

# How Memory-Based Movement Leads to Nonterritorial Spatial Segregation

Louise Riotte-Lambert,\* Simon Benhamou, and Simon Chamaillé-Jammes

Centre d'Ecologie Fonctionnelle et Evolutive, Unité Mixte de Recherche 5175, Centre National de la Recherche Scientifique–Université de Montpellier 2, 1919 route de Mende, F-34293 Montpellier Cedex 5, France

Submitted January 14, 2014; Accepted September 17, 2014; Electronically published February 10, 2015

Online enhancements: appendix figures.

**ABSTRACT:** Home ranges (HRs) are a remarkably common form of animal space use, but we still lack an integrated view of the individual-level processes that can lead to their emergence and maintenance, particularly when individuals are in competition for resources. We built a spatially explicit mechanistic movement model to investigate how simple memory-based foraging rules may enable animals to establish HRs and to what extent this increases their foraging efficiency compared to individuals that do not base foraging decisions on memory. We showed that these simple rules enable individuals to perform better than individuals using the most efficient strategy that does not rely on memory and drive them to spatially segregate through avoidance of resource patches used by others. This striking result questions the common assumption that low HR overlaps are indicators of territorial behavior. Indeed, it appears that, by using an information-updating system, individuals can keep their environment relatively predictable without paying the cost of defending an exclusive space. However, memory-based foraging strategies leading to HR emergence seem unable to prevent the disruptive effects of the arrival of new individuals. This calls for further research on the mechanisms that can stabilize HR spatial organization in the long term.

**Keywords:** home range, space use, territory, foraging, random walk, working/reference memory.

## Introduction

In many animal species, individuals restrict their movements to areas far smaller than expected from their locomotion capacities alone (Börger et al. 2008). This so-called home range (HR) behavior has considerable implications for various ecological processes, such as demography (Moraes et al. 2010), habitat selection (Benhamou 2011), foraging strategies (Mueller et al. 2011), sociality (Galanti et al. 2006), and epidemiology (Kenkre et al. 2007; Vander Wal

et al. 2013). Although the existence of HRs has been empirically acknowledged for a long time (Burt 1943) and has been extensively studied recently thanks to the development of new tracking technologies and methodologies (review in Börger et al. 2008), the theory providing proximate and ultimate explanations for the emergence of HRs and insights into their possible adaptive value is still in its infancy. To date, only a few movement-based models leading to HR emergence have been developed, mainly restricted to territorial (reviewed in Potts and Lewis 2014) and/or central-place (Benhamou 1989; Adler and Gordon 2003; Moorcroft 2012) foragers.

Species experiencing predictable environments often perform HR behavior, whereas those experiencing unpredictable environments tend to be nomadic (e.g., see Mueller et al. 2011 for a comparison of movement behaviors of four ungulate species). HRs should indeed emerge when animals attempt to efficiently exploit resources that are relatively predictable in space and time. Predictability, from the foragers' point of view, not only is a matter of low variability of resource in space and/or time but also requires that foragers attempting to exploit these resources have the ability to process and memorize information about their spatial locations and their dynamics (Van Moorter et al. 2009; Powell and Mitchell 2012; Spencer 2012; Fagan et al. 2013). Memory-based movement behavior dramatically increases foraging efficiency at short timescales (Benhamou 1994), and this should also hold true at larger scales. However, no mechanistic model has yet been developed to determine the extent to which memory-based movement behavior in a competitive context is more efficient than nomadic behavior in foraging terms and what kind of spacing behavior between competing individuals it can produce.

Van Moorter et al. (2009) showed that behavioral rules based on simple assumptions about memory processes can lead to HR emergence. Their model thus offers a general framework to understand HR behavior, but their study suffers from several important limitations. First, there was no

\* Corresponding author; e-mail: louise.riotte-lambert@cefe.cnrs.fr.

comparison of the foraging efficiencies of individuals establishing HRs (using memory) with those of individuals that did not use memory while foraging and were thus nomadic. It therefore still remains to be shown that HR behavior can be energetically adaptive when the environment is relatively predictable. Second, only a noncompetitive situation was considered, and modeled individuals based their expectations about the quality of a patch on perfect knowledge of the maximum amount of food that could be found at this patch rather than on their own experience of the patch quality when they visited it. In nature, HR behavior should have evolved only if it increases the adaptive value of individuals while they compete with others. The simultaneous exploitation of resource patches by several competitors should lead, for each of them, to discrepancies between the amount of resources an individual will find in a given patch and the amount of resources it expects to find in this patch and therefore to a downgrading of the value of memorized information.

Such discrepancies between findings and expectations can be reduced by displaying territorial behavior to secure exclusive access to space and resources, but the increased foraging efficiency so obtained has to be sufficiently high to balance the costs associated with territorial defense (Schoener 1983; Adams 2001; Hinsch and Komdeur 2010). Alternatively, HR overlap, and therefore discrepancies between findings and expectations, may be reduced without displaying territorial behavior by relying on dynamic, adaptable expectations about the quality of patches (Ohashi and Thomson 2005; Spencer 2012). Spatial segregation that occurs despite an absence of apparent territorial behavior, as, for instance, in the African buffalo, in which there is little overlap between HRs of herds without between-herd agonistic behavior (Prins 1996; Cornelis et al. 2011), may rest on such an adaptive process. However, it remains unclear whether memory-based foraging processes alone are sufficient to lead to long-term stable space sharing in a competitive context or whether invoking some other processes (e.g., learning locations of safe places or territoriality) is required.

In this article, we built on and addressed limitations of Van Moorter et al.'s (2009) approach to investigate HR emergence, foraging efficiency, and space sharing that result from memory-enhanced movements. For this purpose, we contrasted three situations: (1) noncompetitive situation, involving a single individual or several individuals exploiting entirely different resources; (2) fair competitive situation, involving several individuals released simultaneously and exploiting the same resources; and (3) unfair competitive situation (to the naive individual), in which a single naive individual is released in an area where several individuals have already established their HRs. In the noncompetitive situation, we investigated how the resource

renewal rate affects the likelihood of HR emergence for individuals using memory-based foraging decisions and compared the resulting foraging efficiency with that of individuals searching for resources by moving either at random or in a straight line, which is one of the optimal strategies (with some other systematic search strategies) when patches are randomly distributed points in space whose locations have not been memorized, as it prevents the forager from doing unrewarding backtracking. In the fair competitive situation, we investigated how the likelihood of HR emergence and the foraging efficiency of individuals depend on the density of competitors and, when HRs have emerged, the extent to which they overlap, thus determining the spatial organization of HRs within a population of nonterritorial individuals. Finally, in the unfair competitive situation, we investigated the resilience of spatial organization in HRs by looking at the extent to which established competitors are disturbed by the arrival of a new individual having no knowledge about the environment and at the fate of this additional individual.

