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

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

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

Here, we advance toward a more holistic understanding of HR formation, by developing what is, to our knowledge, the first theoretical model integrating resource memory and territorial processes to simulate realistic patterns of space use by territorial animals. We extend a two-state memory-based model for non-territorial animals (Bracis *et al.* 2015) to include multiple individuals that interact through scent-mediated conspecific avoidance behaviour. To explore and illustrate the effects of integrating these two components, we investigate how the interplay of memory and territoriality influences: (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).

2 Methods

2.1 Model description

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

2.1.1 Movement process

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

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

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

and searching states, characterised by different values for τ and υ, based on the current resource consumption $C(t)$.

2.1.2 Resource memory

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

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

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

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

2.1.3 Scent-marking, avoidance and attraction

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

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

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

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

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

where Ψ_D is the response strength and$f_w(r)$ is a spatial kernel (here the exponential kernel with length scale γ_w) that represents that decay with distance of scent perception.

2.1.4 Decision rules

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

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

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

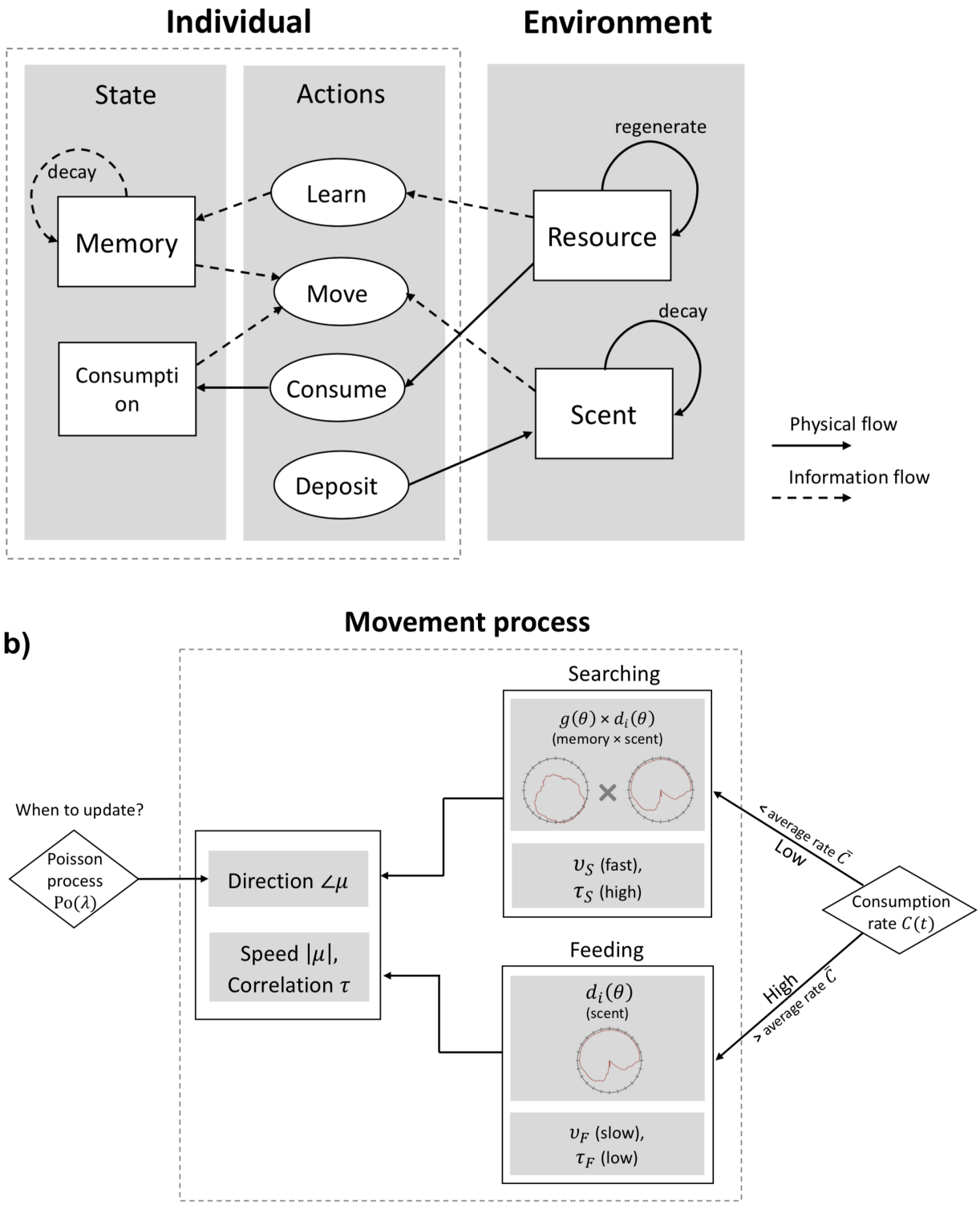

Fig. 1. A graphical representation of the model. a) An overview of all the processes involved. b) The movement process is formulated on continuous time, where the updating of the individual's direction and behavioural state are independent processes. Behavioural state ultimately determines the processes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

