PHILOSOPHICAL TRANSACTIONS OF **THE ROYAL SOCIETY** A | **MATHEMATICAL, PHYSICAL & ENGINEERING SCIENCES**

Modelling the mobility of living organisms in heterogeneous landscapes: does memory improve foraging success?

Denis Boyer and Peter D. Walsh

References	**This article cites 36 articles, 6 of which can be accessed free** http://rsta.royalsocietypublishing.org/content/368/1933/5645.full.html#ref-list-1
Rapid response	Respond to this article http://rsta.royalsocietypublishing.org/letters/submit/roypta;368/1933/5645
Subject collections	Articles on similar topics can be found in the following collections complexity (36 articles)
Email alerting service	Receive free email alerts when new articles cite this article - sign up in the box at the top right-hand corner of the article or click **here**

Modelling the mobility of living organisms in heterogeneous landscapes: does memory improve foraging success?

By Denis Boyer[1,2,*] and Peter D. Walsh[3]

[1]*Laboratoire de Physique Théorique, IRSAMC, CNRS UMR 5152,
Université de Toulouse, UPS, 31062 Toulouse, France*
[2]*Instituto de Física, Universidad Nacional Autónoma de México,
DF 04510, Mexico*
[3]*VaccinApe, 5301 Westbard Circle, Bethesda, MD 20816, USA*

Thanks to recent technological advances, it is now possible to track with an unprecedented precision and for long periods of time the movement patterns of many living organisms in their habitat. The increasing amount of data available on single trajectories offers the possibility of understanding how animals move and of testing basic movement models. Random walks have long represented the main description for micro-organisms and have also been useful to understand the foraging behaviour of large animals. Nevertheless, most vertebrates, in particular humans and other primates, rely on sophisticated cognitive tools such as spatial maps, episodic memory and travel cost discounting. These properties call for other modelling approaches of mobility patterns. We propose a foraging framework where a learning mobile agent uses a combination of memory-based and random steps. We investigate how advantageous it is to use memory for exploiting resources in heterogeneous and changing environments. An adequate balance of determinism and random exploration is found to maximize the foraging efficiency and to generate trajectories with an intricate spatio-temporal order, where travel routes emerge without multi-step planning. Based on this approach, we propose some tools for analysing the non-random nature of mobility patterns in general.

Keywords: mobility patterns; agent-based models; ecology; foraging behaviour;
search processes; random media

1. Introduction

The literature on the movement of mobile agents has long been dominated by random walk models in which movement decisions are first-order Markovian or have rapidly decaying correlations: that is, based entirely on conditions that are proximate in time and local in space. This approach has been extraordinarily successful in describing the behaviour of everything from microscopic particles to simple organisms such as insects and bacteria (Turchin 1998; Colding *et al.* 2008).

Extensions of random walk models beyond Brownian motion, for instance, to processes governed by steps and/or waiting times with heavy-tailed distributions (Shlesinger & Klafter 1986) have also been used to describe the displacements of microzooplankton (Bartumeus *et al.* 2003), spider monkeys (Ramos-Fernández *et al.* 2004), marine predators (Sims *et al.* 2008) or even bank notes (Brockmann *et al.* 2006). Other extensions have considered multiple random walks, which are useful to identify the presence of different behavioural states in foraging data (Morales *et al.* 2004).

However, the Markovian approach has serious limitations and other research frameworks are emerging (Nathan *et al.* 2008; Gautestad & Mysterud in press). In particular, memory storage and processing capabilities allow humans, non-human primates and other large-brained vertebrates to transcend the shackles of a first-order Markov world. Many animals escape the present using episodic memory, the ability not just to associate past events with a particular time and place but also to project how conditions at that place may have evolved since that event (Griffiths *et al.* 1999; Dere *et al.* 2008; Rolls 2008). In fact, animals can even use episodic memories of past states to predict future states (Martin-Ordas *et al.* 2010), a good example being the ability of mangabeys to predict how weather has affected the ripening of fruit (Janmaat *et al.* 2006*a*,*b*). Animals escape their current location with spatial representations such as cognitive maps (Wills *et al.* 2010), Euclidean representations of space, which allow them not only to navigate directly to important habitat features (e.g. resource patches) that are outside of the perceptual range (Normand & Boesch 2009; Presotto & Izar 2010) but also *a priori* to estimate the cost of travelling there (Lanner 1996; Janson 2007; Janson & Byrne 2007; Noser & Byrne 2007). These advanced cognitive capacities mean that movements need not be governed entirely by random decisions based on proximate states but may also be informed by deterministic cost–benefit analyses that compare the predicted benefits for different movement choices with their estimated costs (Walton & Mars 2007; Hillman & Bilkey 2010). Models motivated by observations on spider monkeys (Boyer *et al.* 2006), ungulates (Getz & Saltz 2008) or humans (Lee *et al.* 2009) have explored how such decisions can induce complex movement patterns in heterogeneous environments.

In the realm of Markovian processes, a lot of attention has been devoted in the past decade to identifying efficient search strategies for finding prey or food patches whose locations are unknown to the forager (Viswanathan *et al.* 1999, 2008; Bénichou *et al.* 2005; Oshanin *et al.* 2009). The impressive set of cognitive tools mentioned above offers the promise of more efficient foraging. Nevertheless, efficiently exploiting resources still presents some daunting challenges. Even with perfect information about the size and the location of resource patches, the computational load entailed in choosing the most efficient route through a series of patches rises exponentially with the number of patches, quickly becoming intractable (the classic 'travelling salesman problem'). What's more, in the real world information is rarely perfect. Resources are often ephemeral and unpredictable because of the irregularity of environmental forcing, resource production dynamics and harvesting rates. Consequently, the accuracy of predictions about resource quality tends to decay with time since the last visit to a given location. Because for mobile agents time tends to correlate with displacement, prediction accuracy tends to be greatest within some limited spatial neighbourhood of the agent's current location. This suggests

that the best vertebrate foragers can hope for a combination strategy akin to that employed in search algorithms such as Markov chain Monte Carlo simulations, with deterministic memory-based movements used to move the forager up local maxima in the rugged foraging efficiency landscape and occasional random steps used to explore the constantly evolving landscape for higher maxima.

