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Journal of Theoretical Biology 240 (2006) 241–249
Journal of Theoretical Biology
www.elsevier.com/locate/yjtbi

Searching on patch networks using correlated random walks: Space usage and optimal foraging predictions using Markov chain models

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Received 8 March 2005; received in revised form 14 September 2005; accepted 15 September 2005
Available online 26 October 2005

Abstract

We describe a novel representation of a discrete correlated random walk as the transition matrix of a Markov chain with the displacements as the states. Such a representation makes it possible to utilize results from the theory of absorbing Markov chains, to make biologically interesting predictions without having to resort to Monte Carlo simulations. Our motivation for constructing such a representation is to explore the relationship between the movement strategy of an animal searching for resources upon a network of patches, and its consequent utilization of space and foraging success. As an illustrative case study, we have determined the optimal movement strategy and the consequent usage of space for a central place forager utilizing a continuous movement space which is discretized as a hexagonal lattice. The optimal movement strategy determines the size of the optimal home range. In this example, the animal uses mnemokinesis, which is a sinuosity regulating mechanism, to return it to the central place. The movement strategy thus refers to the choice of the intrinsic path sinuosity and the strength of the mnemokinetic mechanism. Although the movement space has been discretized as a regular lattice in this example, the method can be readily applied to naturally compartmentalized movement spaces, such as forest canopy networks. This paper is thus an attempt at incorporating results from the theory of random walk-based animal movements into Foraging Theory.

Keywords: Optimal foraging; Space usage; Patch networks; Correlated random walk; Markov chain

1. Introduction

The movement rules used by a forager searching for food have important consequences on the foraging success, and hence the fitness of the animal. The study of this cause-effect relationship straddles two more or less independent areas of theoretical ecology, namely the theory of animal movements based on random walks (Okubo, 1980; Blackwell, 1997), and optimal foraging theory (OFT) (Stephens and Krebs, 1986). While the former makes predictions regarding the consequences of an animal moving according to a given stochastic mechanism, the latter seeks to find the behaviour(s) that the animal must use while foraging in order to maximize its fitness. The following questions regarding movement patterns and foraging success form the motivation for this paper.

What is the effect of a given movement rule on the encounter rate with patches containing food resources? Following Charnov's classic work on foraging in a patchy environment (Charnov, 1976), most models of this kind make the critical assumption of Poisson encounter with patches of food resources of different types. On the other hand, the most general model of animal movement is that of a correlated random walk (Bovet and Benhamou, 1988); here, the position in space of the animal at any point of time depends upon its position in the previous two time-points. Also, in the general case, resource patches are distributed in a non-random manner. These two generalizations taken together imply that the Poisson encounter rate assumption is violated more often than not. McNair (1979) has shown that when the Poisson encounter rate assumption is violated, the predictions are drastically different from those of the classical models. However, McNair (1979) did not explicitly incorporate the movement mechanism of the forager into the model. Thus, the

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doi:10.1016/j.jtbi.2005.09.006

relationship between the movement rules of the animal and the encounter rate with patches of different types remains to be explored.

Therefore, the first objective of this paper is to describe a method for determining the encounter rate of patch-based resources in the context of a forager performing a correlated random walk while searching for resources.

Which movement rule will maximize the foraging success of the animal? The previous line of reasoning assumes that movement rules themselves are fixed, and constitute a constraint; however, as explored in a number of models (Cody, 1971; Pyke, 1978a, b; Bovet and Benhamou, 1991; Benhamou, 1992, 1994), the movement rules themselves may be the subject of optimizing selection. Since the movement rules are 'chosen' by the individual and are under selection, we will henceforth refer to the movement rules as constituting the movement 'strategy'. A general theme in most of these models is the determination of the optimal degree of directional correlation that the animal must use in order to maximize its searching efficiency. One shortcoming of these models is that they have either used simulations to arrive at their results (Cody, 1971; Pyke, 1978a; Bovet and Benhamou, 1991; Benhamou, 1992, 1994), or have not come up with explicit, quantitative predictions (Pyke, 1978b). Moreover, most of these studies maximize the average *per bout* energy intake rate, instead of the *long term* average of the intake rate, which is traditionally the currency of choice in OFT. In many contexts involving real world foragers, the former may not be the appropriate fitness currency to be used (see Discussion).

Therefore, the second objective of this paper is to describe an analytical framework for determining the optimal parameters for a given movement rule that the animal must use, in order to maximize its long term average rate of energy intake, while searching on patch networks using correlated random walks.

