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Individual-Level Memory Is Sufficient to Create Spatial Segregation among Neighboring Colonies of Central Place Foragers

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ABSTRACT: Central place foragers often segregate in space, even without signs of direct agonistic interactions. Using parsimonious individual-based simulations, we show that for species with spatial cognitive abilities, individual-level memory of resource availability can be sufficient to cause spatial segregation in the foraging ranges of colonial animals. The shapes of the foraging distributions are governed by commuting costs, the emerging distribution of depleted resources, and the fidelity of foragers to their colonies. When colony fidelity is weak and foragers can easily switch to colonies located closer to favorable foraging grounds, this leads to space partitioning with equidistant borders between neighboring colonies. In contrast, when colony fidelity is strong—for example, because larger colonies provide safety in numbers or individuals are unable to leave—it can create a regional imbalance between resource requirements and resource availability. This leads to nontrivial space-use patterns that propagate through the landscape. Interestingly, while better spatial memory creates more defined boundaries between neighboring colonies, it can lower the average intake rate of the population, suggesting a potential trade-off between an individual's attempt for increased intake and population growth rates.

Keywords: space partitioning, public information, animal movement, species distribution, animal tracking, central place foraging.

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Introduction

Although use of a home base can confer numerous benefits, such as protection from predators or environmental stressors, it also constrains a forager's mobility, leading to local resource depletion, also known as Ashmole's halo (Ashmole 1963; Birt et al. 1987; Gaston et al. 2007). Depletion is particularly likely in gregarious central place foragers (CPFs) who aggregate to form colonies to either rest between feeding trips or nurse young during breeding. Colony members are then forced to expand their foraging range away from the colony, and this may lead to additional competition with individuals from neighboring colonies (Gaston et al. 2007; Jovani et al. 2016). It has been hypothesized that intercolony competition can be reduced by spatial segregation, a pattern that has been demonstrated empirically for many CPFs (Boyd et al. 2002; Lynnes et al. 2002; Grémillet et al. 2004; Robson et al. 2004; Wakefield et al. 2013; Kuhn et al. 2014; Corman et al. 2016; Papastamatiou et al. 2018). Between-colony spatial segregation has recently been suggested to emerge from direct visual, olfactory, or vocal interactions between individuals or groups of individuals (Carpenter 1987; Grémillet et al. 2004; Wakefield et al. 2013). For many inconspicuous CPF species, such as harbor seals (fig. 1; Kirkwood et al. 2015; Brasseur et al. 2018; Aarts et al. 2019), this seems unlikely, and the minimum requirements at the level of individual cognition that are necessary for colony segregation to emerge remain unknown.

Historically, spatial segregation between colonies was assumed to emerge from direct (e.g., aggression) or indirect
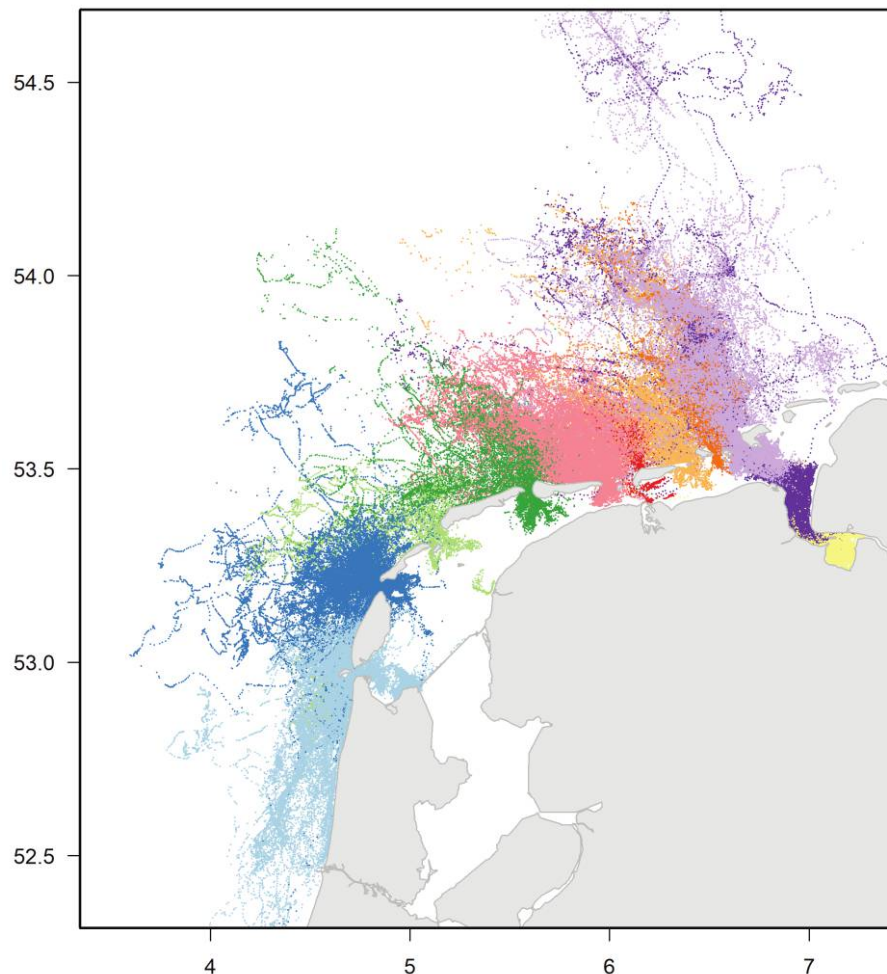
Figure 1: Spatial segregation in harbor seals making return trips from haul-out sites in or near the Dutch Wadden Sea. GPS locations from 207 harbor seals are shown, and locations are colored by haul-out region. For a more detailed description, see appendix S1, available online.

(e.g., scent marking, vocalization) territorial interactions (Carpenter 1987). However, territorial behavior is costly, and many species segregate apparently without using agonistic defense mechanisms (Wanless and Harris 1993; Grémillet et al. 2004; Baylis et al. 2008; Kirkwood and Arnould 2011). Alternatively, if CPFs could freely switch colonies and behave as optimal foragers—that is, maximize their intake rate by always returning to the colony closest to the selected foraging sites—they would ideally distribute themselves, and we would see equidistant boundaries between the location of neighboring colonies (i.e., a Voronoi tessellation of space). This is known as the hinterland hypothesis (Cairns 1989). Indeed, the ideal free distribution predicts that when individuals are perfectly informed and free to relocate, they distribute themselves so as to bring resource depletion and regeneration into balance across space (Fretwell and Lucas 1969). However, the number of resting or

breeding sites at a colony may be limited and costly to acquire, and animals may be reluctant to relocate. Coherently, the hinterland hypothesis has been refuted empirically in several systems. For example, the foraging distributions of breeding Northern gannets (*Morus bassanus*) are spatially segregated, but the foraging ranges of larger colonies often extend well into the hinterland of smaller, neighboring colonies (Wakefield et al. 2013). A hypothesis to explain the discrepancy between the observed spatial distribution of conspicuous CPFs with the hinterland model invoked density-dependent competition between CPFs (Lewis et al. 2001), mediated by transfer of information about the location and quality of foraging patches (Danchin and Richner 2001; Valone and Templeton 2002; Danchin et al. 2004; Grémillet et al. 2004; Wakefield et al. 2013). However, for inconspicuous colonial CPFs, such as pinnipeds, who are often submerged for most of their time and out of reach

of conspecifics, the public information transfer hypothesis seems unlikely.