Here, we use a simulation model of monkeys foraging on fruit trees to explore how spatial and temporal heterogeneity in resource distribution constrain how advantageous it is to have a big brain. More specifically, an adequate balance between deterministic, memory-based movement and random exploration is found to maximize the forager's efficiency. Therefore, some degree of stochastic search is still advantageous for foragers with high cognitive skills and foraging in not so Markov Chain Monte-Carlo scarce environments. We examine how the distribution of fruit tree sizes and the duration of fruiting influence this optimal balance. We show that the concepts of efficiency and order are intricately related in this system: optimal strategies produce the trajectories that have the highest degree of spatio-temporal order. Our simulation model assumes that monkeys have a set of fairly sophisticated skills, including cognitive maps, episodic memory and travel cost discounting. Although there is mounting empirical evidence that monkeys and other vertebrates have these skills (Janson & Byrne 2007), our conclusions do not require them. Rather, they are also valid for a much broader class of models in which the hill-climbing advantages of memory are traded off against the exploratory value of random movement (e.g. Tabone *et al.* (2010) in the context of ant foraging).

2. Model

(*a*) *Medium*

We consider a square lattice of $N \times N$ sites with lattice spacing a, where a random fraction ρ of the sites is occupied by resource patches (fruit trees). A site contains 1 or 0 resource patch. The medium is also heterogeneous in the sense that the resource patches are not of equal value. A tree located at site i has a size k_i representing the total amount of fruits it can produce each year. The tree-size probability distribution function is given by

$$f(k) = Ck^{-\beta}, \quad k_{\min} \le k \le k_{\max}, \tag{2.1}$$

with k a continuous variable, $\beta > 1$ an exponent and $(k_{\min}, k_{\max})$ two constants. The form (2.1) is justified by empirical observations showing power-law distributions for tree sizes in tropical and temperate forests (Enquist & Niklas 2001; Niklas *et al.* 2003). For low values of β (typically, in the range [2, 4]), a few sites concentrate an important quantity of resources, whereas for larger values of β the medium is homogeneous and composed of trees with similar sizes.

Each tree produces fruit once a year during a fruiting period of n_{fruit} consecutive days. $n_{\text{fruit}}(=30$ days in the following, unless otherwise indicated) is assumed to be the same for all trees. However, not all trees start fruiting at the same time. Rather, start dates are randomly and uniformly distributed throughout the year (figure 1*a*). Let us denote $\text{fruit}_i(t)$ as the amount of ripe fruit on tree i at time t.
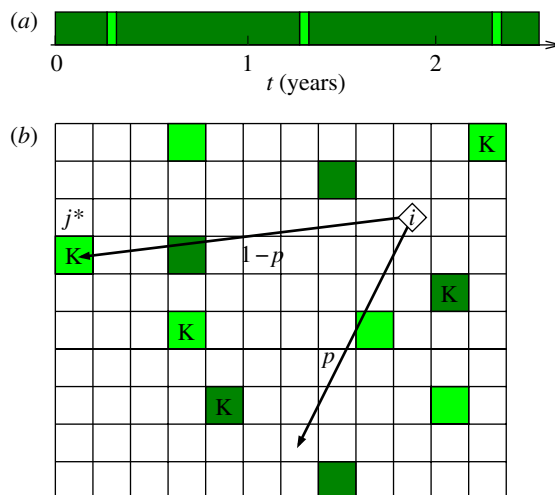
Figure 1. Resource patches, e.g. fruit trees, are randomly distributed on a square lattice with density ρ. (*a*) Each tree produces fruit during a fruiting period (light) of duration n_{fruit} days and is unproductive the rest of the year (dark). The date when a given tree starts fruiting is the same every year, and is randomly and uniformly distributed in the interval [0, 1 year]. (*b*) A forager located at tree i may take a step towards a tree visited in the past (denoted with K, as in 'known' tree) or a random step, with probabilities $1 - p$ and p, respectively. The probability p involves a parameter η (see equation (2.5)), that varies movement between entirely random ($\eta \to \infty$) and entirely deterministic ($\eta \to 0$). (Online version in colour.)

During its fruiting period, i produces k_i/n_{fruit} new ripe fruits per day (i.e. k_i fruits during the whole period). For simplicity, the quantity k_i/n_{fruit} becomes available ('ripens') at the beginning of each simulation day. Ripe fruits remain available for a period of n_{rot} days, after which they rot (become unavailable for consumption).

(*b*) *Forager movement rules*

A mobile agent foraging in this medium is either immobile eating on a fruiting lattice site with a constant feeding rate r (eaten fruits per minute) or moving at constant velocity v_0 (lattice spacings per minute). The elementary simulation time step is Δt ($=0.5$ min in the following). The agent switches its activity from eating to moving when no ripe fruit is left on a tree, and switches from moving to eating when the trajectory crosses a site with ripe fruits. The agent moves in a continuous way along linear steps joining pairs of lattice sites, and cannot exit the $N \times N$ domain. At the end of a step or after a feeding event, the forager takes a new step.

Before describing the movement rules, let us note that the agent has cognitive skills that enable it to remember the locations, sizes and fruiting states of previously visited trees. Hence, during the course of ranging, the agent adds to a list of known trees (marked as 'K' in figure 1*b*) any tree that is visited for the first time: the agent records the tree's location, size k_i, fruiting state (fruiting or not) and ripe fruit crop size. We assume that, once a tree's size and location are known, they are not forgotten. When a known tree is revisited, the agent updates its memory about the tree's fruiting state (for example, from 'non-fruiting' to

'fruiting') and fruit crop size. We assume that each forager has a model of the fruit ripening process that allows it to correctly estimate how much ripe fruit should now be in a known fruiting tree j, $\text{fruit}_j(t)$. When a tree known by the agent to be 'fruiting' actually ends its fruiting period, the forager also changes the tree's state to 'non-fruiting' in its memory. However, foragers can only predict the fruiting state of trees visited during their most recent fruiting period. They cannot remember when the fruiting periods of trees are and, therefore, cannot anticipate fruiting states from one year to another.