2.2 Simulations

We implemented our movement model in the programming language Java and ran the simulations on a High-Performance Computing cluster. Analysis of model outputs was done 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 heterogenous resource landscape generated with a fractional Brownian motion neutral landscape model using the R package *NLMR* (Sciaini *et al.* 2018) with a fractal dimension of 0.75. The initial location of animals in all cases were random, and the boundaries were reflective.

2.2.1 Resource memory and territoriality

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

2.2.2 Effect of removal

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

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

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

3 Results

3.1 Resource memory and territoriality

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

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

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

3.2 Effect of perturbation

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

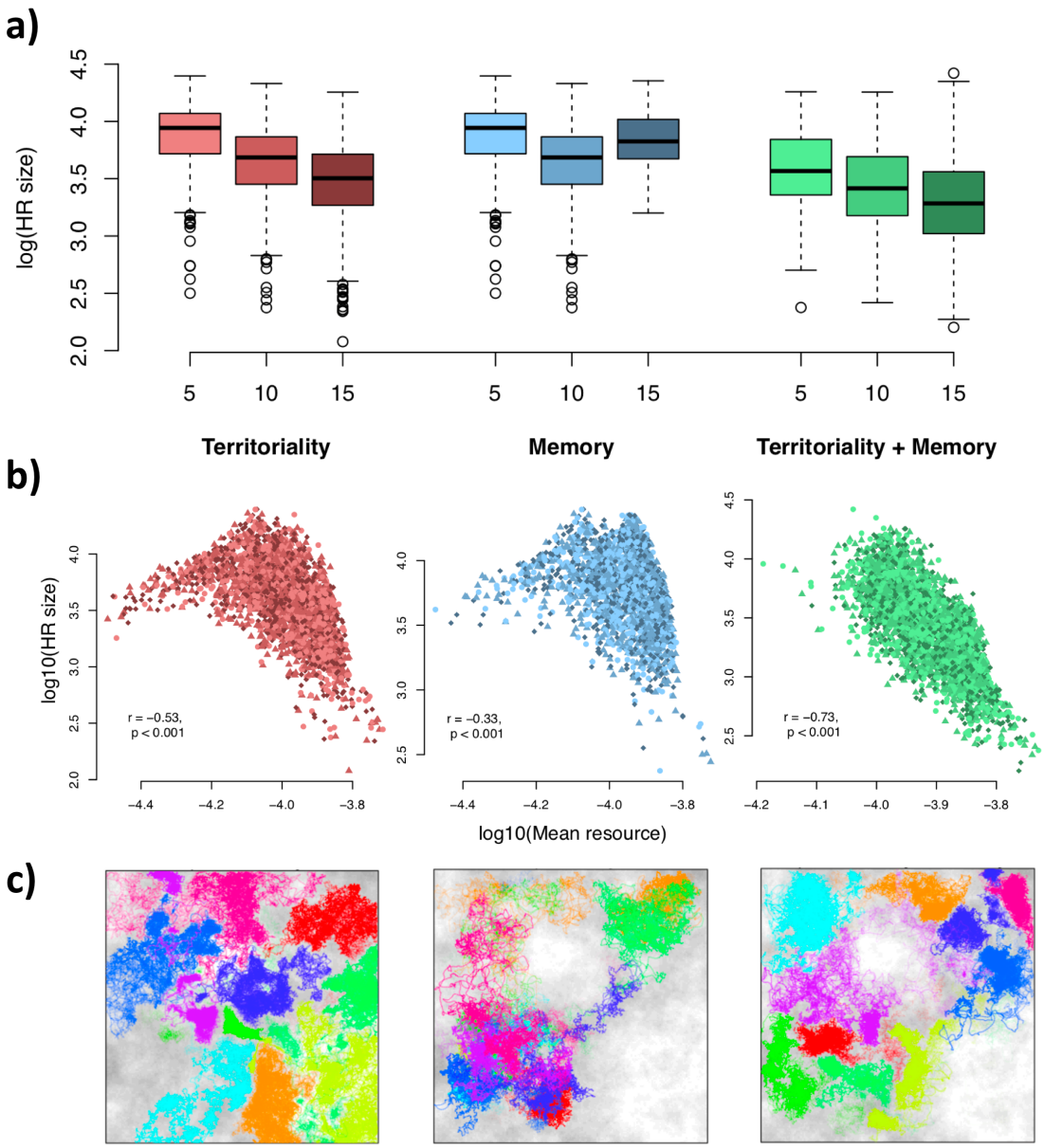

Fig. 2. Simulation results from three scenarios (territoriality, memory, territoriality and memory): relationship between HR size and a) density (n = 5, 10, 15) and b) mean resource value (within HR) from 100 replicates, and c) sample realisations at n = 10. Individual trajectories start at random with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