In this paper, we present a model of a forager using a discrete correlated random walk to search for resources. The unique feature of our model is that we have used a novel representation of a correlated random walk as a Markov chain, by using the displacements of the animal as the states. This representation makes it possible to apply methods from linear algebra and the theory of absorbing Markov chains, in the determination of certain biologically interesting consequences of using a particular movement strategy. Thus, in the general case, the long term relative encounter rate with patches can be determined. In the context of a central place forager, an exact estimate of the long term rate of gain of resource can be obtained. Both these quantities of interest can be determined without having to resort to explicit Monte Carlo simulations.

We demonstrate the utility of this approach by considering the case of a central place forager searching for resources upon a hexagonal lattice using a correlated random walk. The movement strategy in this case is specified by a choice of two parameters. The first parameter constituting the movement strategy is a measure of the intrinsic path sinuosity. Since it is highly conceivable that a central place forager possesses some proximate mechanism that returns it periodically to its home, we have incorporated mnemokinesis into the model. Mnemokinesis (Benhamou, 1994) constitutes a sinuosity regulating mechanism used by animals to polarize their movements towards a central place. Thus, in this case study, the movement strategy constitutes a choice of parameters, namely a measure of the intrinsic sinuosity of the path and the strength of kinetic mechanism. Both parameters involve a trade-off in terms of searching efficiency. As pointed out by Bovet and Benhamou (1991), the intrinsic sinuosity of the search path must be low enough to minimize any overlapping between search paths but high enough to minimize the length of the return journey. Similarly, the strength of the kinetic mechanism must be low enough to allow the animal to perform an extensive search, but again, high enough to minimize the length of the return journey.

Using our model, we determine the optimal movement strategy, i.e. the movement strategy that maximizes the rate of energy intake. The relative encounter rate with patches for an animal using this optimal movement strategy is obtained. We discuss how the methods developed here can be applied to animals foraging in more realistic landscapes.

2. The model

2.1. General model of between-patch movement on a network

2.1.1. Discretization of movement space: the patch network

The movement space is continuous (homogeneous) but discretized, in the manner described by Westerberg and Wennergren (2003). Thus, unlike in the case of contagious movement spaces, there is no 'matrix' outside the patches within which the animal moves. The structure of the movement space is described by the graph $G = (V, E)$, where V, the set of vertices, represents the patches and E, the set of directed edges between vertices. E is thus the set of all possible patch-to-patch (single-step) displacements, in the movement space. $\vec{e}_{ij} \in E$, where $\vec{e}_{ij}$ is the displacement vector from vertex i (centre of patch i) to vertex j (centre of patch j), implies a nearest-neighbour relationship, or non-zero direct accessibility of patch j from patch i. Thus, $|V|$ is the number of patches in the habitat, $|E|$ is the number of possible displacements that can be made in the habitat, and $|\vec{e}_{ij}|$ is the length of the displacement vector, or the actual distance between patches i and j.

The movement space in the illustrative example used in this paper consists of a regular hexagonal patch lattice of size 8×8, a portion of which is shown in Fig. 1. In each time step, the animal can only be displaced to one of the $\leqslant 6$ immediately adjacent patches from the current patch; this describes the locomotion constraint upon the animal. Since we have used a regular hexagonal lattice, the distance