At each movement step, the forager may or may not decide to visit a known tree. It either heads towards a known tree j^* (with probability $1 - p$) or takes a random walk step (with probability p; figure 1b). Hence, despite its knowledge, the forager may decide to take a random walk step, which is drawn from a step length distribution function, $f_{\text{rnd}}(l)$, where $l > a$. In a deterministic step, the forager chooses as a target the known tree that is most efficient, i.e. that provides the best trade-off between ripe fruit crop size and travel distance. For this purpose, we introduce a one-step efficiency function, $e_i(t)$, given by

$$e_i(t) = \max_j \left[\frac{F_j(t)}{d_{ij}} \right] = \frac{F_{j^*}(t)}{d_{ij^*}}, \qquad (2.2)$$

where the index j runs over the list of all known trees and d_{ij} is the distance between forager location i and tree j. The quantity F_j is the estimated amount of ripe fruit in tree j and, if the tree is known as 'fruiting', is given by

$$F_j(t) = \text{fruit}_j(t). \qquad (2.3)$$

If the tree is known as 'non-fruiting' then $F_j(t) = 0$ if the tree has already been visited during the current day; otherwise,

$$F_j(t) = \langle \text{fruit}_j(t) \rangle, \qquad (2.4)$$

the average being taken over an entire year. In equation (2.4), a tree known as 'non-fruiting' can still be considered as a potential destination as the tree may have started fruiting since the latest visit. Nevertheless, it tends to be less attractive than a known 'fruiting' tree of the same size and at the same distance, as $\langle \text{fruit}_j(t) \rangle$ tends to be lower than the typical amount of fruit that j carries during its fruiting period. The rule (2.2) simply indicates that the closer and the larger a known tree is, the more efficient would be a step towards that tree. The particular tree that maximizes equation (2.2), or the 'best' known tree, is j^*. Note that a fruiting tree recently depleted by the forager has $F_j(t) = 0$ and thus will not be considered until it produces new fruits the next day.

As explained above, the agent takes a step towards j^* with probability $1 - p$, where p is given by

$$p = \exp\left(\frac{-e_i(t)}{\eta} \right), \qquad (2.5)$$

with η a constant. The rule (2.5) indicates that the forager is more likely to visit j^* if it is a 'good' tree (large e_i, low p). In turn, if the known trees are far away from the current location of the forager and/or of small sizes, the forager will prefer to take a random step instead ($p \sim 1$). Therefore, the parameter η does not control

the memory capacities of the forager (which are assumed to be perfect), but the use of memory by the forager: known trees with $e_i \gg \eta$ will tend to be visited, while those with $e_i \ll \eta$ will be ignored. The limit

$$\eta \to \infty \tag{2.6}$$

produces random walk trajectories, whereas

$$\eta \to 0 \tag{2.7}$$

corresponds to a forager with movements that are entirely determined by the memory, tending asymptotically to revisit the same fruit trees. With this set of rules, if all known trees have been visited during a single day (i.e. in a time shorter than the refreshing period), then $p = 1$. At $t = 0$, the forager is placed with no previous knowledge of the medium and p is obviously 1. Each time an unknown tree is encountered (during a random walk step or *en route* towards a known tree), it is added to the list of known trees, which grows as time proceeds.

Below, we will investigate the effects of varying three parameters of the model: η (the tendency to take random steps), β (the fruit crop size distribution) and n_{fruit} (the duration of each tree fruiting period). The eating rate (r), displacement speed (v_0) and ($k_{\min}, k_{\max}$) are fixed to realistic values so that the forager visits a number of trees much larger than 1 on average during 1 day (the period of fruit refreshing). The forager often feeds no more than a few minutes on a tree but may occasionally spend a few hours on a very big fruiting tree, which is consistent with observations on spider monkeys, for instance (Ramos-Fernández *et al.* 2004).

3. Results

(*a*) *Foraging efficiency*

We start by computing the foraging efficiency of the mobile agent, defined as

$$E = \left\langle \frac{\mathcal{K}}{\mathcal{L}} \right\rangle, \tag{3.1}$$

where $\mathcal{K}$ is the total amount of fruits eaten and $\mathcal{L}$ the total distance travelled by the forager. An alternative definition is $E = \langle \mathcal{K} \rangle / t$ with t the foraging time, leading to similar results to those presented below. The average in equation (3.1), which tends to a stationary value after a few years, is taken over different realizations of the media and foraging trajectories. Figure 2*a* displays E as a function of the memory parameter η, for different tree-size exponents β. For easier comparison, $k_{\min}$ is adjusted so that the total amount of resources produced in one year in the domain, $\langle k \rangle N^2$, remains the same even though the tree-size distribution varies.