## Methods

### *Resource Configuration and Dynamics*

The landscape was modeled as a  $100 \times 100$ - $u$  (arbitrary length unit) continuous-space square with reflective boundaries, containing 400 patches that are randomly distributed. In most natural environments, resources occur in renewing patches that can be clearly delimited (e.g., fruit trees for baboons [Noser and Byrne 2010], inflorescences for nectarivorous insects such as bumblebees [Ohashi et al. 2013]) or with fuzzy limits (e.g., grasslands for large herbivores [Owen-Smith et al. 2010], areas of high productivity for northern gannets [Wakefield et al. 2013]). In our study, for simplicity, patches were modeled as points in space (i.e., all resources are concentrated at one location instead of distributed within an area representing the patch) because we focused only on behavioral decisions associated with interpatch movements (i.e., intrapatch movements, assumed to correspond to area-concentrated searching, are not considered here). All patches initially contain the same amount of food resources, corresponding to their maximum value. No resources occur outside the patches. When an individual reaches a patch, it consumes almost all available resources, lowering their amount to  $1/1,000$  of their maximum value. Similarly to Van Moorter et al. (2009), we assumed that the amount of resources within any patch is renewed over discrete time steps  $t$  through a logistic growth function with renewal rate  $r$ :

$$P[p]_{t+1} = P[p]_t + rP[p]_t(1 - P[p]_t), \quad (1)$$

where  $P[p]_t$  is the proportion of resources (relative to the maximum amount a patch can contain) within patch  $p$  at time  $t$ . Indeed, resources often grow logistically (e.g., Thomas and Potter 1985; Morris and Silk 1992), and, consequently, logistic growth is classically used to model recovery in biological systems (Garrett 2012). The temporal evolution of the proportion of resources in patch  $p$  is therefore  $P[p]_t = P[p]_0 / \{P[p]_0 + (1 - P[p]_0) \times \exp(-rt)\}$ . With  $P[p]_0$  set to 1/1,000, any patch then requires  $6.9/r$  and  $13.8/r$  time steps to replenish at 50% and 99.9%, respectively. In most of our simulations, the rate  $r$  was set to 0.03 (different values ranging between 0.01 and 0.06 were used in some cases; see below).

### Movements and Memories

For simplicity, every individual systematically moves with a constant speed of 1  $u$  per time step. In our model, both space and time units are arbitrary and can therefore be set to any actual value when needed. For example, in Benhamou's (1990) study on wood mice (*Apodemus sylvaticus*) movements in an environment that was similar to the one modeled here, where shrubs acted as well-defined patches, the patch density (85 shrubs/ha) and the mean speed between patches (about 10 m/min) result in a length unit  $u$  of ca. 2.2 m and a time step of ca. 13 s.

We assume that an individual can detect a patch only when it comes within  $2u$  of the patch, in which case it then goes directly to the patch (in one or two time steps, depending on the distance at which it has detected the patch, as detection occurs only at the end of each time step), and, as noted above, it systematically consumes almost all available resources in one time step. Any energetic cost of movement or handling resources was neglected; only the temporal cost was taken into account, and foraging efficiency was expressed as the amount of food resources (expressed as the number of equivalent fully replenished patches) harvested per 100 time steps.

As in Van Moorter (2009), the location of any detected patch and its expected quality  $Q[p]$  are stored in a long-term memory, referred to as the reference memory, which is used by the individual to revisit high-quality patches. Memorized values about a given patch will be forgotten if the individual does not return to this patch within a duration  $T_R$ . The individual also relies on a short-term memory, referred to as the working memory ( $T_W$ ) and lasting  $T_W \ll T_R$  (where  $T_R$  is the reference memory), to remember that it has recently depleted the patch, so as to avoid coming back there too soon. Time thresholds  $T_W$  and  $T_R$  were set to 200 and 1,000 time steps, respectively, in all simulations (except when conducting the sensitivity analyses; see below). With  $T_W$  set to 200, the forager is prevented from returning to a given patch before it replenishes

at 30% ( $r = 0.03$ ), 75% ( $r = 0.04$ ), 95% ( $r = 0.05$ ), or 99% ( $r = 0.06$ ).

For a given individual, the expected quality of a given patch  $p$  at time  $t$ ,  $Q[p]_t$ , corresponds to the amount of food it expects to find there at the next visit. When this individual visits the patch  $p$  for the first time (or after having forgotten about it) at time  $t$ , the expected patch quality is simply set to the proportion of food present:  $Q[p]_t = P[p]_t$ . When the individual revisits this patch later at time  $t + \tau$  with  $T_W < \tau < T_R$ , the memory time counter is reset to 0. The patch quality is then updated to a new value equal to the arithmetic mean between the amount of resources expected, which reflects its previous experience, and the amount of resources actually found, which reflects its current experience (fig. 1):

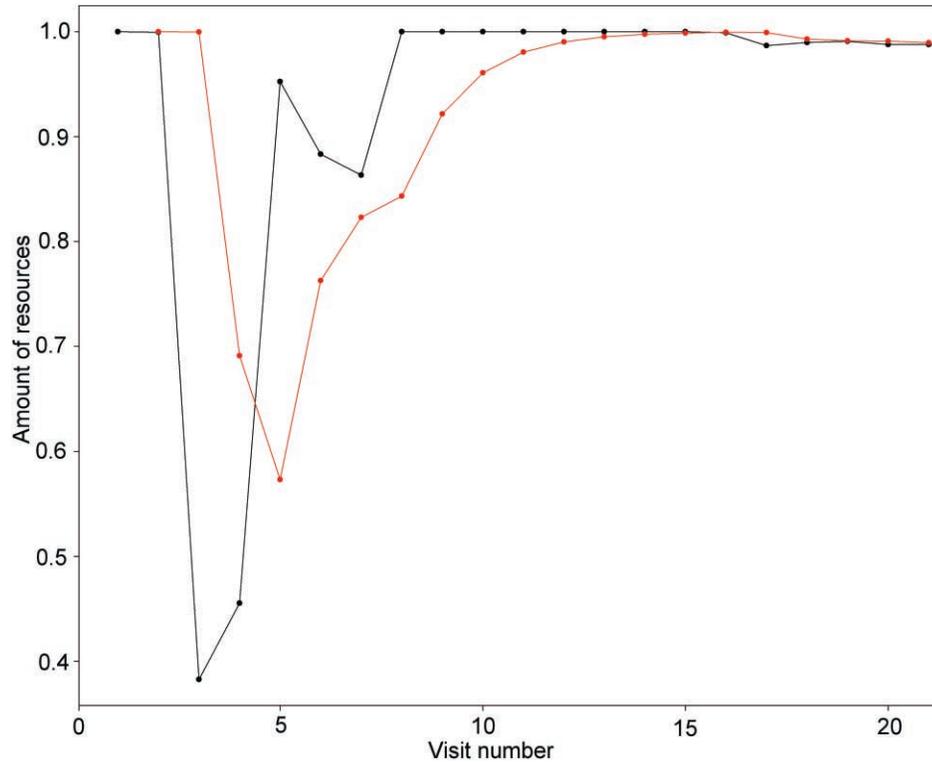
$$Q[p]_{t+\tau} = \frac{Q[p]_t + P[p]_{t+\tau}}{2}. \quad (2)$$

This approach differs from the one used by Van Moorter et al. (2009), who assumed that the expected quality of any patch was always equal to its maximum possible value (corresponding to  $Q[p]_t = 1$  at any time  $t$ ). Thus, the memory system we modeled is made of three components that are thought to be key elements in memory-enhanced movements (see Fagan et al. 2013): a long-term spatial memory to store patch locations, a long-term adaptive (updated at each visit) attribute memory to store the expected quality of the patches, and a short-term temporal memory to store whether a given patch has been recently visited.

