldsymbol{u}-\mathbf{x}_{t-1}\|$ translates polar coordinates into Euclidean coordinates i.e., the conversion of a probability of moving a given distance and direction to a probability of moving to a particular area[9]. Given the temporal resolution of our movement data (every 6 h), we ignored serial correlation in movement direction. Because we fitted our mechanistic movement model to observed movement data in a discretized landscape (square cells of resolution 25 m), we transformed the GPS relocations in the continuous space, $\mathbf{x}_t$, to the centroid of the overlapping cell (see Supplementary S4 for the correction required to calculate the movement kernel on the location currently used by the animal).

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. We assumed that animal movement was influenced by memory, $m(\boldsymbol{u};t)$,

and that, in absence of such information, animals may visit locations in proportion to their intrinsic resource preference value:

$$w(\boldsymbol{u};t,\varepsilon) = \left[\underbrace{m(\boldsymbol{u};t)}_{\substack{Memory \\ component}} + \underbrace{\varepsilon}_{\substack{Intrinsic \\ component}} \right] \underbrace{Q(\boldsymbol{u})}_{\substack{Resource \\ preference}} \qquad Eq.5$$

with ε, the intrinsic component of resource preference. In our model formulation, it is not the absolute value of memory that defines its influence on movement, but rather its value relative to the intrinsic component of resource preference i.e., scaled to the attraction of similar resource conditions in absence of memory. We modelled the preference for location u, $Q(\boldsymbol{u})$, using an exponential resource selection[64]:

$$Q(\boldsymbol{u}) = e^{(\beta_1 slope + \beta_2 slope^2 + \beta_3 cover + \beta_4 cover^2 + \beta_5 LC_{reforested} + \beta_6 LC_{agriculture})} \qquad Eq.6$$

with β_i the selection coefficient for resource variable i – slope (linear and quadratic terms), tree cover (linear and quadratic terms), and reforested and agriculture landcovers – evaluated at location $\boldsymbol{u}$.

We modelled memory, $m(\boldsymbol{u};t)$, as a bi-component mechanism[15–17]. Reference memory, $m_R(\boldsymbol{u};t)$, is the long-term memory of previously-visited spatial locations and has an attractive effect. By contrast, the working memory, $m_W(\boldsymbol{u};t)$, encodes the short-term, temporary repulsion of previously visited locations. The combined memory map is given by:

$$m(\boldsymbol{u};t) = m_R(\boldsymbol{u};t) - m_W(\boldsymbol{u};t) \qquad Eq.7$$

The dynamics of both memory components are governed by learning (i.e., acquisition of information) and decay or forgetting (i.e., loss of information). The learning curve was

513 represented by an asymptotically increasing function of experience[38,39]. Specifically, we
514 formulated learning as an exponentially saturating process with an associated spatial scale such
515 that animals experience maximum learning at their current position, but also gain information
516 about surrounding areas. Decay was modelled as a negative exponential of time since last
517 visit[65,66]. Together this yields the following equations for the dynamics of memory across space
518 $\boldsymbol{u}$, given the animal's current position $\mathbf{x_t}$:

519 $$m_J(\boldsymbol{u}; t, \mathbf{x}_{t-1}) = m_J(\boldsymbol{u}; t-1) + \underbrace{\alpha\big(\boldsymbol{u}; \mathbf{x}_{t-1}, \lambda_J\big) . \Big(1 - m_J(\boldsymbol{u}; t-1)\Big) . l_J}_{Learning}$$

520 $$- \underbrace{\Big(1 - \alpha\big(\boldsymbol{u}; \mathbf{x}_{t-1}, \lambda_J\big)\Big) . m_J(\boldsymbol{u}; t-1) . \delta_J}_{Decay} \qquad Eq. 8$$

521

522 $$\alpha\big(\boldsymbol{u}; \mathbf{x}_{t-1}, \lambda_J\big) = e^{-\lambda_J . \|\boldsymbol{u} - \mathbf{x}_{t-1}\|} \qquad Eq. 9$$

