The use of space by animals as a function of accessibility and preference

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Abstract

Heterogeneous usage of space by individual animals or animal populations is partly due to their preference for particular resources that are, themselves, heterogeneously distributed. When all points in the environment are equally accessible, a direct relationship between usage and preference can be assumed. However, when accessibility is restricted, spatial variations in usage can no longer be attributed entirely to preference. In such cases, it is necessary to control for the effects of accessibility on observed usage before conclusions about preference can be drawn. In this paper, I develop a modelling framework that treats the use of space by animals as a joint function of preference and accessibility. I specify a null version of the framework that assumes no preference and propose that its output can be used to control for the effect of accessibility on the observed, spatial distribution of usage. I briefly discuss how the framework can subsequently be used to provide insights about the animals' preference for different resources and types of movement, and to predict usage in areas where no usage data exist. I explore the properties of the methodology using data from a population of simulated animals and present the first results of its application to a sub-set of the British population of grey seals (*Halichoerus grypus*).
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1. Introduction

Quantifying habitat preference is 'of particular interest because it provides fundamental information about the nature of animals and how they meet their requirements for survival' (Manly et al., 1993). This information is vital for the conservation and management of wildlife and their habitats. However, preference is only indirectly observed through measurements of the usage of space by animals.

Spatial usage (or utilization) is defined as the proportion of time per unit area spent by an animal or group of animals in the neighborhood of a point in space. In most cases, the distribution of usage by an individual or a population will be

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heterogeneous and this is partly a reflection of the spatial distribution of the resources required by the animal(s). This is the motivation for extracting indexes of habitat preference from data of spatial usage (Baker and Brooks, 1981; Holbrook and Schmitt, 1988; Batzli and Lesieutre, 1991; Gorman and Reynolds, 1993; Lubin et al., 1993; Wright and Begg, 1997).

The methods employed for this purpose (Buckland and Elston, 1993; Arthur et al., 1996; Augustin et al., 1996; Boyce and McDonald, 1999; Brito et al., 1999) treat spatial usage as a proxy for habitat preference and, hence, correlate it directly with environmental variables. The assumption in this (Manly et al., 1993, p.30) is that all points in space are freely and equally accessible to the animal(s), which implies practically unlimited speed of movement and/or practically unlimited time for movement. Although this assumption will be valid for some animals (e.g. free-ranging grazers—see case studies in Manly et al., 1993) it will not be for others (e.g. central-place foragers). Evidently, restrictions in accessibility cannot always be treated as a transient phenomenon and this has been recognised in recent theoretical work by other authors (Arthur et al., 1996; Blackwell, 1997; Hjermann, 2000).

Quite apart from environmental preference, animals tend to show preference for particular types of movement. In analyses of individual movement (Harkness and Maroudas, 1985; Bovet and Benhamou, 1988; McCulloch and Cain, 1989; Scharstein, 1990; Benhamou and Bovet, 1992; Blanché et al., 1996; Claussen et al., 1997; Firle et al., 1998; Séguinot et al., 1998) these are typically characterised by the geometrical properties of the trajectories (two-dimensional paths or three-dimensional flights) produced by moving animals. In studies of animals that can be assumed to track the preferred resources (such as ideal free foragers) the effect of the way animals move on the resulting usage distributions is neglected. However, when accessibility is restricted (for example, by the need to periodically return to a central place) preference for a particular type of movement is important and must be modelled in the same framework as environmental preference.

The first objective of this paper is to develop a general framework that models the usage of a point (x) in space as follows

$$\text{Usage}(x) = f(\text{Accessibility}(x), \ \text{Preference}(x)) \quad (1)$$

where

$$\text{Preference}(x)$$
$$= \text{Preference}\begin{pmatrix} \ldots \text{ for environmental attributes of } x, \\ \ldots \text{ for attributes of paths going through } x \end{pmatrix}$$
$$(2)$$

I argue that usage and the determinants of accessibility are somewhat easier than preference to measure in the wild and, hence, that the latter will usually be the unknown in studies of the spatial distribution of animals. Consequently, the second objective is to formulate a null model of usage by assuming no preference and to use it to control for the contribution of accessibility to the observed distribution of usage. Effectively, I solve Eq. (1) for preference

$$\text{Preference}(x) = f'(\text{Usage}(x), \ \text{Accessibility}(x)) \quad (3)$$

In Section 2, I review the biological facts that determine the main features of the modelling framework. In Section 3, I discuss more specific aspects of its implementation. In Section 4, I describe a null version of the modelling framework that assumes no preference. I discuss why the output of this null model can be used to quantify accessibility of different points in space. In Section 5, I explore the potential applications of this methodology using data from a simulated population. In Section 6, I present preliminary results obtained by specifying and parameterising the framework using data from the British population of grey seals (*Halichoerus grypus*). Finally, in Section 7, I present a critical review of the assumptions, practicality and applicability of the framework.

2. Modelling framework

2.1. Representing the environment

In general, an animal's environment and its response to it do not remain constant. At a given

instant, an animal's preference for particular environmental attributes will depend on its current biological requirements. Ultimately, at any given time, preference for a particular type of habitat will be the result of the behavioural activity the animal is performing.

Furthermore, by interacting with its environment an animal may change the real or perceived suitability of a particular location for itself or for other animals. This could happen if the animal changed a location's attributes (by exploiting local resources or simply occupying space) or if it explored (and, possibly, communicated information about) a previously unvisited location. In this paper, I focus on animals performing a single behaviour (e.g. foraging), whose usage of space is not affected by conspecifics and can be assumed constant over the time scale of observation (the so-called 'pseudo-equilibrium' assumption—Guisan and Zimmermann, 2000).

Since most spatial, resource-usage interactions in ecology either occur on, or can be readily projected onto the plane, I focus on animals moving in two-dimensions. I represent space by a regular lattice which consists of cells through which animals can travel and cells that are obstacles to movement. This implies that, in this framework, as is often the case in nature, movement takes place within arbitrarily complex geographical boundaries.

Within these boundaries (i.e. for the domain of all cells that admit movement) I consider a function $h(x)$ which associates a value of preference with the centrepoint x of each lattice cell. The notation $h(\cdot)$ is used throughout the paper to indicate animal preference. The value of the preference function $h(x)$ is solely determined by the response of the animal to the local environmental properties at the cell x. Hence, this function quantifies environmental heterogeneity as seen from the animal's point of view and it is the desired unknown in studies that relate usage to habitat type. It is formally defined as the expected spatial distribution of usage that would occur if the animals could access any point in space with equal ease. Equivalently, $h(x)$ can be defined as the probability of an animal being at x if it can choose to be anywhere at anytime.

2.2. Representing animal movement

Observation records of animal movement are rarely continuous. A typical data set consists of time-ordered sequences of coordinate pairs separated by known time intervals. Particularly in data obtained in the wild (e.g. by telemetry methods), where the observer has less control over the rate of data collection, the time intervals between observations tend to be long and/or irregular. An extreme example of this occurs in studies that observe a single, biologically important, location in space (such as a nest or a burrow) and only record the time interval between two consecutive visits, by the animal, to that location.

Surely, the observer cannot know where the animal was at any time instant between two consecutive observations but knowledge of the animal's position at the beginning and the end of a known time interval can inform about where the animal could have been and this information must form the basis of any quantitative description of accessibility.

I collectively refer to this information as a *trip*. A trip is defined as the movement, of known duration τ, of an animal from one point x_0 in space to another x_T. In *open-ended trips* only the point of origin x_0 is known. In *fixed-endpoint trips*, the point of termination x_T is also known. *Return trips* are a particular kind of fixed-endpoint trip for which $x_0 = x_T$. I call all other fixed-endpoint trips (those for which ($x_0 = x_T$) transitory trips.

Existing investigations of spatial usage (Dusenbery, 1989; Johnson et al., 1992; Andreassen et al., 1993; Gautestad and Mysterud, 1993; Seaman and Powell, 1996; Smith et al., 1997) have most often considered open-ended or return trips and, unlike the work presented here, models (e.g. Don and Rennolls, 1983) that can estimate usage around more than one focal point, assume a homogeneous environment. For the sake of clarity and without loss of generality, I firstly specify the framework to a single, fixed-endpoint trip (known endpoints and duration).

A *path* is the trajectory of the animal during a trip of known x_0, x_T and τ. In order to convert individual movement to spatial usage, continuous paths can be discretised into lattice coordinates.

This can be done either by using a fixed time unit (Δt) and counting the number of path points contained in each lattice cell or by using a fixed unit of length (Δt) and allocating a 'residence duration' value to each point in the discretised path. Both ways can lead to equivalent results but, in this paper, discretising by length leads to a simpler algorithm for path generation.

I therefore consider the Δl-discretization of a path of length l and define the corresponding lattice path $U = \{x_0, \ldots, x_n\}$ as the sequence of centrepoints of lattice cells visited by the discretised path.

This process suffers from the fact that the remainder of the division $l/\Delta l$ will almost never be zero. So, I define the number of points (n) in the lattice path as the integer part of the ratio $l/\Delta l$ incremented by two ($n = [l/\Delta l] + 2$) to account for the two endpoints. The algorithm of path generation (described below) takes account of this fact by treating the length of the discretised path's final segment as a variable, equal to $\Delta l(l/\Delta l - [l/\Delta l])$.

In trying to determine where the animal could have been while it wasn't being observed it is equally important to know how the animal moves. Movement can be described by summarising the geometrical properties of its observable output, the lattice path. These summaries can be characteristics of the entire lattice path (such as overall path length, overall displacement, sinuosity) or moments from the observed frequency distributions of variables (such as step length or turning angles) measured from smaller segments of it. Such a set of path summaries specifies a *path classification scheme*. For a particular classification scheme containing k such summaries, let m_i be the ith summary and let $\mathbf{m} = \{m_1, \ldots, m_i, \ldots, m_k)$ be the *path summary vector* making up the entire scheme.

A particular realization of the path summary vector represents a particular type of path. The degree of specificity with which this is done depends on the number of summaries used in the classification scheme. The most specific classification of lattice paths would use $k = n$ summaries for every lattice path U, one for each of its points, so that $m_i = x_i$, $(1 \leqslant i \leqslant n)$. Under this scheme, a particular realization of the path summary vector would only describe one lattice path and longer

paths would be described by longer summary vectors. Although this trivial classification fully retains the information content of a data set of lattice paths, most of this information would not be required by a model of spatial usage. At the other extreme, one could use too few summaries to be able to capture enough of the features of individual movement that are important in determining the spatial distribution of usage.

