

# **The integrated role of resource memory and scent-mediated territoriality in the emergence of home-ranges**

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## Abstract

Despite decades of extensive animal movement research, we still lack an integrated, process-based understanding behind the movement decisions that individuals make, which ultimately lead to the emergence of home-ranges. Here, we advance toward a more holistic understanding of HR formation, by developing a theoretical model integrating two key processes that have been separately proposed to play important roles in HR formation in territorial animals: (i) optimising resource acquisition by referencing a cognitive memory (i.e., resource memory); and (ii) minimising resource competition through defensive cues (i.e., territoriality). We extend a two-state memory-based model for non-territorial animals to include multiple individuals that interact through scent-mediated conspecific avoidance behaviour. We investigated how the interplay of memory and territoriality influenced: (1) the emergence of individual home-ranges; (2) the relationship between home-range size, density and resource availability; and (3) the response of animal home ranges to perturbations of the conspecific environment (i.e., removing individuals). We showed that integrating both resource memory and territoriality gave rise to spatially distinct and dynamic HRs that follow a negative log-linear relationship with respect to resource distribution (Pearson's  $r = -0.73$ ,  $p < 0.01$ ), congruent with empirical evidence. On its own, neither process resulted in a similar response.

# 1 Introduction

Many animal species constrain their movement to specific home-ranges (HR), which emerge from activities (i.e., processes) engaged in to survive and reproduce (Burt 1943). The emergent HR patterns observed are ultimately caused by movement decisions of individual animals, which are in turn driven by dynamic processes including their need to access resources while avoiding costly interactions with conspecifics and predators (Borger *et al.* 2008; Nathan *et al.* 2008). Despite decades of extensive movement research, the development of models explaining HR emergence through such processes has been relatively few and recent (Ranc *et al.* 2020b). Two key processes have been proposed to play important roles in HR formation in territorial animals: optimising resource acquisition by referencing a cognitive memory (i.e., resource memory) and minimising resource competition through defensive cues (i.e., territoriality) (Borger *et al.* 2008; Powell & Mitchell 2012; Spencer 2012; Fagan *et al.* 2013). While there have been successes in modelling these underlying mechanisms separately, integration of the two to form a general predictive theory of HR emergence has remained a key challenge (Potts & Lewis 2014).

A fundamental characteristic of animal home ranges is the regular revisitation to locations such as foraging areas, dens, watering holes and movement corridors (a.k.a. ‘site fidelity’). Animal memory provides a plausible biological explanation of this phenomenon and recent empirical evidence supports this hypothesis (Merkle *et al.* 2014; Bracis & Mueller 2017; Merkle *et al.* 2017; Ranc *et al.* 2020a; Ranc *et al.* 2021). While quantifying memory is particularly challenging, theoretical analyses have demonstrated that memory-based foraging processes can produce emergent home ranges and more efficient resource use, in line with the theory of optimal foraging (Van Moorter *et al.* 2009; Bracis *et al.* 2015; Riotte-Lambert *et al.* 2015). Modelling memory mechanisms essentially captures the underlying localisation process behind the formation of HR boundaries, and spatio-temporal patterns of site use and fidelity within a HR. Moreover, it could potentially reproduce the dynamic nature of HRs (i.e., longer term shifts in boundaries or sites) as a response to a changing environment (e.g., Potts *et al.* (2013); Bateman *et al.* (2015)). This is a key advance from non-mechanistic movement models, which have commonly assigned localising centres or HR boundaries *a priori* to achieve stable, but unrealistically static HRs (Borger *et al.* 2008).

Since animals rarely exist in isolation, it is also important to consider how conspecific interactions shape HRs. Competitive interactions drive spatial segregation of HRs in a multi-individual context, particularly in territorial animals that maintain and defend exclusive territories against conspecifics. In mechanistic movement models, territoriality is classically modelled as scent-mediated conspecific avoidance (Giuggioli *et al.* 2013; Potts & Lewis 2014). Conspecific scent avoidance has been demonstrated as a significant underlying driver of observed variations in individual HRs and changes in HR patterns following population change in territorial carnivores (Lewis & Murray 1993; Moorcroft *et al.* 2006; Bateman *et al.* 2015). While existing mechanistic models that include territoriality have led to realistic patterns of HR formation, most have imposed a redirect-to-centre response following encounter of scent marks (i.e., focal attraction point) to stabilise the otherwise unconstrained enlargement of HRs caused by diffusive movement (Borger *et al.* 2008; Potts & Lewis 2014). This non-mechanistic component is not only inappropriate for animals that are not central place foragers or denning animals, it also precludes the emergence of dynamic localising behaviours as a response to changing environments (e.g., HR shifts following resource depletion). Moreover, the redirect-to-centre response does not provide an explanation for the

50 underlying localising movement behaviours in the absence of conspecifics (e.g., in sparsely  
51 populated habitats), which would be a result of memory processes.