523

524 where $J = R$ and $J = W$ for reference and working memory, respectively; l_R and l_W are the rates
525 of learning for reference and working memory; the functions $\alpha(\boldsymbol{u}; \mathbf{x}_{t-1}, \lambda_R)$ and $\alpha(\boldsymbol{u}; \mathbf{x}_{t-1}, \lambda_W)$
526 respectively describe how the rates of reference and working memory acquisition attenuate as a
527 function of distance from the animal's previous position (modelled via negative exponential
528 functions); and δ_R and δ_W determine the rates at which the two forms of memory decay over
529 time. According to their biological definition[15,16], reference memory is always larger than
530 working memory, thus imposing the following constraints: $l_R \geq l_W$, $\delta_R \leq \delta_W$ and $\lambda_R \leq \lambda_W$. For
531 missing relocations, no learning occurred but memory decay took place.

532

533 *Model fitting*

We fitted two models representing competing hypotheses pertaining to the biological processes influencing the movements of reintroduced roe deer: resource-only (M_{res}), and interplay between memory and resources ($M_{mem:res}$). For the M_{res} model, the memory parameters were omitted (i.e., no memory learning; $l_R = l_W = 0$). We estimated the model parameters through maximum-likelihood inference. The likelihood function for the parameter set of the information-independent movement kernel $\theta_1 = \kappa_S, \lambda_S$, and of the cognitive weighting function, $\theta_2 = (l_R, l_W, \delta_R, \delta_W, \lambda_R, \lambda_W, \varepsilon, \beta_1{:}\beta_6)$, is given as:

$$L(\boldsymbol{\omega}) = \prod_{i=1}^{N} \prod_{t=1}^{T_i} p(\mathbf{x}_t | \mathbf{x}_{t-1}, \theta_1, \theta_2) \qquad Eq.10$$

with N the number of animals (i.e., 17) and T_i the number of relocations for animal i. Missing GPS relocations were omitted from the likelihood function. We estimated the global minima of the log-likelihood function [$logL(\boldsymbol{\omega})$; i.e., the objective function] using the particle swarm optimization algorithm (PSO[67]; see Supplementary S5 for details). We calculated 95% marginal confidence intervals (CIs) via an asymptotic normal approximation of the objective function in the neighbourhood of the global minima. We then evaluated the contribution of each variable to the model support by calculating the delta Akaike Information Criterion[68] of the reduced model (i.e., excluding the variable of interest) relative to the full model.

Movement simulations and emergent properties

We evaluated whether the two parametrized movement models (M_{res} and $M_{mem:res}$) could characterize the spatial behaviour of reintroduced roe deer by means of movement simulations. For each monitored roe deer, we ran 30 movement simulations (17 animals x 30 runs = 510

556 simulated trajectories per model), initiated on the first observed GPS relocation of each
557 individual (i.e., in the vicinity of the release site). At each time step, a spatial location was
558 randomly selected according to the probabilities defined by the parametrized redistribution
559 kernel. Simulations ran for a duration equivalent to that of the observed roe deer trajectories.
560 We compared observed and simulated trajectories using key emerging properties. First, to
561 evaluate the emergence of spatially-restricted movements, we compared the temporal trend in net
562 squared displacement (NSD). NSD was calculated as the squared distance between the individual
563 position at time t, $\mathbf{x}_t$, and the trajectory start position, $\mathbf{x}_0$:

564 $$NSD_t = \|\mathbf{x}_t - \mathbf{x}_0\|^2 \qquad Eq. 11$$

565

566 At the population-level, we computed the mean NSD for the 17 released roe deer as a 5-day
567 running mean to remove individual noise. For the simulations, we calculated the 5% and 95%
568 confidence bounds for the mean NSD via bootstrapping (1000 random samples of 17 simulated
569 trajectories). Second, we evaluated whether the parametrized movement models captured the
570 empirical distributions of emergent movement properties. We calculated step length as the
571 Euclidean distance between two successive relocations, and turning angle as the angle in radians
572 between the directions of two successive steps (ranges from $-\pi$ to π; 0 indicating no directional
573 change). Third, we investigated whether the parametrized movement models captured roe deer
574 revisitation behaviour (i.e., movement recursions[29]). Revisits, defined as returns to a previously
575 visited area, occurred when an animal (observed or simulated) used a 25 x 25 m spatial cell that
576 had been last visited within > 6 hours (i.e., temporally-disjointed use of a specific location). For
577 each visited cell along the trajectory, we computed its total number of revisits (0 indicating a
578 single visit) and their associated time since last visit.

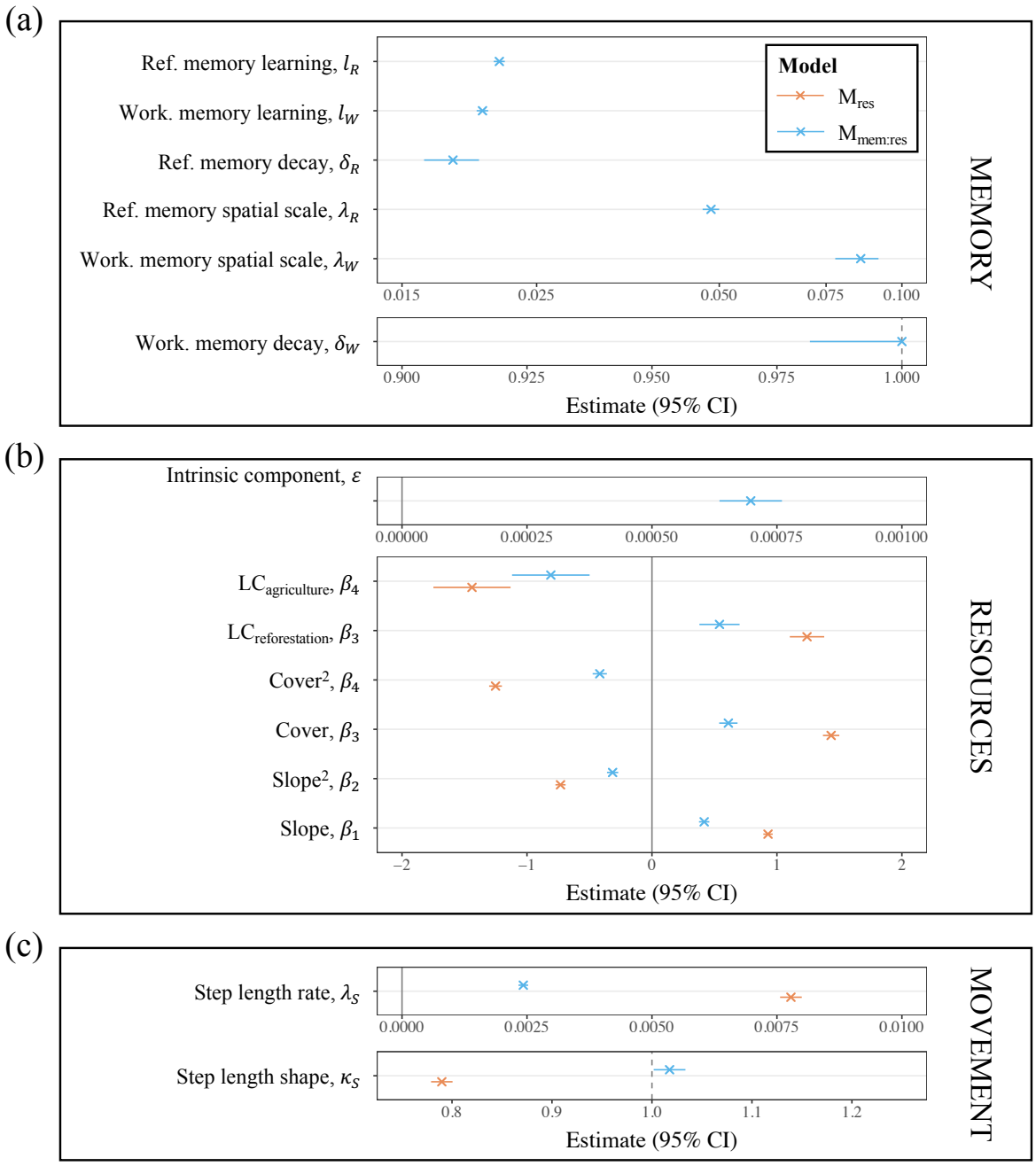
579

580 Equations 1-10 were solved numerically, and simulations performed in C++. The
581 parameters were estimated using the PSO algorithm, implemented within the Global
582 Optimization Toolbox, MATLAB R2017b (MathWorks, Natick, Massachusetts, USA). The
583 optimization ran on a computer cluster using the Distributed Computer Server[69]. We calculated