To formalise this trade-off, let Ω be the event space of all the lattice paths that can be realised on a particular lattice. Let $\Omega_\mathbf{m} \subseteq \Omega$ be the event space of those lattice paths described by the path summary vector m. I refer to all the paths belonging to the space $\Omega_\mathbf{m}$ as being generated by the same mode of movement. Clearly, a more specific and larger path summary vector results in more $\Omega_\mathbf{m}$ subdivisions of the space Ω each with fewer elements in it. At the extreme of maximum specificity there are as many sets $\Omega_\mathbf{m}$ (i.e. as many modes of movement) as the number of lattice paths in Ω and at the extreme of minimum specificity, there is a single set $\Omega_\mathbf{m}$ (corresponding to the true but uninteresting statement 'a path is a path').

2.3. The estimation of usage

To introduce this sub-section, I now focus on the k-dimensional space defined by the different path summaries of a particular classification scheme. For each path summary, I consider an arbitrary but computationally manageable discretization of its range. For example, if the length of a path is used as one of the summaries and path length takes values between 0 and 1000 m this can be discretised in one hundred 10 m bins. This yields the equivalent of a multi-way contingency table (see Fig. 1 for an example of such a contingency table comprising two summaries and two bins for each summary) the bins of which can be used to subdivide the event space (Ω) of all lattice paths.

I next introduce the remaining types of preference function required for the estimation of usage. Let $h(\Omega_\mathbf{m})$ be the probability of occurrence of any path from the event space $\Omega_\mathbf{m}$ so that $\Sigma_{\text{All } \mathbf{m}} h(\Omega_\mathbf{m}) = 1$. Let $h(U|\Omega_\mathbf{m})$ be the probability of
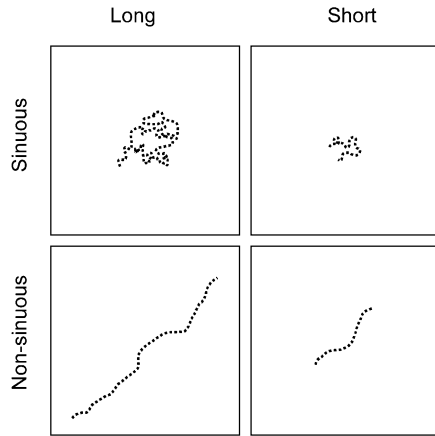
Long   Short

Fig. 1. Paths are the observable, spatio-temporal output of movement. Different modes of movement can be classified by the geometrical properties of paths. These path summaries can be viewed as the dimensions of a space (Ω). Each point in this space uniquely defines a mode of movement. In the idealised example shown here, two summaries are used, path length and sinuosity. Discretising the ranges of the path summaries (in this case by two bins per summary) leads to a path classification scheme. Attaching a probability (the value of a preference function) to each of the categories in the scheme leads to the equivalent of a two-way contingency table for paths.

occurrence of a particular lattice path from the event space $\Omega_{\mathbf{m}}$ so that $\Sigma_{\text{All } U \in \Omega_{\mathbf{m}}} h(U|\Omega_{\mathbf{m}}) = 1$. The notation $h(\cdot)$ is used for these functions to indicate that they quantify the animal's preference for a particular path (U) within a space $\Omega_{\mathbf{m}}$ or a particular type of path ($\Omega_{\mathbf{m}}$) within the space Ω.

Finally, I introduce the different types of usage function estimated. Given the duration and endpoints of a trip and the lattice path (U) generated by the trip, let $s(x|U)$ be the proportion of the trip's duration spent at the cell centred at x (so that if $x \notin U$, then $s(x|U) = 0$). Also, let $s(x|\Omega_{\mathbf{m}})$ be the average proportion of time spent at x as a result of all paths belonging to the event space $\Omega_{\mathbf{m}}$. Finally, let $s(x)$ be the average proportion of time spent at x as a result of any path or, in other words, the average usage of the cell at x resulting from trips of the given duration and with the given endpoints.

The average usage ($s(x|\Omega_{\mathbf{m}})$ of a lattice cell x resulting from paths of a given type will be

$$s(x|\Omega_{\mathbf{m}}) = \sum_{\text{All } U \in \Omega_{\mathbf{m}}} h(U|\Omega_{\mathbf{m}})s(\mathbf{x}|U) \tag{4}$$

The average usage ($s(x)$) of a cell x resulting from any path will be

$$s(x) = \sum_{\text{All } \mathbf{m}} h(\Omega_{\mathbf{m}})s(x|\Omega_{\mathbf{m}})$$

$$= \sum_{\text{All } \mathbf{m}} h(\Omega_{\mathbf{m}}) \sum_{\text{All } U \in \Omega_{\mathbf{m}}} h(U|\Omega_{\mathbf{m}})s(x|U) \tag{5}$$

3. Implementation of the framework

3.1. Choosing path summaries

Animal movement in two dimensions can be naturally described in terms of speed and sinuosity (Bovet and Benhamou, 1988; Marsh and Jones, 1988; Bovet and Benhamou, 1991; Turchin, 1998). Variables traditionally used to characterise discretised paths are the step length and the turning angles between successive steps. General models of movement using these variables that have been applied to animal movement include Pearson's random walk (Hughes, 1995), the biased random walk (Hill and Häder, 1997), the correlated random walk (Bovet and Benhamou, 1988; McCulloch and Cain, 1989) and the Lévy walk (Klafter et al., 1990; Viswanathan et al., 1996, 1999).

The majority of these approaches model movement by describing the probability distribution of variables at the scale of a single step taken by the animal or a single time increment of observation, hence, treating animal movement as a Markov process. However, modelling movement at larger scales may lead to more realistic results. This is because many animals have memory and intention and are therefore more likely to have an overview of their movement (past and future) at any one point of their trip.

If during a trip the animal performs and completes a certain behavioural function (e.g. foraging or patrolling a territory) then the resulting path may be meaningfully summarised at a

time scale equal to the trip's duration. Alternatively, a path may be characterised at multiple time scales. This is equivalent to incorporating higher order temporal dependencies in the model of movement and can easily lead to cumbersome formulations. To avoid such complications, assumptions of self-similarity can be made, or scale-independent properties can be sought, in movement data (Wiens et al., 1995). However, the existence of such properties and their usefulness for models of movement is still open to debate (Turchin, 1996).

In this paper, I employ a simple classification scheme using only two summaries ($k = 2$), the path's total length (l) and its range (ρ)—the maximum distance achieved by the path from its endpoint(s). Classification schemes using more than two summaries are possible, if more computationally demanding.

The usefulness of total path length as an informative path characteristic is evident but the definition of the range and the rationale for using it as a path summary need to be explained further. The values that can be taken by ρ are determined by the path's length and the type of trip that generated the path (Fig. 2). For an open-ended, unobstructed trip (Fig. 2a), of the type most amenable to analytical treatment (Hughes, 1995), the range of the path is identical to its maximum displacement. Note, that this is not the same as the final displacement (the distance between the path's two endpoints). The range can therefore be used as a measure of the region in space containing the path and, for a given path length, the range can be interpreted as a measure of path sinuosity. The concept of the range can be similarly adapted to return (Fig. 2b) and transitory (Fig. 2c) trips.

The existence of obstacles to movement means that the use of Euclidean distances to measure the range can be misleading. Instead, *biological distance* must be used. This is defined as the minimum path length required to get from one point of the lattice to another while avoiding obstacles. Most geographical information systems (GIS) have functions that will calculate exact or approximate biological distances between any two points within a given lattice.

In conclusion, for a given path length, the range provides information about how far the animal has moved away from its origin and termination points during its trip and, hence, how unfolded the path is. More information-rich indices, such as the fractal dimension (Falconer, 1990) or the maximum area covered by the path (Firle et al., 1998; Claussen et al., 1997), can also be used for this purpose.

3.2. Generation of paths—exploration of the event space Ω

The event space Ω contains all the lattice paths that can be realised in a given lattice. The subdivisions of Ω, introduced by the path summaries, classify lattice paths according to their properties (in this classification, total length and range). The model in Eq. (5) requires the function $h(\Omega_{\mathbf{m}})$ which represents the animals' relative preference for a particular type of path (generated by a particular mode of movement) under the classification scheme. In order to quantify this function it is first necessary to generate paths of each type within the lattice.

Most algorithms for path generation use sequential (step-by-step) generation and, as a result, can only control the fine-scale properties (such as step length and turning angles) of their output, possibly with some degree of control over the autocorrelation with previously realised path points. By using more global summaries for the present classification scheme and, also, by requiring that fixed-endpoint paths must be generated on demand, sequential generation of points in a path becomes impractical. So, for example, using a random walk approach to sample the event space of paths resulting from a return trip from and to a central place would lead to enormous wastage as very few paths of the required length would return to the point of origin after exactly n steps. Instead, I introduce an algorithm that generates paths that are specified in terms of length and endpoints but are otherwise unspecified. This algorithm, explores the event space Ω randomly but not uniformly (see

Open-ended trip

$0 \le \rho \le l$

Return trip

$0 \le \rho \le l/2$

Transitory trip

$\lambda(\mathbf{x}_O, \mathbf{x}_T) \le \rho \le l$
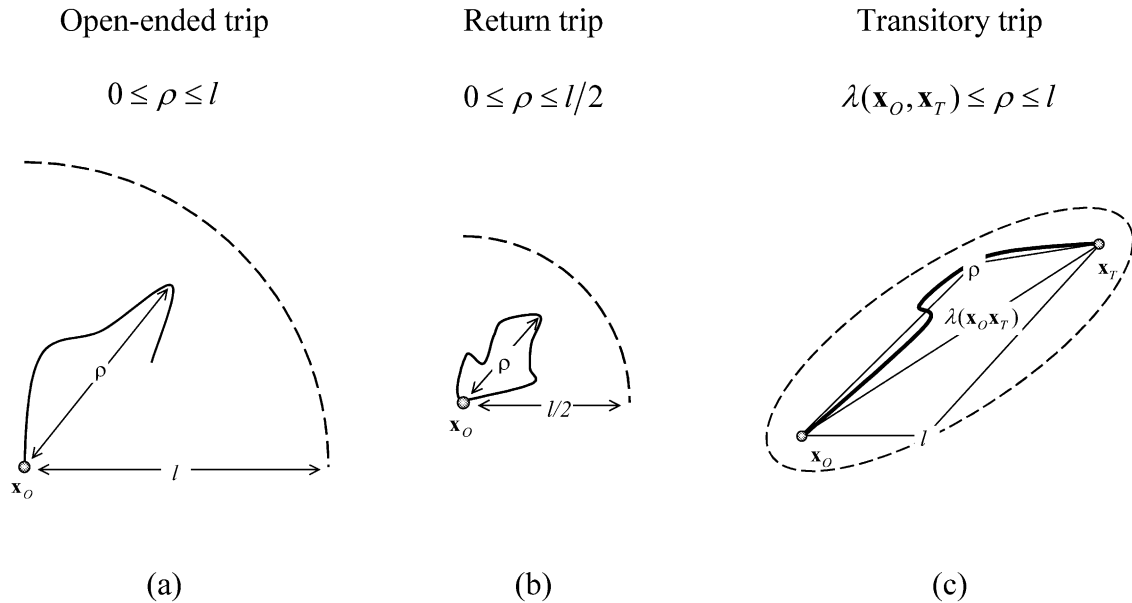
(a)   (b)   (c)

Fig. 2. The range (ρ) of a path is defined as the maximum distance reached during a trip from the trip's endpoint(s). In environments that contain obstacles to movement, biological distance must be used to measure the range. This is simply the smallest path length ($\lambda(x_1, x_2)$) required to get from one point (x_1) in space to another (x_2) while circumnavigating obstacles. The maximum attainable value of the range depends on the type of trip that generated the path. In open-ended trips (a) the animal can unfold its path completely so that the maximum attainable value of the range is equal to the path's length (l). In return trips (b), the range cannot exceed half the path's length. In transitory trips (c), the path's length must be greater than the biological distance ($\lambda(x_0, x_T)$) between the trip's endpoints. In this case, the range is defined $\rho = \max\{\lambda(x_0, x) + \lambda(x_0, x_T), \forall x \in U\}$ and its value cannot exceed the path's total length.

below) and then groups the resulting paths according to the classification scheme at hand.