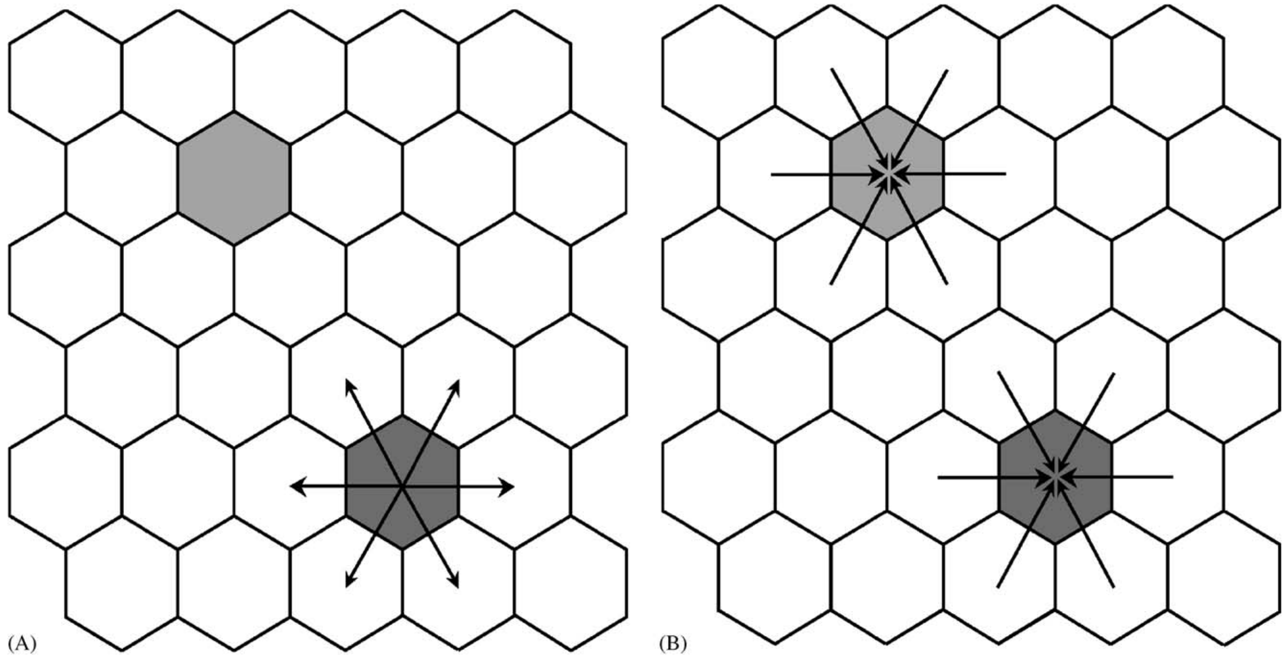

Fig. 1. A section of the hexagonal movement space showing starting states (A) and absorbing states (B) of the Markov chain. The dark grey patch is the central place, and the light grey patch is the *m*th patch. Each arrow represents a (potential) displacement vector. (A) The arrows originating from the central place make up the set *SV*. Any one of these, with uniform probability, is the first displacement made by the animal in a particular bout. (B) The arrows leading to patch *m* constitute A_m (displacements which end in patch *m*). The arrows leading to the central place constitute A_{cp} (displacements which end in the central place). The other members of *E* are not shown explicitly.

between each pair of adjacent patches is the same; this is taken to be one unit distance ($|\overrightarrow{e}_{ij}| = 1$ for all i,j).

2.1.2. First-order correlated random walk

In the context of foraging upon patch networks, the random walk only describes the movements between the patches, and not within the patches. The movement of an animal performing a first-order correlated random walk on *G* is represented by a continuous-time Markov chain with the *potential displacement vectors* (*E*) as the states. Thus, the Markov chain is not a temporal sequence of patches, but a temporal sequence of patch-to-patch displacements. Two displacement vectors are considered to be (potentially) successive if the endpoint of the first is the start-point of the second. For the sake of clarity, we use the term 'displacement' to denote an event involving a pair of successive patches in a path, and the term 'transition' to denote an event involving a pair of successive displacement vectors in a path. Thus, if an animal has moved from patches *j* to *k* in a single time step (described below), with patch *i* as the previous patch, the same event is a displacement from patch *j* to patch *k* and a transition from edge $\overrightarrow{e}_{ij}$ to edge $\overrightarrow{e}_{jk}$. The time taken between successive transitions is assumed to be an exponentially distributed random variable, whose mean is proportional to the distance between the patches.

2.1.3. Transition matrix

The $|E| \times |E|$ transition probability matrix *P* is obtained as follows. Let a_{ij} be the turn angle going from the *i*th edge to the *j*th edge ($-\pi < a_{ij} < \pi$, in radians); then,

$$p_{ij} = \frac{f(a_{ij})}{\sum_{j=1}^{d_i} f(a_{ij})}, \tag{1}$$

where $f(a_{ij})$ is a function describing the tendency of the animal to turn in a given direction and d_i is the number of adjacent patches of the patch forming the endpoint of the *i*th edge. $f(a_{ij})$ has the following properties: (i) $f(a_{ij})$ is non-negative over the domain $-\pi < a_{ij} < \pi$, (ii) $f(a_{ij})$ has a maximum at $a_{ij} = 0$, and (iii) $f(a_{ij})$ is symmetric about $a_{ij} = 0$. Obviously, $p_{ij} = 0$ if the *i*th edge and the *j*th edge are not successive. In this paper, we have used the normal probability distribution function with parameters 0 and σ' as in Bovet and Benhamou (1988). Thus, $f(a_{ij})$ is given by $(\sigma'\sqrt{2\pi})^{-1}e^{-\frac{1}{2}(\frac{a_{ij}}{\sigma'})^2}$. It is important to note that although σ' is a measure of the angular dispersion, it does not refer to the standard deviation of turn angles (since firstly, the domain of $f(a_{ij})$ is truncated to $-\pi$ to π and secondly, the standard deviation of turn angles can only be calculated after the normalization step in Eq. (1)). We define the 'inherent sinuosity' of the animal's movement strategy as $\sigma'.l^{-1/2}$, where *l* is the mean step length. We use the term 'inherent' to distinguish this parameter from the path sinuosity defined by Bovet and Benhamou (1988) as $\sigma.l^{-1/2}$ where σ is the realized, or actual standard deviation of the turning angles.