The attractiveness value  $V[p]_t$  of a patch  $p$  at time  $t$  increases with its expected quality but decreases with its remoteness and is estimated as

$$V[p]_t = I_M[p]_t \left( \frac{Q[p]_t}{D[p]_t} + \varepsilon \right), \quad (3)$$

where  $D[p]_t$  is the distance between the patch  $p$  and the individual at time  $t$  and  $I_M[p]_t$  is a memory indicator function that specifies whether the patch is known and has not been visited too recently:  $I_M[p]_t = 1$  if the last visit was made between times  $t - T_R$  and  $t - T_W$  and  $I_M[p]_t = 0$  if the patch was never visited or if the last visit was made less than  $T_W$  or more than  $T_R$  time steps ago. The ratio  $Q[p]_t / D[p]_t$  acts as a proxy for the expected rate of intake (the time required to reach a patch being proportional to its remoteness). It is classically used both in theoretical (e.g., van Moorter et al. 2009) and empirical (e.g., Boyer et al. 2006) studies. The parameter  $\varepsilon$  represents the uncertainty in the estimation of the patch attractiveness. It takes into account the imperfect knowledge that an animal may have about the quality of a patch and/or the time required to reach it. It was modeled as a zero-centered random variable with a standard deviation set to 0.002. In "Sensitivity



**Figure 1:** Amount of resources (expressed as the proportion of resources available in a fully replenished patch) expected (red) and found (black) in a patch on successive visits. At the first visit, the individual does not know the patch (or has forgotten it) and reaches it by chance. Hence, there is no expected value (no red dot for the first visit). On the following revisits, the individual remembers the patch and visits it when it chooses to, depending on the amount of resources expected at this and other patches. The averaging algorithm enables the animal to progressively adjust its revisit schedule to obtain almost the maximum amount of resources.

Analyses” we checked that other values within the same order of magnitude (0.001 or 0.004) have only limited effects on our results. Note, however, that much larger values result in a decrease in foraging efficiency and in a lack of HR stabilization due to very inaccurate estimation of patch values by individuals.

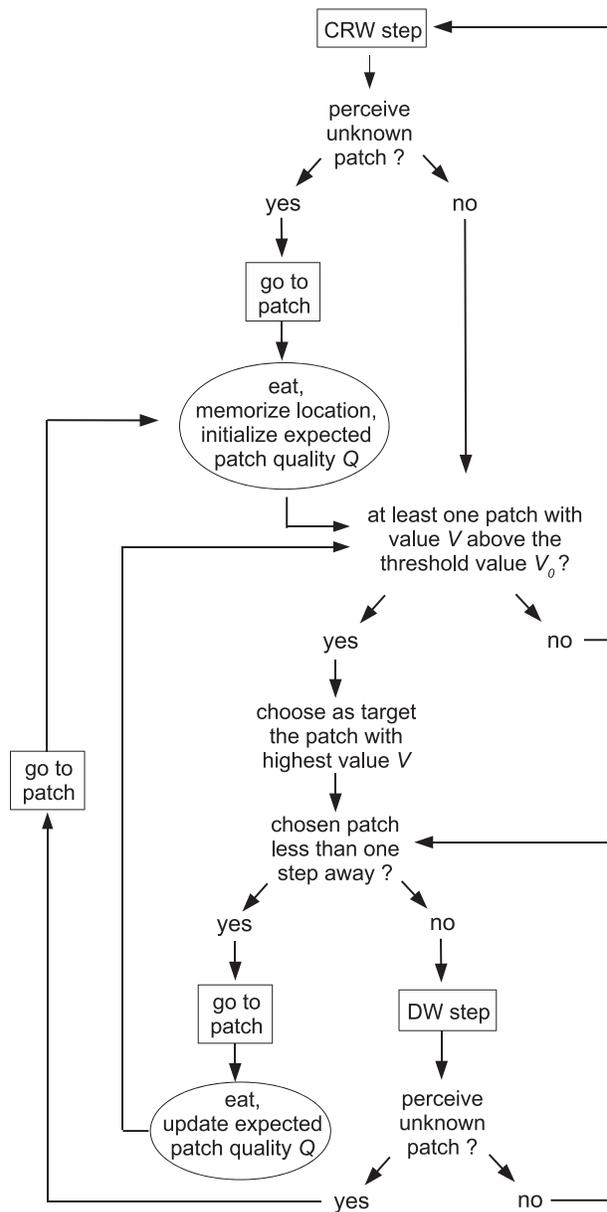
When an individual has finished exploiting a patch, it compares the value  $V$  of all known patches with a given threshold  $V_0$ . If at least one patch has a value  $V > V_0$ , the individual goes in a straight line to the patch with the highest value. Patch values  $V$  are not reevaluated during this directed movement. If the individual detects an unknown patch, it, however, changes focus and walks directly toward this new patch and reevaluates the values of all known patches just after having fed there. If no patch has a value  $V > V_0$ , the individual performs a random search behavior modeled as a correlated random walk (CRW) characterized by a constant step length set to  $1 u$  and a zero-centered wrapped normal distribution of turns with a mean cosine set to 0.8 and reevaluates the values of the known patches after each time step. With these CRW parameters,

it takes  $5.94 \pm 6.74$  time steps to reach a new patch from a previous one (vs.  $2.50 \pm 0.65$  for an animal that would move directly toward the closest neighboring patch). At the beginning of the simulation, the individual has no knowledge about its environment. It therefore systematically performs random searching and starts to memorize the locations and qualities of the patches it detects en route. The individual stops its random searching behavior to switch to memory-based directed movement as soon as at least one patch has reached a value  $V > V_0$  and resumes random searching when all known patches have a value  $V < V_0$ . This differs markedly from Van Moorter et al.’s (2009) approach where, after a predefined period of time during which the individual performed only random searching behavior, it switched to a memory-based behavior determined by an attraction field that is generated by the whole set of known patches and updated at each time step. The  $V_0$  threshold was empirically determined using computer simulations so as to obtain the highest foraging efficiencies (see below). When modeling situations with several individuals exploiting the same landscape,

the same  $V_0$  threshold was attributed to all individuals. The work flow of the model is shown in figure 2.

### Noncompetitive Situation

A single individual was released at the center of the landscape and moved for 105,000 time steps according to the rules mentioned above. In pilot simulations based on 20 replicates, we explored how the foraging efficiency depends on both the resource renewal rate  $r$  and the  $V_0$  threshold.



**Figure 2:** Work flow of the model. CRW = correlated random walk; DW = directed walk.

It visually appeared that, for each value of  $r$ , there is a range of  $V_0$  values leading to higher foraging efficiencies. Therefore, for each  $r$  value considered, we ran batches of 100 replicates with  $V_0$  values within this range to determine the  $V_0$  value leading to the highest mean foraging efficiency during the last 5,000 time steps of the simulation. Then, we generated 900 additional replicates with this  $V_0$  value, so as to obtain 1,000 replicates for each  $r$  value (and associated optimal  $V_0$  value) considered.