The foraging efficiency exhibits a maximum at an intermediate level of memory use, η_{opt}. Somewhat surprisingly, the deterministic, memory-based steps (2.2), which at small η are increasingly common relative to random choices, do not necessarily have a positive impact on the long-term efficiency. This property can be qualitatively understood by noticing that, given the dynamical rules of §2, random steps are often taken at the beginning of a run because of limited knowledge. When the number of known trees becomes large enough, a forager with very small η can forage exclusively on known trees between two fruit production
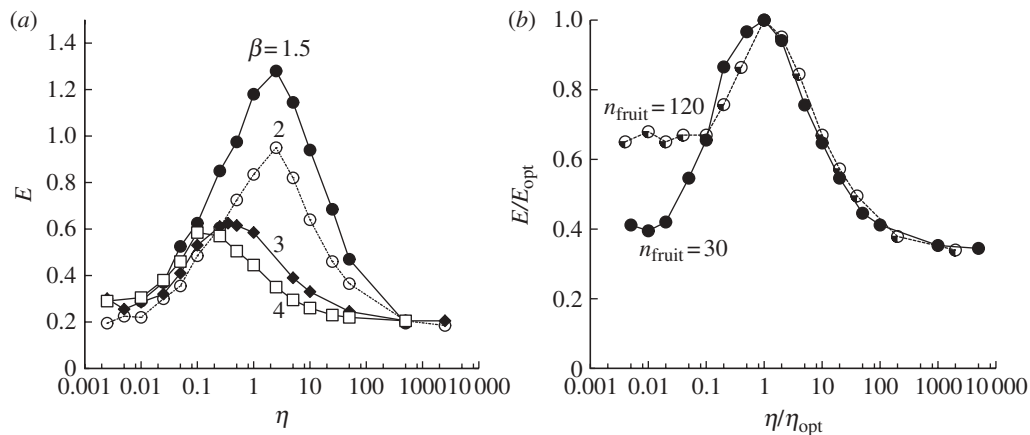
Figure 2. (*a*) Foraging efficiency in media with different levels of fruit crop size heterogeneity ($\beta = 1.5, 2, 3, 4$). The other parameters are $a = 1$, $\Delta t = 0.5$ min $N \times N = 4 \times 10^4$, $\rho = 0.75$, $\langle k \rangle = 19.9$, $k_{\max} = 2000$, $n_{\text{fruit}} = 30$ days, $n_{\text{rot}} = 7$ days, $r = 0.2$ eaten fruits min^{-1}, $v_0 = 2a$ min^{-1}, $f_{\text{rnd}}(l) \propto l^{-\alpha}$ with $\alpha = 2.5$ (the curves are little affected by other choices of f_{rnd}). (*b*) Same quantity for $\beta = 3$ and two different fruiting durations: $n_{\text{fruit}} = 30$ days and 120 days.

events (i.e. a 1 day interval). Hence, a forager with $\eta \to 0$ will tend to revisit the same set of learned tree locations, reducing the exploration of other areas where other fruiting trees could be encountered. On the contrary, a random forager (η large) visits a larger number of different trees but does not use its knowledge to improve efficiency by moving directly to large and/or nearby trees. Note that no fine-tuning of the one-step cross-over efficiency η that controls the use of random search relative to memory is necessary to bring the forager in the efficient region: the long-term forager's efficiency varies with $\log \eta$ rather than with η.

A mixed strategy is the most efficient in this context, especially if resource patches have heterogeneous sizes (small β). Whereas the foraging success of random and deterministic foragers is rather independent of the tree-size distribution, efficiency increases with medium heterogeneity in the range of intermediate strategies (figure 2*a*). In other words, the optimal strategy becomes increasingly advantageous with respect to others when fruits are unevenly distributed in space. In general, the selection of the best tree j^* is biased towards large tree sizes, i.e. thanks to rule (2.2), the forager selects preferentially a subset of trees with larger sizes than those given by a random sampling of the distribution (2.1). When β decreases, this effect becomes more noticeable. As previously shown analytically on a very simple foraging model (Boyer & Larralde 2005), the single-step efficiency (2.2) of a forager knowing many trees tends to be higher when heterogeneity increases: on average, F_{j^*} increases faster than the travel cost to j^*. This explanation does not hold, however, at low values of η in the present model, when the number of places susceptible to being visited is reduced by the lack of previous random exploration.

Another significant aspect that favours the use of a mixed foraging strategy is the fruiting duration n_{fruit} of a tree. When $n_{\text{fruit}} \ll 365$, the medium is unpredictable to the forager: at a given time only a small fraction of the trees are fruiting ($n_{\text{fruit}}/365 = 0.082$, in figure 2*a*), and they fruit for a relatively short period of time. To show that behaviours exclusively based on memory ($\eta \sim 0$) are

not adapted to rapidly changing environments, we have varied n_{fruit}. As shown by figure 2b, the use of the optimal strategy brings a greater relative advantage than the more deterministic strategies when n_{fruit} is small. Nevertheless, for $\eta > \eta_{\text{opt}}$, i.e. for behaviours more random than at optimality, the relative efficiency is not affected by the tree fruiting duration.

In the following sections, we investigate connections between the foraging efficiency and the spatio-temporal structure of the walks.

(b) *Spatial order of occupation patterns*

Processes involving memory are *a priori* more predictable than random walks. Predictability has been addressed empirically in the context of human displacements by means of entropy measures (Song *et al.* 2010). Assume that the forager is optimal because it better 'knows', at any time, where the most profitable resource sites in the disordered environment currently are and how to exploit them. Do the corresponding walks have an ordered spatio-temporal structure that would make it easier for an external observer unaware of the movement rules to predict the forager's position? Among the possible quantities related to the degree of predictability of a trajectory, we will consider two entropies: the average occupation entropy,

$$S = -\left\langle \sum_i p_i \ln p_i \right\rangle, \tag{3.2}$$

where p_i is the probability of finding the forager on site i during a time window of duration T (the average being taken over successive time windows), and the average visitation entropy,

$$S_v = -\left\langle \sum_i v_i \ln v_i \right\rangle, \tag{3.3}$$

where v_i is the number of visits that site i has received during a time window of duration T, normalized to unity ($\sum_i v_i = 1$). Contrary to S, S_v does not take into account the time spent on i, but the number of steps that arrived at i. Figure 3 displays E, S and S_v as functions of η, for media of varying heterogeneity. We set $T = n_{\text{fruit}}$ ($= 30$ days) as other choices give similar results.

S_v has lower values when η is low, meaning that the visits among sites are unequally distributed. As new fruits are produced each day, the same fruiting trees can be revisited after being depleted. The biased choice towards larger trees also amplifies uneven visits: evident in the fact that S_v decreases as β decreases, i.e. when the probability of finding large trees in the system increases. In a given medium, after a plateau (in the cases $\beta = 2$ and 6), the visitation entropy increases with η, as more frequent random steps even out the number of visits received by the different trees.