Algorithm 1 *(Path generation).*   (i) Initialization: Initialise the algorithm with the trip's endpoints (x_0, x_T) and duration (τ).

(ii) Path length: Take the next value of l from the discretised domain of possible path lengths.

(iii) Overall feasibility: Examine if the trip can be performed with a path of length l. This involves, firstly checking if the biological distance between the trip's endpoints is at most as large as l and, secondly, if the maximum speed of the animal (see next section) enables it to cover a length l in the available time τ. If the trip is not feasible then go to step (ii).

(iv) Path discretization: Use the length unit Δl to discretise the path length l. This gives a total of n points. The endpoints are specified as parameters in step (i). The intermediate points have not yet been placed in the lattice. The length of the path

segments generated in this way is Δl except for the length between the $n-1$th point and x_T which is equal to $\Delta l(l/\Delta l - [l/\Delta l])$.

(v) Next point to be placed: From the set of points that have yet to be placed in the lattice, select one at random.

(vi) Find the feasible region for this point: Let l' be the length of the path segment between the currently selected point and the immediately preceding point that has already been placed in the lattice (say, at x'). Similarly, let l'' be the length of the path segment between the current point and the first point after it that has already been placed in the lattice (say, at x''). The values of l' and l'' are fixed and, in most cases, integer multiples of Δl. The value of l'' will be a non-integer multiple of Δl only if $x'' = x_T$. The feasible region for the current point is the intersection of the two discs (x', l') and (x'', l''). It therefore consists of all points x that satisfy the inequalities $\|x' - x\| \le l'$ and $\|x'' - x\| \le l''$. Conceptually, the, as yet un-

placed, point x is tied to two pieces of string of length l' and l'' which are anchored at the points x' and x''. The region within which the point can be placed will be determined by these constraints and its boundaries can be calculated in general using simple geometrical arguments (Appendix A).

(vii) Placement of point: Select a set of coordinates uniformly randomly from the feasible region. Position the current point at those coordinates.

(viii) Recalculate combinatorial weight for this path. This algorithm is computationally expedient but step (vii) means that not all paths of a given type (i.e. paths belonging to an event space $\Omega_{\mathbf{m}}$) have the same probability of being generated. A correcting weight is therefore derived in Appendix B.

(ix) Repeat steps (v)–(vii): Continue until all n points have been placed.

(x) Obtain lattice path: Convert path coordinates to the centrepoints of the corresponding lattice cells.

This procedure shares common elements with the midpoint displacement method (Mandelbrot, 1982). An example of a path generated using this algorithm is shown in Fig. 3. This algorithm allows the positioning of points in a path in any order, rather than sequentially. In this case, the endpoints are placed first and the intermediate points are placed in random order after them.

Note, however, that there is a computational price to be paid in terms of the number of iterations of the whole algorithm required to explore the event space Ω. For combinatorial reasons, some types of paths are easier to generate than others. An example is shown in Fig. 4. Using the summaries of length and range, we see that, for a given path length, extreme values of the range are less likely to occur by chance. Therefore, the types of paths that are more difficult to generate with this algorithm will determine the sampling intensity required to adequately explore the event space Ω. This problem will become more severe when modes of movement are specified in detail, but, as I argued above, a few path summaries will usually be sufficient for the estimation of usage.

It must also be stressed that this is only a computational problem. This algorithm is used to generate the relative usage of different lattice cells

resulting from the same type of path. The frequencies with which different types of paths are generated by this algorithm are ignored in the estimation of usage. This is because the preference associated with a given mode of movement should be determined by the animals' behaviour and not by combinatorics.

3.3. Time allocation along a lattice path

Having discretised a path by length, it is then necessary to allocate a time of residence to each point in the resulting lattice path. In this subsection, I describe my approach to this problem.

If the animal moves at a constant speed, so that equal length increments along the path correspond to equal time intervals of movement, then the proportion of time spent in a cell will be $s(x|U) = n_x/n$, where n_x is the number of points of the lattice path (U) that are in the cell x. Once again, a suitable correction needs to be made to take account of the fact that the last segment of the path will not be exactly equal to Δl.

However, for a particular lattice path (U), it is more reasonable to expect that the animal would regulate its speed so that it spends more time in cells of higher preference. The simplest way to incorporate this is to assume that the time spent in each of the cells visited by the path is proportional to the value of the preference function $(h(x))$ for that cell. However, this neglects the fact that animals are limited by their maximum speed (For example, an animal could not travel infinitely quickly through a cell of zero preference).

Let $t_{min}(l)$ denote the minimum time required by the animal to perform a path segment of length $l = v \Delta l$ $(v = 1, \ldots, n)$. Covering this fixed length in the minimum possible time $t_{min}(v \Delta l)$ implies that the animal is moving at its maximum average speed. In this and subsequent uses of the term 'maximum average speed', 'maximum' refers to the restrictions imposed on speed by the animal's physiology and 'average' refers to the fact that the value of speed is not instantaneous but measured over the entire path segment l.

Note, that maximum average speed and segment length may not be linearly related. For example, animals may be able to cover small lengths in
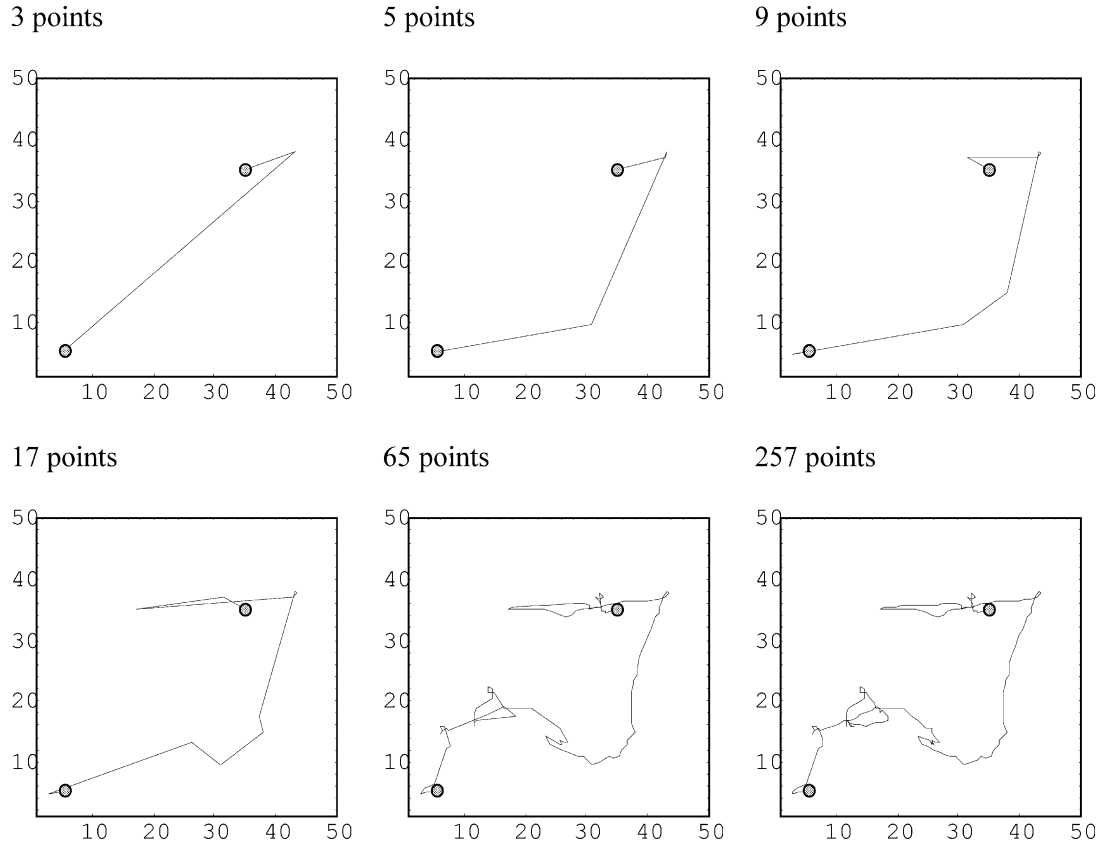
Fig. 3. An example of a path generated using Algorithm 1. The algorithm is initialised with the path's length and the positions of the trip's endpoints. It then fixes the remaining points along the path in random order.

bursts of high speed but they may not be able to maintain such speed for longer path lengths. An empirical function or a behaviourally/physiologically realistic model for $t_{\min}(v\Delta l)$ is therefore required (see Appendix C for an example of such a model).

The allocation of time over the elements of U can be done using the following algorithm:

Algorithm 2 (*Time allocation along a lattice path*). (i) Initialization: Generate an initial residence duration distribution along the lattice path such that $s(x|U) \propto h(x)$ and $\Sigma_{\text{All } x \in U} s(x|U) = 1$.

(ii) Feasibility test: If the minimum time $t_{\min}(v\Delta l)$ required to perform the entire path is more than the trip's duration τ then declare the path unfeasible and exit.

(iii) Loop for length scale: Examine next length scale v ($v = 1, \ldots, n$).

(iv) Minimum time for that scale: Calculate the minimum time ($t_{\min}(v\Delta l)$) required to perform a path at the current length scale v.

(v) Loop for path segment at current length scale: Examine next segment $\{x_i, \ldots, x_{i+v}\}$ at the scale v in the lattice path.