Individual spatial memory, leading to the emergence of stable home ranges (Van Moorter et al. 2009), has recently been proposed as an alternative explanation for the emergence of spatial segregation in free-ranging foragers. In the presence of scramble competition between individuals, spatial memory can lead to nonterritorial, spatially segregated individual home ranges (Riotte-Lambert et al. 2015). However, a similar explanation has not been formulated for CPFs, which differ from free-ranging foragers in two key aspects. First, they regularly return to a communal site where individuals aggregate. Second, their central places are often fixed within the landscape, for example, because suitable nesting sites are limited or because colonies only establish gradually (e.g., due to Allee effects; Stephens and Sutherland 1999) and persist by means of tradition (Matthiopoulos et al. 2005). In this setting, the location of colonies may constrain the foraging distribution of CPFs.

In this study, we investigate whether resource depletion and individuals' memory of resource distribution can lead to the emergence of spatial segregation between CPFs from neighboring colonies, without the need for transfer of information about foraging locations between conspecifics or antagonistic behavior. While the study was motived by the spatial segregation observed in harbor seals (fig. 1; app. S1; apps. S1, S2 are available online), species-independent individual-based simulations were used to discover the minimum biological requirements for the emergence of the space-use patterns of CPFs seen in nature. The simulated CPFs made foraging trips away from the colony, gaining information on resource abundance at the sites they visited. We investigated the effect of varying levels of stochasticity in resource encounters and levels of exploration on foraging efficiency and space-use patterns. We show that minimal foraging rules can lead to anisotropic foraging distributions and clear spatial segregation between neighboring aggregations of foragers.

Methods

Spatial Distribution of Colonies and Resources

The 600 simulated CPFs were distributed among six colonies located within a resource landscape with impenetrable boundaries. The landscape consisted of a regular grid (20 × 20 grid cells; see table S2.2; tables S2.1, S2.2 are available online) where the initial resource distribution was spatially homogeneous. We considered three different designs (A, B, and C) to show how different spatial configurations of colonies influence the emerging foraging distribution (fig. 2; for a more detailed motivation, see fig. S2.3; figs. S1.1, S2.3–S2.8 are available online). In design A, 600 individuals were equally distributed among the six colonies. One colony (no. 1) was placed in the corner of the grid to study how CPFs responded to restrictions in available foraging space. Two colonies (nos. 3 and 4) were placed side-by-side to explore how CPFs responded to competition from nearby individuals. One colony (no. 6) was located far from all other colonies to study the distribution of CPFs when competition from neighboring colonies was low. Two other colonies (nos. 2 and 5) were added to impose additional
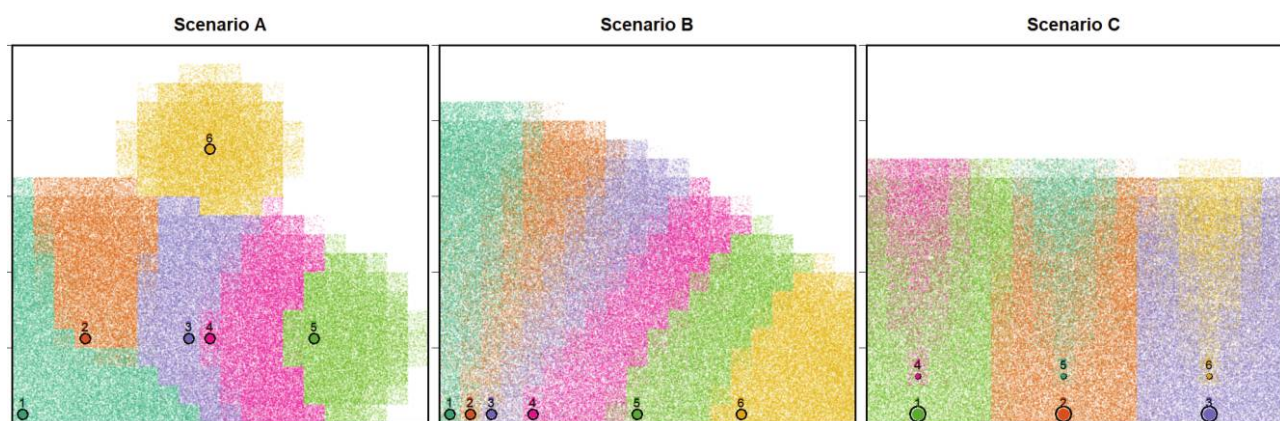
Figure 2: Simulation designs showing how different spatial configurations of six colonies influence the emerging foraging distribution (for a more elaborate description and motivations, see "Methods" and fig. S2.3, which is available online). In scenarios A (baseline) and B, each colony contained 100 central place foragers. In scenario C, the larger colonies (nos. 1–3) contained 150 individuals each, whereas the smaller colonies (nos. 4–6) contained 50 individuals each. Each point (colored by colony) represents the foraging location of one trip. If the density of animals and subsequent resource depletion was high in one region, individuals in other less densely populated regions would avoid these areas, leading to a spatial cascade in the foraging distributions across the landscape.

competition. In design B, we investigated the emergence of spatial cascades, where high densities of animals in the west (colonies 1–4) influenced the foraging distribution of animals in the east (colonies 5 and 6). In design C, we investigated how CPFs from three larger colonies (colonies 1–3, 150 individuals each) responded when enclosed between the landscape boundaries and a series of smaller colonies (colonies 4–6, 50 individuals each).

CPFs' Foraging Decisions

Characteristics of the Simulated CPFs. The focus of the simulations was to investigate the effect of different fixed foraging strategies and spatial configuration of colonies on the CPFs' foraging ranges and intake rate. The model does not describe the colonies' population dynamics (i.e., there are neither birth nor death events). Furthermore, within each simulation scenario, all individuals had the same foraging and exploration strategy, which was kept constant for the duration of the simulation.

Grid Cell Selection Rules. Each individual started a new foraging trip every 24 h. At the start of the simulation, the environment was spatially homogeneous, and the cognitive map of all individuals was set to this initial homogenous resource landscape. During each foraging trip, the individual selected the grid cell i with the largest anticipated trip intake rate R_i' (Olsson et al. 2008). All primed symbols represent anticipated (or remembered) quantities within each individual's cognitive abilities. Rate R_i' was defined as the ratio between the amount of resources collected per trip (z; see table S2.2) and the anticipated total trip duration T_i' (the sum of travel time $T_{t,i}$ and anticipated foraging time $T_{f,i}'$):

$$R_i' = \frac{z}{T_i'} = \frac{z}{T_{t,i} + T_{f,i}'}. \tag{1}$$

Since z was assumed to be fixed for each trip (e.g., representing animals with fixed loading capacity), maximizing R_i' corresponds to minimizing anticipated total trip duration T_i'.

The travel time to cell i ($T_{t,i}$) was defined as twice the distance (d_i) between the colony and the foraging site i, divided by the animals' speed (v):

$$T_{t,i} = \frac{2d_i}{v}. \tag{2}$$

The anticipated foraging time $T_{f,i}'$ was defined as the (fixed) amount of resources acquired during a foraging trip (z, expressed in weight), divided by the anticipated intake rate π_i', which was defined as the product between searching efficiency (α, effective area covered per unit of time) and anticipated resource density X_i' (in units of weight/area):

$$T_{f,i}' = \frac{z}{\pi_i'} = \frac{z}{\alpha X_i'}. \tag{3}$$

Since the individuals were not foraging under conditions of superabundance, we assumed a linear dependence between intake rate and resource density, which corresponds to a type I functional response, where handling time was considered negligible compared with searching time.