52

53 Though critical insight has been gained from modelling resource memory and territoriality  
54 separately, the integration of these two important aspects of HR formation is yet to be  
55 explored. Each component essentially provides a mechanistic explanation for what the other  
56 lacks: resource memory is an attractive (overall) driver for individuals to preferentially  
57 acquire resources from a memory of previously visited sites, while territoriality is a repulsive  
58 driver for individuals to establish exclusive HRs in a multi-individual context (Potts & Lewis  
59 2014). Integrating them into a single framework could provide the basis for understanding  
60 and simulating more complex localisation behaviours, such as the spatial allocation of  
61 resources in a competitive context.

62

63 Here, we advance toward a more holistic understanding of HR formation, by developing what  
64 is, to our knowledge, the first theoretical model integrating resource memory and territorial  
65 processes to simulate realistic patterns of space use by territorial animals. We extend a two-  
66 state memory-based model for non-territorial animals (Bracis *et al.* 2015) to include multiple  
67 individuals that interact through scent-mediated conspecific avoidance behaviour. To explore  
68 and illustrate the effects of integrating these two components, we investigate how the  
69 interplay of memory and territoriality influences: (1) the emergence of individual home-  
70 ranges; (2) the relationship between home-range size, density and resource availability; and  
71 (3) the response of animal home ranges to perturbations of the conspecific environment (i.e.,  
72 removing individuals).

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74

## 75 **2 Methods**

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### 77 **2.1 Model description**

78

79 We created a model of scent-marking and conspecific scent avoidance into an existing  
80 modelling framework (Bracis *et al.* 2015) in which foragers move around a dynamic resource  
81 landscape, learning as they consume about the intrinsic quality of the landscape (**Fig. 1a**).

82

#### 83 **2.1.1 Movement process**

84

85 An animal's movements through the landscape are described by a continuous trajectory with  
86 a current position of  $Z(t) = \int_0^t V(t') dt' + Z_0$ , with a velocity of  $V(t)$  and initial position  
87 of  $Z_0$ . The autocorrelated, directed, continuous movement process is given by

88

$$89 \quad dV = \frac{1}{\tau} (\mu(t) - V) dt. \quad (1)$$

90

91

92 This is similar to the Ornstein-Uhlenbeck process where  $\tau$  is the time scale of autocorrelation  
93 and instead of the white noise component, stochasticity is introduced through the bias vector  
94  $\mu(t)$  of magnitude  $\|\mu(t)\|$  (controlling average speed) and angle  $\angle\mu(t)$  (direction) (**Fig. 1b**).  
95 A Poisson process with rate parameter  $\lambda$  determines when angle  $\angle\mu(t)$  is updated, which is  
96 then selected from an angular probability distribution derived from resource memory or scent  
97 processes, depending on the behavioural state. Finally, individuals switch between feeding

98 and searching states, characterised by different values for  $\tau$  and  $\nu$ , based on the current  
99 resource consumption  $C(t)$ .

100

### 101 **2.1.2 Resource memory**

102

103 The resource  $Q$  is modelled as continuously varying in space across the landscape. Resources  
104 deplete as they are consumed by individuals and logistically regenerate at a rate of  $\beta_R$ , but do  
105 not shift in space. Thus, it is advantageous for the individual to leave recently depleted  
106 patches but return to high quality areas over the long term. Animals consume resources  
107 according to a spatial kernel (a bivariate normal distribution with length scale  $\gamma_C$ ) and  
108 consumption rate  $\beta_C$ . Animals have a resource memory with two different streams of  
109 information: a short-term stream  $S$  that pushes the animal away from recently visited  
110 locations even if they are attractive, and a long-term stream  $L$  that attracts the animal to back  
111 to high quality areas (Van Moorter *et al.* 2009). The latter can either be initiated fully  
112 informed, with the intrinsic resource quality  $Q_0$ , or naively, with a homogenous map of value  
113  $M^*$  indicating the animal's prediction for unvisited areas which can be more optimistic or  
114 pessimistic and thus affect exploratory tendency (see Bracis & Wirsing, In review).  $M^*$  is  
115 also the value that long-term memory  $L$  decays to. The two streams are combined into a  
116 single memory map  $M$ , which is used to inform the movement process.