Determining whether a HR has emerged, that is, whether the movement process leads to locational stationarity, can be tricky (Van Moorter et al. 2009; Benhamou 2014). In the present context, an interesting parameter is the mean-squared distance between the patches visited and their barycenter (weighted arithmetic mean location). For each replicate, we computed the mean-squared distance  $MSD_{1/1}$  between the locations of the patches visited between the 95,000th and 100,000th time steps and their barycenter  $\mathbf{B}_1$ , as well as the mean-squared distance  $MSD_{2/1}$  between the locations of the patches visited between the 100,001th and 105,000th time steps and the point  $\mathbf{B}_1$ .  $MSD_{2/1}$  can be decomposed into two additive components:  $MSD_{2/2}$ , which is the mean-squared distance between the patches visited for the last 5,000 time steps and their barycenter  $\mathbf{B}_2$ , and  $(\mathbf{B}_1 - \mathbf{B}_2)^2$ , which is the squared distance between the two points  $\mathbf{B}_1$  and  $\mathbf{B}_2$  ( $MSD_{2/1} = MSD_{2/2} + (\mathbf{B}_1 - \mathbf{B}_2)^2$ ). Thus, comparing  $MSD_{1/1}$  and  $MSD_{2/1}$  makes it possible to detect both a shift in barycenter and a change in dispersion in the locations of the patches visited. If a HR has emerged, one expects  $MSD_{1/1} \approx MSD_{2/2} \approx MSD_{2/1}$ . We considered that a HR has emerged if the absolute difference between  $MSD_{2/1}$  and  $MSD_{1/1}$  is smaller than 10% of the mean-squared dispersion of patches exploited for 5,000 time steps ( $MSD_{1/1}$  or  $MSD_{2/2}$ ), that is,  $R = |MSD_{2/1} - MSD_{1/1}| / (MSD_{1/1} + MSD_{2/2}) < 0.05$ . For comparison, using computer simulations, we found  $MSD_{1/1} \approx MSD_{2/2}$  but  $R \approx 2.0 \pm 1.8$  with a diffusive walk (any kind of CRW).

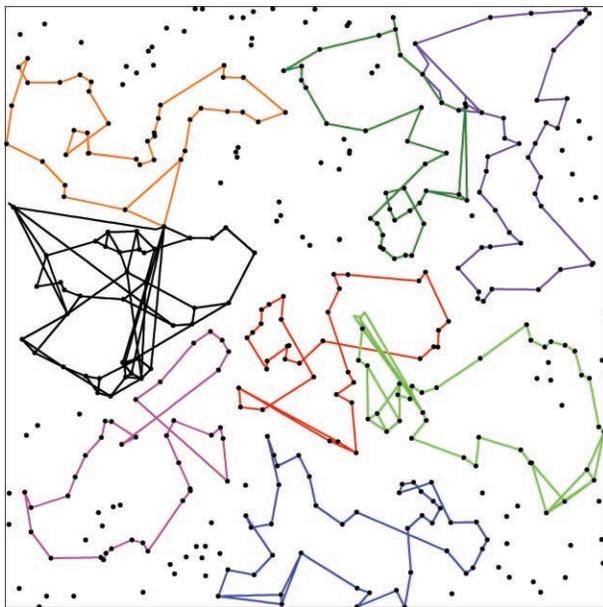
For any emerging HR, we delimited the set of patches included in the minimum convex polygon (MCP) encompassing all patches visited during the last 5,000 time steps and estimated the HR compactness as the proportion of patches within the polygon that had been actually visited. We compared the mean foraging efficiencies during the last 5,000 time steps of the simulations of individuals behaving as described above, differentiating those that succeeded or failed to settle in a HR, with the mean foraging efficiencies of individuals that always either performed CRW-based random searching (with the same parameters as those used during their exploratory phases by individuals that use memory) or moved along a straight line (except for short-scale reorientations to reach detected patches and bouncing at landscape boundaries). Speed of movement (1  $u$  per time step) and radius of detection (2  $u$ )

were the same for individuals, irrespective of their memory capacities.

#### *Fair Competitive Situation*

Six to eight individuals were simultaneously released at the center of the landscape. As in the noncompetitive situation, the results do not markedly depend on the renewal rate  $r$  for  $r > 0.02$ , and we ran all our simulations with  $r = 0.03$  (see fig. A8 for results obtained with additional simulations run with  $r = 0.02$  and  $r = 0.06$ ; figs. A1–A8 available online). With  $r = 0.03$ , at least six HRs may emerge in the competitive situation. Indeed, HRs that emerge in the noncompetitive situation encompass about 60–70 patches, that is, roughly one-sixth of the number of available patches. Consequently, we released  $n = 6$ ,  $n = 7$ , or  $n = 8$  individuals in the same conditions to study the situations with a density of competitors equal to or slightly higher than the assumed theoretical saturation density. In all cases, we used the same procedure as in the noncompetitive situation to determine the optimal  $V_0$  values. An example of emerging HRs in the competitive situation is illustrated in figure 3. This kind of movement pattern can be seen in real-world studies (e.g., HRs of wood mice in fig. 2 in Benhamou 1990).

All simulations were replicated 1,000 times. We considered that a given simulation led to HR emergence if at



**Figure 3:** Example of the final (last 5,000 time steps) space use patterns of eight individuals that all succeeded in establishing a home range (illustrated using different colors) in the competitive situation. All parameters were set to default values.

least  $n - 1$  individuals settled in a HR at the end of the simulation (based on the same criterion as for the noncompetitive situation). This tolerance of one individual possibly remaining partly nomadic was added because in a bounded landscape, the patches remaining available for the last individual not yet settled in a HR may be overdispersed along the landscape boundaries, and such a situation often led to values  $V < V_0$  for all known patches, preventing the remaining individual to be able to settle in a HR.

As in the noncompetitive situation, we compared the foraging efficiency reached by individuals able to establish a HR in all replicates leading to HR emergence (i.e., where at least  $n - 1$  individuals established HRs) with the foraging efficiency reached by  $n$  individuals using the random search strategy (CRW) or moving along a straight line. We also computed the overlap between HRs of any two individuals as the ratio, over the last 5,000 time steps, of the number of different patches used by both individuals divided by the total number of different patches used by one and/or the other. With six to eight individuals in a landscape of  $100 \times 100 u$ , the mean distance between HR barycenters is about 35–40  $u$ . As the overlap between distant HRs is necessarily null and meaningless, we restricted overlap computations to pairs of HRs whose barycenters are less than 50  $u$  of each other. In the absence of a theoretical reference that would be useful to appreciate the overlap values obtained in this competitive situation, we contrasted it with a multi-individual noncompetitive situation fully similar to the competitive one, except that each patch is made of  $n$  independent sets of resources, with each set being accessible only to a specific individual. Several individuals could therefore exploit the same patch without affecting the resources available to each other.

#### *Unfair Competitive Situation*

We considered two types of unfair competitive situation. In the first type, an additional, naive competitor is introduced in an established population of HR owners. We ran simulations of 105,000 time steps with  $n = 6$  individuals released simultaneously at the landscape center (and with the threshold  $V_0$  set to the optimal value for  $n = 6$ ) until we obtained 1,000 replicates in which six HRs had emerged and then introduced the naive competitor at the center of the landscape and let the system evolve for 105,000 additional time steps (with  $V_0$  then set to its optimal value for  $n = 7$ ). In the other type of unfair competitive situation, a naive competitor replaces a HR owner (assumed to have died or emigrated) in an established population of HR owners. We ran simulations over 105,000 time steps with  $n = 7$  individuals released simultaneously at the landscape center (and with the threshold  $V_0$  set to

the optimal value for  $n = 7$ ) until we obtained 1,000 replicates in which seven HRs had emerged and then replaced a randomly chosen individual by a naive competitor and let the system evolve for 105,000 additional time steps.

For both types of unfair situation, the renewal rate  $r$  was set to 0.03, and we looked at the same output variables as in the fair competitive situation (HR emergence, compactness, overlap, and foraging efficiencies). We compared the values obtained for the period from 100,000 to 105,000 time steps (i.e., just before the seventh individual was introduced) with those obtained for the period from 205,000 to 210,000 time steps. We additionally measured the mean displacement between the two periods of the barycenters of the HRs having restabilized.