(vi) Modification of residence time: The total time allocated to that segment by the current residence duration distribution is $t_i = \tau\Sigma_{j=i}^{i+v} s(\mathbf{x}_j|U)$. If $t_i < t_{\min}(v\Delta l)$, then increment the existing residence times at the points of the current segment in proportion to the preference for the lattice cells involved and so that the total time increment for the segment brings it up to $t_{\min}(v\Delta l)$, the minimum time required to perform the segment.
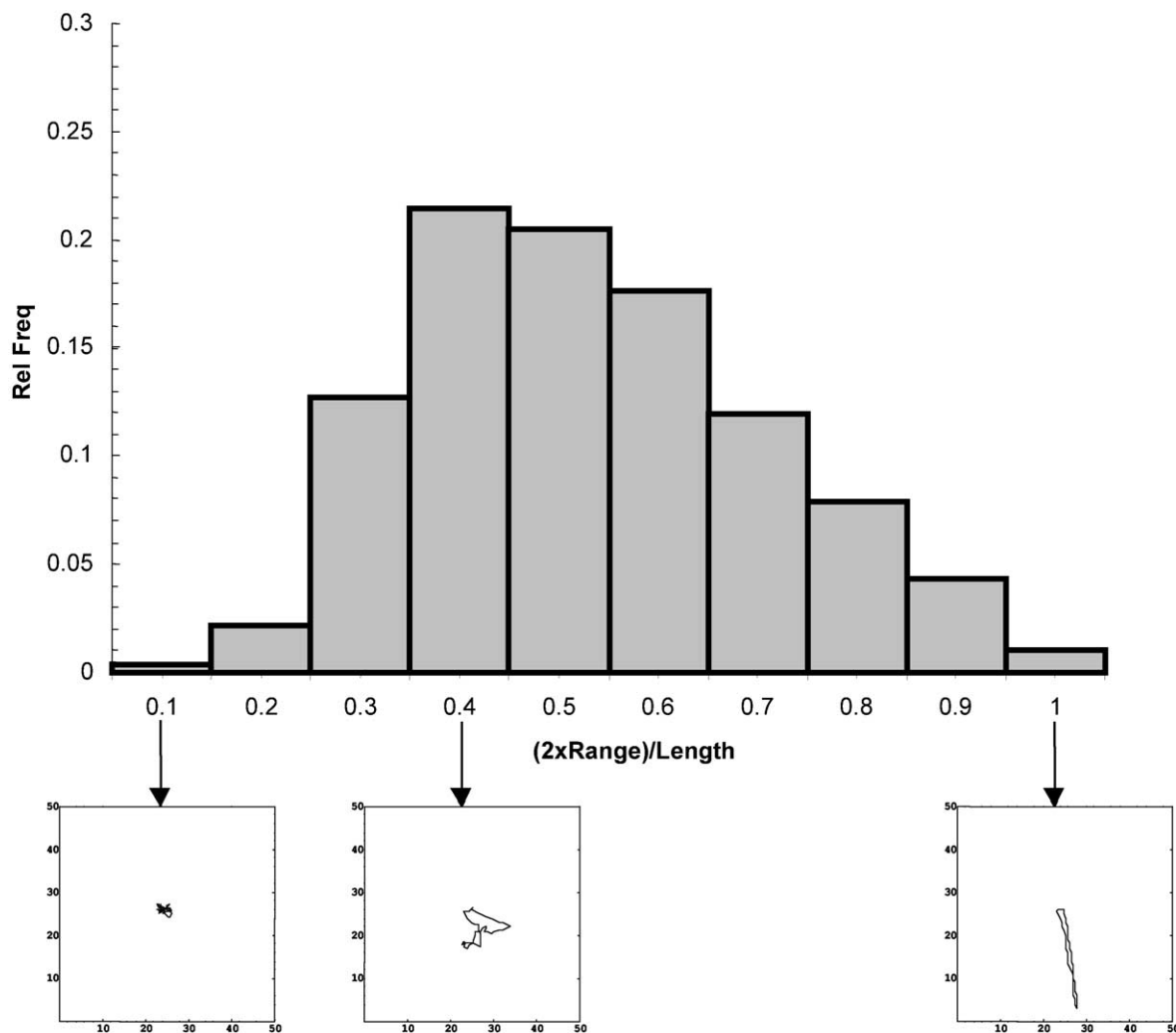
Fig. 4. For combinatorial reasons, under Algorithm 1, some types of paths are easier to generate than others. I used Algorithm 1 to generate 1000 paths of the same length (50 points each) and classified them according to the simple scheme of this paper (employing path length and range). It is clear from this example that extreme values of the ratio $2\rho/l$ occur less frequently. This implies that the event spaces to which these paths belong will be less intensively explored by the algorithm.

(vii) Repeat steps (v)–(vi) until all segments have been examined.

(viii) Renormalise the entire residence duration distribution so that, once again, $\Sigma_{\text{All}\mathbf{x}\in U}s(\mathbf{x}|U) = 1$.

(ix) Repeat steps (v)–(vii) until no further corrections are necessary.

(x) Repeat steps (iii)–(ix) until all length scales have been examined.

Sample output of this algorithm for a given environment and a given lattice path is given in Fig. 5.

When not limited by the animal's maximum speed, the algorithm allocates time in proportion to preference (steps (i) and (vi)). This assumes that the animal has, in the past, explored and accurately perceived the profitability of all the points
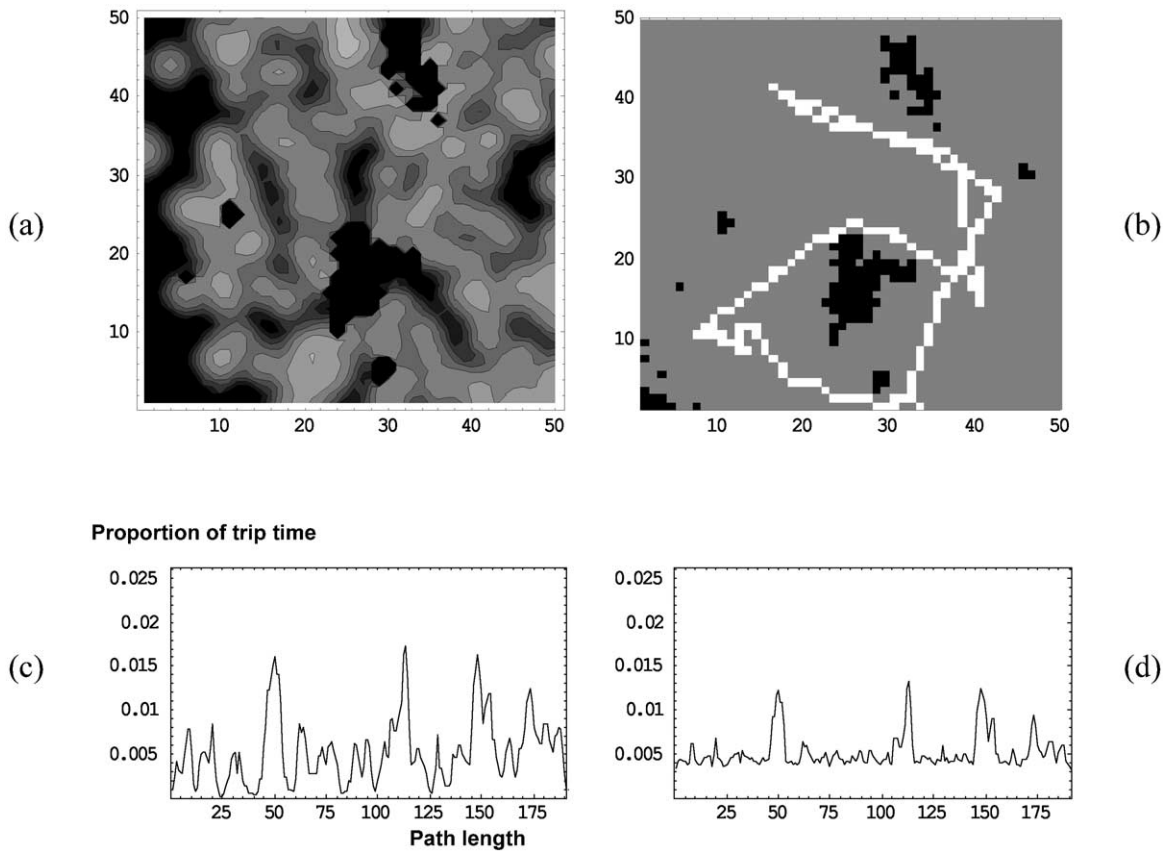
Fig. 5. Sample output of the path generation and time allocation algorithms (Algorithm 1 and Algorithm 2 respectively). The lattice path (b) is generated independently of the preference function (a). The algorithm is initialised with a time allocation trace (c) that is directly proportional to the preference values of the cells that the lattice path goes over. Restrictions in maximum average speed at all scales of length are then considered and the final time allocation trace (d) is arrived at. This determines the usage $(s(x|u)$ of lattice points along a path.

visited by the lattice path U. Although in this paper, I use (and validate under conservative conditions) this assumption, steps (i) and (vi) of the algorithm can be modified (e.g. by using error terms in the perception of the preference function) to enable it more accurately to represent the effect of deficient knowledge and imperfect memory.

Finally, the algorithm needs to be corrected for the fact that animals cannot travel over obstacles. Those lattice paths generated by Algorithm 1 that go over an obstacle are deemed unfeasible for a given lattice and must therefore be excluded from the corresponding event space $\Omega_{\mathbf{m}}$.

Conceptually, this does not require an 'If… then…' test in addition to that of step (ii)

of Algorithm 2 since, the time required for an animal to travel over an obstacle is infinite and so is the minimum time required to perform the path, whatever the path's duration. Instead of the binary treatment of maximum average speed used in this paper, one could envisage more complicated models of time allocation in which the animal moves at a variable speed not because it chooses to but because its maximum average speed is affected by the medium it moves through or the habitat it moves over. If the way in which maximum speed is affected by the environment of movement is known, then this information can readily be incorporated in the above algorithm.

