

From random walks to informed movement

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Abstract

The analysis of animal movement is a large and continuously growing field of research. Detailed knowledge about movement strategies is of crucial importance for understanding eco-evolutionary dynamics at all scales — from individuals to (meta-)populations. This and the availability of detailed movement and dispersal data motivated Nathan and colleagues to published their much appreciated call to base movement ecology on a more thorough mechanistic basis. So far, most movement models are based on random walks. However, even if a random walk might describe real movement patterns acceptably well, there is no reason to assume that animals move randomly. Therefore, mechanistic models of foraging strategies should be based on information use and memory in order to increase our understanding of the processes that lead to animal movement decisions.

We present a mechanistic movement model of an animal with a limited perceptual range and basic information storage capacities. This ‘spatially informed forager’ constructs an internal map of its environment by using perception, memory and learned or evolutionarily acquired assumptions about landscape attributes. We analyse resulting movement patterns and search efficiencies and compare them to area restricted search strategies (ARS) and biased correlated random walks (BCRW) of omniscient individuals. We show that, in spite of their limited perceptual range, spatially informed individuals boost their foraging success and may perform much better than the best ARS. The construction of an internal map and the use of spatial information results in the emergence of a highly correlated walk between patches and a rather systematic search within resource clusters. Furthermore, the resulting movement patterns may include foray search behaviour. Our work highlights the strength of mechanistic modelling approaches and sets the stage for the development of more sophisticated models of memory use for movement decisions and dispersal.

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Introduction

The ability to move is fundamental to life and very relevant to the fitness of most animal species. It influences foraging success, the ability to escape predators, or to target mating partners — to name just a few aspects. Similarly, the impact of dispersal — a large-scale phenomenon resulting from the movement of individuals — on the eco-evolutionary dynamics of animal populations cannot be overestimated. The exchange of individuals between populations, respectively habitat patches, is central for the persistence of spatially structured populations (metapopulations: Levins 1969, 1970; Hanski 1998, 1999). Furthermore, dispersal is a key life-history attribute which may shape evolutionary trajectories of populations significantly (for recent comprehensive reviews see Bowler and Benton 2005; Ronce 2007). Yet, despite the central role movement plays in ecology and evolution the process is often not considered explicitly in models of spatially structured populations (e.g. Travis and Dytham 1998; Hanski 1999; Poethke et al. 2011; Fronhofer et al. 2011). Instead, dispersal is approximated by diffusion processes or random walks (for a recent review see Codling et al. 2008) or the statistical properties of some dispersal kernel. These approaches typically do not consider the movement process at all but (only) the emergent consequences, i.e. the translocation of individuals from one place to another.

A number of models of animal movement and resulting inter-patch dispersal assume that the movement process can be described as a modified version of a random walk (Codling et al. 2008). Such models account for e.g. limited perceptual capabilities (detection range), directional persistence, i.e. correlation in the direction of consecutive movement steps (e.g. Bartumeus and Levin 2008), or a bias in movement directions (e.g. Conradt et al. 2003; Bartoń et al. 2009). They are based on the assumption that movement can be described by the statistical attributes of step length and turning angle distributions, for example. Movement decisions are seen as inherently random. However, the fact that the statistical properties of movement trajectories can adequately be described in this way should not be taken as evidence that the underlying generating processes are equally well described by such distributions (Benhamou 2007; Plank and James 2008; Boyer et al. 2009).

A first approach towards modelling movement as a more context-dependent process based on the ability to memorize a sequence of temporal events is found in the concept of the area restricted search (ARS Kareiva and Odell 1987; Benhamou 1992). In nature resources are often spatially autocorrelated (Conradt et al. 2003; Jelinski and Wu 1996), i.e. food plants are frequently surrounded by other food plants. Given that resources are rare and distributed in more or less discrete clusters (patches) encounters with resources reveal information on the probability of finding additional resources nearby. ARS models assume that individuals remember the time since past encounters (possibly integrated by their hunger level, see Bartoń and Hovestadt 2013) and decrease the straightness (correlation) of their random walk upon detecting a resource item. Such patterns have been observed in various taxa, from microbes (Keller and Segel 1971) and invertebrates (Hassell and Southwood 1978) to birds (Tinbergen et al. 1967). Tailored to the search for spatially clustered resources this movement rule leads to a more intense search in areas of high resource density. If we equate ‘resource aggregations’ with the term ‘habitat patches’ — as frequently done in the metapopulation literature (for reviews see Hanski 1999; Hanski and Gaggiotti 2004) — ARS models generate more or less straight inter-patch movement that can be differentiated from intra-patch foraging behaviour and the earlier may be qualified as dispersal (Ronce 2007). Note that ARS models do not assume any spatial memory or orientation: memory is only related to the temporal order of events, i.e. recent encounters with resource items. Furthermore, the ARS still is a modified random walk (‘composite random walk’; Benhamou 2007) with a context-dependent directional correlation. Due to the lack of spatial memory the choice of the movement direction remains nonetheless a random process.

Like more simple random walk models the ARS models thus still assume that movement can be adequately described according to the statistical mechanics underlying the movement of physical particles, i.e. that movement can indeed be modelled as random walk. Only the statistical properties of the walk may change according to conditions. However, most animals possess (highly developed) perceptual and cognitive capabilities (including the ability to memorize, process information, and take decisions, as noted by Gautestad 2011). Individuals with such capacities can be expected to actively take informed, non-random decisions. Individuals from many taxa have indeed been shown to store information about their environment and use this memory to influence their behaviour (e.g. cognitive maps for navigation; for reviews see Moser et al. 2008; Moser and Moser 2008).