Foraging and Prey Encounter. Once the individual arrived at the selected grid cell, it would start foraging and continue until the required amount of resources z (in weight) was obtained. In most natural systems, animals encounter discrete resource units (e.g., prey), and such encounters are stochastic. Here, we assumed that resource items were randomly distributed within each cell, which corresponds to a homogeneous Poisson process (Pielou 1969). Under this process, the time needed to acquire one resource item in a cell i can be described by an exponential random variable, with a rate λ_i representing the resource encounter rate (i.e., the number of resource items encountered per unit of time) in cell i:

$$\lambda_i = \alpha X_i \omega^{-1}, \tag{4}$$

where ω is the average weight of each resource item and X_i is the real resource density in cell i (in weight). The time needed to acquire a total resource weight z—or, equivalently, $n(= z\omega^{-1})$—is the sum of n $\exp(\lambda_i)$ random variables, which corresponds to a Gamma random variable,

$$T_{f,i} \sim \text{Gamma}(\alpha = n, \beta = \lambda_i), \tag{5}$$

with mean $E(T_{f,i}) = \mu_i = n/\lambda_i$ and variance $\sigma^2 = n/\lambda_i^2$. Based on the realized foraging duration in cell i at time t ($T_{f,i,t}$), the individual calculated the realized resource encounter rate $n/T_{f,i,t} = \lambda_{i,t}'$ and subsequently estimated the resource density as $\lambda_{i,t}' \omega \alpha^{-1} = X_{i,t}'$. The individual's cognitive map (Fagan et al. 2013) was updated by replacing the old anticipated resource density X_i' by the resource density estimated by the individual during the visit, $X_{i,t}'$. These memorized X_i' could be replaced but did not wane with time. After foraging, the real resource density $X_{i,t+T_{f,i,t}}$ of the selected cell was reduced by the amount z consumed (i.e., $X_{i,t+T_{f,i,t}} = X_{i,t} - z$). In the unlikely event that resource density would become negative, $X_{i,t+T_{f,i,t}}$ was set to $X_{i,\min} = 0.01$.

Exploration. After foraging, the individual either returned straight to the colony or continued exploring to update information on resource density elsewhere, at no cost in

terms of intake rate. Starting from the foraging cell, the expected trip intake rate of each cell was reevaluated (by the criterion of eq. [1]). This time, however, the travel distance *d* in equation (2) was redefined as the distance between the individual's current position and the target cell plus the distance between the target cell and the colony. Next, the individual randomly sampled a cell with a probability proportional to this anticipated intake rate R_i^t. Once the individual arrived at the selected target cell, it started searching for resources but without feeding, since it was already sated. Once completed, resource density was memorized, and the individual returned to the colony.

Resource Renewal

In each cell, independent resource renewal took place at an hourly interval. We implemented a logistic renewal function allowing the resource $X_{i,t}$ in the *i*th cell to recover at an intrinsic rate *r*, up to a local carrying capacity K_i:

$$X_{i,t+1} = rX_{i,t}\left(1 - \frac{X_{i,t}}{K_i}\right), \quad \text{when } X_{i,t} < K_i,$$
$$X_{i,t+1} = X_{i,t}, \quad \text{when } X_{i,t} \geq K_i. \tag{6}$$

In pilot simulations, we explored different values of *r* (between 1.000167 and 1.000833), and eventually we set *r* to 1.000583 to ensure that resources would get neither completely depleted nor saturated. In the main simulations, K_i was assumed to be spatially homogeneous ($K_i = 3,000$; see table S2.1). In supplementary analyses (figs. S2.4, S2.5), we also explored the effect of spatially heterogeneous *K* (sampling from a random uniform distribution between 100 and 5,900).

Varying Information on Resource Distribution

Individuals acquire information by visiting places and memorizing their spatial location and resource density. In our simulations, we varied the individual's exploration tendency and ability to acquire and memorize information (see also table S2.1):

Scenario 1. The exploration proportion (γ), defined as the proportion of foraging trips that were followed by exploration, was varied between 0.05 (i.e., exploration in one out of 200 foraging trips) and 1 (i.e., exploration after each foraging trip).

Scenario 2. Stochasticity in resource encounter. By varying *n* (the number of resource items to be collected during a trip) while keeping the daily energetic requirement *z* (in weight) constant, the expected time needed to meet *z* remains the same; that is,

$$E(T_{f,i}) = \frac{n}{\lambda_i} = \frac{n}{\alpha X_i n z^{-1}} = \frac{1}{\alpha X_i z^{-1}}, \tag{5}$$

but the variance changes,

$$\sigma_i^2 = \frac{n}{\lambda_i^2} = \frac{z^2}{n(\alpha X_i)^2}.$$

Decreasing *n* while keeping *z* constant means that the average weight *w* of resource items increases and that a given resource density in weight X_i corresponds to a smaller resource density in terms of number of prey items per unit area. For example, if a forager feeds on larger prey items (bigger *w*) that occur in proportionally lower densities, the mean time spent foraging remains unaffected, but the variation in foraging time increases, and therefore, the individual will estimate and memorize the encountered resource density less accurately.

Scenario 3. Memory size (*m*), here defined as the number of unique cells each individual could memorize, where *m* was varied between two and 400 (i.e., all) cells. Whenever the individual performed an exploration trip, the food density estimated by the individual in the selected cell was memorized, but the resource density of the cell visited *m* exploration trips back in time was erased from memory.

Alternative Simulation Scenarios Explored

The simulations described above were based on individuals that (1) were faithful to a colony (i.e., did not switch colonies), (2) competed for resources with individuals from the same and neighboring colonies, and (3) acquired information on resource density based on individual memory. We also explored the effect of the following alternative settings:

No competition between neighboring colonies. In this scenario, the foraging distribution of individuals from each colony was simulated in isolation from all others (i.e., it excludes intercolony competition but includes intracolony competition). The between-colony overlap was estimated as if all colonies were present in the landscape. This scenario thus served to estimate the expected overlap between neighboring colonies in the absence of competition between them.

Between-colony switching. An individual would always and immediately switch to another colony if a selected cell was closer to the other colony (akin to the Hinterland hypothesis, whereby individuals only use the foraging sites that are closer to their home colony than to any other colony; Cairns 1989).