117

118 The resource memory contribution to this angular probability distribution is computed by  
119 integrating transects of the resource memory map radiating out from the individual's location  
120  $r$  with the resource memory value at each point weighted by distance,

121

$$122 \quad g(\theta) = \frac{\int_0^r M(r, \theta) f_z(r) dr}{\int_0^{2\pi} \int_0^r M(r, \theta') f_z(r) dr d\theta'}, \quad (2)$$

123

124 where  $f_z(r)$  is the kernel function that weights according to distance (here exponential with  
125 length scale  $\gamma_z$ ). The foraging memory movement model is described in further detail in  
126 Bracis *et al.* (2015).

127

### 128 **2.1.3 Scent-marking, avoidance and attraction**

129

130 As individuals move about the landscape, they also deposit scent, which decays over time,  
131 thereby marking their territory. The amount of scent,  $D$ , is governed by the deposition rate,  
132  $\beta_D$ , how much scent is deposited, and the deposition spatial scale,  $\gamma_D$ , how broadly the scent  
133 is deposited in the vicinity of the forager. The amount of scent deposited is then adjusted  
134 according to how much scent is already present, to a maximum value of 1 ( $D_0 = 1$ ). The  
135 scent decays uniformly in space according to the exponential decay rate,  $\phi_D$ . Thus, the  
136 change in scent for each forager at location  $z = (x, y)$  is given by the equation

137

$$138 \quad \frac{\partial D}{\partial t} = \beta_D f_D(|z - Z|)(D_0 - D) - \phi_D D, \quad (3)$$

139

140

141 where  $f_D$  is the spatial kernel (here exponential with scale  $\gamma_D$ ). Scent deposition is tracked per  
142 individual, and in the simplest case, foragers are indifferent to their own scent, but repulsed  
143 by the scents of all other conspecifics.

144

145 The repulsion of individuals by the scent of conspecifics is represented with an angular  
146 conspecific safety metric that scales between 0 and 1 but is not constrained to sum to 1 (e.g.,  
147 like predation risk; (Bracis *et al.* 2018)). It represents the relative ‘safety’ in each direction in  
148 terms of avoiding conspecifics, with 0 meaning not safe (high levels of conspecific scent) and  
149 1 meaning safe (no conspecific scent). It is calculated by integrating the summed values of all  
150 other foragers’ deposited scent according to

151

$$152 \quad d_i(\theta) = 1 - \max \left( 1, \int_0^r \Psi_D \sum_{n \neq i} D_n(r, \theta) f_w(r) dr \right), \quad (4)$$

153  
154 where  $\Psi_D$  is the response strength and  $f_w(r)$  is a spatial kernel (here the exponential kernel  
155 with length scale  $\gamma_w$ ) that represents that decay with distance of scent perception.

156

#### 157 **2.1.4 Decision rules**

158

159 In order to create the angular probability distribution from which the angle  $\theta$  is drawn to  
160 inform the movement process, several pieces of information are combined. The angular  
161 probability distribution based on the resource memory  $g(\theta)$  is multiplied by the conspecific  
162 safety metric  $d_i(\theta)$  for individual  $i$ , then normalised, giving