2.1.4. Estimation of long term usage of space

The expected proportion of visits to the various states of the Markov chain is its stationary distribution vector *w*, given by the dominant eigenvector of the transition matrix. We define the vector $U = \{u_1, u_2, u_3, \ldots u_n\}$ as the expected proportion of visits to each of the patches, where $u_i = \sum_{j=1}^{d_i} w_j$, d_i is the degree of vertex i, w_j is the relative frequency of traversal for the jth displacement vector ending in patch i, and n is the number of patches in the movement space. U is thus the 'relative encounter frequency' vector, which means that it represents the long term probability of encountering each patch. In the example shown here, since all the patches are of the same size, U also represents the long term usage of space. In the general case of unequal patch sizes, U must be weighted by the size of the patches to obtain the long term usage of space.

2.2. Central place foraging using random search on a patch network

Our model of a randomly searching central place forager is similar to that of Bovet and Benhamou (1991). Consider an animal with a central place (such as a burrow or a nest), which is located on one of the patches. As in all central place foraging models, the animal is obliged to return to the central place periodically in between bouts, which are return trips originating from and ending at the central place.

In this example, the forager uses mnemokinesis to return to the central place, which means that the inherent sinuosity is a function of the rate of change in proximity, with each step, of the central place. The change in proximity is estimated by the animal using the direction of the previous step relative to the direction of the central place. The model is adapted from Benhamou (1989) and Benhamou (1994), wherein it is shown that such a mechanism consistently leads the animal to periodically return to its home along looping paths.

The mnemokinetic mechanism is described by the equation

$$\begin{aligned} S_i &= S_b(1 - k\cos(\theta_i - \Phi_i)) \\ &\simeq S_b(1 + k(D_i - D_{i-1})), \end{aligned}$$

where S_i is the inherent sinuosity used by the animal at the end of the ith edge traversed in a path, S_b is the basic (or intrinsic) sinuosity, θ_i is the orientation of the ith edge, Φ_i is the direction of the central place from the start-point of $\overrightarrow{e}_i$, D_i is the distance of the endpoint of i from the central place and k is the dimensionless kinetic factor ($0 \leqslant k \leqslant 1$). When $k = 0$, the animal relies upon drift to return to the central place. It is important to distinguish between the basic sinuosity S_b and inherent sinuosity S_i. S_b is a global parameter representing the tendency of the animal to turn, in the absence of mnemokinesis. The values of S_i are obtained as a consequence of the interaction between the animal's intrinsic tendency to turn (S_b) and the mnemokinetic mechanism. Thus, S_b and k constitute the decision variable. The unit of S_b is rad unit distance$^{-1/2}$.

A patch in the centre of the movement space was arbitrarily chosen as the central place. When the animal encounters the boundary of the patch network, at low values of S, the transition probabilities to the successive edges are sometimes too close to zero to be computed. In such cases, it is assumed that the animal takes the next successive edge with the least turn angle and continues on the random walk.

2.2.1. Searching, resource depletion, and renewal

Each bout is a random search, with the animal possessing no knowledge of the location of resources. Each of the patches has some non-negative amount of food resource that the animal can consume, with the expected amount of resource within a patch given by $E\{R_p\}$. However, with each visit to a patch, all the *utilizable* resource present in the patch is depleted. It is assumed that the forager has a 'patch leaving rule' (Stephens and Krebs, 1986), which states that the animal will not forage in a patch if the intake rate in the patch falls below a certain threshold.

The forager 'rests' in the central place for a time period. During this period, the resource in the patch is renewed, such that the potential intake rate is now above the threshold. This renewal occurs only between bouts. Consequently, visiting a patch more than once in the same bout is redundant. We define the efficiency as the ratio of the average number of unique patches encountered during a bout, υ, to the expected distance travelled during the bout, $E\{D\}$.

2.2.2. Determining the long term average rate of net energy intake

The standard 'currency' of fitness in optimal foraging models is the long term average rate of net energy intake (Stephens and Krebs, 1986). If $E\{T_c\}$ is the expected time taken for a single bout and s is the average speed, then $E\{T_c\} = E\{D\}/s$. If $E\{R\}$ is the expected energy gained during a bout and c is the energetic cost per unit distance travelled, then the long term average rate of net energy gain, ρ_c is given by

$$\rho_c = \frac{E\{R\} - cE\{D\}}{E\{T_c\}}.$$

After some substitution and rearrangement,

$$\begin{aligned} \rho_c &= s.\left[\frac{E\{R\}}{E\{D\}}\right] - cs \\ &= sE\{R_p\}.\left[\frac{\upsilon}{E\{D\}}\right] - cs. \end{aligned}$$

It follows that the forager has to maximize efficiency $[\upsilon/E\{D\}]$, in order to maximize the long term rate of energy intake. It is interesting to note that the optimal movement strategy is independent of both the energetic cost per distance travelled, and the average speed.