Omniscient individuals. In this scenario, the individuals had, at every instant, perfect knowledge of the quality of each cell in the landscape. This scenario was used to evaluate the effect of a perfect informational state of individuals, compared with individuals relying solely on their personal experience of the landscape.
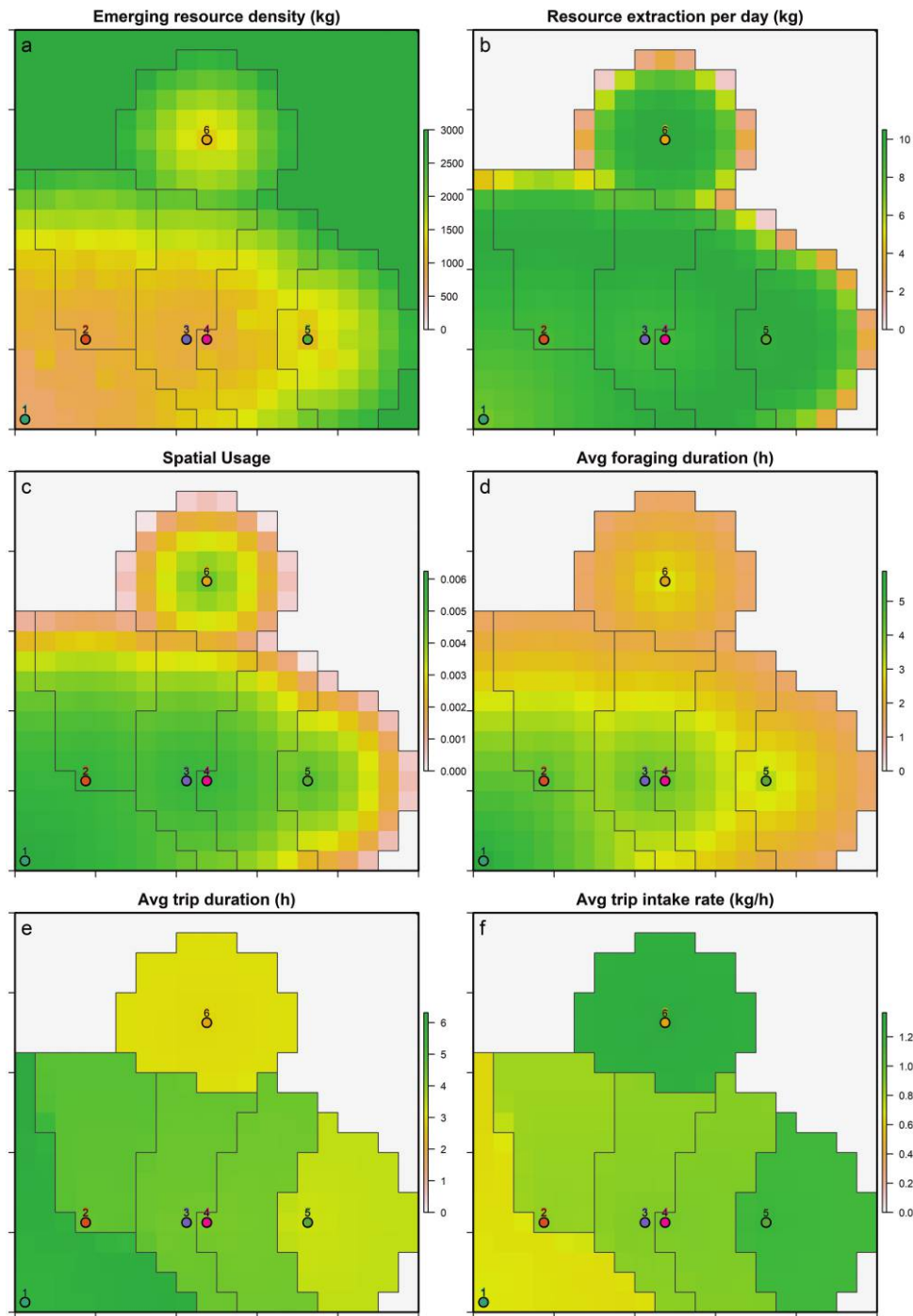
Figure 3: Spatial maps of the emerging distribution of resources and foragers at the end of the baseline simulation (table S2.1, available online). The gray lines separate cells where the majority of usage came from different colonies, and these lines indicate the emerging borders between the colonies' foraging ranges. *a*, Resource density. Near each colony, resource density could be as low as 500 kg, whereas resource density was at carrying capacity (3,000 kg) in cells far away from any colony. *b*, Average resource extracted per day. Note the lower resource extraction close to the colonies, particularly colony 1, which was the result of the logistic renewal function causing a lower replenishment at extremely low (and extremely high) resource densities. *c*, Spatial usage, that is, time spent foraging in each cell divided by the total foraging time. *d*, Average forage duration. The cells with the lowest food density (and shortest travel distance) required the longest foraging duration. *e*, Average trip duration. Trip duration was homogenously distributed within each colony's foraging range. *f*, Average trip intake rate, also spatially homogenous within each colony's foraging range (similar to trip duration).

Quantifying Between-Colony Overlap in Foraging Distributions

We used Bhattacharyya's affinity (BA; Fieberg and Kochanny 2005) to measure the degree of overlap between the space use of animals from colony i and all other J_i neighboring colonies ($J_i = \{j\epsilon\{1, \cdots, 6\}, j \neq i\}$):

$$\text{BA} = \iint\limits_{-\infty}^{\infty} \sqrt{\text{UD}_i(x,y)}\sqrt{\text{UD}_{J_i}(x,y)}\,dxdy.$$

The utilization distribution of colony i was defined as

$$\text{UD}_i(x,y) = \frac{u_i(x,y)}{\iint_{-\infty}^{\infty} u_i(x,y)\,dxdy},$$

where $u_i(x,y)$ was the total foraging time spent in each cell (located at the coordinates x and y). Similarly, the overall utilization distribution of the other colonies was defined as

$$\text{UD}_{J_i}(x,y) = \frac{\sum_j u_j(x,y)}{U_{J_i}},$$

where

$$U_{J_i} = \iint\limits_{-\infty}^{\infty} \left(\sum_j^{J_i} u_j(x,y)\right) dxdy.$$

Simulation Settings

To ensure asynchrony between the foraging of different population members, the time of the first trip of each of the 600 individuals was drawn from a uniform distribution between $t = 0$ and $t = 365$ days. All the simulations contained a burn-in period (3 years, well after average trip duration stabilized), and the subsequent simulation was run for at least 3 years and stored for further analysis. All analyses and simulations were carried out in R (R Development Core Team 2019).

Results

Convergence Toward an Equilibrium Distribution of Resources and Foragers

At the start of the burn-in period, when resources were homogenously distributed, individuals first extracted resources from the cells closest to the colonies. Local depletion led to an expansion of their foraging range until the distribution of resources reached an equilibrium (fig. 3*a*), whereby resource renewal and extraction (fig. 3*b*) were in balance. Since individuals attempted to minimize the trip duration and maximize the trip intake rate R_i, longer travel times to the more distant but resource-rich cells were compensated by shorter foraging times (fig. 3*d*). Therefore, the distribution of foraging effort (fig. 3*c*) would ultimately lead to an emerging resource distribution whereby both the average trip duration (fig. 3*e*) and the trip intake rate (fig. 3*f*) were approximately equal everywhere within the colony's foraging range. However, between colonies, individuals experienced different average trip intake rates; colonies with the most competition from their neighbors (e.g., colony 1) had the lowest average intake rates (figs. 3*f*, 4).

Between-Colony Differences in Trip Intake Rate and Spatial Overlap

On average, individuals from secluded colonies had larger trip intake rates and shorter trip durations compared with individuals from colonies that were close to other colonies or landscape boundaries. For example, individuals from colony 6 (the most isolated colony; figs. 2, 4*b*) had average travel and foraging durations of 1.0 h and 2.0 h, respectively, whereas individuals from colony 1 had average travel and foraging durations of 2.1 h and 4.1 h.

The location of the colonies relative to one another also influenced the amount of overlap between colonies. Colonies 3 and 4 were close neighbors and had the largest overlap indexes (BA = 0.22 and 0.19, respectively; fig. 4*b*, 4*e*). The BA value of colony 3 was slightly larger, because it also experienced competition from colonies 1 and 2. The isolated colony 6 in the north had the smallest overlap index (BA = 0.003). By comparison, in the simulation scenario with no intercolony competition, the overlap between colonies was substantially larger, particularly for those colonies near one another (e.g., colony 3, BA = 0.50, and colony 4, BA = 0.48; fig. 4*a*, 4*e*).

When the local resource carrying capacity was spatially heterogeneous, spatial segregation among colonies also emerged (fig. S2.4), secluded colonies experienced higher average intake rates, and average trip duration and trip intake rates were equal for all exploited cells in each colony's foraging range (fig. S2.5).