The behaviour of S is quite different as it is not the minimum at $\eta = 0$ but at an intermediate value close to η_{opt}. In the case $\beta = 3$, the location of the minimum is actually indistinguishable from the maximum for the efficiency. Low values of S can be related to uneven visits and/or uneven occupation times (hence, $S < S_v$).
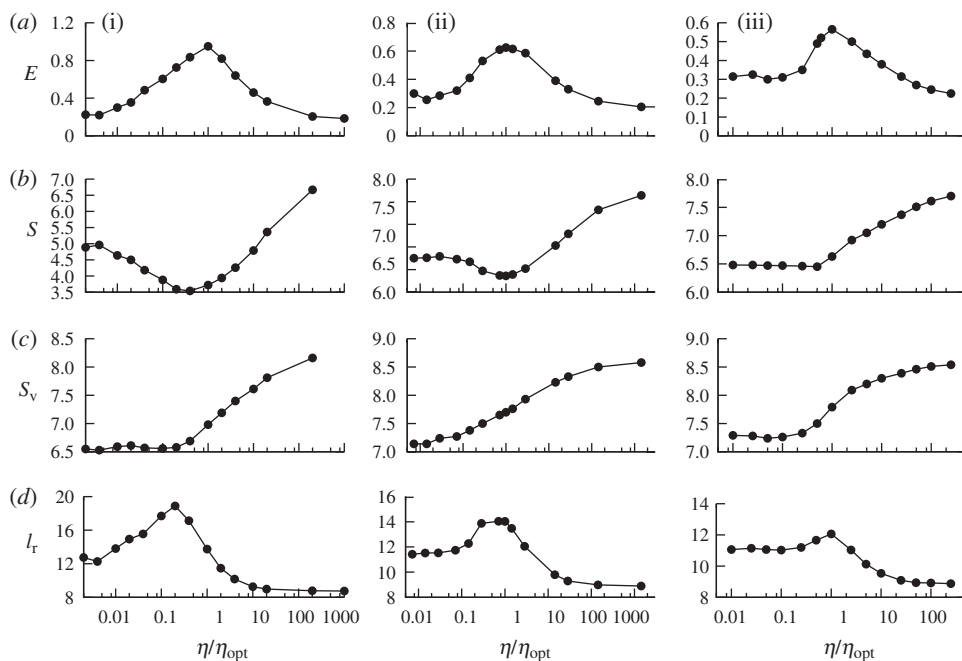
Figure 3. (a) Foraging efficiency (E), (b) occupation entropy (S), (c) visitation entropy (S_{v}) and (d) mean route length (l_{r}) as a function of the parameter for memory use (η), for (i) highly heterogeneous ($\beta = 2$), (ii) moderately heterogeneous ($\beta = 3$) and (iii) homogeneous ($\beta = 6$) landscapes.

The time spent at a tree is determined by its ripe fruit content. Given the power-law distribution of the tree sizes, one may *a priori* expect very unequal feeding times in media with small β, thus lowering the entropy. In a given medium, the curves of S show that this effect is maximal in the vicinity of the optimal strategy, when many of the trees visited in a given foraging time are currently fruiting. For $\eta < \eta_{\mathrm{opt}}$, however, the higher entropy indicates that residence times are more even: as confirmed by measures of $\mathcal{L}$ and $\mathcal{K}$ (not shown), the forager spends more time travelling and less time feeding. In this case, the fruiting trees are more rapidly depleted and non-fruiting trees are more often chosen as target sites, from rule (2.4). If a visited tree is not fruiting, the forager stays for a short time at the site, no matter the tree size. Similar patterns are observed at large η; in this situation, this is because trees are visited more randomly and most of the trees are non-fruiting.

In homogeneous media ($\beta = 6$, figure 3), visitation and occupation patterns become more similar. The minimum in S disappears and is replaced by a flat plateau: S becomes remarkably constant for $\eta < \eta_{\mathrm{opt}}$.

(c) Travel routes

The above entropy measures capture the spatial heterogeneity of the occupation and visitation patterns but not their temporal correlations. To gain some insight into the time regularity with which some sites are visited, we now look for repeated sequences in the trajectories.
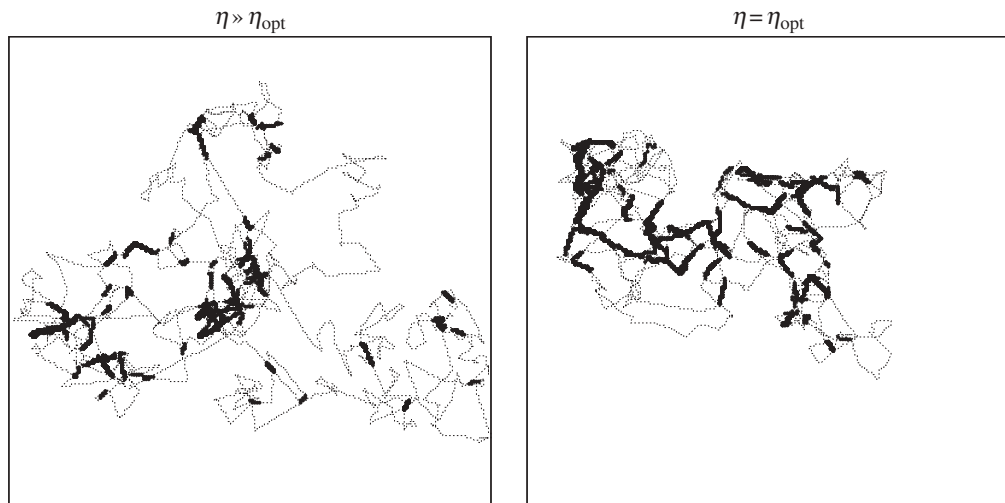
Figure 4. One-month trajectories in a homogeneous landscape, above and at optimality (same scale). The dark thick lines indicate the routes defined as subsequences of $k = 6$ or more consecutive sites that appear more than once in the trajectory (see text for details).