2.2.3. Computing υ, the expected number of unique patches encountered during the bout

The expected number of unique patches encountered during the bout is given by $\upsilon = \sum_{m=1}^{|V|} h_m$, where h_m is the probability of hitting the mth patch at least once per bout. If the edges leading to the mth patch and the central patch are considered to be the absorbing states of the Markov chain, then h_m is simply the probability of being absorbed into an edge leading to the mth patch, and is computed using the following algorithm:

For each patch, define an absorbing Markov chain as follows. The absorbing states are $A = A_m \cup A_{cp}$ with ($r = |A|$, $t = |E| - r$), where A_m is the set of all the edges with m as the endpoint, and A_{cp} is the set of all the edges with the central place as the endpoint, as shown in Fig. 1. Compute $B = NR$, where $N = (I - Q)^{-1}$ is the Fundamental Matrix of the absorbing Markov chain, Q is the submatrix of P formed by eliminating the rows and columns corresponding to the absorbing states, R is the submatrix of P formed by eliminating the rows corresponding to the absorbing states and columns corresponding to the transient states, and I is the identity matrix. B is a $t \times r$ matrix giving the probability of absorption, starting from each of the transient states, into each of the absorbing states (Grinstead and Snell, 1997). h_m, the probability of hitting m at least once per bout, is now the probability of being absorbed into any A_m, i.e. $h_m = \sum_{i=1,j=1}^{i=|SV|,j=|A_m|} b_{ij}$, where the i are the rows of B corresponding to $\vec{e}_i \in SV$, where SV is the set of all the edges with the central place as the start-point, and j are the columns of B corresponding to $\vec{e}_j \in A_m$. This process is repeated to obtain each value of h.

However, this algorithm is computationally intensive. A much quicker and more elegant approximation method is presented in the Appendix.

2.2.4. Computing $E\{D\}$, the expected distance travelled per bout

A similar argument can be used to determine the long term average distance travelled per bout, which is given by

$$E\{D\} = \sum_{i=1}^{t} \tau_i |\vec{e}_i| + \sum_{j=1}^{r} p\{absorption\ into\ \vec{e}_j\} |\vec{e}_j|,$$

where τ_i is the expected number of times edge $\vec{e}_i$ is traversed, $\vec{e}_i \notin A_{cp}$ and $\vec{e}_j \in A_{cp}$.

We define an absorbing Markov chain as follows. The absorbing states in this case are A_{cp} with ($r = |A_{cp}|, t = |E| - r$), where A_{cp} is defined as above. We compute $N = (I - Q)^{-1}$ and $B = NR$ as before. N is a $t \times t$ matrix giving the time spent in each transient state starting from each transient state of the Markov chain (Grinstead and Snell, 1997). Thus, $\tau_i = \sum_{k=1}^{|S|} n_{ki}$ and $p\{absorption\ into\ \vec{e}_j\} = \sum_{k=1}^{|S|} b_{kj}$, where k are the rows of B and N corresponding to $\vec{e}_k \in SV$, where SV is defined as before, i are the columns of N corresponding to $\vec{e}_i \notin A_{cp}$, and j are the columns of B corresponding to $\vec{e}_j \in A_{cp}$. Thus, the expected distance travelled by the forager before returning to the central place can be determined.

2.2.5. Finding the optimal movement strategy: computation

The efficiency of a forager was computed using the exact method described above for 100 linearly spaced values each of S_b (ranging from 0.2 to 2 rad unit distance$^{-1/2}$) and k (ranging from 0 to 1). We used the FMINCON function from the MATLAB™ Optimization Toolbox to determine the maximum of the efficiency function. This finds the minimum of a constrained nonlinear multivariable function (Coleman and Zhang, 2001).

3. Results

Fig. 2 shows the efficiency as a function of S_b and k. The surface has a peak at $S_b = 1.6572$ rad unit distance$^{-1/2}$ and $k = 0.7551$, respectively, corresponding to a 77.22% chance of hitting an undepleted resource patch for every step the forager takes. The surface shows a single peak, with a relatively steep slope on the side leading to $S_b = 0$. This indicates that (a) there are no 'local peaks' which natural selection cannot take the population out of, and (b) going straighter than the optimal strategy is much more expensive than increasing the turn angle.

An animal using the optimal movement strategy generates a kernel of space usage centred around the forager's home, depicted in Fig. 3. For comparison, we have included the usage of movement space as determined both by the matrix method described earlier and from a simulation, which involved generating 20 paths of 100 steps each using the movement rules described by the optimal strategy. As apparent from the figure, the usage kernel determined by the two methods is the same.