### Sensitivity Analyses

The model structure implies that results will not change if the resource renewal rate and the movement speed are  $k$  times larger and the memory thresholds  $k$  times smaller or if the patch density is  $k$  times larger and the movement speed and the detection radius are  $k$  times smaller (other parameters remaining unchanged). For other combinations of parameters, we ran additional simulations (100 for each parameter setting) to investigate the sensitivity of key output variables (likelihood of HR emergence, HR size, foraging efficiency, HR compactness, and, for  $n > 1$ , HR segregation) to variations in the values of four key parameters (in addition to the renewal rate, already mentioned above): reference and working memory thresholds  $T_R$  and  $T_W$  (default values 1,000 and 200 time steps, respectively), detection radius (default value  $2u$ ), and standard deviation of the uncertainty in estimating patch values (default value 0.002). This was done by setting all these parameters except one to their default values and setting the remaining one to a value either twice or half the default value. All simulations and analyses were performed using R (ver. 2.15.1; R Core Team 2012).

## Results

### Noncompetitive Situation

For a given  $r$  value, there is a range of optimal or sub-optimal  $V_0$  values (i.e., leading to mean intake rates that are close to the maximum possible value; fig. 4A). For  $r \geq 0.03$  and  $V_0$  set to the optimal value (0.074; see fig. 4A), the proportion of HRs that emerge does not depend on  $r$ , and the mean intake rate increases slowly with  $r$  (fig. 5A). A HR emerges in more than 85% of simulations for  $r > 0.0175$  (when using the corresponding optimal  $V_0$  value) versus in only 15% of simulations for  $r = 0.0125$  (not shown). Furthermore, for  $r \geq 0.015$ , the mean intake rate

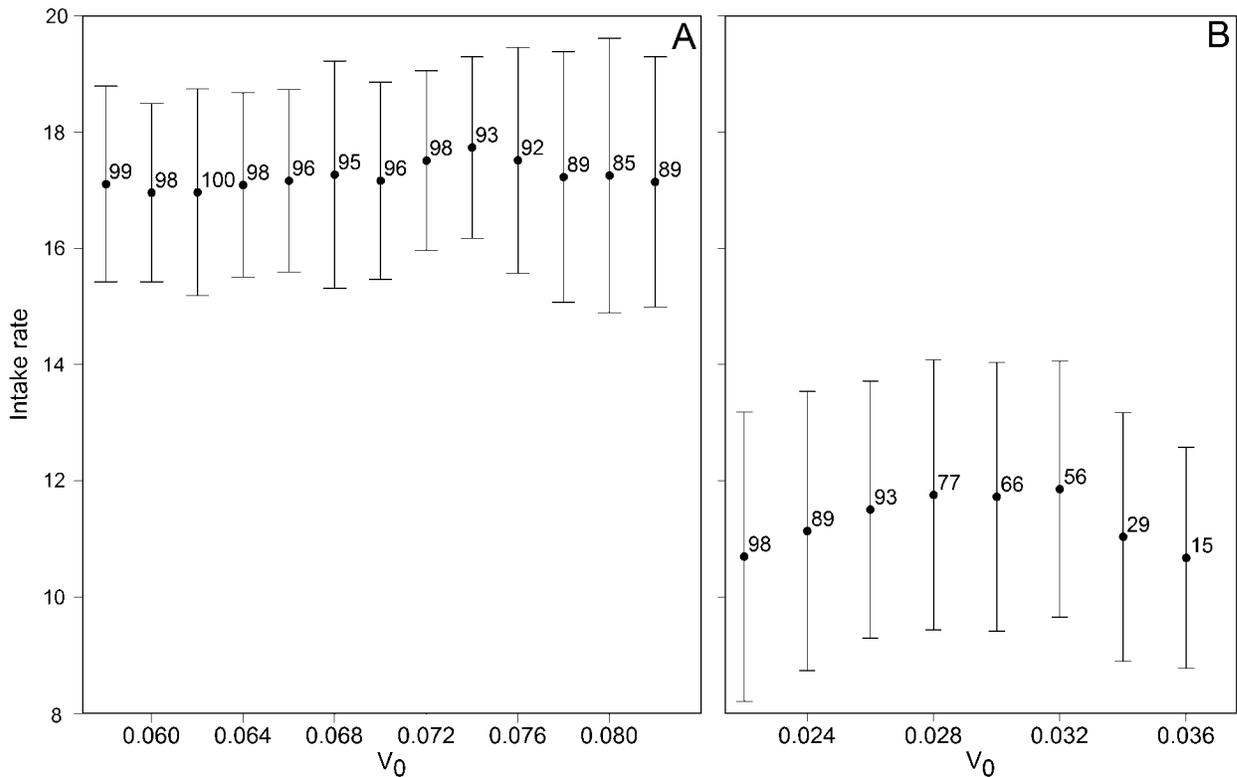
of individuals that use memory and are able to establish a HR (at the corresponding  $r$ -dependent optimal  $V_0$  value) is on average 25% higher than that of individuals that use memory but are unable to establish a HR (fig. 5A). It is also far higher (by more than 60% for  $r \geq 0.03$ ) than the mean intake rate of individuals moving along a straight line, which is the best no-memory strategy, or than the rate reached by the random search strategy, which is unsurprisingly the least efficient (fig. 5A). As expected, the mean HR size decreases when  $r$  increases (it is about 47% lower for  $r = 0.06$  than for  $r = 0.015$ ; see fig. 6). The mean compactness of HRs (number of patches used over the total number of patches encompassed within the MCP defined by the most outer patches used) is about  $0.66 \pm 0.12$  for  $r = 0.03$ .

### Fair Competitive Situation

When six competitors are released at the same time at the center of the landscape, with the renewal rate set to  $r = 0.03$  and  $V_0$  to the optimal value for this density and renewal rate (here the mean intake rates for  $0.028 \leq V_0 \leq 0.032$  are almost the same [fig. 4B] and we chose  $V_0 = 0.028$  as the optimal value, which leads to the maximum HR emergence rate), HRs emerge with a frequency just a little bit lower than in the noncompetitive situation (fig. 5B). However, with higher densities ( $n = 7$  or  $n = 8$ ) and corresponding optimal  $V_0$  values (0.026 and 0.024, respectively), the frequency of emerging HRs is lower (fig. 5B). Furthermore, competition for resources leads to a decrease in the mean intake rate (fig. 5B) and mean HR size (table 1). Thus, for  $r = 0.03$ , the mean intake rate of individuals having established a HR at the theoretical saturation density ( $n = 6$ ) is approximately 31% lower than in the noncompetitive situation, and the mean HR size is about 27% smaller. However, the mean intake rate of individuals that use memory and establish a HR in the competitive situation is approximately 53% ( $n = 6$  or  $n = 7$ ) or 50% ( $n = 8$ ) higher than the mean intake rate reached by the best no-memory strategy (straight line) in the same conditions (fig. 5B). The mean intake rate of individuals that use memory but failed to establish a HR is usually a little lower (by about 12%) than the rate reached by HR owners. With respect to the noncompetitive situation, HRs emerging in the fair competitive situation are more compact and their overlaps (mean percentages of patch locations shared by pairs of individuals) are 7–11 times lower (table 1).