As in the previous section, we decompose a whole trajectory in time windows of duration T ($= n_{\text{fruit}}$ days in the following). We then convert the continuous forager positions within the same time window into a series of visited lattice sites $\{i_1, i_2, \ldots, i_n\}$. As we focus here on the paths followed by the forager, we do not count the amount of time spent at each site (therefore, two consecutive sites are necessarily different). In the series of visited sites, we denote a k-route as a sequence of at least k consecutive sites, which appear more than once. For practical purposes, two sequences that are locally distant by no more than one lattice spacing a are considered to be part of the same route. With $\rho = 0.75$ and $n_{\text{fruit}} = 30$ (the values chosen for figure 3), the mean separation distance between two neighbouring fruiting trees is approximately $6a$. As a route is likely to join two fruiting trees, we choose $k = 6$ as the minimal sequence length.

In media with homogeneous tree sizes and for the range of values of η considered in figure 3, the six routes represent about 30 per cent (higher η) to 90 per cent (lower η) of a trajectory in a given time window T. Figure 4 shows two trajectories with their routes highlighted. In this example, at optimality, about 52 per cent of the sites of a trajectory are located on the routes, the mean number of routes is 57 and each route is used 3.3 times on average by the forager. With decreasing randomness, the number of routes slightly decreases but each route is used much more frequently.

We denote the average length of a route as l_{r}. This quantity is analogous to a correlation length and indicates the persistence of the forager when it is engaged in a route. In other words, it measures the predictability of the forager's movements when it starts repeating previous positions in the same order. As shown in figure 3, this quantity reaches a maximum in the vicinity of η_{opt}, or at the minimum of the occupation entropy S. Other choices of k slightly change the values obtained for l_{r} but not the existence of the maximum near η_{opt}.

These results suggest that the optimal forager uses the routes as well as its persistence along the routes to revisit several fruiting trees consecutively (a number of the order of $l_r/6 + 1 \simeq 3$ to 4). Nevertheless, the complexity of the optimal trajectories is probably not fully described by observing a single object. At $\eta = \eta_{\text{opt}}$, the spatial structure of the routes, which is not captured by l_r alone, reveals a relatively regular, interconnected network (figure 4). In this case, the trajectory is never very far from a route. By contrast, for $\eta \gg \eta_{\text{opt}}$, the spatial distribution of the routes is less uniform, some routes become isolated whereas others are clumped.

4. Discussion and conclusion

We have shown that trading off between random and memory-based decisions can be advantageous for a forager searching for food. A mixed strategy is especially rewarding if the resources are heterogeneously distributed in space and their production period is short. Memory is in general useful, as it allows the forager to revisit resource patches without searching. But excessive memory use over stochastic decisions prevents the forager from updating its knowledge in rapidly changing environments.

Ideally, optimizing foraging efficiency in our model medium requires combined activities: (i) to deplete nearby or large known trees, (ii) to stay in the vicinity of known areas in order to revisit at low travel costs the depleted trees once they have refreshed, and (iii) to continuously search for new fruiting trees that will replace the known ones when these stop fruiting. Finding the rules that reach the absolute maximum efficiency is a task prohibitively complex. Nevertheless, an animal that uses a one-step optimization procedure such as the one considered here (instead of many-steps planning, for instance) in combination with random steps can increase its efficiency by a factor of about 3–7 compared with the uncombined behaviours. This efficiency gain is quite high. In purely random search problems with memoryless agents, optimal strategies (obtained, for instance, by tuning the Lévy exponent of a step-length distribution) typically increase the efficiency by 30–40% in scarce environments (Viswanathan *et al.* 1999). Notwithstanding, our results suggest that stochastic decisions are still playing a crucial role for organisms with extremely high cognitive skills and foraging in not so scarce environments. These findings open other perspectives in the debate on the relevance of random searches in Biology (Bartumeus & Catalan 2009; Smouse *et al.* 2010).

Memory leads to unexpected emergent patterns of habitat use, many of which still need to be studied. As shown by a recent multiple random walk approach, revisits are not independent events when memory effects are at play (Gautestad & Mysterud in press). In our model, high efficiencies coincide with movements of higher predictability or order. We find that order is enhanced in environments with broad tree-size distributions, where a few patches concentrate many resources. Low values are found for an entropy based on time-averaged spatial occupation patterns. Trajectories also become more predictable from a dynamical point of view, with longer repeated sequences of visited sites. Similar measures have revealed the regular nature of human displacements (Song *et al.* 2010), and their application to real ecological data could be useful to unveil how

animals exploit resources. In this context, predictability also has implications for the risk of predation: if one associates low forager's entropy levels with higher predation risks, a deviation from optimal foraging may decrease that risk. This may be achieved by increasing the randomness of the displacements, for instance.

At optimality, the model forager spends about half of its travelling time revisiting previous places in an orderly way, an activity that is reminiscent of the travel routes used by real animals (Noser & Byrne 2007). In fact, observation that monkeys persistently visit the same sequence of trees has been used to argue that monkeys navigate by choosing from a limited set of multi-step routes rather than Euclidean cognitive map calculations (Di Fiore & Suarez 2007). What our simulations show is that persistent use of the same sequence of trees need not imply the use of a pre-ordained, multi-step route. Rather, what looks like a multi-step route can emerge spontaneously from a one-step optimization algorithm. In areas that are well known, the forager's cognitive map of the size and location of trees is essentially the same at every visit. As the forager tends to make the same sequence of decisions each time it visits an area, its episodic memory of local fruiting states is also similar between visits. This might occur if depletion dynamics resulted in a characteristic return time such that trees tended to be at the same state of refresh at each visit. Or characteristic return time might be so long that fruiting states were poorly known. In both cases, the predicted value for each tree would be proportional to its size and the relative values of alternative choices at each step of the chain would be consistent between visits.