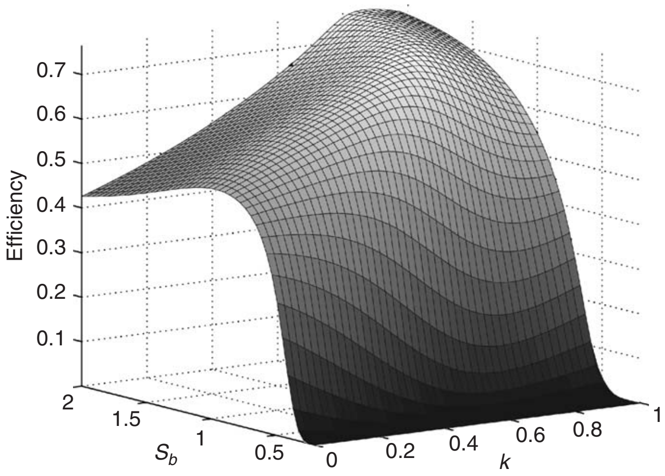

Fig. 2. Contour surface interpolated from the numerical estimation of the efficiency of foraging against k and S_b. 100 values each of S_b and k were used to generate the surface.

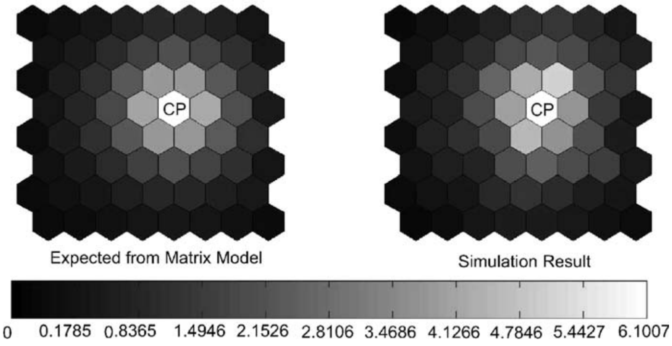

Fig. 3. Long term usage of the movement space by an animal using the optimal movement strategy, as determined by the space usage vector U (left), compared with that determined by a simulation (right), which consisted of generating 20 paths of 100 steps each. The intensity gradient bar below represents the brightness associated with percentage of time spent in the patch. CP is the central place. The differences in between the expected space usage and the simulated space usage were not significant (χ^2 test, $d.f. = 63$, $p \gg 0.01$).

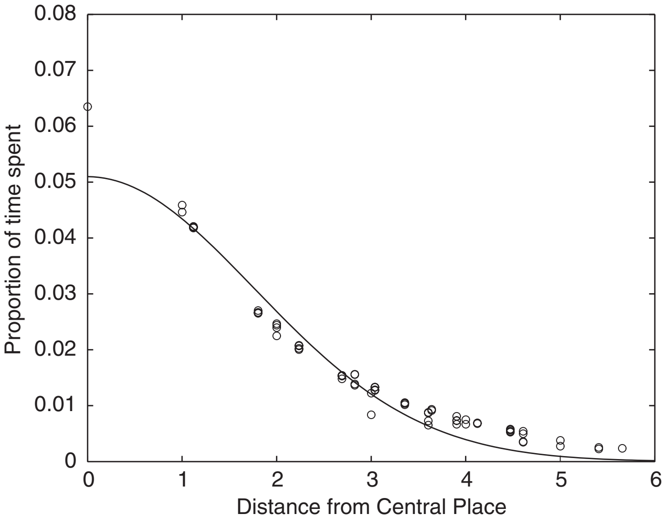

Fig. 4. Distribution of usage of movement space around the central place. The circles depict the expected usage determined by the matrix method (U). The curve represents one tail of a normal distribution with $\sigma = 1.693$.

The usage kernel is similar to a bivariate normal distribution centred on the home. With the objective of characterizing this usage kernel, we fitted the optimal space usage kernel, determined from U, to a bivariate normal distribution, using the Gauss-Newton method. The best fit distribution has a standard deviation of 1.693 distance units (root mean squared error = 0.0029), as shown in Fig. 4. Thus, if the home range of the animal were to be described as the area in which the animal spends 95% of its time, then the home range corresponding to the optimal movement strategy is an area described by a radius of 4.131 units around the central place.

4. Discussion

We have described a novel representation of a correlated random walk as a Markov chain with the displacements as the states. In this paper, we demonstrate how this approach is useful in determining (a) the usage of space and (b) the rate of energy gain of a central place forager. While the latter result is in the tradition of OFT, we do not believe that all real world foraging behaviours must necessarily be optimal, or even that the sole currency of fitness is the long term rate of energy gain. Since much has been said about the use and abuse of optimality modelling (see Parker and Maynard Smith, 1990), we do not intend to elaborate on that subject here. However, we agree with Stephens and Krebs (1986) and Parker and Maynard Smith (1990), that optimality modelling serves as a useful tool for providing directions to research. Departure from predicted optimality would be as interesting and useful to study as actual agreement with predictions. It is in this spirit, and with this caveat, that the predictions of our model should be interpreted. A discussion of the applicability of the results presented here to real-world foraging scenarios follows.