### Unfair Competitive Situation

The arrival of a naive individual leads to similar effects whether it represents an additional competitor in a “close-



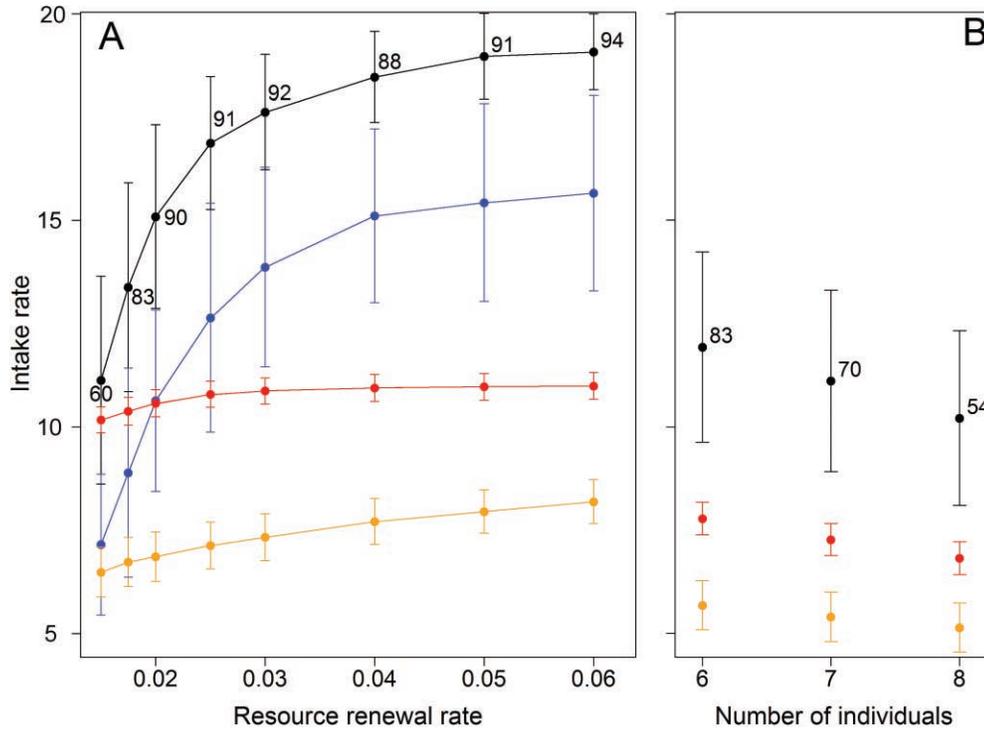
**Figure 4:** Intake rate (mean  $\pm$  SD; based on 100 replicates, expressed as the amount of resources, in full-patch equivalents, harvested per 100 time steps, during the last 5,000 time steps of the simulation, independent of the fact that individuals established a home range [HR] or not) in the noncompetitive situation (A) and in the competitive situation (B) for  $n = 6$ ,  $r = 0.03$ , as a function of the threshold value  $V_0$  (all other parameters set to default values). Numbers give the percentages of replicates leading to the emergence of a HR in the noncompetitive situation (A) or where at least  $n - 1$  individuals were able to establish a HR in the competitive situation (B).

to-saturation” landscape (i.e., where six competitors have already-established HRs), or it replaces one competitor out of seven having established a HR. In both cases, the competitors initially present are led to modify their use of space, but in more than 75% (78% and 79% for “addition” and “replacement,” respectively) of the simulations, the situation restabilizes (based on the same stability criterion as in the fair competitive situation) within 105,000 time steps following the introduction (in  $55,313 \pm 31,512$  time steps for addition and  $54,710 \pm 32,399$  time steps for replacement). The barycenters of HRs before the arrival of the new individual and after further 105,000 time steps are on average displaced by  $14.03 \pm 12.39 u$  in the addition case and  $13.45 \pm 12.31 u$  in the replacement case (for comparison, the mean distance between the patches used within the HR and its barycenter is about  $20 u$ ). After restabilization, the situation is similar to the fair competitive situation with seven competitors in terms of net intake rate, HR emergence, HR size, compactness, and overlap, and there is no noticeable difference between the new competitor and the ones that were initially present in terms of

intake rate or of HR size, compactness, and overlap (table 1). However, during the first 1,000 time steps following the addition or the replacement, the mean intake rate of the naive individual is less than half that of the familiar individuals (addition:  $4.7 \pm 1.3$  vs.  $11.3 \pm 2.3$ ; replacement:  $5.0 \pm 1.3$  vs.  $10.8 \pm 2.2$ ) but similar to the one of seven naive individuals arriving in a partly depleted landscape (i.e., where seven individuals have established HRs and are all replaced by naive individuals:  $5.5 \pm 1.3$ ).

#### Sensitivity Analyses

In the noncompetitive situation, intake rates and HR sizes are not sensitive to halving or doubling (with respect to default values) the uncertainty in estimating patch value ( $\epsilon$ ), but they increase with the reference memory time threshold ( $T_R$ ) and the perception range (figs. A1, A2). Intake rates are not sensitive to the working memory time threshold ( $T_W$ ), but HR sizes and compactness increase when  $T_W$  increases. HR compactness is not sensitive to  $\epsilon$  but slightly decreases when  $T_R$  increases and increases when



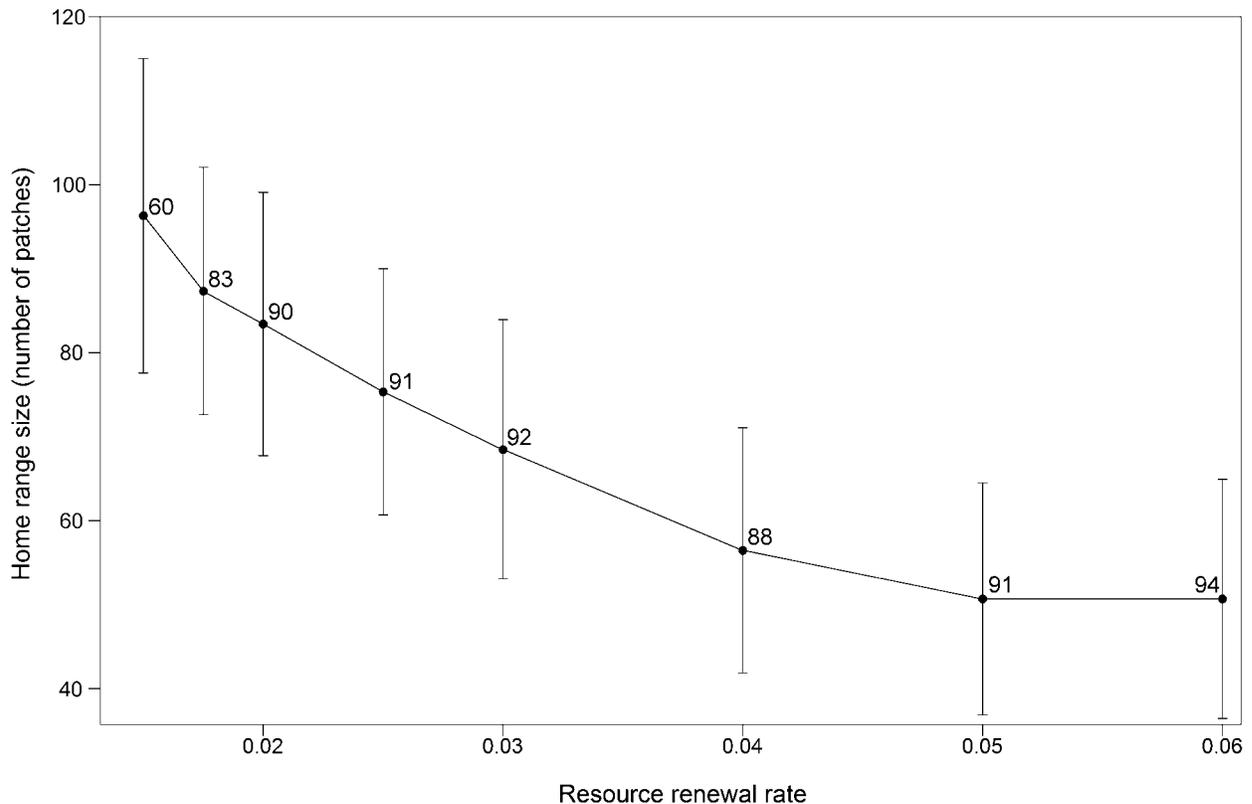
**Figure 5:** Intake rate (mean  $\pm$  SD; based on 1,000 replicates, expressed as the amount of resources, in full-patch equivalents, harvested per 100 time steps, during the last 5,000 time steps of the simulation) of individuals in the noncompetitive situation as a function of the resource renewal rate  $r$  (A; all other parameters set to default values) or in the competitive situation as a function of the number of individuals, for  $r = 0.03$  (B; all other parameters set to default values). In the noncompetitive situation (A), we contrasted individuals that use memory and were able (black) or unable (blue) to establish a home range (HR), with individuals performing a correlated random walk (with the same characteristics of individuals that use memory in exploratory phases; orange) or moving in a straight line (red). In the competitive situation (B), black dots represent mean intake rates of individuals able to establish a HR within replicates where at least  $n - 1$  individuals were able to do so. Numbers give the percentages of replicates in which either the individual was able to establish a HR (A) or at least  $n - 1$  individuals were able to establish a HR (B).