Directional persistence is another observation often interpreted to support multi-step route planning over the use of one-step, Euclidean cognitive map navigation. Here, model foragers also tended to show a high level of directional persistence, continuing on in the same direction after feeding on a tree. Directional persistence occurred in our simulations because a forager *en route* to a high-yield large tree often passed close enough to a smaller tree to make a short detour cost-effective (Janson 2007).

These examples raise a much broader issue in the study of animal movement. Many previous empirical studies have attempted to test alternative models of animal navigation in terms of relatively simple, intuitive predictions such as 'follows route or not' or 'takes direct path or not'. What the example above illustrates is not just that alternative models often make the same prediction (Janson & Byrne 2007), but the fact that a given alternative model predicts a particular movement pattern is not always intuitively obvious. That a one-step optimization algorithm can cause repeated or directionally persistent sequences of movement is not a foregone conclusion that flows necessarily from the algorithm's assumption. It is an emergent consequence of the algorithm's application in a heterogeneous environment.

More importantly, just as alternative models can non-intuitively predict the same emergent patterns, alternative models can also predict very different emergent patterns that often cannot be anticipated from the decision algorithms themselves. These emergent patterns represent a huge and a virtually untapped body of data for discriminating between animal navigation mechanisms and motivations. However, which emergent patterns that are predicted by complex navigation models such as the one we describe can only be evaluated through

simulation? This necessitates a shift in statistical inference towards methods such as approximate Bayesian computation (ABC), which allows the fitting of arbitrarily complex simulation models to real field data (Beaumont *et al.* 2002). What makes ABC particularly attractive for inference on movement models is the fact that it can use observations not just on the turning angle or velocity of particular path segments, but on multiple ensemble properties of movement such as the mean, variance or autocorrelation of angles or velocities and their cross correlation with environmental features. We expect ABC and similar methods to play pivotal roles in shifting the axis of research on animal movement from theory and experiment towards field observation.

References

Bartumeus, F. & Catalan, J. 2009 Optimal search behavior and classic foraging theory. *J. Phys. A Math. Theor.* **42**, 434002. (doi:10.1088/1751-8113/42/43/434002)

Bartumeus, F., Peters, F., Pueyo, S., Marrasé, C. & Catalan, J. 2003 Helical Lévy walks: adjusting searching statistics to resource availability in microzooplankton. *Proc. Natl Acad. Sci. USA* **100**, 12 771–12 775. (doi:10.1073/pnas.2137243100)

Beaumont, M. A., Zhang, W. & Balding, D. J. 2002 Approximate Bayesian computation in population genetics. *Genetics* **162**, 2025–2035.

Bénichou, O., Coppey, M., Moreau, M., Suet, P. H. & Voituriez, R. 2005 Optimal search strategies for hidden targets. *Phys. Rev. Lett.* **94**, 198101. (doi:10.1103/PhysRevLett.94.198101)

Boyer, D. & Larralde, H. 2005 Looking for the right thing at the right place: phase transition in an agent model with heterogeneous spatial resources. *Complexity* **10**, 52–55. (doi:10.1002/cplx.20068)

Boyer, D., Ramos-Fernández, G., Miramontes, O., Mateos, J. L., Cocho, G., Larralde, H., Ramos, H. & Rojas, F. 2006 Scale-free foraging by primates emerges from their interaction with a complex environment. *Proc. R. Soc. B* **273**, 1743–1750. (doi:10.1098/rspb.2005.3462)

Brockmann, D., Hufnagel, L. & Geisel, T. 2006 The scaling laws of human travel. *Nature* **439**, 462–465. (doi:10.1038/nature04292)

Colding, E. A., Plank, M. J. & Benhamou, S. 2008 Random walk models in biology. *J. R. Soc. Interface* **5**, 813–834. (doi:10.1098/rsif.2008.0014)

Dere, E., Zlomuzica, A., Huston, J. P. & De Souza Silva, M. A. 2008 Animal episodic memory. *Handb. Behav. Neurosci.* **18**, 155–184. (doi:10.1016/S1569-7339(08)00210-5)

Di Fiore, A. & Suarez, S. A. 2007 Route-based travel and shared routes in sympatric spider and woolly monkeys: cognitive and evolutionary implications. *Anim. Cogn.* **10**, 317–329. (doi:10.1007/s10071-006-0067-y)

Enquist, B. J. & Niklas, K. J. 2001 Invariant scaling relations across tree-dominated communities. *Nature* **410**, 655–660. (doi:10.1038/35070500)

Gautestad, A. O. & Mysterud, I. In press. The home range fractal: from random walk to memory-dependent space use. *Ecol. Complex.* (doi:10.1016/j.ecocom.2009.11.005).

Getz, W. M. & Saltz, D. 2008 A framework for generating and analyzing movement paths on ecological landscapes. *Proc. Natl Acad. Sci. USA* **105**, 19 066–19 071. (doi:10.1073/pnas.0801732105)

Griffiths, D., Dickinson, A. & Clayton, N. 1999 Episodic memory: what can animals remember about their past? *Trends Cogn. Sci.* **3**, 74–80. (doi:10.1016/S1364-6613(98)01272-8)

Hillman, K. L. & Bilkey, D. K. 2010 Neurons in the rat anterior cingulate cortex dynamically encode cost-benefit in a spatial decision-making task. *J. Neurosci.* **30**, 7705–7713. (doi:10.1523/JNEUROSCI.1273-10.2010)

Janmaat, K. R. L., Byrne, R. W. & Zuberbhuler, K. 2006*a* Primates take weather into account when searching for fruits. *Curr. Biol.* **16**, 1232–1237. (doi:10.1016/j.cub.2006.04.031)

Janmaat, K. R. L., Byrne, R. W. & Zuberbhuler, K. 2006*b* Evidence for a spatial memory of fruiting states of rainforest trees in wild mangabeys. *Anim. Behav.* **72**, 797–807. (doi:10.1016/j.anbehav.2005.12.009)

Janson, C. H. 2007 Experimental evidence for route integration and strategic planning in wild capuchin monkeys. *Anim. Cogn.* **10**, 341–356. (doi:10.1007/s10071-007-0079-2)

Janson, C. H. & Byrne, R. 2007 What wild primates know about resources: opening up the black box. *Anim. Cogn.* **10**, 357–367. (doi:10.1007/s10071-007-0080-9)

Lanner, R. M. 1996 *Made for each other: a symbiosis of birds and pines.* New York, NY: Oxford University Press.