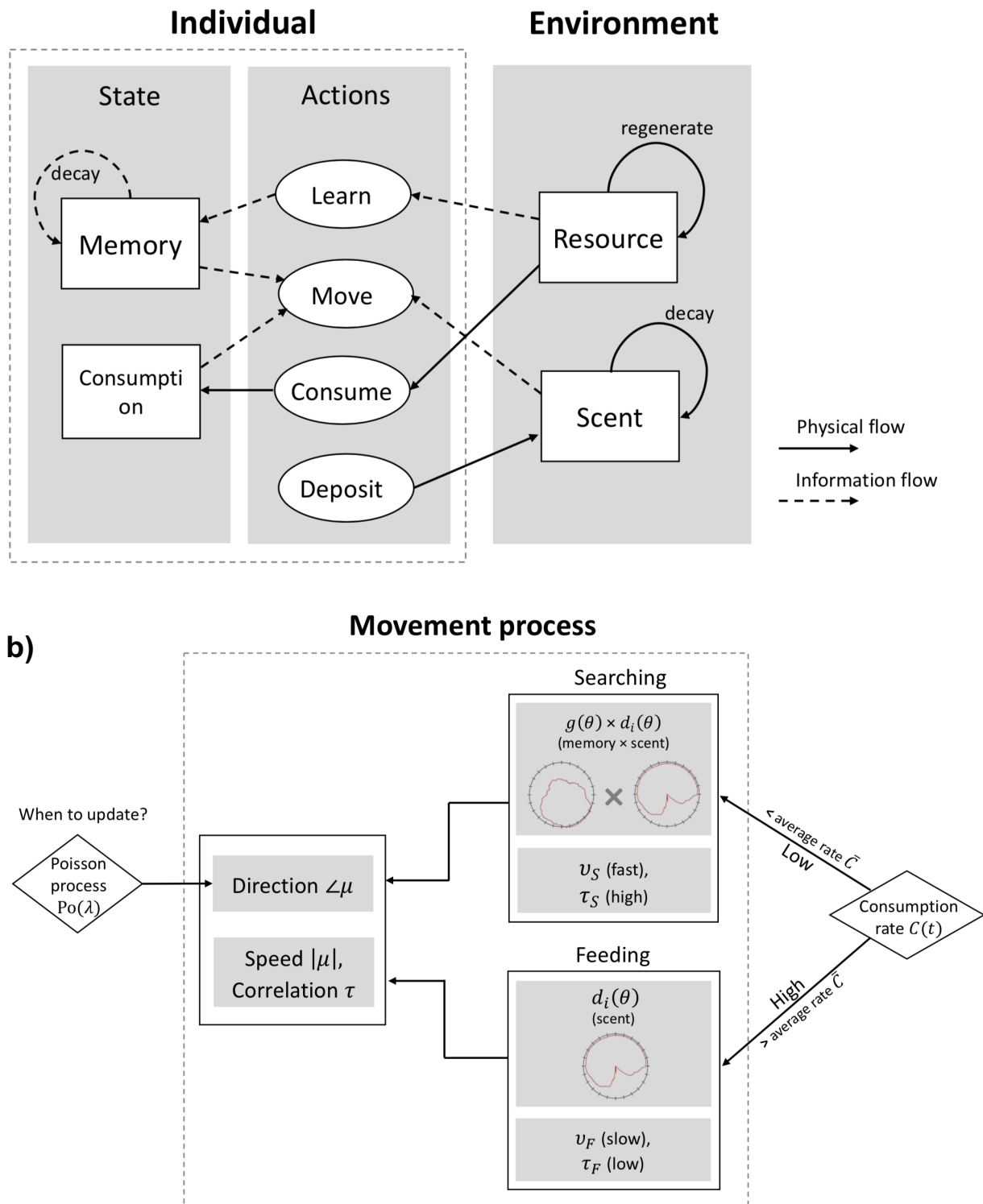
163  
164

$$165 \quad h_i(\theta) = \frac{g(\theta)d_i(\theta)}{\int_0^{2\pi} g(\theta')d_i(\theta')d\theta'}, \quad (5)$$

166

167

168 the angle of the bias term  $\theta(t) = \angle\mu(t)$ , in the movement process is then drawn from  $h_i(\theta)$ ,  
169 which is specific for each individual.



**Fig. 1.** A graphical representation of the model. a) An overview of all the processes involved. b) The movement process is formulated on continuous time, where the updating of the individual's direction and behavioural state are independent processes. Behavioural state ultimately determines the processes used in selecting the next direction (represented by an angular probability density function of memory and scent) and the speed/correlation values.

## 170 2.2 Simulations

171  
172 We implemented our movement model in the programming language Java and ran the  
173 simulations on a High-Performance Computing cluster. Analysis of model outputs was done  
174 in R version 3.6.1 (R Core Team 2020). For Section 2.2.1 and 2.2.2, we used a 200 by 200  
175 heterogenous resource landscape generated with a fractional Brownian motion neutral  
176 landscape model using the R package *NLMR* (Sciaini *et al.* 2018) with a fractal dimension of  
177 0.75. The initial location of animals in all cases were random, and the boundaries were  
178 reflective.

### 179 2.2.1 Resource memory and territoriality

180  
181  
182 To test the effect of territoriality on emergent HRs within a memory-based framework, we  
183 first ran simulations for three scenarios: (1) territoriality only, (2) memory only; and (3)  
184 territoriality and memory. In scenario 1, the movement process is a resource-dependent two-  
185 state random walk, with  $g(\theta)$  in Eq. 5 being uniform while scenarios 2 and 3 use the memory  
186 process of Eq. 2. All three scenarios were run across three different densities of individuals ( $n$   
187 = 5, 10, 15) according to parameter values in **Table S1**, and 100 replicate simulations per  
188 combination were run for each scenario and density combination. We then showed variance  
189 in each individual's HR size with respect to density and resource availability. HR size was  
190 estimated from the simulation output using a kernel density estimator function *kernelUD* in  
191 the R package *adehabitatHR*. The 95% HR polygons were used to extract resource values  
192 within the landscape using the R packages *sp* and *raster*, after which the mean resource value  
193 within each HR was computed.