the perception range increases (fig. A3). In the fair competitive situation, we performed the sensitivity analysis on densities close to the theoretical saturation density given the HR sizes observed in the noncompetitive situations. When  $T_W$  is halved, no simulation leads to HR emergence (fig. A4). Intake rates are not sensitive to halving or doubling  $\varepsilon$  but increase with  $T_R$ ,  $T_W$ , the perception range, and the resource renewal rate  $r$  (figs. A4, A8). HR sizes are not sensitive to  $\varepsilon$  but increase with  $T_R$ ,  $T_W$ , and the perception range and decrease with  $r$  (figs. A5, A8). HR compactness is not sensitive to  $T_W$  or to  $\varepsilon$  but decreases with  $T_R$  and increases with the perception range and  $r$  (figs. A6, A8). Finally, HR overlaps in the fair competitive situations decrease with  $r$  (fig. A8) but are sensitive to none of the other parameters for which we evaluated the sensitivity ( $T_W$ ,  $T_R$ , the perception range, and the uncertainty in estimating patch value  $\varepsilon$ ; fig. A7). In both noncompetitive and competitive situations, intake rates of HR owners were always higher than those of individuals following straight

lines (by on average 65%), whatever the parameter values (figs. A1, A4, A8), and overlaps of HRs were always larger in the noncompetitive situation than in the competitive one (on average 10 times larger; figs. A7, A8). These analyses thus show that our results are qualitatively robust to changes in the values of key parameters of our model.

## Discussion

HR behavior should be an efficient foraging solution when environmental resources are relatively predictable in space and time (Wiens 1976; Stamps 1995; Powell 2000; Van Moorter et al. 2009; Mueller et al. 2011). A widespread component of predictability experienced by numerous species is resource patchiness. Patchiness enables a forager to find additional resources in close proximity when a first resource has been discovered by intrapatch area-concentrated foraging (Benhamou 1994), but there remain various sources of unpredictability linked to the dynamics of the



**Figure 6:** Home range (HR) size (mean  $\pm$  SD; based on 1,000 replicates) in the noncompetitive situation as a function of the resource renewal rate  $r$  (all other parameters set to default values). Numbers give the percentages of replicates leading to HR emergence.

patches. Moreover, space sharing, by which a patch can be depleted by several competitors, can dramatically increase environmental unpredictability and thus decrease the value of memorized information for all individuals. Our study shows, however, that a simple rule to combine past and current information allows individuals to learn appropriate return times from experience. In this context, individuals relying on a simple memory system that stores information about resource patches and a simple optimization rule (moving toward the memorized patch with the best quality/distance ratio) spontaneously restrict their movements to a specific subset of patches (i.e., perform HR behavior) and are, even under intense competition, more efficient than not only random searchers but also the most efficient foragers that do not rely on memory (by more than 50%, provided the resource renewal rate is not too low), which avoid any backtracking by moving in a straight line.

We developed our model in accordance with currently available knowledge. However, to parameterize it fully for any specific system, we lack empirical knowledge of the settlement process of naive individuals in environments where patch resource renewal would be known. In one of the scarce empirical studies that tracked introduced indi-

viduals at various scales, Fryxell et al. (2008) monitored the movement of introduced elks (*Cervus elaphus*) but did not monitor all the processes that we modeled. Also, in most species, memory capabilities are uncertain. The three-component memory system we modeled can be seen as a basic implementation of “win-stay” and “win-shift” strategies, which have long been used as basic paradigms in cognitive neurosciences. For example, the ability of hungry rats, due to their short-term (working) memory, to visit each arm of a multiarm maze that contains a single, non-renewed food reward only once reflects a win-shift strategy. In contrast, their ability to return repeatedly to the same rewarding place, such as the hidden platform in water maze experiments, whose location is encoded in a long-term (reference) memory, reflects a win-stay strategy (see Poucet and Benhamou 1997 for a review of spatial memory processes in the rat). Win-stay and win-shift strategies are obviously not restricted to rats but appear to exist within numerous taxa (e.g., cows [Hosoi et al. 1995] or echidnas [Burke et al. 2002]). Exploiting a HR typically requires using both strategies, as food is usually distributed in patches that can be depleted in the short term and renewed in the long term. This appears consistent with what has been

**Table 1:** Home range (HR) characteristics and intake rate of individuals that use memory under contrasted situations of competition

	Noncompetitive	Fair competitive			Unfair competitive		
		$n = 6$	$n = 7$	$n = 8$	Addition	Replacement	
HR emergence (%)	92	83	70	54	78	79	
HR size	68.48 ± 15.45	49.55 ± 7.52	47.89 ± 7.27	46.94 ± 7.73	New: 48.60 ± 8.27 Old: 47.49 ± 6.84	New: 47.52 ± 7.99 Old: 47.23 ± 6.62	
HR compactness	.66 ± .12	.75 ± .16	.77 ± .15	.79 ± .15	New: .76 ± .27 Old: .76 ± .16	New: .81 ± .28 Old: .77 ± .15	
HR overlap	$n = 6$ : 18.27 ± 7.20 $n = 7$ : 14.19 ± 12.38 $n = 8$ : 14.61 ± 12.89	1.54 ± 2.60	1.69 ± 3.07	2.06 ± 3.82	New: 1.83 ± 2.54 Old: 1.54 ± 2.57	New: 1.45 ± 2.04 Old: 1.59 ± 2.69	
Intake rate	17.6 ± 1.4	11.9 ± 2.3	11.1 ± 2.2	10.2 ± 2.1	New: 11.4 ± 2.3 Old: 11.1 ± 2.2	New: 11.1 ± 2.2 Old: 11.0 ± 2.2	

Note: The results (means ± SD) presented are based on 1,000 replicates for a resource renewal rate  $r = 0.03$ . The intake rate is expressed as the amount of resources (in full-patch equivalents) harvested per 100 time steps and averaged over the last 5,000 time steps of the simulation, calculated for individuals that were able to establish a HR. The intake rate of individuals that failed to establish a HR was lower by about 20% for  $n = 1$  and 12% for  $n > 1$ . For the unfair competitive situation, values are given for the last 5,000 time steps following the introduction of a naive individual (called "new" in the table) in a population of established HR owners (called "old" in the table).

found in nectar-feeding birds that show a short-term win-shift strategy but a win-stay strategy matching the rate of nectar replenishment (Burke and Fulham 2003).