In summary, if we want to understand the (microscopic) mechanisms of movement the random walk framework appears to be ill suited. At a small scale mechanistic movement models should instead ac-

count for the physiological and behavioural processes that generate a sequence of (informed) movement decisions. This does not exclude, however, that random walk models may serve well as integrative tools for the description of large scale movement phenomena. While individual movement decisions may have a completely mechanistic and deterministic basis, the unpredictability of external conditions and signals (typically not recorded by a human observer) impacting upon individuals result in an apparent randomness of movement, especially over larger spatial and temporal scales.

Over the last years a number of approaches have been developed that model movement decisions based on individually or even evolutionarily ‘learned’ information about the spatial distribution of e.g. food resources. Some of these follow the ‘patch-matrix’ approach and thus do in fact not model movement but only emigration (Klaassen et al. 2006; van Gils 2010). Others still adhere, to a certain degree, to the random walk approach (Gautestad and Myrsetrud 2010a,b; Gautestad 2011; van Moorter et al. 2009) or assume that individuals learn optimal movement rules for a specific landscape during their life (Mueller et al. 2011).

In a conceptual paper, expanding the movement ecology paradigm of Nathan et al. (2008), Getz and Saltz (2008) have compiled the general elements that are necessary to build mechanistic movement models. Their paper provides a framework for the construction of such models that account for an individual’s motivation as well as its ability to perceive, memorize, or make inference based on past experience (see also Mueller and Fagan 2008). Here, we generally follow this framework, yet focus on the specific case of foraging behaviour (or more generally the search for any resource, i.e. host plants, oviposition sites) and expand it to account in more detail for the process of perception, memory building and use.

With great diligence Getz and Saltz (2008) explain the concept of ‘fundamental movement elements’ and ‘canonical activity modes’ — we will ignore these complexities here and simply assume that individuals move at constant speed. Further, Getz and Saltz (2008) point out that movement can be driven by different motivations and that movement decisions will be a consequence of some weighting of the different needs of the moving animal. Here, we will focus on movement motivated only by a single reason, i.e. the motivation to find food or host plants suitable for e.g. egg deposition. We do not account for competing motivations. In our model we are, however, more specific than Getz and Saltz (2008) with respect to three issues: (1) We clearly distinguish whether information about the landscape is based on perception or on memory of locations visited in the past; we allow for both (see also Mueller and Fagan 2008). (2) Furthermore, in our model an individual has the ability to make an informed guess (inference) about the state of unknown locations (neither perceived nor visited in the past) based on the information it has gathered. As outlined above, such an inference is sensible when the landscape is informative, i.e. when resources are distributed non-randomly. Note that this reasoning is always applicable, regardless of whether an observed cell was occupied or empty. This allows the focal animal to construct a ‘spatial inference map’ of the expected resource distribution based on the perceived and memorized locations of resources, and the learned or inherited knowledge about the statistical properties of the spatial distribution of these resources. Such an ability is also the core attribute of a ‘Bayesian forager’ (e.g. Klaassen et al. 2006; van Gils 2010). (3) Finally, any movement decision is the basis for future movement decisions, and therefore influences the availability of new options. Optimal movement decisions should therefore not only account for the immediate benefits of an action, but take into account the consequences for future movement. This aspect of ‘anticipation’ lays at the heart of the ‘travelling salesman problem’ (e.g. Wong et al. 2010; Lihoreau et al. 2012) and has not been discussed by Getz and Saltz (2008).

The model we propose in the following is a first step towards a mechanistic model of animal movement that simultaneously accounts for perception, memory, inference and anticipation. Although we make a number of severe simplifying assumptions. Already a very basic introduction of these processes leads to promising results, such as the emergence of highly efficient movement patterns that include (1) straight line search between patches (Zollner and Lima 1999), (2) systematic, grid-line search within patches and (3) foray search, i.e. loops returning to not yet fully depleted patches (e.g. Conradt et al. 2003).

Model description

Landscape

We modelled the movement of a single individual searching for resources distributed in a landscape of finite size, e.g. an insect foraging or searching for host plants. To simplify the storage (memory) and use of information our landscape is modelled as a hexagonal grid (500 x 500 cells). Cells are either

empty or contain one resource item. To allow for different degrees of spatial correlation, resources were distributed using a Thomas process (R 2.14.1; package “spatstat” version 1.25-0). This allows us to control the number of clusters (κ), the degree of clustering (σ ; standard deviation of the displacement from the cluster centre) and the number of items per cluster (μ). The resulting (continuous) coordinates were rounded to fit the underlying grid. No more than one non-renewable resource item was placed into a cell, i.e. duplications were omitted (resource content of cell i at time t : $C_{i,t} \in \{0, 1\}$). In addition to simulations with dense (1: $\kappa = 500$, $\sigma = 1$, $\mu = 150$) and three intermediate degrees of resource clustering (2: $\kappa = 500$, $\sigma = 2$, $\mu = 34$; 3: $\kappa = 500$, $\sigma = 4$, $\mu = 28$; 4: $\kappa = 500$, $\sigma = 6$, $\mu = 26$) we ran our model using a landscape with approximately randomly distributed resources (5: $\kappa = 500$, $\sigma = 20$, $\mu = 26$). Furthermore, we include results from one landscape that is heterogeneous in cluster size (6: including an equal number of clusters generated according to landscape 1 and additionally to $\kappa = 50$, $\sigma = 5$, $\mu = 1000$) and one that is heterogeneous in the degree of clustering (7: including an equal number of clusters generated according to landscapes 1 and 4). Parameters (especially μ) were tailored such that in all generated landscapes about 5% of cells contained a resource item (probability of containing a resource item $E_0 \approx 0.05$). Note that the initial landscape parameters do not correspond exactly to the resulting landscapes since the Thomas landscape is distorted by fitting the coordinates to the hexagonal grid. For every replicate simulation run a new landscape was generated. 100 replicates were used for the results presented below.