### 194 2.2.2 Effect of removal

195  
196  
197 To further demonstrate that HRs are both an emergent property and dynamic to changing  
198 conditions in our model, we removed individuals and quantified the effects on the HRs of the  
199 remaining individuals. We ran a set of simulations with individual removal and a control  
200 scenario (no removal) with the same set of parameters given by **Table S1** (50 replicates  
201 each). These simulations were separated by three phases:

- 203 1) initialisation to allow for 'home-range establishment' ( $t = 1-20,000$ ),
- 204 2) removal of four out of ten individuals ( $t = 20,001$ ), followed by a transition period to  
205 allow the scent of removed individuals to decay ( $t = 20,001-30,000$ ), and
- 206 3) finally, to allow exploration by remaining individuals ( $t = 30,001-50,000$ ).

207 To quantify the effects of removal, we compared the aggregate overlap between initial area  
208 covered by removed individuals (calculated from phase 1 with a burn-in of 5,000 timesteps)  
209 and the remaining individuals before and after (calculated from phase 1 and 3 respectively  
210 with a burn-in of 5,000 timesteps) removal, and test for statistical significance through a  
211 dependent Wilcoxon signed rank test. For control simulations, identities of the four  
212 'removed' individuals (not actually removed) were randomly selected for a similar  
213 comparison to be made. Aggregate overlap in area covered (95% HR) between removed and  
214 remaining individuals was computed using the R package *rgeos*.



## 215 **3 Results**

216

### 217 **3.1 Resource memory and territoriality**

218

219 The differences in simulation trajectories and space use with or without the inclusion of the  
220 behavioural processes were apparent (**Fig. 2c**). Simulated individuals in the territoriality-only  
221 scenario established distinct territories restricted by surrounding conspecifics but space use  
222 was not in accordance with resource availability. In the memory-only scenario, individual  
223 space use appeared stable but overlapped heavily and was concentrated in high resource areas  
224 in the landscape. With both the territorial and resource memory processes enabled in the last  
225 scenario, individuals established distinct territories that spread across resource areas with  
226 little overlap in movement trajectories.

227

228 Density of individuals did not significantly affect space use patterns in all three scenarios  
229 (**Fig. 2a**). The increase in density caused a slight decrease in HR size in the first (territoriality  
230 only) and third (territoriality and resource memory) scenarios, but the difference was not  
231 significant. In both these scenarios, the variance in HR size increased with increasing density,  
232 a result of individuals being ‘trapped’ into a small area by surrounding conspecifics (causing  
233 the lower limit) and larger ranging behaviour by individuals which were relegated to lower  
234 quality areas (causing upper limit) (**Fig. S1**). In the memory-only scenario, there appeared to  
235 be no relationship between density and HRA.

236

237 The simulated individual’s environment influenced realised space-use patterns (**Fig. 2b**).  
238 Although all three scenarios reflected a negative relationship between HR size and mean  
239 resource value, only the third scenario was strongly log-linear ( $r = -0.73$ ). Without both  
240 mechanisms in place, the trend tended towards a negative quadratic regression.