584 the CIs, produced the effect size plots and comparison between observed and simulated
585 trajectories in R[70].

Table 1 Variable contributions to the memory-based model ($M_{mem:res}$).

Variable(s) removed from the full model	Equation(s)	Parameter setting(s)	Number of removed parameters	Δ AIC
Ref. memory (i.e., M_{res})	7, 8	$l_R = 0$*	6	17,355
Ref. memory spatial scale	8, 10	$\lambda_R = \infty$	1	7,444
Step length decay	2	$\lambda_S = 0$	1	4,945
Ref. memory learning	8	$l_R = 1$	1	3,434
Ref. memory decay	8	$\delta_R = 0$	1	2,631
Working memory	7, 9	$l_W = 0$**	3	1,278
All resources	6	$\beta_1 : \beta_6 = 0$	6	304
Slope + Slope^2	6	$\beta_1 = \beta_2 = 0$	2	138
Landcover – reforested	6	$\beta_6 = 0$	1	83
Landcover – agriculture	6	$\beta_5 = 0$	1	59
Cover + Cover^2	6	$\beta_3 = \beta_4 = 0$	2	34
Step length rate	2	$\kappa_S = 1$	1	4

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 *Methods* section. Parameters setting refers to the conditions imposed to exclude the variable. *Reference (Ref.) memory was removed by setting its learning rate, $l_R = 0$, resulting in the effective removal of all memory parameters (i.e., equivalent to a resource-only model): λ_R and δ_R are irrelevant if there is no reference memory learning, and because $l_W \leq l_R$, the three working memory parameters (l_W, λ_W and δ_W) were dropped as well. **Similarly, removing working memory by setting $l_R = 0$, led to the effective removal of λ_W and δ_W.



595

596 **Figure 1: Parameter estimates.** The estimates for the resource-only (M_{res}; orange), and the memory-based

597 ($M_{mem:res}$; blue) models are plotted with the corresponding 95% marginal confidence intervals. Memory

598 (panel a), resource preference (b) and movement (c) parameters are shown separately for readability.