Spatial Cascades in the Foraging Distributions

The pattern of the foraging distribution of each colony was influenced by the location and size of neighboring colonies. For example, in design A, individuals from colony 1 located in the southwest corner were limited in space and competed for resources with individuals from other colonies (mostly colony 2). As a result, they expanded their foraging range toward the north and east and forced individuals from colony 2 to do the same (fig. 2, design A). This spatial cascade was even more apparent for design B, where several colonies were located in the southwest corner of the study area. Individuals from these colonies avoided competition by moving in a northeasterly direction. Even the distribution of individuals from colony 6, in the far-right corner, were
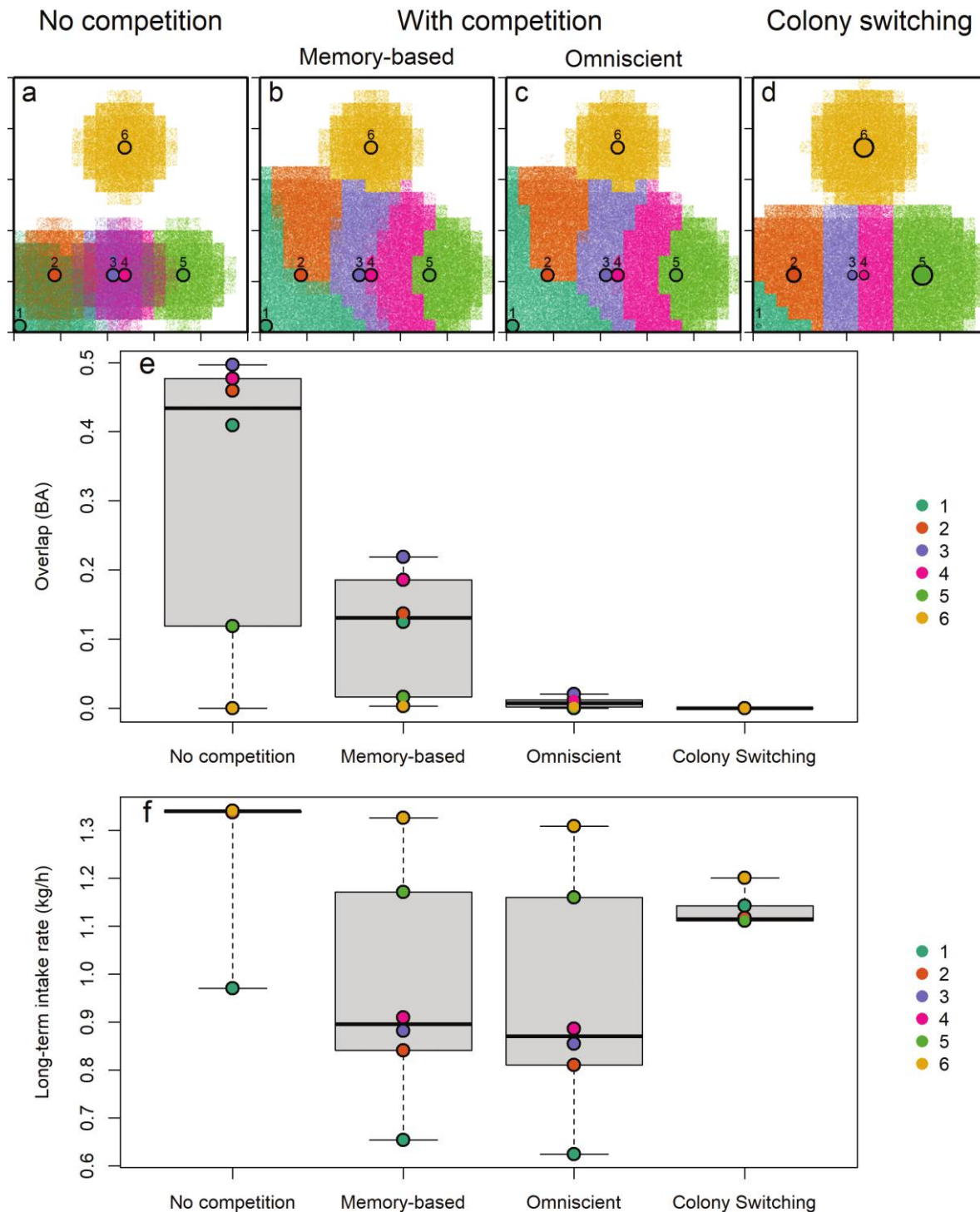
Figure 4: Spatial distribution of the foraging distributions of colonial central place foragers who did not experience any resource competition from neighboring colonies (*a*), competed for resources with neighboring colonies and relied on memorized resource density (baseline scenario; *b*), were omniscient (*c*), or always switched to the nearest colony relative to the selected foraging cell (hinterland model; *d*). *e*, Spatial overlap (Bhattacharyya's affinity) between the foraging distribution of one colony relative to the combined foraging distribution of all other colonies. Overlap was highest when individuals did not perceive the presence of their neighbors (*a*) and lowest when individuals were omniscient (*c*) or obeyed the hinterland theory (*d*). *f*, Average trip intake rate of each colony for the different simulation scenarios. The trip intake rate of the scenario in panel *a* was logically high because the simulation was run as if the other colonies were absent.

influenced by individuals from the most western colonies (fig. 2, design B). A similar effect occurred in scenario C, where individuals from larger colonies were effectively blocked by smaller colonies and, as a result, used U-shaped areas surrounding the foraging distributions of the northern colonies (fig. 2, design C).

Effect of Stochasticity in Resource Encounter on Overlap and Trip Intake Rate

When there was little stochasticity in resource encounters (small σ^2 for the Gamma distribution; eq. [5]), the individuals could accurately assess and memorize the resource density in the selected cell, and their foraging distributions showed little overlap with the foraging distribution of individuals from neighboring colonies (BA = 0.008; fig. 5*d*). In contrast, when individuals were unable to accurately assess resource density in each cell because of large stochasticity in resource encounters (i.e., large σ^2), overlap between colonies was substantially larger (BA = 0.65; see fig. 5*a*). Interestingly, despite this larger overlap, intermediate levels of stochasticity in resource encounters led to higher intake rates (fig. 6).

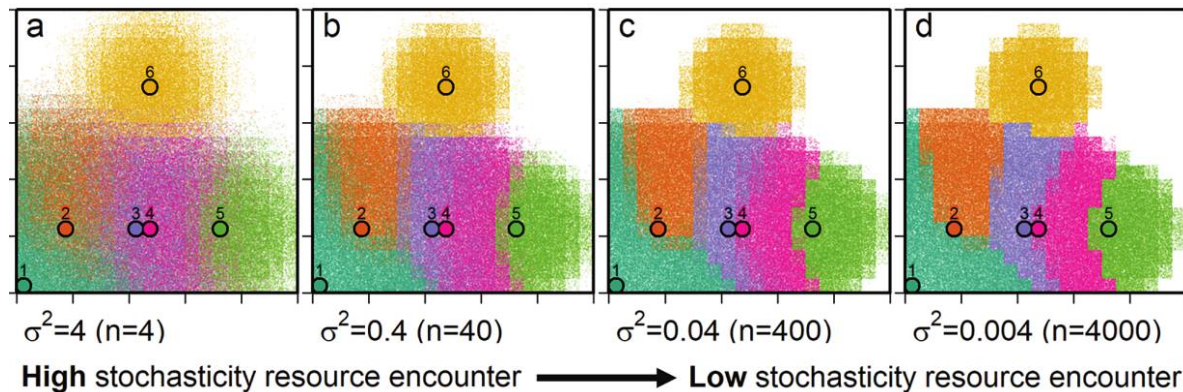### Effect of Exploration Frequency on Overlap and Trip Intake Rate

After the start of the simulation, individuals expanded their foraging range, and as a result, the overlap in foraging distribution between colonies increased. Eventually, the overlap stabilized to low average values (BA = 0.06)

when individuals explored frequently ($\gamma = 1$) and high values (BA = 0.09) when the CPFs explored infrequently ($\gamma = 0.05$; fig. S2.6). When we look at the overlap in the foraging distribution between individuals from the same colony, higher exploration ($\gamma = 1$) caused individuals to have a more homogeneous distribution within the foraging range, with more overlap between the individuals from the same colony (fig. 7, middle row). These results resembled the simulation scenario with omniscient individuals (fig. 7, bottom row). In contrast, when individuals were less explorative (baseline scenario, $\gamma = 0.05$), each individual was more site faithful to a smaller number of cells (fig. 7, top row). Thus, higher-quality information led to less overlap among individuals of different colonies but more overlap among individuals from the same colony.