3.4. Preference for a particular lattice path of known characteristics ($h(U|\Omega_\mathbf{m})$)

As discussed in the previous subsection, along a given path, an animal might be expected to spend more time in cells of high preference. It is also plausible to assume that, in choosing between paths of a given type, the animal will be more likely to perform paths that, overall, allow it to spend more time in locations of high preference. If the animal spent an equal proportion of its trip's duration at every cell in the lattice path then the overall preference for a particular path could be expressed as the average of the preference values $h(x)$ of the cells visited by the path. However, since residence time will not, in general, be the same for all cells, overall preference for a path can be expressed as the average of the preferences ($h(x)$) of the individual cells visited along the path, weighted by the proportion of time the animal spends there

$$h(U|\Omega_\mathbf{m}) = K \sum_{\text{All } x \in U} h(x)s(x|U) \qquad (6)$$

Preference for paths of a given type must satisfy the condition $\Sigma_{\text{All } U \in \Omega_\mathbf{m}} h(U|\Omega_\mathbf{m}) = 1$. The constant of proportionality in Eq. (6) is therefore the result of normalization,

$$K = \left(\sum_{\text{All } U \in \Omega_\mathbf{m}} \sum_{\text{All } x \in U} h(\mathbf{x})s(\mathbf{x}|U) \right)^{-1} \qquad (7)$$

3.5. Preference for a mode of movement ($h(\Omega_\mathbf{m})$)

The animal's preference ($h(\Omega_\mathbf{m})$) for a particular mode of movement will depend on external and internal factors (e.g. Scharstein, 1990). The contribution ($h_\mathrm{E}(\Omega_\mathbf{m})$) of external factors to the function $h(\Omega_\mathbf{m})$ depends on the underlying preference function $h(x)$ for environmental attributes and is therefore dependent on the positioning and orientation of the path within the environment. The contribution $h_\mathrm{I}(\Omega_\mathbf{m})$ of internal factors (such as physiological constraints on speed, or an inherent tendency to maintain the same direction while moving) will be shift- and rotation-invariant. As a first approach to the problem, I assume a multiplicative relationship between the contribution of internal and external factors,

$$h(\Omega_\mathbf{m}) \propto h_\mathrm{I}(\Omega_\mathbf{m})h_\mathrm{E}(\Omega_\mathbf{m}) \qquad (8)$$

This formulation gives equal importance to internal and external preference. This is not a strict assumption. Admittedly, some animals' movement may be uninfluenced by their environment so that one may be tempted to weight $h_\mathrm{I}(\Omega_\mathbf{m})$ and $h_\mathrm{E}(\Omega_\mathbf{m})$ differentially. However, this situation is, in fact, the result of a uniform preference function $h(x) = \text{const}$. Also, a multiplicative relation such as Eq. (8) behaves like a logical 'OR' operator. This is a desirable property because it ensures that, if a particular mode of movement does not occur, it is either because the animals do not inherently tend to use it or because it is not encouraged by the distribution of resources in the environment. The biological interpretation and implications of Eq. (8) are examined further in the paper's discussion. Here, I discuss how the components of Eq. (8) can be specified.

Preference for a mode of movement due to external factors $h_\mathrm{E}(\Omega_\mathbf{m})$ can be derived as a weighted average of the preference for the cells visited by paths generated by this mode of movement,

$$h_\mathrm{E}(\Omega_\mathbf{m}) = \sum_{\text{All } x} h(x)s(x|\Omega_\mathbf{m}) \qquad (9)$$

Internal preference for a mode of movement $h_\mathrm{I}(\Omega_\mathbf{m})$ can be expressed as an empirical function of path summaries and their higher-order interactions. Given the rather small number of biological studies carried out on inherent patterns of animal movement it is not clear what form that function should take. In the examples presented below I tentatively use a log-linear model with four parameters,

$$h_\mathrm{I}(\Omega_\mathbf{m}) = \exp(\beta_0 + \beta_1 l + \beta_2 \rho + \beta_3 l\rho) \qquad (10)$$

The expression in Eq. (10) carries no biological or statistical significance. It is not based on any biological principle and its similarity with a generalised linear model (GLM) is only superficial. It is just one of many possible formulations that give positive values which can then be re-normal-

ised to satisfy the condition $\Sigma_{\forall\ \mathbf{m}}h_{\mathrm{I}}(\Omega_{\mathbf{m}}) = 1$. In Eq. (10) this is done by setting $\beta_0 = -\ln(\Sigma_{\forall\ \mathbf{m}}\exp(\beta_1 l + \beta_2 \rho + \beta_3 l\rho))$.

3.6. Modelling usage

Prior to estimating usage it is necessary to create the data structures that will receive the results from Algorithm 1 and Algorithm 2 (path generation and time allocation). These are (1) an array identical in structure to the spatial lattice and, (2) for each cell (x) in the spatial lattice, a corresponding array identical in structure to the contingency table of path types. The first of these will eventually store the predicted, total usage of each location in space and the second will store the relative contribution, by each mode of movement, to the predicted usage of each lattice cell.

The second of these data structures enables the program to track usage in a cell x resulting from each mode of movement. It is also the main determinant of the program's memory requirements. For example, in a path classification scheme consisting of k summaries where the domain of the ith summary has been discretised into z_i intervals (bins) the contingency table will consist of a total of $\Pi_{i=1}^{k}z_i$ distinct classes (each corresponding to a distinct mode of movement). In a relatively small, 50×50 lattice, using only two path summaries, each discretised into 10 bins, the storage requirement is for 2.5×10^5 high-precision numbers.

Overall, this framework is characterised by a trade-off between the size and resolution of the spatial lattice and the specificity (number of summaries) and resolution (number of bins per summary) used to describe the geometry of paths.

To generate a usage distribution resulting from trips with known endpoints and of known duration, the following procedure is applied:

Algorithm 3 *(Modelling usage).* (i) Generate lattice path U (using Algorithm 1).

(ii) Allocate residence time to each of the points of U (using Algorithm 2).

(iii) Estimate the preference $h(U|\Omega_{\mathbf{m}})$ for the path relative to other paths resulting from the same mode of movement (Using Eq. (6)), normal-

ization of these values of preference and hence the calculation of K under Eq. (7) can be left until after step (v)).

(iv) Estimate the additional usage of each cell x visited by the lattice path U from the occurrence of this path. Increment existing usage $s(x|\Omega_{\mathbf{m}})$ at each cell accordingly.

(v) Repeat steps (i)–(iv) until the path summary space has been adequately explored.

(vi) Estimate preference $h_{\mathrm{E}}(\Omega_{\mathbf{m}})$ for a mode of movement due to external factors (Using Eq. (9)).

(vii) Combine it with the model (e.g. Eq. (10)) of preference $h_{\mathrm{I}}(\Omega_{\mathbf{m}})$ for modes of movement due to internal factors to produce the preference function $h(\Omega_{\mathbf{m}})$.

(viii) Finally, use Eq. (5) to generate the usage distribution.

4. A null model of usage

The modelling framework described in Sections 2 and 3 estimates usage at a point in space as a function of accessibility and preference. In most biological systems, data relating to accessibility (speed of movement, trip durations, trip endpoints and obstacles to movement) are more easily obtainable, through direct and, often localised observation, than information pertaining to preference. In this section, I specify a null version of the general framework that is as informed as it can possibly be on matters of accessibility and as naïve as it often has to be on matters of preference. Hence, the null model incorporates information about the animals' speed and the duration and endpoints of their trips, but assumes that animals show no preference either to specific locations in space or particular modes of movement.

In general, such a partly specified model serves two purposes. Firstly, it synthesises all the readily obtainable data into a spatial description of accessibility and, secondly, it formalises the investigator's ignorance on matters of preference. As I will discuss in Section 5, below, the null model described here is the start of a line of enquiry that aims to provide insights about animal preference.
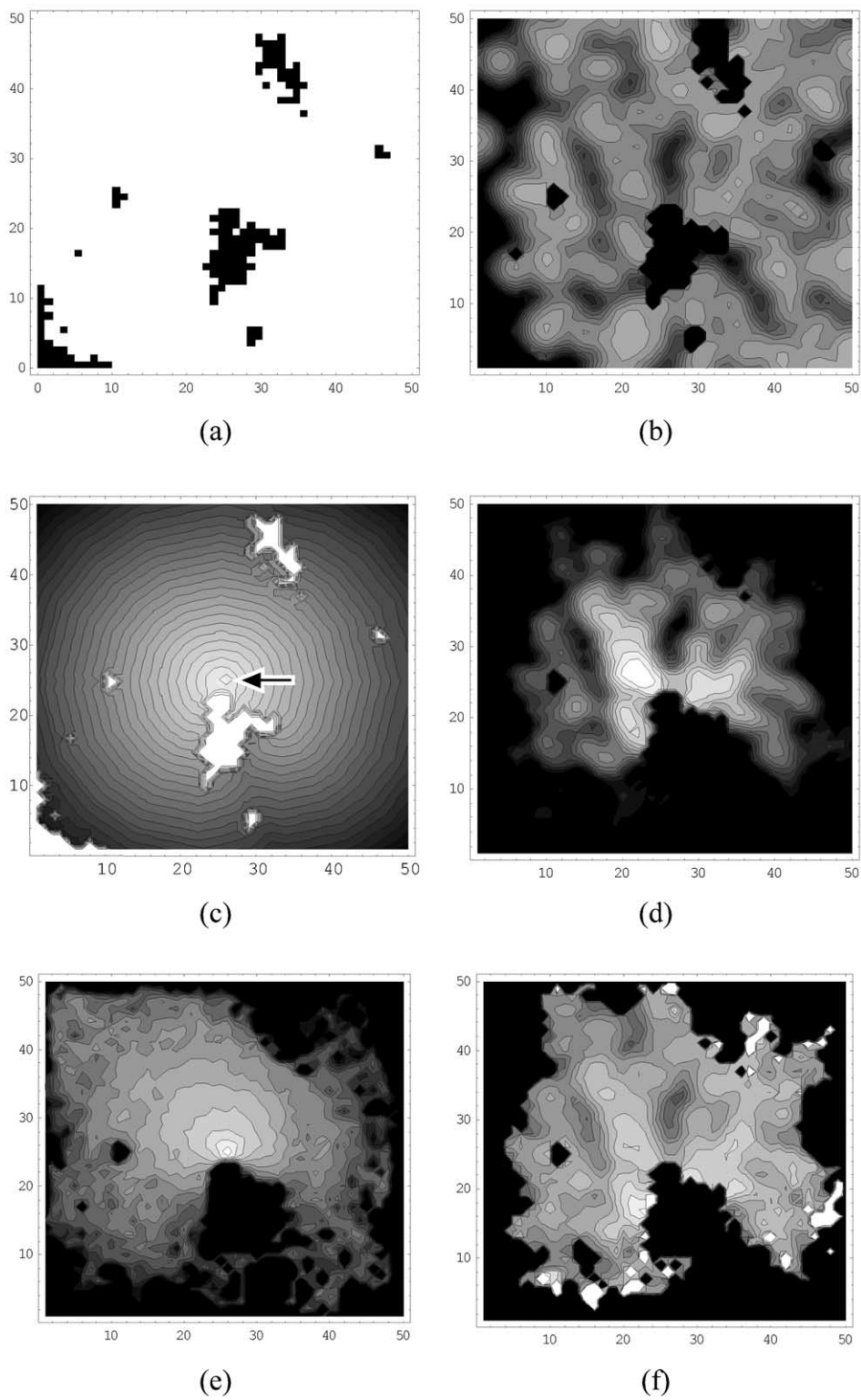
Fig. 6

4.1. Quantifying the determinants of accessibility

Advances in remote sensing and GIS have greatly increased the ease with which data on geomorphology and habitat features are collected and processed. In addition, the investigator is often aware of the type of environmental feature that obstructs the movement of the animal being studied (for example, land for marine, and water for terrestrial organisms). It is therefore likely that the investigator will be able to include information about obstacles. It must be noted that this is not a necessary input to the model. If this information is not available or if the investigator is not certain about what constitutes an obstacle the model can still generate results.