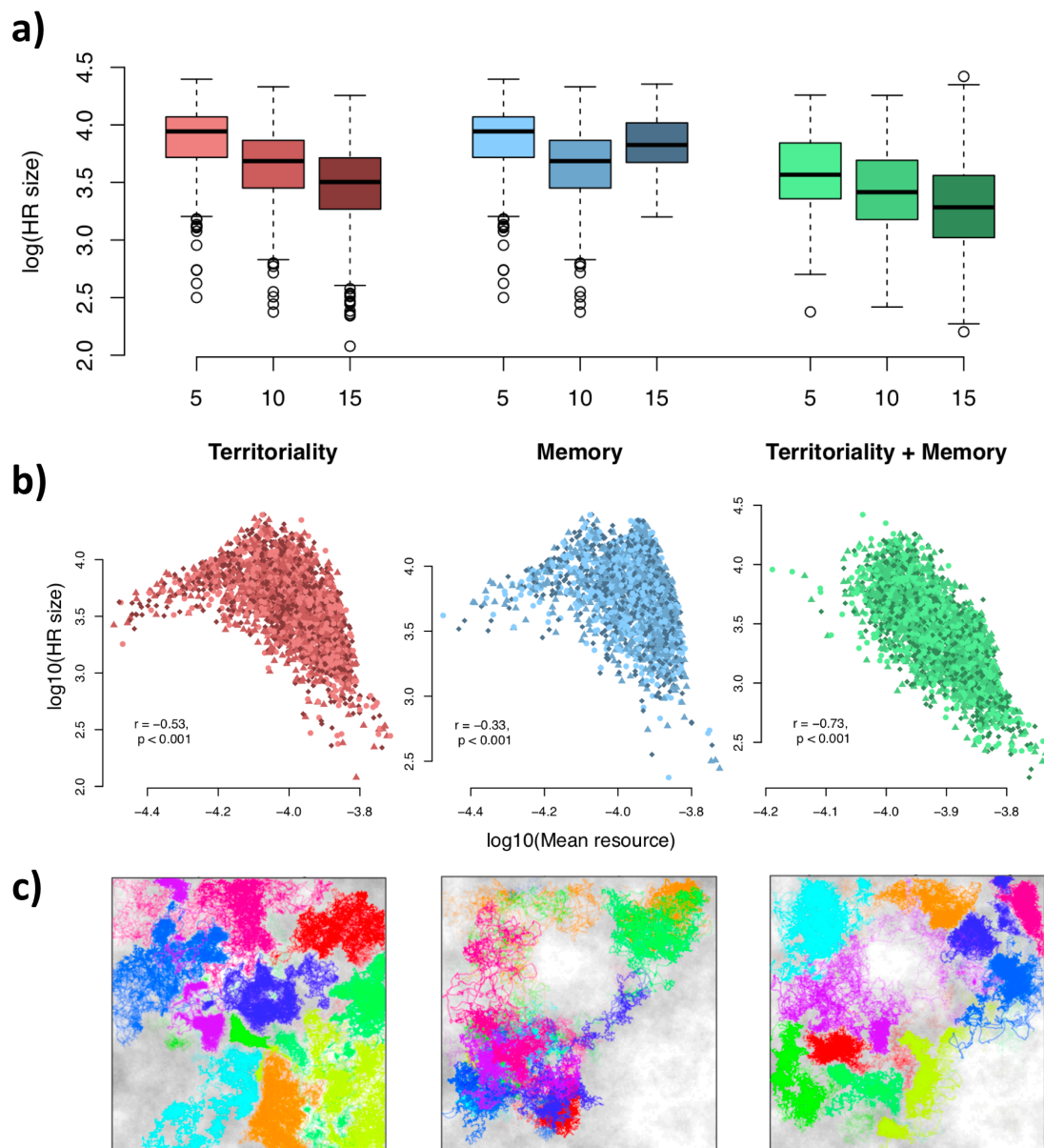
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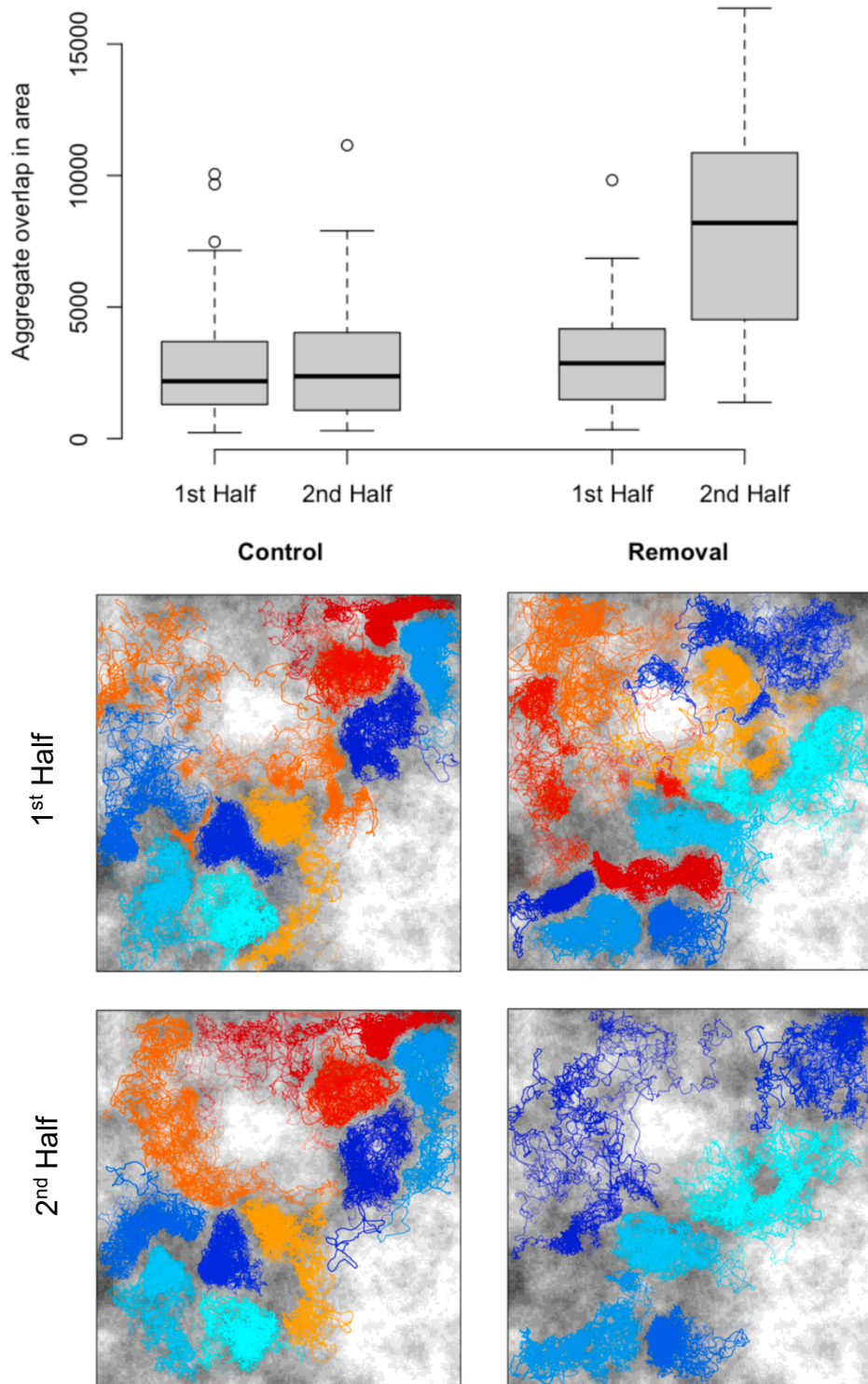
### 243 **3.2 Effect of perturbation**