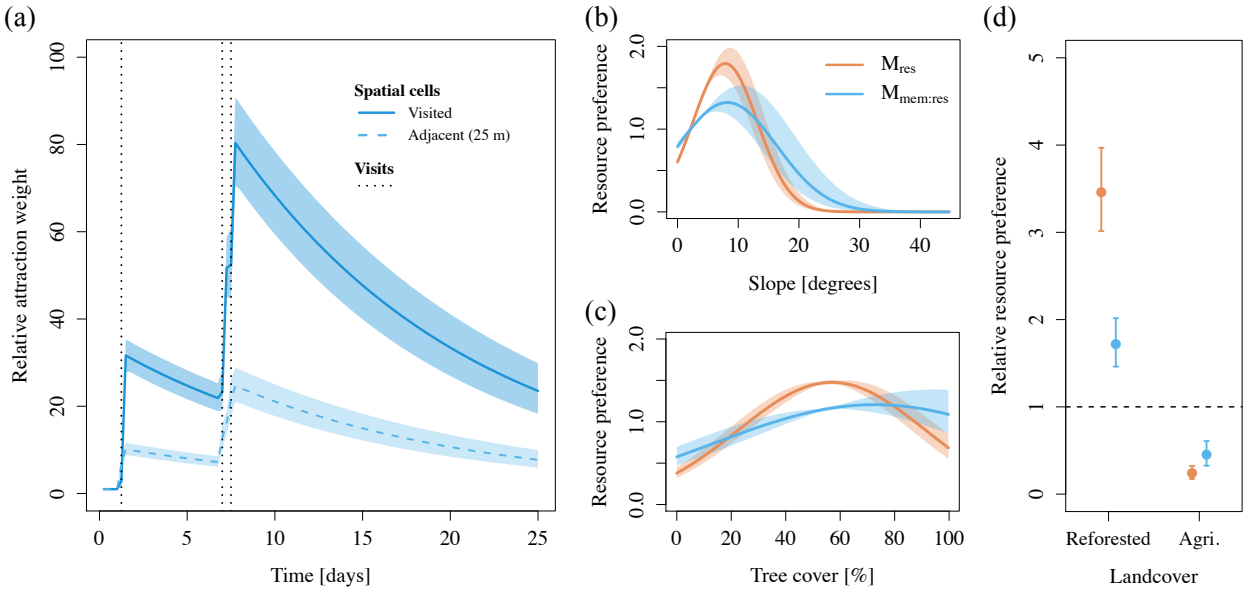
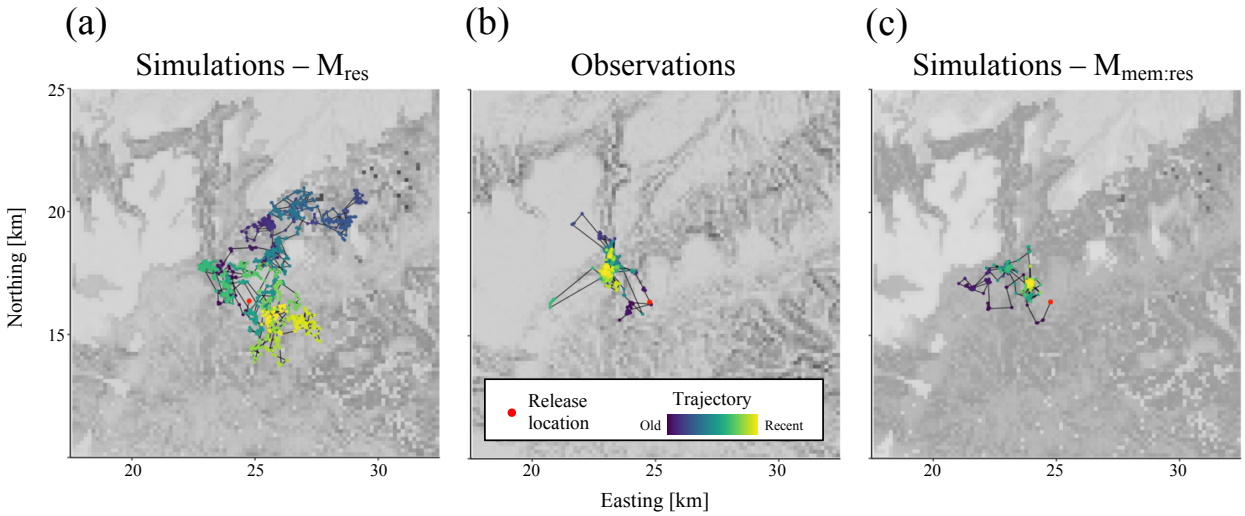