Lee, K., Hong, S., Kim, S. J., Rhee, I. & Chong, S. 2009 SLAW: a mobility model for human walks. In *Proc. IEEE INFOCOM 2009: IEEE Conference on computer communications, Rio de Janeiro, Brazil, 19–25 April 2009.*

Martin-Ordas, G., Haun, D., Colmenares, F. & Call, J. 2010 Keeping track of time: evidence for episodic-like memory in great apes. *Anim. Cogn.* **13**, 331–340. (doi:10.1007/s10071-009-0282-4)

Morales, J. M., Haydon, D. T., Frair, J., Holsinger, K. E. & Fryxell, J. M. 2004 Extracting more out of relocation data: building movement models as mixtures of random walks. *Ecology* **85**, 2436–2445. (doi:10.1890/03-0269)

Nathan, R., Getz, W. M., Revilla, E., Holyoak, M., Kadmon, R., Saltz, D. & Smouse, P. E. 2008 A movement ecology paradigm for unifying organismal movement research. *Proc. Natl Acad. Sci. USA* **105**, 19 052–19 059. (doi:10.1073/pnas.0800375105)

Niklas, K. J., Midgley, J. J. & Rand, R. H. 2003 Tree size frequency distributions, plant density, age and community disturbance. *Ecol. Lett.* **6**, 405–411. (doi:10.1046/j.1461-0248.2003.00440.x)

Normand, E. & Boesch, C. 2009 Sophisticated Euclidean maps in forest chimpanzees. *Anim. Behav.* **77**, 1195–1201. (doi:10.1016/j.anbehav.2009.01.025)

Noser, R. & Byrne, R. W. 2007 Travel routes and planning of visits to out-of-sight resources in wild chacma baboon, *Papio ursinus. Anim. Behav.* **73**, 257–266. (doi:10.1016/j.anbehav.2006.04.012)

Oshanin, G., Lindenberg, K., Wio, H. S. & Burlatsky, S. 2009 Efficient search by optimized intermittent random walks. *J. Phys. A Math. Theor.* **42**, 434008. (doi:10.1088/1751-8113/42/43/434008)

Presotto, A. & Izar, P. 2010 Spatial reference of black capuchin monkeys in Brazilian Atlantic Forest: egocentric or allocentric? *Anim. Behav.* **80**, 125–132. (doi:10.1016/j.anbehav.2010.04.009)

Ramos-Fernández, G., Mateos, J. L., Miramontes, O., Larralde, H., Cocho, G. & Ayala-Orozco, B. 2004 Lévy walk patterns in the foraging movements of spider monkeys (*Ateles geoffroyi*). *Behav. Ecol. Sociobiol.* **55**, 223–230. (doi:10.1007/s00265-003-0700-6)

Rolls, E. T. 2008 The primate hippocampus and episodic memory. *Handb. Behav. Neurosci.* **18**, 417–438. (doi:10.1016/S1569-7339(08)00223-3)

Shlesinger, M. F. & Klafter, J. 1986 Lévy walks versus Lévy flights. In *On growth and form: fractal and non-fractal patterns in physics* (eds H. E. Stanley & N. Ostrowsky), pp. 279–283. Boston, MA: Martinus Nijhoff.

Sims, D. W. *et al.* 2008 Scaling laws of marine predator search behaviour. *Nature* **451**, 1098–1102. (doi:10.1038/nature06518)

Smouse, P. E., Focardi, S., Moorcroft, P. R., Kie, J. G., Forester, J. D. & Morales, J. M. 2010 Stochastic modelling of animal movement. *Phil. Trans. R. Soc. B* **365**, 2201–2211. (doi:10.1098/rstb.2010.0078)

Song, C., Qu, Z., Blumm, N. & Barabási, A.-L. 2010 Limits of predictability in human mobility. *Science* **327**, 1018–1021. (doi:10.1126/science.1177170)

Tabone, M., Ermentrout, B. & Doiron, B. 2010 Balancing organization and flexibility in foraging dynamics. *J. Theor. Biol.* **266**, 391–400. (doi:10.1016/j.jtbi.2010.07.004)

Turchin, P. 1998 *Quantitative analysis of movement: measuring and modelling population redistribution in animals and plants.* Sunderland, MA: Sinauer Associates.

Viswanathan, G. M., Buldyrev, S. V., Havlin, S., da Luz, M. G. E., Raposo, E. P. & Stanley, H. E. 1999 Optimizing the success of random searches. *Nature* **401**, 911–914. (doi:10.1038/44831)

Viswanathan, G. M., Raposo, E. P. & da Luz, M. G. E. 2008 Lévy flights and superdiffusion in the context of biological encounters and random searches. *Phys. Life Rev.* **5**, 133–150. (doi:10.1016/j.plrev.2008.03.002)

Walton, M. E. & Mars, R. B. 2007 Probing human and monkey anterior cingulated cortex in variable environments. *Cogn. Affect. Behav. Neurosci.* **7**, 413–422. (doi:10.3758/CABN.7.4.413)

Wills, T. J., Cacucci, F., Burgess, N. & O'Keefe, J. 2010 Development of the hippocampal cognitive map in preweanling rats. *Science* **328**, 1573–1576. (doi:10.1126/science.1188224)