When individuals made frequent explorations ($\gamma = 1$), the distribution of foragers and resource and the trip intake rate quickly stabilized around an equilibrium ($R = 0.94$). By contrast, when individuals explored only sporadically (i.e., $\gamma = 0.05$), the average trip intake rate continued to decline to low values but eventually increased and stabilized at around ~1.05, above the trip intake rate of the regular explorers (figs. 6, S2.6*d*).

### Effect of Memory Size on Overlap and Trip Intake Rate

When individuals memorized only a very small set of recently visited cells, the overlap between the foraging distributions of neighboring colonies was substantially larger (e.g., for $m = 2$, BA = 0.32; see fig. 6*c*). However, the overlap was still much smaller compared with the scenario

$\sigma^2=4$ (n=4) $\sigma^2=0.4$ (n=40) $\sigma^2=0.04$ (n=400) $\sigma^2=0.004$ (n=4000)

High stochasticity resource encounter ⟶ **Low** stochasticity resource encounter

Figure 5: Effect of increasing stochasticity in encountered resource density on the spatial distribution and overlap of central place foragers (CPFs). When stochasticity was large (*left*), there was a large overlap between the foraging distribution of CPFs from neighboring colonies (see also fig. 4*b*), and the overlap decreased with decreasing stochasticity in the encountered and memorized resource density (*right*). Stochasticity in prey encounters was varied by modifying *n*, the number of resource items that need to be collected to meet the daily energetic requirement (*z*, kept constant). Small *n* resembled a forager feeding on large resource items occurring at low density, and large *n* resembled a forager feeding on small resources occurring at high density. See "Methods" for details.
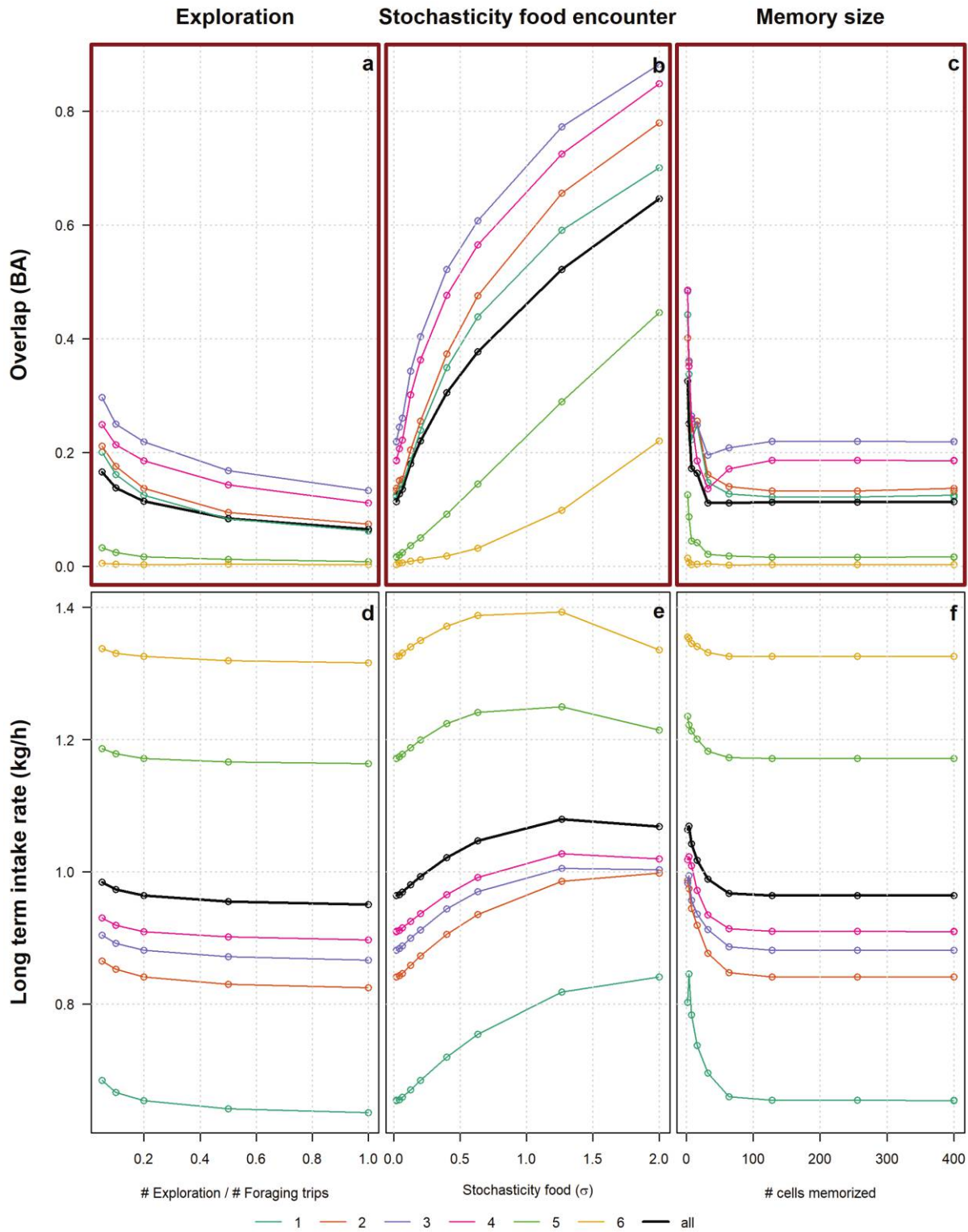
Figure 6: Effect of the exploration frequency, the stochasticity in encountered resource density, and the size of memory on the overlap and trip intake rate for each colony under simulation scenario A. Increased exploration, smaller environmental stochasticity, and larger memory size lead to less overlap (*a–c*) and decline in trip intake rate (*d–f*). Stochasticity in encountered and memorized resource density (expressed as the standard deviation, $\sigma = \sqrt{n/\lambda^2}$) had the largest effect on overlap and intake rate.
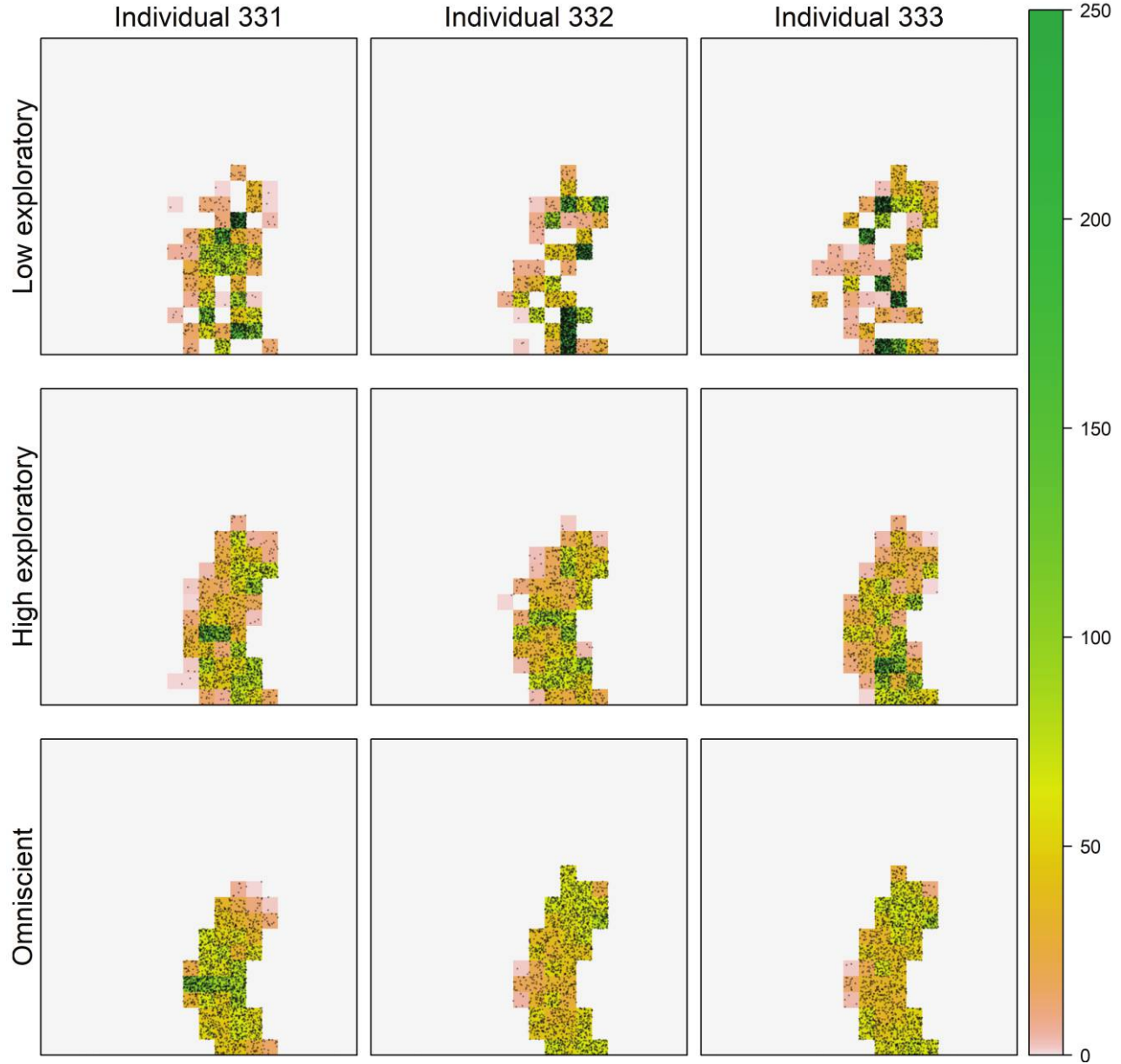
Figure 7: Number of times each cell was visited (based on the last 2,000 foraging trips) by three arbitrary individuals (from colony 4) emerging from three simulation scenarios. Individuals who selected cells based on memorized resource density and made an exploration trip only every fifth foraging trip (i.e., baseline scenario) had a strong tendency to be more site faithful and aggregated in a smaller number of cells (*top row*). In contrast, individuals who made very regular exploration trips (i.e., all foraging trips were succeeded by exploration; *middle row*) or who had perfect information on the distribution of resources (*bottom row*) had a tendency to distribute themselves more homogeneously within the foraging range of each colony. So, in summary, higher-quality information led to less overlap between individuals of different colonies but more overlap between individuals of the same colony.