244

245 The removal of individuals mid-simulation had a significant effect on space use in the  
246 remaining individuals (**Fig. 3**). The aggregate overlap in area covered by remaining  
247 individuals and removed individuals was significantly higher (dependent Wilcoxon signed  
248 rank test;  $V = 7$ ,  $p < 0.001$ ) in the second half of the removal simulations, while there was no  
249 significant difference in overlap between individuals (dependent Wilcoxon signed rank test;  
250  $V = 668$ ,  $p = 0.77$ ) in both halves of the control simulations. One example realisation showed  
251 exploration by remaining individuals into areas previously occupied by removed individuals  
252 (Fig. 3).



**Fig. 2.** Simulation results from three scenarios (territoriality, memory, territoriality and memory): relationship between HR size and a) density ( $n = 5, 10, 15$ ) and b) mean resource value (within HR) from 100 replicates, and c) sample realisations at  $n = 10$ . Individual trajectories start at random with opacity increasing through time (colours represent individuals).



**Fig. 3.** Aggregate overlap in area (95% HRA) between removed and remaining individuals before (1<sup>st</sup> half of simulation) and after removal (2<sup>nd</sup> half of simulation) in the control and removal scenarios (50 replicates each). Beneath each scenario is a sample realisation of movement trajectories in the first half (top panel) and 2<sup>nd</sup> half (bottom panel) the simulation. Individual trajectories decrease in opacity according to the rate of scent decay, thus only the most recent 10,000 time-steps are illustrated. Cool colours represent remaining individuals,

## 253 4 Discussion

254  
255 We showed that integrating two key drivers of HR formation, resource memory and  
256 territoriality, can give rise to spatially distinct and dynamic HRs that vary in size according to  
257 resource distribution. We also demonstrated how recreating stable HR patterns is ultimately a  
258 balance between an animal's inherent exploratory tendency and its desire to avoid  
259 conspecifics.