Movement model and rules

Movement decisions are deterministic. Exceptions may occur if two or more movement directions are equally attractive according to the criteria given below. The process leading to an individual’s decision has four central elements: (1) perception, (2) memory, (3) inference and (4) anticipation. Firstly, information about the resource content ($C_{i,t}$) of visited and perceived locations (cells i at time t) is stored in the animal’s memory. We assume here that perception and memory are free of errors. Secondly, the focal animal may infer from its memory (position of occupied and empty cells) and from learned or inherited knowledge about general landscape properties (mean resource density and correlation) the state of unknown cells. Initially, the probability of finding a resource at a given location i equals the mean resource content (E_0). With inference the probability of finding a resource may be higher or lower than this uninformed guess. Finally, while considering its movement options based on perception, memory and inference the individual may not only evaluate the direct benefits of the next movement step but also ‘anticipate’ — and take into account — how this decision affects its prospects for future movement. In the following, we will explain the rules implemented for each of the four components of the movement model in more detail.

Perception and memory

We assume that animals have a restricted perceptual capacity and can thus only perceive the content of cells within a defined perceptual range (radius of the perceptual range: P). The focal animal stores this perceived information in a map of the landscape. The internal map has two components: firstly, it contains information about the present resource content of a cell (cells containing a resource item: $C_{i,t} = 1$; empty cells $C_{i,t} = 0$). Secondly, it contains information about whether the cell has been previously harvested ($H_{i,t}$) or not (harvested cells are empty: $C_{i,t} = 0$ and $H_{i,t} = 1$; non-harvested cells: $H_{i,t} = 0$). This additional information is important because, on the one hand an individual should avoid revisiting a harvested cell (resources do not regrow), but on the other the information that the cell contained a resource item in the past remains valuable for the inference of the state of neighbouring cells.

Inference

In addition to the certain knowledge provided by direct perception and memory, an individual may also estimate the resource content of unobserved cells. Such an inference becomes possible if the general statistical attributes of the spatial distribution of resources (i.e. mean resource density and correlation) are known to the individual. If these general properties show temporal persistence it is very likely that such information is learned evolutionarily, i.e. saved in the genome. Without any prior information about the correlation of resources the expected probability that a cell contains a resource item equals the mean

resource density in the landscape (E_0) — in our simulations $E_0 \approx 0.05$. However, when resources are correlated in space, information about the state of a cell confers information about the state of other cells in its vicinity: cells in the vicinity of an occupied cell have themselves an increased probability of containing a resource item (figure 1 A). Vice versa, the probability of finding a resource item in the surroundings of an empty cell is reduced (figure 1 B).

In our simulations we use a very simple approximation to calculate the expected resource content of a

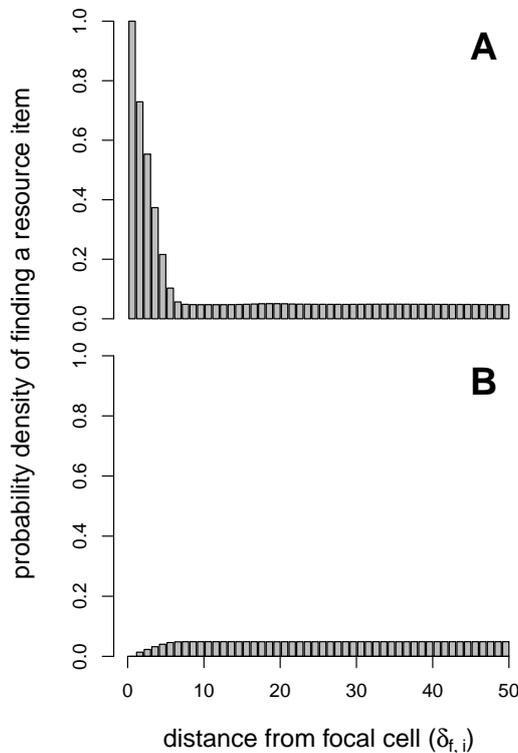


Figure 1: Probability of finding an occupied cell in the surroundings of a focal cell (occupied cells in panel A; empty in panel B) at a given distance ($\delta_{f,i}$) for a densely clustered landscape ($\sigma = 1$). For the meaning of the parameter values see text.

focal cell ($E_{f,t}$) based on averaging the information of its surroundings (with inference radius R). This is only done for a cell that has not directly been observed. The expected probability that a cell f contains a resource item at time t is calculated as follows:

$$E_{f,t} = \begin{cases} 0 & \text{if } C_{f,t} = 0 \\ \frac{1}{n} \sum_{r=1}^n (C_{r,t} + H_{r,t}) & \text{if } C_{f,t} = \text{unknown} \\ 1 & \text{if } C_{f,t} = 1 \end{cases} \quad (1)$$

with $C_{r,t} = E_0$ for so far unobserved cells. $n = 6 \cdot \sum_{i=1}^R i$ is the number of cells in the inference radius R around the focal cell f . As pointed out above, including $H_{r,t}$ in this calculation allows to derive correlative information from formerly occupied cells even when they have been harvested. Note that inference is only used when the state of the focal cell is unknown. Furthermore, inferred information is not saved for use in the next time step, i.e. inference is always based on secure knowledge. Note that the optimal inference radius (R), i.e. the inference radius that leads to the highest foraging success, should correlate with the average degree of clustering (σ).

As foraging is destructive in our model, i.e. resources do not regrow, inference is only spatial and not temporal. This is a valid approximation as long as the time scale under consideration is shorter than resource regrowth. At larger time scales temporal inference could, for example, be a driving force for the establishment of home ranges (e.g. van Moorter et al. 2009).