with the largest stochasticity in resource encounters (i.e., $BA = 0.65$; see fig. 6*b*). A slight increase in memory size (e.g., from $m = 2$, 0.5% of all cells, to $m = 4$, 1% of all cells) led to a rapid decrease in overlap between neighboring colonies (fig. 6*c*). A larger memory size also resulted in a lower average trip intake rate (fig. 6*f*).

Alternative Scenarios: Colony Switching under the Hinterland Model

When individuals could switch colonies, they redistributed in correspondence with the size of their hinterlands, resulting in higher average trip intake rates and more similarity in trip

intake rates between the colonies than in the memory-based and omniscient simulations (fig. 4). Colony 1 (southeast), with the smallest hinterland, contained 24 individuals at the end of the simulation, whereas the isolated colony 6 (northwest), with the largest hinterland, contained 187. The rules imposed by the simulation results in sharp and equidistant borders between the foraging distributions of the different colonies (fig. 4).

Discussion

Previous work suggests that spatial segregation between colonies can be driven by density-dependent competition combined with animals' use of public information to avoid regions with high density of competitors from neighboring colonies (Wakefield et al. 2013). Here, we show that spatial segregation between colonies can also emerge more parsimoniously, as a result of localized (i.e., imperfect) awareness of resource density at an individual level. These results concur with Riotte-Lambert et al. (2015), who reached a similar conclusion for noncolonial foragers. In other words, animals do not need to know the whereabouts of their neighbors to segregate. If each individual animal can memorize the resource density in a subspace of the foraging range, this is sufficient to create spatial segregation between neighboring colonies.

Individually acquired information on resource density might be the most likely driver for the observed spatial segregation in inconspicuous species. For example, some species rarely encounter conspecifics when feeding (e.g., seals), and discriminating between individuals from their own or other colonies can be challenging for those species. Even if animals can measure competitor density, this measure could be a poor proxy for expected resource intake. For example, competitor density might depend on other drivers that are unrelated to resources, like proximity to breeding or resting sites. So, clearly, spatial memory can be an effective alternative instrument to minimize overlap between neighboring colonies, without the need for costly agonistic interactions (Riotte-Lambert et al. 2015).

Higher-Quality Information Increases Spatial Segregation

More accurate information on the distribution of resources, due to smaller stochasticity in food encounters or higher exploration rates, led to stronger spatial segregation between neighboring colonies (figs. 4 and 6, left and middle panels). We assumed here that foragers fed individualistically on hidden resources in a predictable spatially homogeneous environment. In natural systems, resources are often aggregated into hierarchical patches (Fauchald 1999). As resource patchiness increases the environment's predictability and constitutes a source of information for foragers

(Fauchald 1999; Riotte-Lambert and Matthiopoulos 2000), we expect that it would strengthen our results. In contrast, when food patches are ephemeral and reappear randomly in space after depletion, this would annul the effect that memory could have on the emergence of spatial segregation. Under those circumstances, rapid information transfer between individuals could be a more efficient way for individuals to predict the distribution of resources (Wakefield et al. 2013). However, more inconspicuous CPFs cannot rely on such mechanisms and must explore the environment in isolation. For those species, spatial segregation between individuals from neighboring colonies is expected to emerge when CPFs gradually deplete resources and when individuals make informed foraging decisions by memorizing predictable resource distributions based on either spatial location or environmental features.

Spatial Cascades

A colony's foraging distribution can be shaped by indirect interactions with other colonies, even ones that are not direct neighbors (fig. 2). Especially when members of a colony have limited exclusive access to nearby high-quality foraging locations, they are forced to select lower-quality locations. In turn, these foraging locations become less attractive, driving individuals from neighboring colonies to forage elsewhere, even if they must travel farther and compete with individuals from yet another colony. The general principle of this process is illustrated in video S1 (available online) and fig. S2.8. This process can cascade throughout the landscape and may have important implications for understanding and modeling species habitat associations. For example, consistent directional movement of GPS-tagged animals away from their colony and avoidance of areas closer to neighboring colonies (Boyd et al. 2002; Grémillet et al. 2004; Robson et al. 2004; Wakefield et al. 2013; Kuhn et al. 2014; Corman et al. 2016) might be incorrectly interpreted as habitat avoidance, while in fact it may be the result of depletion by competitors.

Spatial Segregation between CPFs from the Same Colony

The quality of information on resource distribution not only determined the amount of intercolonial overlap, it also strongly influenced the amount of intracolonial overlap between colony members. In the high-exploration scenario, individuals often selected a different cell after each foraging trip (a pattern also observed in the field; e.g., Courbin et al. 2018), and this led to more overlap between individuals from the same colony (fig. 7). By contrast, when individuals were less exploratory, they often remained site faithful to specific cells for a long time, because they were unaware of increases in resource densities elsewhere.