A first glimpse at the energy gains brought by spatial segregation emerging from information-updating processes, limited, however, to the special case of traplining, was given by Ohashi and Thomson (2005). Using computer simulations, they showed that individuals that use information can be more energy efficient by shifting to less competitive areas. In our model, a similar, although more general, process is at work: when an individual comes to a patch that has recently been visited by another individual, the apparent quality of this patch that is memorized by the second individual tends to be lower than the apparent quality memorized by the first individual. As individuals tend to return to the memorized patches of the highest quality, they are collectively led to use mainly patches that are not exploited by others and thus to segregate spatially to a greater or lesser extent. As envisioned by Spencer (2012), taking the imperfection and dynamic nature of learned information into account is clearly required to build a unifying theory of animal space use and HR behavior, as spatial segregation may spontaneously emerge from these dynamics. However, Spencer (2012) argued that spatial segregation may be due to a more efficient exploitation of patches by competitors familiar with the patches, whereas in our model segregation emerges despite the absence of any such difference between familiar and nonfamiliar individuals. The rule we used to adjust expectation about patch quality with experience (arithmetic means between what is expected and what is found) is certainly one of the simplest ways to model how information can be updated. A more elaborate possibility would be to use a Bayesian rule (e.g., see Marshall et al. 2013 for Bayesian patch-departure rules). However, McNamara et al. (2006) showed, by reviewing biological contexts where Bayesian updating rules have been used to describe behavioral decision making, that simple rules can often perform very well and be highly robust. Exploring how other rules would perform was beyond the scope of this work. The key point here is that using a simple adaptive memory is sufficient to limit HR overlaps and that, with a reduced number of intrusions from other competitors in its HR, an individual then experiences a reduced loss of value of information compared to the expectations based on the behavior of isolated individuals.

Recently, several studies have emphasized the role of density-dependent competition and public information in driving spatial segregation between neighboring social groups, in the special case of central-place foragers, the northern gannets (Wakefield et al. 2013) and the red harvester ants (Adler and Gordon 2003). Here we show in a more general context that neither public information nor spatial restriction in space use involving territorial behav-

ior or central-place foraging is required to explain low HR overlap between memory-driven foragers. This raises the question of the evolutionary advantage of territoriality. Actively defending an area and displaying keep-out signals implies costs that should be compensated for by some advantages that territoriality might provide (Schoener 1983; Adams 2001; Hinsch and Komdeur 2010). Beyond the exclusive use of resources per se, territorial behavior is likely to improve environmental predictability by preventing the resource landscape from being altered by other competitors. As we showed here, HRs with little overlap do not require territorial behavior to emerge, however, for population densities up to a value slightly higher than the theoretical saturation level (as determined from the size of HRs in the noncompetitive situation; at higher population densities, most competitors fail to establish HRs, and their intake rates are quite low, even for competitors that have established a HR). However, only food resources were considered in our study, whereas many territories documented in the wild are linked to other resources, in particular, resources specific to reproduction purposes, such as nest sites or mates, which can be limiting. For example, in field voles, males defend a territory covering the HRs of several females and prevent other males from mating with them (Pusenius and Viitala 1993).

A key point in our study is that the introduction of a naive individual, in addition to already established individuals or in replacement of one of them, led to moderate spatial rearrangements of established individuals. As expected, the intake rate of this new individual is at the beginning (for the first 1,000 time steps following its introduction) far lower than the one of established individuals, which are familiar with their environment. It is, however, not significantly lower than the rate that would be experienced if all competitors were naive. Consequently, the new individual should not be more likely to die before establishing a HR among experienced competitors than when attempting to colonize a new area in the presence of unexperienced competitors. In other words, the initial low intake rate of a newcomer is mainly due to the lack of information about the resource distribution in the landscape and to the high population density and only marginally due to the fact that the individuals with which it is in competition are experienced. An important consequence is that successfully exploiting a HR based on the simple rules we modeled does not protect established individuals against invasion when little free space is available. Once the new individual has established a HR, the intake rate and HR characteristics are those expected given the population density.

To remain stable in the long term, the spatial organization of HRs should allow the replacement of previously established neighbors (which die or emigrate) by new ones

but be resistant to the continuous establishment of additional competitors. As the low initial intake rates of new competitors are similar in both the replacement and addition situations, it cannot be argued that the additional competitors would not be able to survive up to HR establishment. Consequently, in the absence of mechanisms preventing additional competitors from attempting to establish, the population density is likely to increase up to a point where the initial intake rates of newcomers should be so low that they may not survive the establishment phase and would either die or disperse before. At such a high density, individuals already familiar with the landscape should have an intake rate that is sufficient to survive, but they may not be able to establish HRs and thus will be led to display somewhat nomadic movements. This indicates that the spatial organization of HRs with little overlap makes it possible for competitors to reach a high level of foraging efficiency but that it will not persist in the long run if based only on memorized information about patch values. In the absence of territorial behavior, the maintenance of HRs at high population density is likely to rest on additional benefits provided by familiarity of the landscape. For example, it can be argued that established individuals may exploit patches more efficiently (Spencer 2012) but also that they can learn escape routes and shelter locations (Stamps 1995). Newcomers could also take advantage of direct presence signs of a HR owner (e.g., odors in mammals or songs in birds) to distinguish between areas that are already intensively exploited by resident individuals and those that are still underexploited, beyond the simple monitoring of the patch quality. This would enable them to experience a higher intake rate by focusing on “free” patches and also consequently lead to less disturbance of established HR owners and thus to a more stable organization of HRs. Thus, territoriality may become an energy-efficient strategy only when benefits provided by familiarity are not sufficient to keep a stable organization of HRs. For example, Baker et al. (2000) and Potts et al. (2013) showed that when density decreases in a population of territorial foxes, the remaining foxes enlarge their territories so as to keep contiguous territories between neighbors, which facilitates the exclusion of potential invaders.

To sum up, our model showed that using memory enables individuals to forage much more efficiently than individuals performing the most efficient foraging strategy not using memory and that this holds both in isolation and in a competitive context, particularly because individuals that use memory are naturally driven to segregate by passive avoidance of patches used by others. This striking result questions the common assumption that low HR overlaps reveal territoriality. We note, however, that empirical data allowing testing of the assumptions, or re-

sults, of this model are few (but see Merkle et al. 2014). We urge field ecologists to start designing experiments that will provide evidence or falsification of the processes studied here.

### Acknowledgments

Our study greatly benefited from the Montpellier Bioinformatics Biodiversity computing cluster platform. L.R.L. thanks the Ecole Normale Supérieure of Paris for financial support. Editor Fred Adler and reviewers Dick Green and Jonathan Potts provided suggestions that improved the manuscript. We also thank editor in chief Judith Bronstein for improving the English.

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