4.1. *Extending the model to more 'realistic' landscapes*

For illustrative purposes, we have used a movement space with a hexagonal lattice structure. In principle, our method can be applied to any irregular or regular lattice-based movement space. Most interestingly, the method is readily applicable to naturally compartmentalized movement spaces, such as forest canopy networks. Here, the crown of each tree can be considered to be internally homogeneous. In a closed canopy forest, the crowns of individual trees form a space-filling, or tessellation. Each crown can be visualized as an irregular polygon, with a varying number of neighbours. The forest canopy thus forms an irregular patch network. Our approach would be particularly useful in the modelling of the movements of obligately arboreal small mammals, such as the Malabar Giant Squirrel, *Ratufa indica*. While such animals are constrained to move only to the nearest patch in a single step, this constraint would not apply in the case of animals able to leap, glide or fly beyond adjacent patches in a single step. For modelling these situations, it would be straightforward to incorporate different dispersal kernels into the transition probability matrix. Thus the approach would still be useful in this more general case. Also, constraints on accessibility, such as forest clearings and other discontinuities arising out of spatial heterogeneity can also be easily incorporated into the transition probability matrix. Thus, the method described in this paper can be applied to much more general situations than the illustrative example described here.

4.2. *Correlated random walk—biological justification*

The use of a correlated random walk for a patch-network movement space requires some justification, in terms of biological realism. Bovet and Benhamou (1988) point out that the correlated random walk is a necessary consequence of bilateral symmetry and cephalocaudal polarization of animals. However, the step length relative to the body size is mostly large in the case of a random walk upon patch networks. To what extent bilateral symmetry and cephalocaudal polarization cause a correlation in the turn angle, when the step length is very large compared to the body size of the animal, is unclear, since the standard deviation of the turn angles increases proportionally with the square root of the step length (Bovet and Benhamou, 1988); as the standard deviation increases, the path becomes more and more similar to that of a simple random walk. However, higher animals have the ability to remember the direction of the previous patch from the current one; thus, any correlation in the turn angles of the path upon a patch network is likely to be due to an active behavioural decision on the part of the forager, and not merely a consequence of its physical structure-movement relationship. This brings the degree of correlation, or inherent path sinuosity, under the purview of optimality theory.

4.3. Applicability of the optimal movement predictions

The predictions of optimal movement strategy that have been made in this paper are applicable only in the context of a central place forager, whose resting period at the central place is necessary and sufficient for renewal of resources to occur. This assumption is not entirely unreasonable. Nocturnal renewal of nectar sources of diurnal bees is known to occur (Schaffer et al., 1979); conversely, daily afternoon winds are known to replenish seed patches depleted by nocturnal desert gerbils (Ben-Natan et al., 2004).

Benhamou (1994) has shown that the 'looping' search paths adopted by many central place foragers such as desert ants (Wehner and Srinivasan, 1981) and isopods (Hoffmann, 1983) can be explained by a kinetic mechanism such as mnemokinesis. Such a looping search behaviour has also been demonstrated in house flies (Fromm and Bell, 1987) and savannah baboons (Baker, 1978). While we have used mnemokinesis as a movement mechanism in this study, it is straightforward to represent any movement mechanism in the transition matrix.

It is important to note that the 'optimal strategy' that we have determined in this paper is restricted to that of an animal already committed, in evolutionary terms, to the use of mnemokinesis for random search-based central place foraging. Other mechanisms, such as taxis might yield higher efficiencies than what we have obtained for the optimal strategy. In fact, a systematic search strategy (Zollner and Lima, 1999) is obviously more efficient than a random search strategy. A comprehensive survey of the efficiency of a wide range of qualitatively different mechanisms is beyond the scope of this paper. However, we have demonstrated the use of Markov chain theory as a tool for exact estimation of the efficiency in each possible case.