Figure 2: Predictor effects. The response curves for the resource-only (M_{res}; orange) and the memory-based ($M_{mem:res}$; blue) models are plotted with the corresponding 95% marginal confidence intervals. Panel (a) shows the attraction of a visited spatial cell (continuous line) and an adjacent cell (25 m away; dashed line) relative to a cell that has never been visited (attraction = 1) resulting from the fitted memory-based model. Hypothetical visits (at t = 1.25, 7.00 and 7.50 days) are shown in dotted vertical lines. Panel (b) and (c) illustrate the preference for slope and tree cover, respectively. Panel (d) shows the relative preference for reforested and agriculture landcovers.



608

609 **Figure 3: Movement trajectories**. Three typical trajectories are shown for the resource-only simulations
610 (M_{res}; panel a), observed roe deer movements (panel b), and memory-based simulations ($M_{mem:res}$; panel c).
611 The release location is shown as a red dot and the time since release illustrated as a colour gradient (blue
612 = old, yellow = recent). The trajectories were selected from the sample displayed on Figure 4.

613

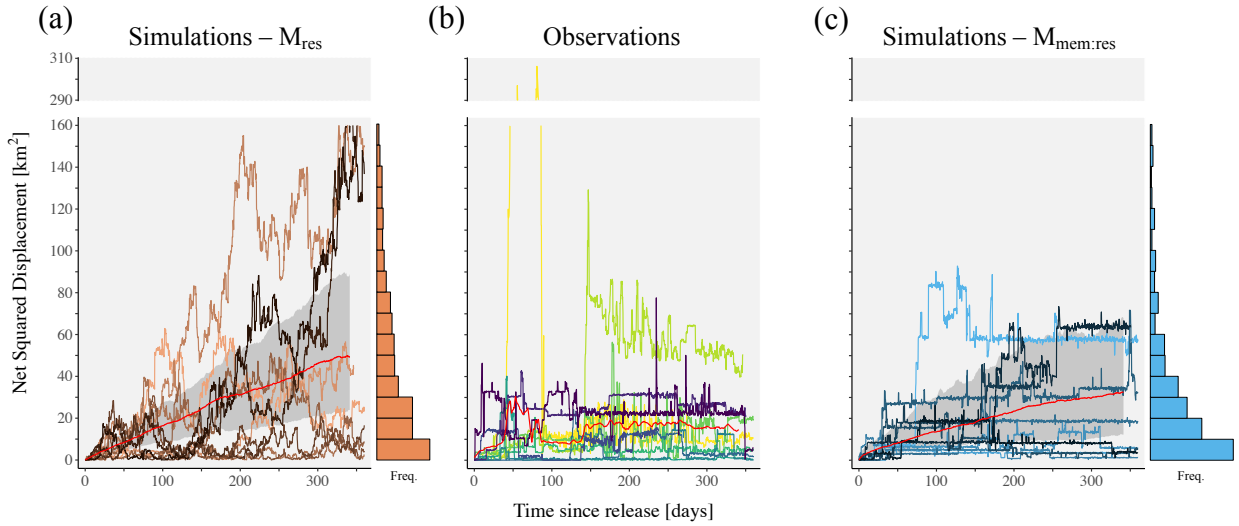


Figure 4: Trends in net squared displacement (NSD) with time since release. Panel (a): resource-only simulations (M_{res}). Panel (b): observed roe deer movements. Panel (c): memory-based simulations ($M_{mem:res}$). For the sake of clarity, only the individuals with more than 230 days of monitoring are shown (n = 10). For the simulations, one run for each of the selected individuals was randomly chosen. The trends in 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.