Anticipation

During each time step the animal decides to move to one of its six neighbouring cells (movement direction $\alpha = 30^\circ, 90^\circ, \dots, 330^\circ$; see figure 2), i.e. step length is fixed to 1. Based on its internal map which contains perceived and memorized as well as inferred information about these cells an individual will decide on its next movement step. Clearly, a rational forager should choose the direction resulting in the largest foraging success. It could thus choose the neighbouring cell with the largest $E_{i,t}$ value. Yet, as every step into a particular direction changes the position of the individual, it also influences the potential foraging success of following steps. Thus, individuals should base their movement decision not only on the resource content of the six directly neighbouring cells but also on that of subsequent cells. Indeed, the larger the area covered by the internal map the more the problem of an ideal anticipation resembles that of solving a ‘travelling salesman problem’. We sidestep the issue of resolving this rather complex problem here. Instead, we assumed that the movement decision is taken according to a simple hierarchical rule of thumb: (1) Generally, the animal moves into the directly neighbouring cell (direction α) with the highest expected resource content $E_{i,t}$. (2) If this is ambiguous, i.e. two or more cells have the same expected content, the animal will additionally take into account the content of neighbours to the potential target cells (see figure 2 for a detailed description of the process). We then calculate the specific attractivity of a direction α as the sum of the probability of resource encounter ($E_{i,t}$) in the target cell and the cells directly adjoining the target cell in that direction (see figure 2). If this does not yield an unambiguous result the refinement is repeated until a maximum of three cell rings have been used for the assessment. If at that moment two or more directions are still equally attractive the animal chooses randomly between these options. Exploratory simulations show that this happens rarely and that further increasing the number of cell rings used for anticipation does not change our results importantly.

Note that these movement rules, although being memory based, are rather local. Attraction by known resource patches far beyond the perceptual range (e.g. as known from primates: Normand and Boesch 2009; Presotto and Izar 2010) and the inference radius is not included. This simplification will not alter our results significantly, especially since foraging is destructive (see above).

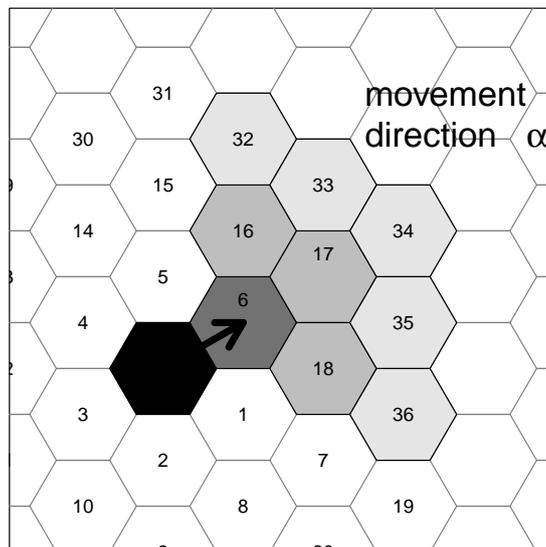


Figure 2: The attractivity of a movement direction (in this case $\alpha = 30^\circ$ i.e. a movement to cell 6) is determined by the sum of the probability of resource encounter ($E_{i,t}$) in the focal cell in direction α (cell 6) and the three neighbours of this cell (cells 16, 17, 18) which are not themselves neighbouring the current position (cell 0) of the individual. If this does not yield an unambiguous result the refinement is repeated until a maximum of three cell rings have been used for the assessment. Here cells 32–36 could be used additionally.

Simulation experiments

In all simulation experiments the focal animal was released in the centre of the landscape. Simulations ended, whenever the foraging individual reached the border of the landscape (absorbing boundary conditions) or when the maximum number of movement steps ($N = 1000$) was reached. In order to compare the performance of different movement strategies we calculated the foraging success of a strategy as the number of resource items collected divided by the number of iteration steps (e.g. Bartumeus and Levin 2008) over all 100 replicate simulations runs. We analysed the influence of the parameters of our model by varying the perceptual range ($P \in \{0, 1, 2\}$) and the inference radius ($R \in \{0, 1, 2, \dots, 10\}$).

We compared the foraging success of our spatially informed forager with two implementations of a modified random walk: (1) an area restricted search (ARS) and (2) an omniscient, biased correlated random walk (BCRW). This is done in seven landscapes differing in the degree of clustering of resources (see above).

Area restricted search (ARS)

The concept of the area restricted search introduces the idea that individuals have the ability to memorize a sequence of temporal events. In such an ARS the correlation, i.e. the straightness of the walk, increases as a function of the time since the last encounter with a resource item (Kareiva and Odell 1987; Benhamou 1992). The correlation coefficient is calculated as $\rho_t = 1 + (\rho_{t-1} - 1) \cdot e^{-d \cdot \Delta t}$, with $\Delta t = 1$, and is thus bounded between 0 (no correlation, i.e. diffusion) and 1 (maximal correlation, i.e. straight walk). After each resource encounter ρ is reset to zero. In biological terms this means that a resource encounter fully satiates the focal animal; d can then be interpreted as the decay rate of the satiation. Step length was set to 1 cell as for the spatially informed forager and turning angles were drawn from a wrapped Cauchy distribution (e.g. Bartumeus and Levin 2008, for a discussion see Codling et al. 2008; R 2.13.1; package ‘‘CircStats’’ version 0.2-4) and transformed to the grid. We ran simulations for $d \in \{0.01, 0.1, 1, 10\}$. A maximum was always found within this interval.

Biased correlated random walk (BCRW) of omniscient individuals

In contrast to the ARS, this strategy is based on the assumption that an individual has an unlimited perceptual range and thus always perceives the complete landscape, i.e. is omniscient. In addition to a correlation of turning angles as in the ARS (see above) the BCRW thus assumes that the turning angles are biased towards a target. Here, the target is always the nearest resource item.