260  
261 In our multi-individual simulation environment, two mechanisms were required to replicate  
262 realistic patterns of HR formation in territorial animals: one that inherently tended towards  
263 fidelity to previously visited, high quality areas (resource memory); and another that drove  
264 spatial avoidance between individuals (territoriality). Further, our model captured realistic  
265 responses to density with the emergence of transient behaviour by some individuals as  
266 density increased and all higher quality areas were occupied. The absence of territoriality  
267 meant that foragers were acting independently, which caused large overlaps in emergent HRs  
268 (**Fig. 3b**). Whereas the absence of resource memory resulted in unrealistic HR formation that  
269 was not in accordance with resource quality; movement was inherently diffusive and only  
270 constrained by the scent of surrounding conspecifics (**Fig. 3a**). The combination of both  
271 mechanisms led to the emergence of distinct individual HRs distributed across high resource  
272 areas of the landscape (**Fig. 3c**). In addition to being spatially realistic, biologically  
273 meaningful relationships were also captured. Simulated individuals' HR sizes correlated  
274 negatively with both resource availability and population density, which is congruent with  
275 ecological evidence from both field and experimental studies (Boutin & Schweiger 1988;  
276 Baker *et al.* 2000; Dahle *et al.* 2006; Santangeli *et al.* 2012; Šálek *et al.* 2014; Schoepf *et al.*  
277 2015). This is biologically intuitive: when resources are abundant, the individual needs less  
278 space to meet its metabolic needs; when population density is high, the amount of available,  
279 unoccupied space is smaller, which limits individual HR sizes (Schradin *et al.* 2010).

280  
281 Home-ranging was a dynamic property emergent from our model, continuously shaped by the  
282 dynamic resource landscape and presence of surrounding conspecifics. This was emphasised  
283 in our perturbation simulations, where remaining individuals migrated into areas previously  
284 occupied by removed individuals once their scent decayed. The phenomenon of expanding  
285 into newly vacated habitat can be found in numerous species, such as mice (Schoepf *et al.*  
286 2015), chipmunks, (Mares *et al.* 1976), coyotes (Moorcroft *et al.* 2006), and red foxes (Potts  
287 *et al.* 2013). Non-mechanistic models (e.g., with imposed HR centres and/or boundaries) fail  
288 to respond to changing environments (e.g., individuals leaving or dying, fluctuating resource  
289 availability) in contrast to our model in which dynamic behaviour arises as a consequence of  
290 underlying mechanisms. Notably, the memory mechanism in our model can approximate the  
291 empirical phenomenon of HR stabilisation, which has (until now) remained an imposed  
292 property in existing mechanistic territorial models (Potts *et al.* 2012; Giuggioli *et al.* 2013;  
293 Potts & Lewis 2014). It is these dynamic and stochastic elements of mechanistic movement  
294 models that are key to modelling complex, realistic movement patterns.

295  
296 Our flexible modelling framework could be applied to a variety of populations exhibiting  
297 cue-based territorial behaviour once calibrated and validated against empirical data. The  
298 continuous-time movement trajectories emergent from the model allows for parameterisation  
299 to fine spatio-temporal resolution movement data, which is becoming increasingly available  
300 (Kays *et al.* 2015). Though ancillary data required for parameterisation of consumption,  
301 memory and scent remains difficult to collect and quantify, indirect methods of measurement  
302 are possible. For example, existing MHRAs on carnivores have been able to quantify the

303 influence of scent-mediated conspecific avoidance with measures of scent decay and  
304 deposition parameters similar to that of our model (Moorcroft *et al.* 2006; Potts *et al.* 2013;  
305 Bateman *et al.* 2015), and hence, potentially transferable. However, similar efforts for  
306 memory do not yet exist. Hence, future work could explore methods for inferring memory  
307 rates from high-resolution movement data (e.g., short-term memory decay could be related to  
308 the time between site revisits). If close correspondence of model outputs to observed patterns  
309 can be achieved, testing its efficacy as a conservation tool for predicting and evaluating  
310 natural and human-induced perturbations is an important next step.

311  
312 Further applications include studies which require a framework for simulating generic animal  
313 space use. One such area is in simulation-based evaluations of methods such as the analysis  
314 of behavioural structure in animal movement (e.g., Gurarie *et al.* 2016), and population  
315 estimation of mobile animals (e.g., Theng *et al.*, In review). Another potential area of  
316 application is in animal-mediated seed dispersal research, which has identified the need to  
317 integrate frugivory and disperser movement (Côtés & Uriarte 2013). A recent study  
318 highlighted the implications of using generic phenomenological movement representations  
319 (e.g., correlated random-walk) on dispersal model outcomes, and suggested more process-  
320 based movement approaches (Nield *et al.* 2019).

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