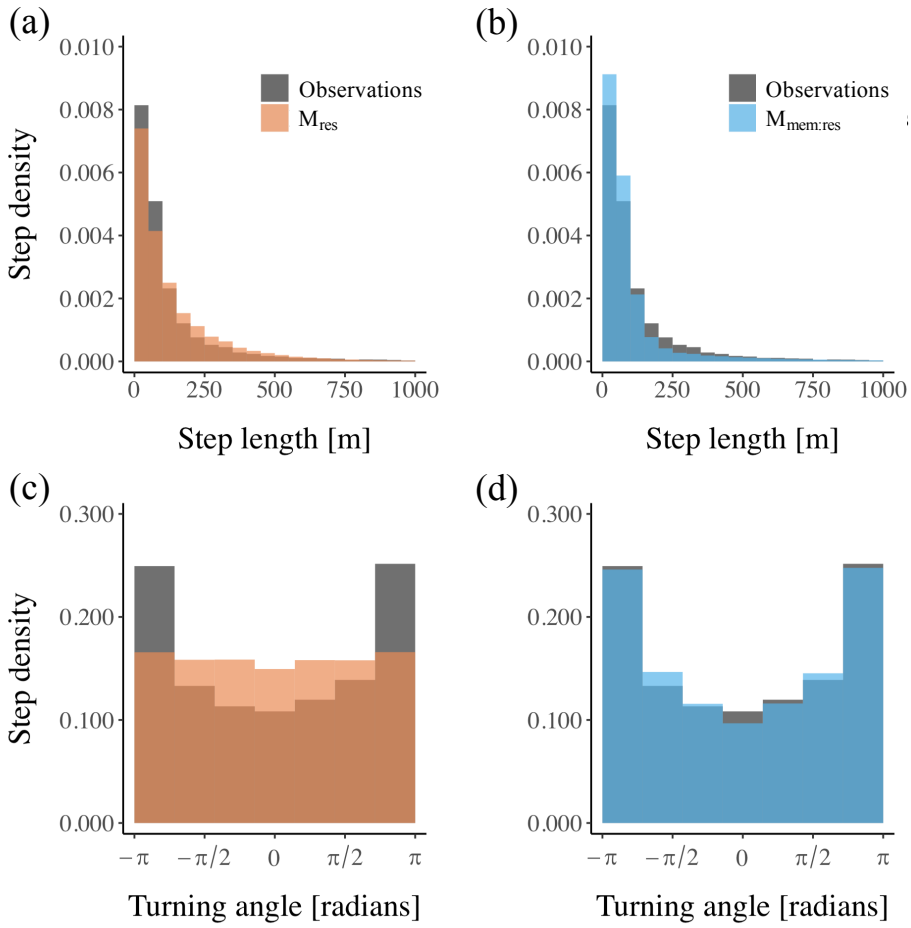
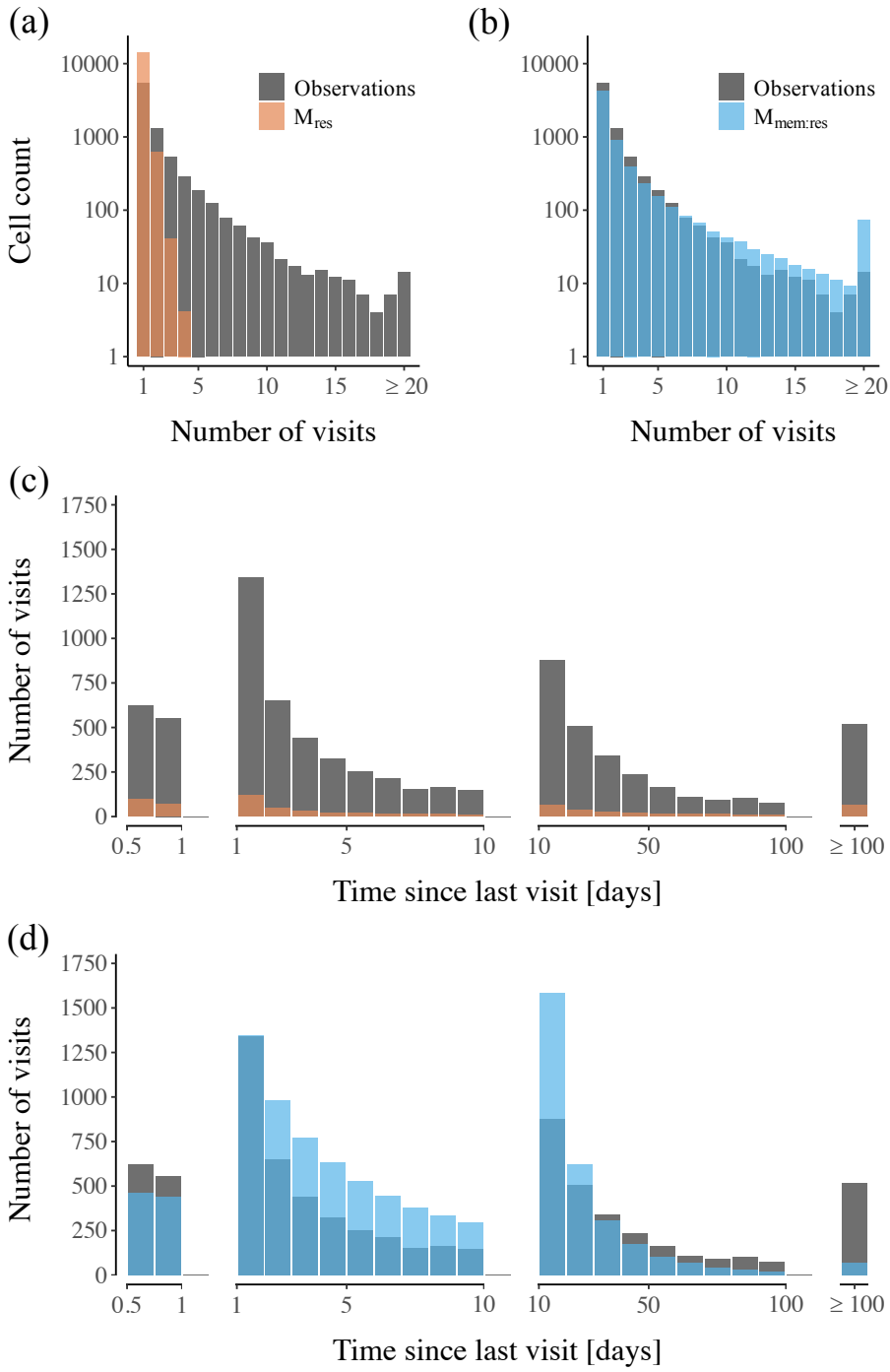


Figure 5: Emergent movement properties. The distributions of step length (panels a and b) and turning angle (panels c and d) are shown for observed roe deer movements (grey), the simulated trajectories from the resource-only model (M_{res}; orange), and the simulated trajectories from the memory-based model ($M_{mem:res}$; blue).



628

629 **Figure 6: Emergent revisitation properties.** The distributions of revisits (panels a and b) and time since
630 last visit (panels c and d) are shown for observed roe deer movements (grey), the simulated trajectories
631 from the resource-only model (M_{res}; orange), and the simulated trajectories from the memory-based model
632 ($M_{mem:res}$; blue).

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Competing Interest Statement

The authors declare no competing interests.

Data Availability Statement

The datasets generated and/or analysed during the current study are available from the authors on request.

Ethical Statement

The roe deer (*Capreolus capreolus spp. italicus*) reintroduction project was carried out under the technical approval and ethical requirements of the Institute for Environmental Protection and Research (ISPRA, public body for research under the vigilance of the Italian Ministry of the Environment; protocols #47427 and #45826). The capture of roe deer in the population of origin

were conducted under authorization #1555 by the Director of the Wildlife Resources and Natural Reserve Service of the Province of Sienna.

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