4.4. The "fallacy of averages" revisited: maximize average rate per bout, or average rate over all bouts?

In most previous studies on optimal movement strategies (Pyke, 1978a; Bovet and Benhamou, 1991; Benhamou, 1992, 1994), the fitness currency that is maximized is the per bout average net rate of energy intake, with each bout itself constituting a large number of steps. Thus, what has been maximized is $E\{R_N/T\}$, where R_N is the net energy gained in a single bout. However, many animals accumulate reserves over extended periods of time, which cover many bouts. These accumulated stores of energy are converted into reproductive success. If there is no minimum per bout requirement, $E\{R_N\}/E\{T\}$ would be the appropriate fitness currency, as described here. Such a long term average net rate maximizer would probably have more 'bad bouts' (bouts with low R_N/T values) and hence would need an energy reserve mechanism that enables it to survive through bad bouts. This is not an unreasonable assumption; for e.g., we have observed the Malabar Giant Squirrel (*Ratufa indica*) not infrequently having days in which little or no feeding takes place (Borges, 1998). It is our opinion that the appropriate currency to be used must be selected based on an understanding of the biological context of the forager.

4.5. Optimal movement strategy determines the optimal home range

The movement strategy, namely, the choice of inherent path sinuosity and the strength of mnemokinesis, automatically determines the usage of movement space and hence the extent of the home range utilized by the animal. Any change in the size of the home range would necessarily involve a change in movement strategy, and therefore a decrease of foraging efficiency. Thus, for a territorial animal, the optimal movement strategy automatically determines the size of the home range worth defending. It should be noted that the above verbal argument has many implicit assumptions. For example, it is assumed that the only benefit that could possibly be gained from fighting is increased movement space; this argument also does not take into account differential ability to defend areas, non-uniform cost of fighting and nutritional hotspots (Borges and Mali, 2001). Nevertheless, it is our opinion that this feature of our model may prove useful in predicting changes in home range size used by an animal under different resource availability and landscape features, notably lacunarity and connectivity (as studied in With et al., 1997, and With and King, 1999), which can easily be represented in the transition probability matrix.

4.6. Conclusion

For an animal whose movements are described teleonomically as seeking to locate a suitable habitat, food resource or mate, three kinds of factors describe its success:

the structure of the landscape, the locomotion constraints upon the animal and the movement strategy used by the animal. In this paper, we have described a representation of the movement of the animal in the form of a transition matrix of a Markov chain. Such a representation opens up the possibility of using tools from the theory of absorbing Markov chains to make predictions regarding the space use by the animal, and its foraging success. It is our opinion that this approach would be particularly useful in exploring the relationship between optimal movement strategy, locomotion constraints, landscape structure and space use.

Acknowledgements

We thank N.V. Joshi, Finn Kjellberg, Vidyanand Nanjundiah, and Vivek Nityananda for valuable comments on earlier drafts of this manuscript, and for the stimulating discussions that followed. The useful comments of three anonymous reviewers are also gratefully acknowledged.

Appendix. Finding h_m, the probability of visiting the mth patch during each bout

h_m, the probability of visiting the mth patch during each bout, could be interpreted as follows. If τ_m is a realization of the number of transitions that have occurred between leaving the central place and the first visit to the mth patch (hereafter referred to as the first passage ‘time’), and τ_{cp} is a realization of the number of transitions in the bout (hereafter referred to as the return ‘time’), then $h_m = p\{\tau_m < \tau_{cp}\}$. Owing to the ‘memoryless’ property of the Markov chain, the first passage time between any pair of displacement vectors can be approximated by an exponential distribution. The mean of this distribution is given by the matrix $\mu = 1/\lambda = (I - Z + (E \times Z_{dg})) \times D$, where $Z = (I - P + W)^{-1}$ is the fundamental matrix for the ergodic Markov chain, W is a matrix with all rows equal to the stationary distribution $\{\pi_1, \pi_2, \pi_3, \dots \pi_n\}$, I is the identity matrix, E is the matrix with all entries 1, Z_{dg} results from Z by setting off-diagonal elements to 0, and D is the diagonal matrix with elements $d_{ii} = 1/\pi_i$ (Grinstead and Snell, 1997). The mth patch can be visited by traversing any of the n_m displacement vectors leading to it, with each of these displacement vectors having an exponentially distributed first passage time from the central place associated with it, with rate parameters $\{\lambda_{m1}, \lambda_{m2}, \lambda_{m3}, \dots, \lambda_{mn_m}\}$. Similarly, the return to the central place can be through any of the n_{cp} displacements leading to it, with the return times having rate parameters $\{\lambda_{cp1}, \lambda_{cp2}, \lambda_{cp3}, \dots, \lambda_{cpn_{cp}}\}$.Thus, the number of transitions needed to reach either the mth patch or return to the central place forms a hyperexponential distribution. The probability of the ith displacement leading to m occurring before any of the $n_{cp} + n_m$ displacements can be shown to be $\lambda_{mi}/(\sum^i \lambda_{mi} + \sum^j \lambda_{cpj})$ (Ross, 2000). It follows that $h_m = \sum^i \lambda_{mi}/(\sum^i \lambda_{mi} + \sum^j \lambda_{cpj})$. This method is considerably less computationally intensive than the method described in Section 2.2.3.

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