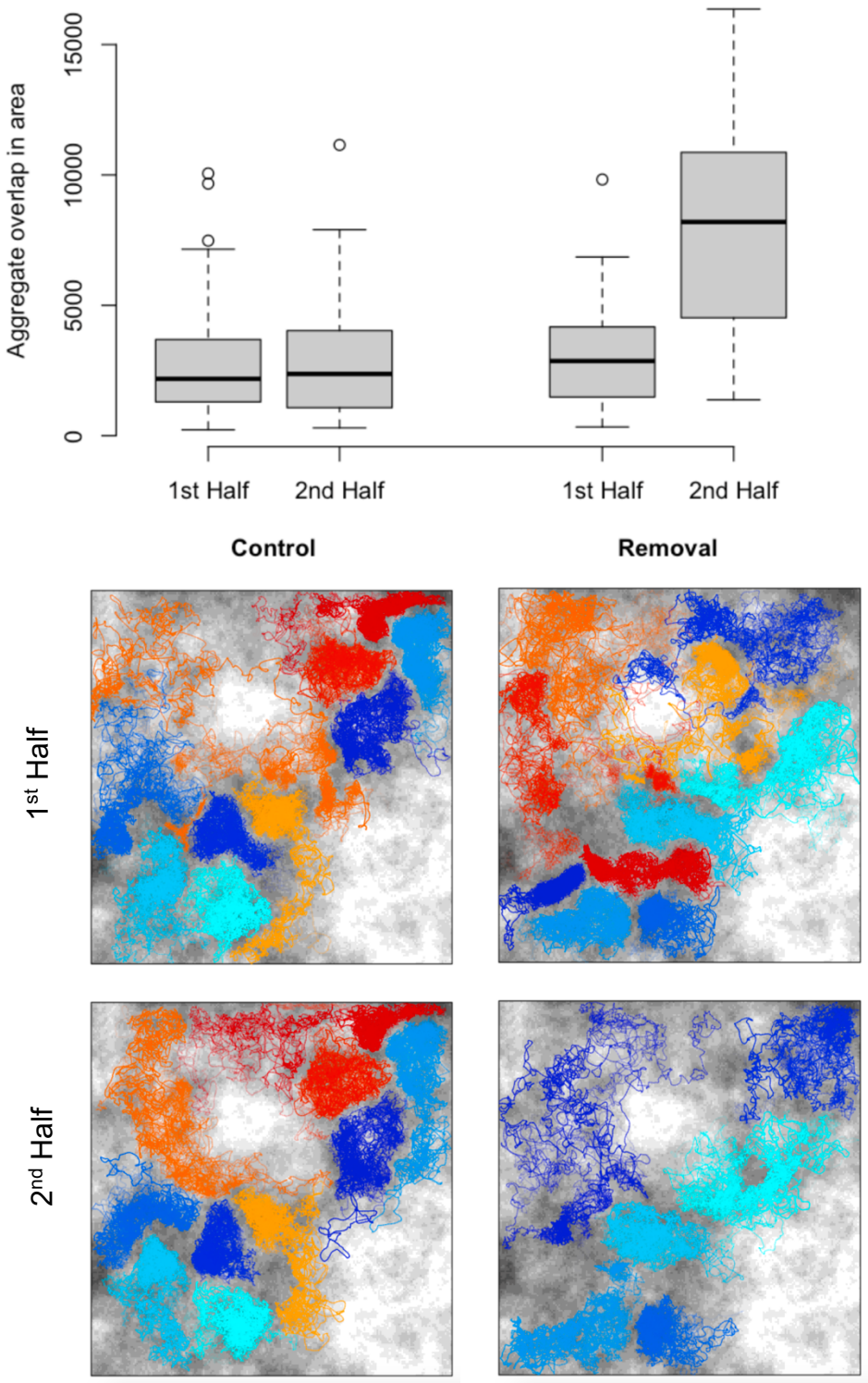

Fig. 3. Aggregate overlap in area (95% HRA) between removed and remaining individuals before (1st half of simulation) and after removal (2nd half of simulation) in the control and removal scenarios (50 replicates each). Beneath each scenario is a sample realisation of movement trajectories in the first half (top panel) and 2nd 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,

4 Discussion

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

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

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

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

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

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

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