We will use an implementation of a BCRW as proposed by Bartoń et al. (2009). The directional bias (β) is a function of the distance to the next resource item ($\delta_{f,i}$, measured as number of cells between the focal cell f and the next resource cell i): $\beta = \tanh(b\delta_{f,i})$ with b as the strength of the bias (for a detailed analysis of this movement strategy see Bartoń et al. 2009). The resulting mean turning angle of the BCRW (Φ_t ; location parameter; modal angle of the wrapped Cauchy distribution) is influenced by both, the turning angle of the last time-step (Φ_{t-1}) and by the angle to the nearest resource item (Ψ_t): $\Phi_t = (1 - \beta)\Phi_{t-1} + \beta\Psi_t$. For simplicity the correlation coefficient (concentration parameter ρ) is fixed. Although no grid is needed for these simulations we used the same landscapes as described above and set step length to 1 for a better comparability. We ran simulations for $b \in \{2, 3, 4\}$ and $\rho \in \{0.8, 0.9\}$ (sensible parameter values were extracted from Bartoń et al. 2009).

Results

Qualitative description and influence of perception, memory and inference

Our implementation of a spatially informed forager generates a broad spectrum of movement patterns. These show two characteristic attributes (see figure 3 B): (1) inter-patch movement is typically very straight and (2) larger turning angles emerge during a more or less systematic, grid-line (‘meandering’) search behaviour inside resource patches. To this respect the pattern resembles that generated by an ARS and is in good accordance with the behavioural dichotomy (correlated movement in the matrix and uncorrelated random walk in resource patches) observed e.g. in butterflies (Schtickzelle et al. 2007) or grasshoppers (Kindvall 1999; Hein et al. 2003). Depending on the landscape attributes (degree of

clustering σ) the spatially informed forager is, however, much more efficient than the best ARS strategy (see below).

The driving mechanism behind these emergent path properties is the joint effect of perception, memory,

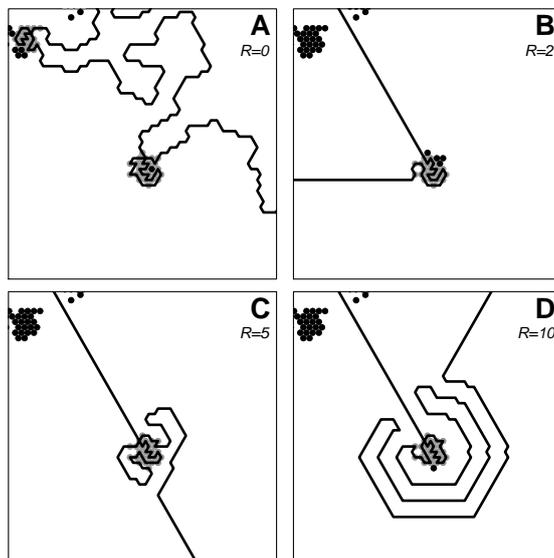


Figure 3: Influence of the inference radius (R) on the resulting movement path of a forager with a perceptual range of one cell ($P = 1$) in a densely clustered landscape ($\sigma = 1$). Panel A depicts the movement path of an animal with memory, but without spatial information (inference; $R = 0$). The movement path of a spatially informed forager using all cells in a radius of $R = 2$ to assess the status of so far unvisited cells is shown in panel B. The systematic, grid-line search pattern within patches is mainly a result of perception and memory use. In addition, the use of spatial information (inference) leads to straight walks between resource patches. A further increase of the inference radius (R) leads to foray loops (panel C) and an intense systematic search for new resources in the vicinity of patches discovered (panel D). Black dots are resource items, grey dots are harvested resource items.

inference and anticipation on movement decisions. Figure 3 illustrates the influence of the inference radius (R) on the movement pattern of an animal moving in a landscape with a high degree of resource clustering ($\sigma = 1$). Even in the absence of any inference ($R = 0$; figure 3 A) the movement pattern of an individual using an internal map is clearly different from that of individuals following a pure random walk (not shown): the movement in the matrix is obviously (relatively highly) correlated. This pattern emerges, because animals with memory typically do not reverse the direction of their walk — except if resources were detected — because they have memorized that the observed cells behind them are empty. The most attractive, because unexplored, movement directions are thus the three cells lying ahead of the animal.

Introducing inference, i.e. the capacity to make an informed guess about the state of an unknown cell (e.g. inference radius $R = 2$; figure 3 B), leads to straight line walks as long as no resources have been detected. This is due to the fact, that the cell directly in front of the animal has the highest inferred $E_{i,t}$ value, since the distance to observed empty cells (behind the animal) is maximal. As soon as a resource patch has been detected this strategy shows a very systematic, grid-line search behaviour, because it has the capacity to memorize detected, but not yet harvested, resource items. Note that this pattern does not depend on inference in densely clustered resource aggregations, the size of the perceptual range and anticipation are decisive here.

In addition to this, foray searches — i. e. looping trajectories — may be observed if the inference radius (R) is further increased (e.g. $R = 5$; figure 3 C). This happens because the animal reorientates its movement towards a resource patch it has recently left, on the one hand due to the attractivity of perceived, but not yet depleted cells, and, on the other, due to a decline in its expectation (inferred probability of positive encounter) for the cells ahead. This expectation gradually declines the longer it moves without detecting a resource item. As such foray searches limit the total area an individual

covers within a certain time interval they may reduce search efficiency in our simulations, as resources do not regrow (see figure 4). For very large inference radii ($R = 10$, figure 3 D) animals keep searching systematically in the surroundings of detected resources. If there is a large discrepancy between the assumed correlation distance (reflected by R) and the real correlation of resources in the landscape as in this example (figure 3 D), the animal will search intensely outside resource patches. This reduces the efficiency of inter-patch movement and leads to very inefficient search strategies.

Detailed model analysis

A more systematic analysis of the influence of perceptual range (P) and inference radius (R) is shown in figure 4. We compare the foraging success of the spatially informed strategy with area restricted searchers (ARS) and individuals following a biased correlated random walk (BCRW). Note, that for the sake of simplicity we only show the most efficient types of ARS and BCRW. For the ARS this value was a function of the decay rate (d) of the correlation: depending on the correlation of the landscape intermediate values of d ($d = 0.1$ for $\sigma = 1$, i.e. highly clustered landscape) or high values of d ($d = 1$ for $\sigma = 20$, i.e. random landscape) were optimal (see also Bartoń and Hovestadt 2013). The most efficient BCRW had high values for both correlation ($\rho = 0.9$) and strength of bias ($b = 4$). This ultimately leads to a straight (deterministic) walk towards the next resource item. While for the BCRW the perceptual range (P) covers by definition the whole landscape we restricted our simulation experiment with ARS to a detection radius of $P = 0$, i.e. the individual can only see the cell it presently occupies.