It can also be assumed that at least one of the trip's endpoints and the trip's duration are known. For most of this paper, for reasons of presentational clarity, I have assumed that knowledge of the trip's duration is exact. However, the framework can easily be extended to the case when the duration of a trip is known in distribution (see application to grey seals in Section 5, below).

The one remaining unknown influencing accessibility is the animal's maximum average speed of movement used in the time allocation algorithm (Algorithm 2). If high-resolution, long-term, individual movement data exist, then one can tabulate maximum average speed as a function of path length. However, such data may not be available. It will then be necessary to extrapolate from fine-scale/short-term data by using a physiologically/behaviourally realistic model.

Fine-scale/short-term movement data can be obtained using methods such as radio tracking (White and Garrott, 1990) or video tracking (Bell, 1991; Häder, 1990). Although these data may not be sufficient to provide a comprehensive under-

standing of the animals' large-scale movement behaviour, they can, nevertheless, be used to obtain extrapolated estimates of their maximum average speed at greater time scales than those observed (see example of such a model in Appendix C).

4.2. Modelling the lack of preference

Assuming that animals show no preference for environmental characteristics implies that the function $h(x)$ has a constant, non-zero value h in all lattice cells that are not obstacles to movement. Preference for modes of movement due to environmental characteristics ($h_E(\Omega_m)$) can then be derived from Eq. (9) as $h_E(\Omega_m) = h\Sigma_{All\ x}s(x|\Omega_m) = h$.

Similarly, in the null model, internal preference for different modes of movement should be uniform. For example, in the case of the model in Eq. (10) parameter values should be set to $\beta_1 = \beta_2 = \beta_3 = 0$.

5. Applications to simulated data

In this section, I outline three, potentially important, applications of this framework in research dealing with habitat selection and usage estimation. There is extensive literature on the investigation of habitat selection (reviewed by Manly et al., 1993). The aim of this paper is simply to extend the applicability of the existing statistical methodology to animals whose usage of space is influenced by accessibility restrictions. Therefore, rather than present a detailed statistical analysis of the simulated data, I restrict attention to how the framework fulfils its objective.

Fig. 6. Simulation setup for applications I and II. Obstacles (shown in black) were placed on a 50×50 lattice (a) and a resource distribution was added to the remaining cells (b). The biological distances ($\lambda(x_0, x)$) of all cells from the point of origin (indicated by the arrow) were estimated (c) and 10 000 paths were simulated to generate the 'observed' usage distribution (d) which is partly determined by the underlying resource distribution (b). However, because accessibility restrictions also influence the observed usage distribution, the direct correlation between the usage and resource distributions was rather weak. Accessibility restrictions were accounted for by running the null model (incorporating no preference for environmental attributes or modes of movement) and using its output (e) to control for the effects of accessibility on usage. The ratio (f) of observed over null usage was a clearer indicator of preference for environmental attributes (compare (b) with (d) and (b) with (f)).

5.1. Application I: investigating preference for environmental attributes

I first examine the common scenario in which the investigator has knowledge of the spatial distribution of environmental attributes (e.g. food or other resources) and of the usage distribution of the animal(s), but lacks knowledge of how the two are connected. The aim is to investigate preference for environmental attributes.

In order to generate a data set on which to test the model framework, I constructed an individual-based simulation of animals performing return-trips of fixed duration from a fixed origin, within a synthetic environment. The environment was a 50×50 lattice consisting of cells that either allowed or obstructed movement (Fig. 6a). Using an algorithm similar to that described in Wiengand et al., (1999), I then generated fictitious preference values $h(x)$ for those cells that the simulated animals could move over (Fig. 6b). To allow correct categorization of paths according to their range (ρ), I produced a map of biological distances with reference to the point of the trips' origin (Fig. 6c). In this lattice, I simulated a total of 10 000 return trips to obtain the 'observed' usage distribution $s(x)$ (Fig. 6d).

Simple movement rules were used. An individual remained at its position or moved to any of the eight neighboring lattice cells with probability proportional to the preference values of these cells. The simulated animals were therefore random walkers on a square grid, whose movement was biased only by the local gradient of habitat quality, one of the simplest set of rules that incorporates a response of the simulated animals to their environment (Okubo, 1980). In a homogeneous environment, the distribution of usage resulting from these simulations would be given by time-integrated, simple diffusion. In a heterogeneous environment, the simulated animals were captured by local maxima of the function $h(x)$ close to their starting point. Importantly, this property of the individual-based simulation makes it a conservative platform on which to validate the proposed modelling framework (see discussion in Section 7).

I then parameterised and ran the null model described in Section 4, for this test system, hence generating a null usage distribution $s'(x)$ (Fig. 6e). To graphically illustrate how the output of the null model can control for the effects of accessibility on usage, I divided the value of each cell of the observed usage distribution by that of the corresponding cell of the null usage distribution. This resulted in a new distribution (Fig. 6f) that was found to be a better predictor of preference (Spearman rank correlation between ratio $s(x)/s'(x)$ and $h(x) = 0.482$) than either one of its components (Spearman rank correlation between
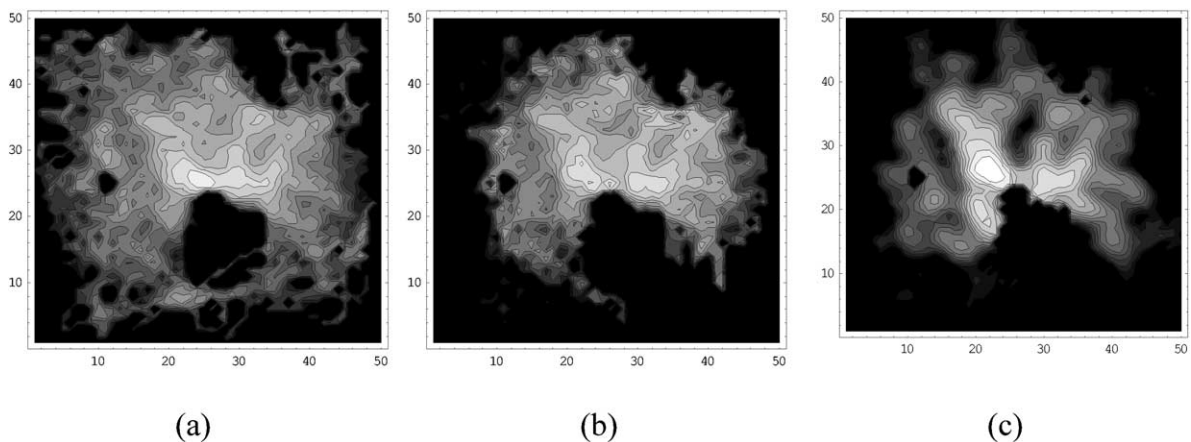

Fig. 7. Investigating preference for modes of movement. Using a known preference function and the null version of the internal preference ($\beta_1 = \beta_2 = \beta_3 = 0$) leads to a usage distribution (a) that can then be modified by finding the parameter values β_0, β_1, β_2 and β_3 that result in a distribution (b) which deviates minimally from the observed usage distribution (c).
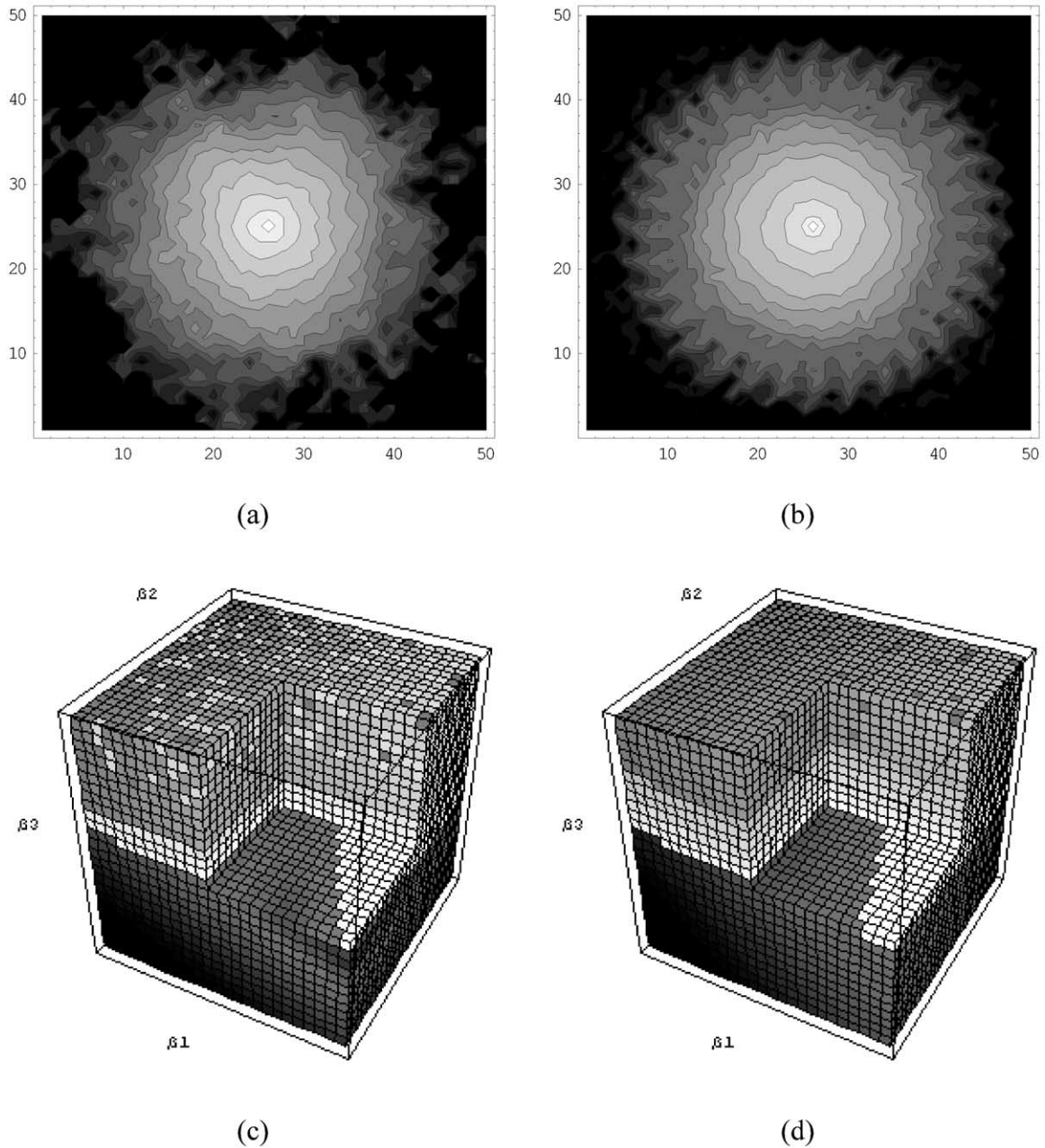
(a)