The strength of foraging site fidelity in natural systems probably depends on how animals memorize resource density (Shettleworth 1993). In our simulation, individuals remembered only resource density encountered during their most recent visit, and a perturbation in encountered resource density could quickly lead to an abandonment of the foraging cell. In contrast, when animals integrate experiences over longer time periods—for example, by using Bayesian updating (Olsson and Holmgren 1998; McNamara et al. 2006; van Gils 2010) or relying on physiological state variables (e.g., current energy reserves; Higginson et al. 2018) or psychological state variables (e.g., feelings as information; Schwarz 2012; Ruotolo et al. 2019)—their memory and decisions should be less susceptible to stochastic changes in resource density. Therefore, under those alternative rules, we expect foraging site fidelity to be stronger, resulting in even less intracolonial overlap.

What Behavioral Mechanisms Are Responsible for the Spatial Segregation Observed in Nature?

Here, we have shown that spatial segregation between neighboring colonies of CPFs can emerge simply from the individuals' use of memory, without the need for either social information use or territoriality. However, unraveling the mechanisms responsible for the spatial segregation between neighboring colonies based on field data (e.g., as observed in fig. 1) remains challenging. It requires knowledge about the sources of information individuals use, their sociality and cognitive abilities, and insights into the predictability of resources (Riotte-Lambert and Matthiopoulos 2020). When resources are highly unpredictable, for example, because they are ephemeral, we would expect social information use to be most effective. In contrast, when resources are more predictable, we would expect individual memory to be involved. We suggest that developing species-specific individual-based models (e.g., Chudzinska et al. 2021) and fitting these models to movement and distribution data using methods like approximate Bayesian computing (van der Vaart et al. 2015) would help reveal the most likely hidden behavioral and environmental mechanisms underlying the observed patterns.

Higher-Quality Information May Lower Population-Level Trip Intake Rate

While higher information quality led to less overlap between the foraging distributions of neighboring colonies, the effects on the average trip intake rates were much less intuitive. During the initial phase of the simulation, low exploration levels led to a dip in the average trip intake rate. In natural systems, such critically low intake rates could result in high mortality and impose a strong

selection pressure toward information-hungry, explorative individuals. These results are in line with other studies showing that, particularly in novel environments, acquisition of information is most valuable (McNamara and Dall 2010; Berger-Tal and Avgar 2012). However, interestingly, once the distribution of foragers and resources reached an equilibrium, the population with omniscient foragers had a lower trip intake rate. The foragers who were less well informed—because either they relied on outdated memory or their encountered and memorized resource density did not accurately reflect the true resource density—were more likely to make misjudgments and occasionally choose to forage beyond the margins of the core foraging area (fig. 5). By foraging in the peripheral area, they reduced the amount of depletion near the colony, leading to higher average trip intake rates at the population level (fig. S2.7). A logistic resource renewal function could amplify this effect: a (temporary) release of predation pressure near the colony where resource density was very low would lead to increases in the rate of renewal and stimulate higher exploitation in the future (akin to the maximum sustainable yield concept; Stigter and Van Langevelde 2004).

This positive effect of individual-level misjudgments on population-level mean fitness can also be found in the literature on the evolution of dispersal. Several simulation studies have shown that dispersal may provide almost no benefit to the dispersing individuals, but when a local population is close to its carrying capacity, dispersal leads to reduced competition, on top of the occasional benefits of finding new vacant patches (Hamilton and May 1977; Parvinen et al. 2003). Such results suggest that short-term suboptimal movement decisions at the individual level can be beneficial for a population or community in the long term.

Connecting Central Place Foraging to Spatial Demography

In our simulations, we explored the emergence of spatial segregation when CPFs remained either site faithful or switched to other colonies to gain access to more profitable regions of space. When individuals were free to switch colonies to minimize their trip duration, this led to equidistant borders between colonies (hinterland model), and the average trip intake rate became substantially higher. Although switching to other colonies could be beneficial from an optimal foraging perspective, some individuals might be unable (e.g., while parenting) or unwilling (e.g., due to philopatry) to relocate instantaneously. For example, colonial breeding species could assess the performance of different colonies by prospecting movements among

the colonies (Boulinier and Danchin 1997; Valone and Templeton 2002), but once settled, all subsequent foraging effort must take place from the chosen colony. This could lead to a regional imbalance between resource demand and availability, and complex space use patterns that deviate from the hinterland model can emerge (fig. 2).

Furthermore, even if intake rate is higher elsewhere and individuals could switch, it might still be beneficial to remain site faithful, since intake rate is not the only variable influencing fitness (Pierce 1987). For example, specific colonies may provide safety in numbers (Allee effect; Stephens and Sutherland 1999) or offer protection from environmental stressors, predation, or disturbance. Based on these properties, animals may favor some colonies and might be willing to travel longer distances or feed in areas with lower resource availability. Hence, colony properties—but also the ability and propensity of central place foragers to disperse between colonies (Ponchon et al. 2015)—can strongly influence the distribution of animals' foraging distribution and this can lead to complex spatial segregation patterns. Overall, to fully understand the drivers of the spatial distribution of CPFs at and away from the colonies, it will be necessary in the future to design an individual-based model integrating foragers' behaviors, cognition, and demography, as was done by Riotte-Lambert et al. (2017) for noncentral place noncolonial foragers. Such a model should also consider the effect of dispersal among colonies, by implementing age-specific dispersal behavior and prospecting (Ponchon et al. 2015), and interactions with migratory behavior occurring at other times of the year (Frederiksen et al. 2012). This kind of process-based approach will be even more critical when attempting to predict changes in the distribution and population dynamics as a function of environmental changes (Grémillet and Boulinier 2009; Bost et al. 2015; Ponchon et al. 2015).

Statement of Authorship

E.M. and G.A. initiated the simulations. G.A. completed the analyses and simulations with major contributions from L.R.-L., J.M., E.M., J.F., S.B., and J.v.G. All authors contributed to writing and revising the manuscript.

Data and Code Availability

R code is provided in a zip file, available online.[1]

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1. Code that appears in *The American Naturalist* is provided as a convenience to readers. It has not necessarily been tested as part of peer review.

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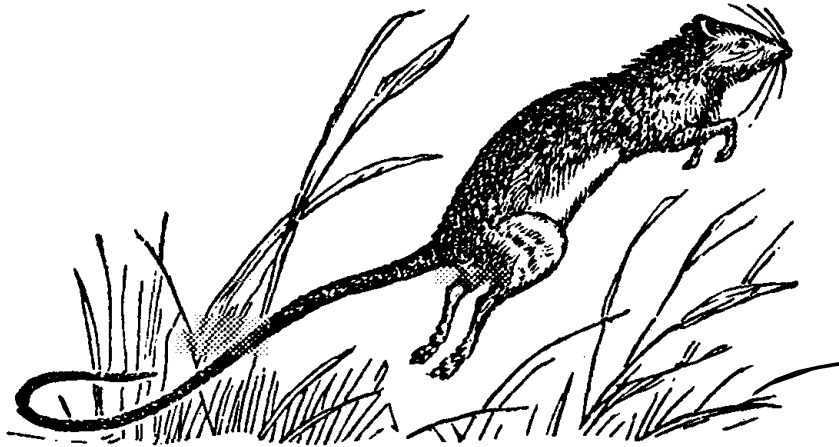
"In this nest was a Jumping Mouse (*Jaculus Hudsonius* Baird) apparently dead. It was coiled up as tightly as it could be, the nose being placed upon the belly, and the long tail coiled around the ball-like form which the animal had assumed. . . . As the mouse became warmer the signs of life became more and more marked; and in the course of the same afternoon on which I brought it into the warm room it became perfectly active, and was as ready to jump about as any other member of its species." From "Hibernation of the Jumping Mouse" by Sanborn Tenney (*The American Naturalist*, 1872, 6:330–332).