Obviously, the perceptual range (P) has an enormous influence on the search efficiency of individuals. Consequently, in all landscapes search efficiency increases with perceptual range and the BCRW searcher consistently outperforms any search strategy with a finite perception.

However, the results also show the enormous influence of spatial information use (i.e. inference) on foraging success. When individuals use an internal map but no inference ($R = 0$) they are not only outperformed by individuals following a BCRW but also by those following an ARS (obviously only if also $P = 0$ as assumed for the ARS). This holds for all types of landscapes analysed. Yet, as soon as individuals use spatial information (inference, $R > 0$) they perform better than those following an ARS. This particularly holds if the resource distribution is clustered (high information content of the landscape) and the assumed inference radius (R) fits the correlation distance of resources in the landscape (maxima in figure 4; see below). In this case (e.g. figure 4; left panel; $P = 0$, $R = 2$) spatially informed individuals are over three times as successful as those following an ARS. In general, the optimal inference radii, i.e. maxima in figure 4, correlate quite well with the degree of clustering σ (see table 1).

The benefit of inference clearly depends on the statistical pattern of the resource distribution. The

Table 1: Optimal inference radii (R) depending on the degree of clustering (σ) of the landscape. The upper row shows the degrees of clustering (σ) assumed for each of the five tested landscape settings. The lower row sums up the results shown in figure 4 and shows the resulting optimal inference radii (R) for each landscape. Optimal values for R are those that lead to the highest foraging success. Note that since the landscape is grid-based R may only take integer values. The difference between the landscape clustering parameter (σ) and its estimate, i.e. the optimal inference radius (R), may be due to the distortion of σ while fitting the Thomas landscape to the hexagonal grid.

landscape clustering (σ)	1	2	4	6	20
optimal inference radius (R)	2	3	5	6	<i>no optimum</i>

difference in search efficiency between area restricted searchers and spatially informed foragers decreases with decreasing resource clustering. Without any correlation of resources — i.e. in a random landscape — observations do not provide information about the status of unobserved cells (see figure 4, right panel). In these landscapes there is no difference in performance between individuals following an ARS, and those using an internal map with or without spatial information.

Heterogeneity in cluster size (figure 5; left panel) does not alter the general findings reported above. The presence of larger clusters leads to a clear increase in foraging success for the optimal informed strategy in comparison to the ARS. The informed strategy shows a highly efficient intra-patch search behaviour (see figure 3) and avoids leaving a resource cluster before having harvested it thoroughly.