(b)

(c)

(d)

Fig. 8. The values of the parameters β_0, β_1, β_2 and β_3 that have been obtained by fitting the model to the observed usage distribution can be treated as a characteristic of the animals and not of their environment. Hence, removing all environmental features (no obstacles and a uniform resource distribution) and re-running, firstly, the individual-based simulation and, secondly, the model results in similar usage distributions (a) and (b). Further to illustrate that the values of the parameters defining internal preference do not depend on environmental features, the goodness of fit resulting from all parameter combinations was explored over the parameter space of β_1, β_2 and β_3 (β_0 is just a rescaling constant). The 3D density plots in (c) and (d) show the goodness of fit of different parameter combinations for the cases of the heterogeneous and homogeneous environments, respectively.
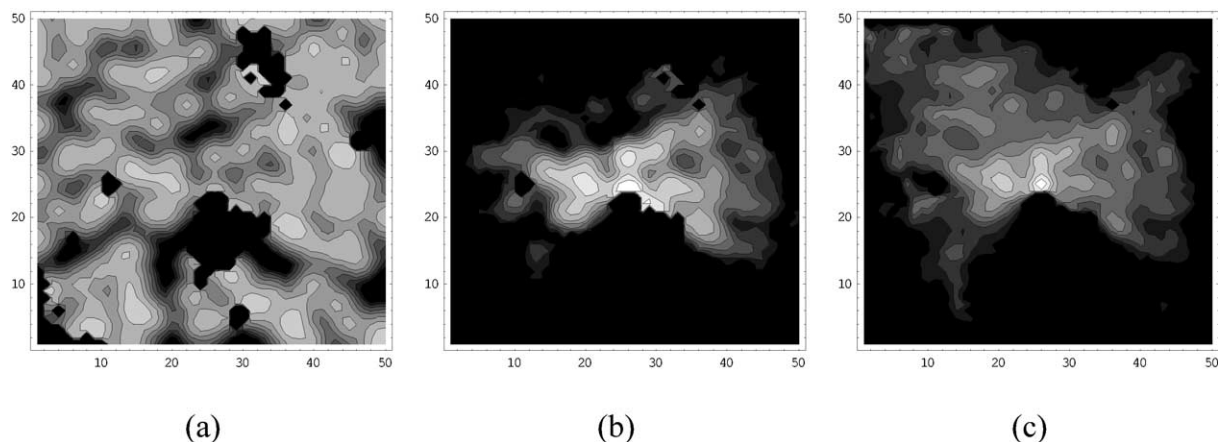
Fig. 9. For a new resource distribution (a) new usage distribution (b) is obtained. If preference is truly invariant under such changes, then we can use previously extracted information on preference to predict what this new usage distribution will look like (c).

$s(x)$ and $h(x) = 0.274$, Spearman rank correlation between $s'(x)$ and $h(x) = -0.146$).

The implication of this is that, in cases where accessibility influences the usage distribution, it is potentially advantageous to obtain a standardised index of usage by employing a null model such as the one presented here. During the exploratory stage of data analysis, this index will enhance the investigator's ability to identify environmental variables that could be covariates of preference.

In a formal analysis of habitat selection (e.g. Rosenberg and McKelvey, 1999) one would take advantage of the information on relative accessibility (as quantified by the output of the null model) by using it directly, as one of the explanatory variables in a multivariate statistical model. This approach has the advantage of actually quantifying the power of the null model's output in explaining the observed usage distribution. Under certain conditions (see Bishop et al., 1975), the accessibility dimension of the resulting empirical model could then be collapsed to yield a standardised estimate for environmental preference in a freely accessible environment.

5.2. Application II: investigating internal preference for different modes of movement

As mentioned above, it is advisable to quantify the explanatory power of the null model's estimate

of accessibility by using it as yet another explanatory variable in a statistical model of environmental preference. There is good cause for allowing this flexibility. The null model assumes that, in a homogeneous environment, animals have no inherent preference for one mode of movement over another. In the examples of this section this is represented by setting $\beta_1 = \beta_2 = \beta_3$ in Eq. (10). The resulting estimate of accessibility is therefore a composite of all modes of movement equally weighted. Although, this is a good initial assumption, it may reduce the null model's ability correctly to quantify accessibility. At some stage, it is necessary to fine-tune the parameters of the internal preference function $h_I(\Omega_m)$. This could follow the investigation for external preference (as is done here) or precede it although, ideally, the two should be investigated simultaneously, or, even, iteratively.

For this application, I assume that, following a formal analysis of preference, the investigator has an estimate of the animals' preference for environmental attributes, of the spatial distribution of these environmental attributes, and, also, of the animals' usage of space. The first two of these three types of information can be used to derive a spatial preference function $h(x)$ The third is used as the truth to which the model is fitted.

At a first stage, I ran the model, this time using the known preference function $h(x)$ and parameter

values $\beta_1 = \beta_2 = \beta_3 = 0$ for the internal preference function. With the introduction of a non-uniform preference function for environmental attributes, the time allocation algorithm (Algorithm 2) and the maximum average speed model (Appendix C) must also come into play. For the function $t_{\min}(l)$ I used the formulation and parameter values derived in the example of Appendix C. The initial output of the model (Fig. 7a) was then improved by fitting the parameters β_0, β_1, β_2 and β_3 to the observed usage. This was done by minimising the sum of squared deviations of the model's spatial output from the observed usage distribution (Fig. 7c).

This recursive procedure is facilitated by the data structures used by the model which store the relative contribution of each mode of movement to the usage of each lattice cell. Hence, a change in the parameters β_0, β_1, β_2 and β_3 is equivalent to a simple reweighting of known information and it is therefore not necessary to generate new paths every time a new set of values for the parameters is examined.

The best-fitting parameters were $\beta_1 = 2.67$, $\beta_2 = 3.90$ and $\beta_3 = -0.34$ the negative sign of the interaction coefficient β_3 suggesting a trade-off between longer paths and wider ranges. Despite their similarities, the distribution predicted by the model (Fig. 7b) was less heterogeneous than the true usage distribution (Fig. 7c).

To illustrate the independence of internal preference from the environment in which movement takes place, I ran both the individual-based simulation and the model in a homogeneous lattice (no obstacles, uniform preference function). For the model of internal preference, I used the previously obtained values $\beta_1 = 2.67$, $\beta_2 = 3.90$ and $\beta_3 = -0.34$ to generate a prediction of usage in this featureless environment. The resulting distributions of usage (Fig. 8a and b, respectively) were comparable in their spread.

Yet, it is possible that more than one combination of values for the parameters β_1, β_2 and β_3 can result in a good fit between the predicted and observed usage distributions. Also, simply looking at how well a single set of parameter values, obtained from one usage distribution, manages to emulate another usage distribution is a rather weak indicator of the independence of internal preference from environmental conditions. Consequently, I performed an exhaustive exploration of how the quality of fit varies over the parameter space of β_1, β_2 and β_3 in the two (heterogeneous and homogeneous) test environments. Once again, the overall aim was to see which parameter values for β_1, β_2 and β_3 would have been suggested as plausible by the present approach under fundamentally different environmental conditions. The results (Fig. 8c and d) illustrate that there is, indeed, considerable similarity between the two cases.

5.3. Application III: predicting usage

Of the three applications presented here, this is the one with the highest degree of risk. The aim was to predict the distribution of usage in a new environment using information on the study species, previously extracted from other sites. The best way of extrapolating to new environments on the basis of information collected either elsewhere or at another point in time is still being debated in the literature (Arthur et al., 1996; Boyce and McDonald, 1999; Mysterud and Ims, 1999 and reply by Boyce and McDonald, 1999). Incorporating a continuous measure of accessibility to an analysis of habitat preference (see Application I, above) should lead to increased robustness in the results but will not take account of other factors such as complex behavioural constraints and interactions between resource requirements. Therefore, this section is purely illustrative and of limited value to the debate of how best to deal with preference when habitat availability changes.