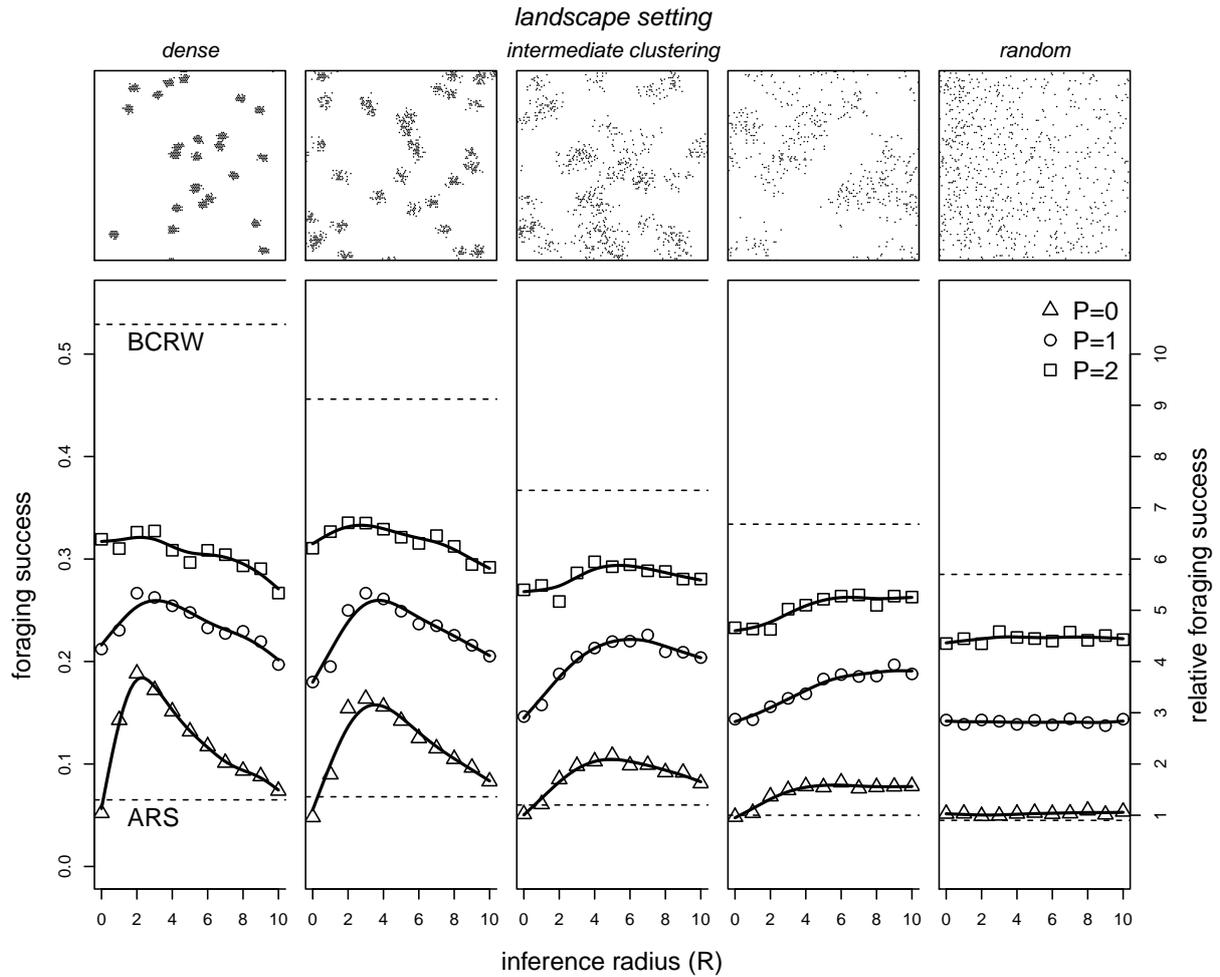


Figure 4: Systematic model analysis: influence of inference radius (R), perceptual range (P) and of landscape attributes (from left to right: dense clustering to a random landscape, depicted at the top; $\sigma = 1, 2, 4, 6, 20$) on foraging success, i.e. resource items found per iteration for 100 replicates. The relative foraging success can be read from the right y-axis (relative to the mean resource content of 5%, i.e. the foraging success of a straight line search). For comparison foraging success of the best ARS and BCRW are shown as dashed lines. The continuous smoothed lines are smooth spline regressions ($\lambda = 0.45$).

Evidently, heterogeneity in the degree of clustering (figure 5; right panel) reduces the efficiency of all search strategies (including ARS and BCRW) since, without any behavioural plasticity, it is difficult to find an optimal strategy for such a landscape. Yet, as long as the landscape is not completely random (as in figure 4; right panel) the optimal informed strategy still performs better than an ARS.

Discussion

In the past several concepts and models for the movement of informed foragers have been presented (e.g. van Gils 2010; van Moorter et al. 2009; Mueller et al. 2011; Nathan et al. 2008; Getz and Saltz 2008). To our knowledge the above presented model is among the first, however, to combine the effects of four fundamental cognitive abilities: perception, memory, inference and anticipation. In addition, it is not implemented as a derivative of a random walk (Gautestad and Myrsetrud 2010a,b; Gautestad 2011; van Moorter et al. 2009). Admittedly, the solutions employed here to save information in an internal map, to account for inference and implement anticipation are very simple and probably not optimal solutions

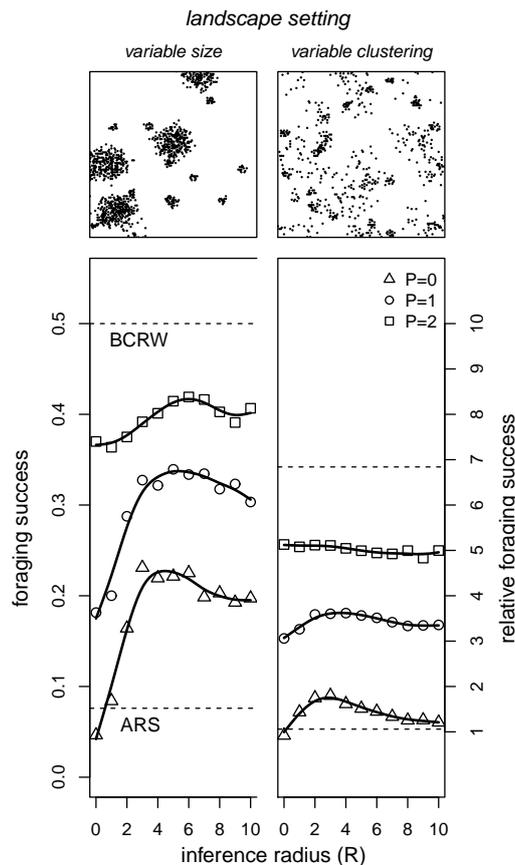


Figure 5: Heterogeneous landscapes: influence of inference radius (R), perceptual range (P) and of landscape attributes (from left to right: heterogeneity in cluster size, heterogeneity in degree of clustering) on foraging success, i.e. resource items found per iteration for 100 replicates. The relative foraging success can be read from the right y-axis (relative to the mean resource content of 5%, i.e. the foraging success of a straight line search). For comparison foraging success of the best ARS and BCRW are shown as dashed lines. The continuous smoothed lines are smooth spline regressions ($\lambda = 0.45$).

for each of these sub-problems. For the problem of inference, for example, Bayesian approaches (e.g. Klaassen et al. 2006) may provide optimal solutions. Yet, note the good fit between the degree of resource clustering (σ) and the estimate provided by the optimal inference radius (R ; see figure 4 and table 1). Modified solutions of the travelling salesman problem (e.g. Wong et al. 2010) would constitute ideal anticipation algorithms. We chose not to combine these approaches — which are typically complex on their own — into a single unified movement model in order not to blur the main message we intend to convey. Moreover, nature itself may often provide only simple ‘rules of thumb’ that perform approximately as well as theoretically optimal solutions.

Due to the use of an internal map, the spatially informed search strategy improves efficiency of foraging at two scales: within patches and during the transition between patches. This can be seen in figure 3 B where the focal animal clearly changes from an (optimally) straight walk between resource clusters to a systematic search within such patches. Particularly in densely clustered landscapes foraging success may be more than tripled compared to an ARS (figure 4, left panel). Crucially, these patterns emerge from our implementation of basic cognitive attributes (perception, memory, inference and anticipation). Note that similar hybrid search strategies with high search efficiency have been described by Zollner and Lima (1999): their ‘average-distance rule’ incorporates straight-line search and a circling path. Yet, in their model these patterns are explicitly implemented and not emergent properties of an underlying mechanistic movement model (Mueller and Fagan 2008; Getz and Saltz 2008).

Here, we show that inference and anticipation based on perception and memory are crucial components

of foraging behaviour leading to high search efficiencies. This is quite different from an ARS where search effort is also concentrated to resource patches but is nonetheless random and thus less efficient. Evidence for systematic searching has been found in numerous animal taxa (see Bartumeus and Catalan 2009, and literature cited therein). The adequacy of inference in our model crucially depends on the radius (R) used to infer the state of cells not yet visited. The optimal choice of R must reflect information about the statistical properties of the landscape (in particular the degree of clustering σ ; figure 1, figure 4 and table 1). Individuals may learn such information in the course of their life. However, for many taxa that live in stable environments we may also assume that this information is ‘learned’ evolutionarily and stored in the genome.

We have also analysed the effect of increasing the radius of perception (P). We show that increasing the range of perception obviously increases foraging efficiency. At the same time it reduces the value of inference (figure 4 and 5). As a consequence a BCRW which assumes an infinite perceptual range does not need any inference. Note that for the ARS inference is implicitly included in the decay rate.

Interestingly, in addition to rather straight movement between patches and a grid-line search behaviour within patches our model may also generate looping behaviour (figure 3 C) similar to the ‘foray searches’ reported for many insect species, mammals and birds (e.g. Conradt et al. 2003; Conradt and Roper 2006). In our model the responsible mechanism underlying the emergence of this movement pattern is the use of spatial memory in combination with inference and anticipation. Individuals remember locations in which resources were present and assign a higher probability of finding resources to cells in the surroundings. Depending on the assumed correlation distance of resources this area may extend beyond a resource patch. This zone of influence of observed occurrences is further increased by anticipation. Foragers leaving a resource patch may then be re-attracted to a patch left a short while ago.

In our model we did not allow for any memory decay. Individuals remember everything they have perceived throughout their life. However, the ability to memorize presumably comes with a cost. It is thus interesting to ask how well our search strategy would perform if memory were restricted to a certain time span. Additional simulation runs with such limited memory show that restricting memory to even just the last 10 movement steps has a minor effect on foraging success. In fact, when individuals use much too large and suboptimal inference radii (e.g. $R = 10$ in a densely clustered landscape with $\sigma = 1$) limited memory may even increase foraging success. Such an overestimation of the degree of clustering of a landscape leads to intense search in the vicinity of resources (see figure 3 D). Limited memory compensates this error and, in this case, drives the individual away from already explored landscape areas. This phenomenon is similar to the observation of Boyer and Walsh (2010) who find in a BCRW model that — besides the inclusion of random steps — an intermediate use of memory is optimal. This happens because the use of memory alone results in a lack of exploratory behaviour which is important in changing landscapes. This idea also applies to our model, although the landscape changes only in space (resources are clustered) and not over time as in Boyer and Walsh (2010). Of course, the robustness of our model to memory loss is due to the destructive foraging scenario. If resource dynamics were included a movement strategy which infers resource content over space and time would be advantageous. Including an estimate for regrowth speed could be done in analogy to the inference radius.

The landscapes shown in figure 4 evidently assume a fairly constant degree of resource clustering (σ). Most natural landscapes though will be heterogeneous in this respect. This strict assumption is relaxed in figure 5. Although it might be impossible to find a truly optimal strategy in such cases (under the premise of no behavioural plasticity) we show that our movement rules are still advantageous in comparison to an ARS, regardless whether the landscape is heterogeneous in cluster size or the degree of clustering (see figure 5). From figures 4 and 5 it is clear that the inference radius becomes less important with increasing randomness of the landscape. The optimal spatially informed strategy still may have an advantage over an ARS since information use leads to a good exploitation of the dense clusters and is not relevant in those parts of the landscape showing only more or less randomly distributed resource items. In summary, for intermediate cases the efficiency of the informed strategy will be reduced in comparison to landscapes with homogeneous clustering and diminish with increasing proportions of less densely clustered resources, just as figure 4 suggests. Note that this only relates to heterogeneity in clustering, i.e. to the form of the boundary of resource clusters. Our results are not affected by varying cluster core sizes (see figure 5), since foraging success in a cluster core is not dramatically affected by suboptimal inference radii (see figure 3).

Our model focuses on the search for a single critical resource, which does not need to be food, but could also be e.g. plants suitable for oviposition. However, if the internal state of the focal animal was to

shift from foraging to e.g. oviposition, mate finding, or search for shelter, several layers of internal maps representing the known or inferred distribution of different commodities could be included into the model (see Getz and Saltz 2008). Such multiple maps — appropriately weighted according to current needs and motivations — could then be overlaid and integrated to generate a more realistic movement decision.

The development of appropriate movement and dispersal models is central for a better understanding of population and evolutionary dynamics. This has important implications in applied ecology and conservation (e.g. metapopulation viability see Heinz et al. 2006). Nathan et al. (2008) and also Mueller and Fagan (2008) have pointed out that modelling of animal movement should be more firmly based on mechanisms. Inspired by growing evidence that a large number of taxa use more or less complex internal maps for navigation (rodents: Hafting et al. 2005; Manns and Eichenbaum 2009; Wills et al. 2010; apes: Normand et al. 2009; Normand and Boesch 2009; birds: Thorup et al. 2007; for reviews see Moser et al. 2008; Moser and Moser 2008), we have proposed a very simple, yet novel model including perception, limited spatial memory and the use of spatial information. We could show that these simple assumptions lead to wide array of emergent phenomena reaching from optimal within and between-patch search to foray loops. To a certain degree our model is an approximation of a Bayesian forager with restricted perception who updates its prior information about the landscape to a posterior expectation depending on learned or inherited information about the resource distribution in the landscape. As it stands, the model represents a first step to a better understanding of the mechanisms behind movement behaviour. Further refinements should include a better statistical model for memory based inference of the state of so far not visited cells, a model of anticipation that allows to plan more than one movement step into the future and the inclusion of distance dependent (imprecise) perception as well as restricted and imprecise memory.

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