I assumed that the investigator has knowledge of the preference functions $h(x)$ and h_i $(\Omega_{\mathbf{m}})$, and of the distribution of environmental attributes, but no knowledge of usage. In a lattice of the same dimensions as before, I generated a new resource distribution (Fig. 9a) and, on it, I simulated a set of 10 000 paths to obtain a new usage distribution ($s(x)$—Fig. 9b) which I kept hidden from the model. I then parameterised the model with the
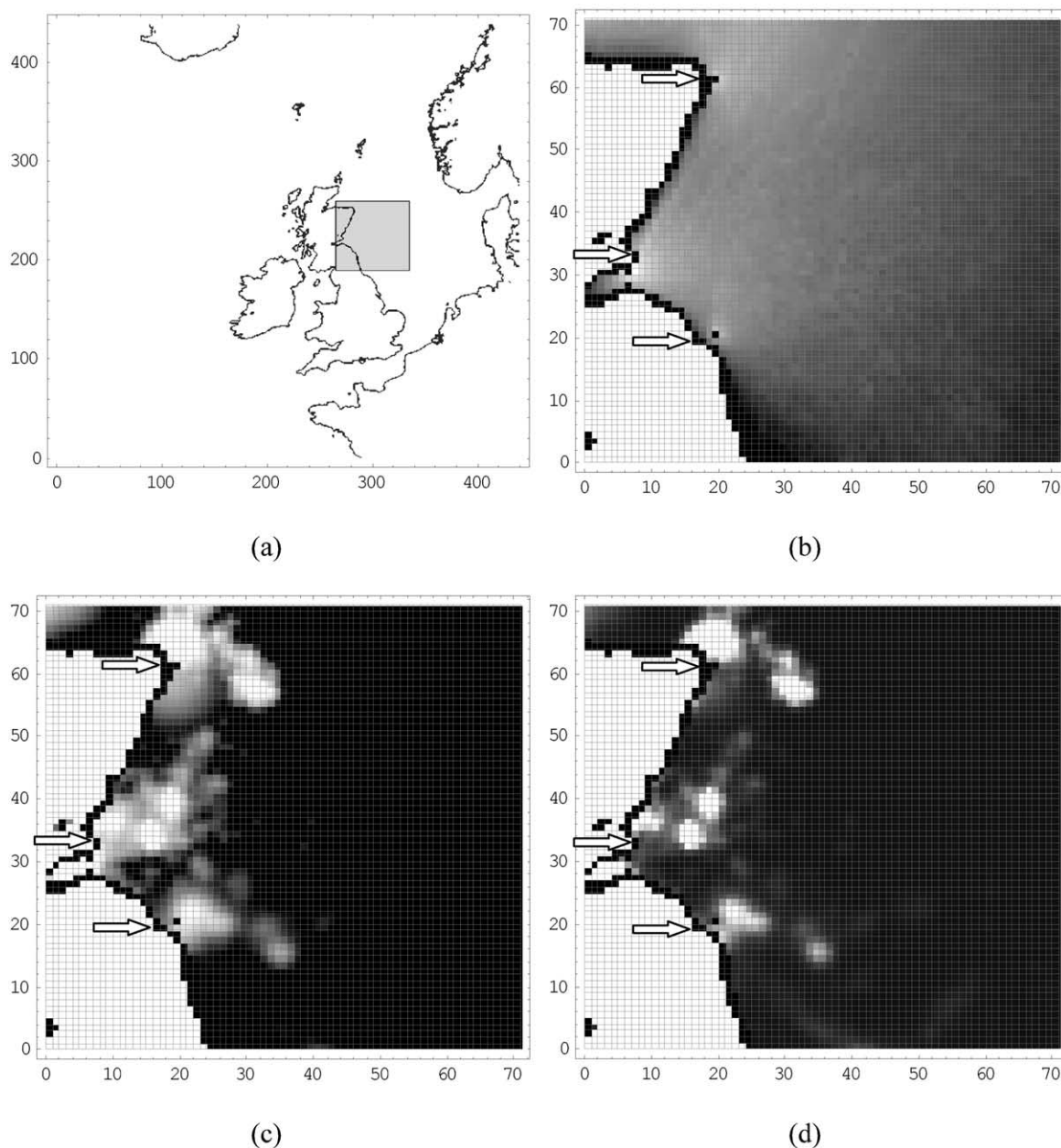
Fig. 10. This qualitative analysis of grey seal habitat usage focuses on a subset of the British population, off the east coast of Britain. Return-trip durations and the coordinates and observed population sizes of three haulouts (indicated by arrows) were used in conjunction with fine-scale data on maximum speed to compile a null distribution of usage (b). This map quantifies the relative accessibility of different points at sea from the three haulouts. Locations from a sample of 30 individuals tagged with SRDL's were used to generate a map of observed spatial usage (c). Taking the ratio the corresponding cells of these two maps (observed usage/ accessibility) yields a standardised map (d) in which the hotspots of usage are more clearly visible. During the exploratory stages of data analysis this makes it easier to determine which environmental attributes are promising candidates as covariates of preference.

known preference functions $h(x)$ and $h_1(\Omega_{\mathbf{m}})$, and generated a prediction for $s(x)$ (Fig. 9c). The spatial features of the true usage distribution were predicted by the model but the prediction was more spread-out around the central place and more homogeneous than the truth.

6. Application to British grey seal data

As a partial application of the methodology developed in this paper, I present preliminary results from an analysis, currently underway, of the habitat preference of the British grey seal.

6.1. Biology of study species

Grey seals (*Halichoerus grypus*) are an important predator of the marine ecosystems around the British coasts, particularly the North Sea. The size of this population (currently estimated to be in the region of 120 000) comprises a large proportion of the species' worldwide distribution and though the species as a whole is not considered endangered, conservation of the British population is seen as important.

On the other hand, fish consumption by grey seals (estimated by Hammond et al., 1994 at ≈ 78 000 tonnes) is anecdotally presented as one of the reasons for the decline of commercially important fish stocks. Knowledge of the spatial distribution and habitat preference of grey seals is therefore of particular importance in the design of policy that satisfies the requirements of fishery management and grey seal conservation.

Outside the breeding season, grey seals apportion their time between the terrestrial and marine environments. Satellite observation of tagged seals (McConnell et al., 1999—see below) indicates that, on average, an individual spends 43% of its time aggregating with other grey seals close to or at sites on shore (haulouts). During the remainder of its time, it performs foraging trips to sea. Most of those trips (~86%) are return trips to the same haulout site.

The position of haulouts and the relative abundance of seals at these sites are monitored by aerial surveys performed regularly by the Sea Mammal Research Unit (SMRU). Data on the large-scale movement of individual seals during their trips at sea have been collected over the last 10 years with the aid of Argos Satellite Relay Data Loggers (SRDLs), developed by SMRU and described in detail elsewhere (McConnell et al., 1992; Fedak et al., 1996). These data sets are typically long-term (average duration of observation 104.3 days), of low frequency (average number of locations per day 6.46) and provide information about the distribution of seals at sea and the duration of their trips.

Short-term (typical duration of observation 24 h) and fine-scale (typical interval between observations 10 min) data on movement have also been collected by following a small ($n = 8$) number of acoustically-tagged individuals (Thompson and Fedak, 1993). These data (McConnell et al., 1999) provide fine-scale information about the animals' speed of movement.

6.2. Extending the framework

To extend the framework for application to a population of animals making trips of variable duration within a network of central places, let T be a random variable with probability density function $g_{ij}(\tau)$ representing the duration of a trip between the ith and jth central place in the network. The distribution of usage resulting from a trip of duration $T = \tau$ can be obtained from Eq. (4).

$$s_{ij}(x|\tau) = \sum_{\text{All } \mathbf{m}} h(\Omega_{\mathbf{m}}) \sum_{\text{All } U \in \Omega_{\mathbf{m}}} h(U|\Omega_{\mathbf{m}}) s_{ij}(x|U) \quad (11)$$

To generate predictions of usage resulting from trips of variable duration under an arbitrary discretization of the domain of the variable T, Eq. (11) must be modified as follows

$$s_{ij}(x) = \sum_{\text{All } \tau} g_{ij}(\tau) \sum_{\text{All } \mathbf{m}} h(\Omega_{\mathbf{m}})$$
$$\times \sum_{\text{All } U \in \Omega_{\mathbf{m}}} h(U|\Omega_{\mathbf{m}}) s_{ij}(x|U) \quad (12)$$

6.3. Application of the framework and results

I examined the usage of space by seals performing return trips from three haulout sites on the east coast of Britain (Fig. 10a). I parameterised the null model using the coordinates of the three haulouts, and data on the durations of trips and the shoreline. The fine-scale speed data were used to parameterise the model of maximum average speed developed in Appendix C giving the values $\mu = 23.97$ m/min, $\sigma = 16$ m/min and $\eta = 3.4$.

Firstly, I generated a map of null usage for each of the three haulouts separately and then combined these into a single map (Fig. 10b) by weighting them according to the relative abundance of animals at each site.

I then generated a map of true usage for each haulout as follows. Each observation in the SRDL data-set was allocated to a trip. Each trip was associated with a haulout. This gave three, haulout-specific data-sets of SRDL observations. Each of these was used to generate a map of observed usage. This was obtained from the SRDL data by kernel-smoothing and using least-squares cross-validation (Silverman, 1986) to select the smoothing coefficient. The three resulting maps were then weighted by the relative abundance of animals at the haulouts and combined into a single map of observed usage (Fig. 10c).

Finally, as with the simulated data, I generated a map of usage standardised by accessibility by dividing observed by null usage. This led to a clearer representation (Fig. 10d) of the hotspots of usage by grey seals in the geographical region examined.

It must be noted that this is just a graphical demonstration of the usefulness of the maps of accessibility in highlighting spatial preference. Accessibility is currently being used as an explanatory variable in conjunction with other information such as sea depth, sediment type and prey density as part of a GLM of habitat preference for these grey seals. The final model (to be published separately) can explain a high percentage of observed variability in usage and accessibility is, consistently, retained as a highly significant term.

7. Discussion

7.1. Overview

The aim of this work, to provide a tool for analysing the spatial distribution of animals whose movement is restricted by temporal and spatial constraints, is reflected in the framework's structure. Preference functions $h(\cdot)$ are used to represent what the animals would do if their movement were not restricted. By defining preference with respect to points in space ($h(x)$), points within a given path ($h(x|U)$), whole paths of a given type ($h(U|\Omega_{\mathbf{m}})$), or groups of paths under a given classification ($h(\Omega_{\mathbf{m}})$), the framework simultaneously deals in stages with the dimensionality of animal movement and breaks down a complicated process into biologically meaningful constituent parts. Preference functions are then corrected for the effect of accessibility to generate usage functions ($s(x|\cdot)$). Usage can be estimated for parts of paths, whole paths, or groups of paths, but always refers to a point in space (a cell in the lattice).

The effect of accessibility restrictions on the observed usage distribution is modelled using first principles. This is possible because, by definition, accessibility is restricted by a small number of factors (speed, obstacles, trip duration and endpoints) that, unlike preference, are observable and, in principle, measurable in the wild.

7.2. Data requirements

The behavioural data required for parameterization of the model are minimal. This is primarily due to the model's Eulerian nature (Turchin, 1996) and to the fact that it can be used repeatedly to generate its own parameters. However, at the initial stages, the model depends on detailed usage data and, at every stage, the quality of its predictions relies on the available data on the spatial distribution of environmental variables.

7.3. Review of the framework's assumptions and simulation results

Although most of the assumptions used in this paper were selected to increase generality, two

assumptions were selected with a view to simplicity. Specifically, (i) preference for points within a path, paths within a group of paths, or groups of paths within the event space Ω was derived as a weighted average of the preferences of the elements of the set in question (the path, the group of paths and the event space Ω, respectively) and (ii) a multiplicative relationship was assumed between internal and external preferences i.e. internal preference was independent of environmental features.

The weights used for deriving preference functions for paths and groups of paths were related to residence time and no other variable. This was linearly related to preference for different cells in the lattice. Animals were therefore assumed to have an overview of both the environment and the relative profitability of paths or groups of paths. Hence, assumption (i), above, implicitly requires the existence of memory or some other inherent mechanism that enables the animals to make efficient use of their environment. Although the model invokes no optimality arguments—mechanistic models such as that of Ollason (1980) can support such assumptions if memory is present—its predictions will be inaccurate if applied to animals that have no memory, animals with no previous experience of their environment, or animals living in rapidly changing environments.

A case in point is the comparison between the predicted and observed usage distributions in the simulations of the present paper. The movement rules used for the individual-based simulation assumed no memory on the part of the individual. The simulated animals were only influenced by the local preference gradient and neither initially had, nor later gained a global overview of their environment. This explains why predicted usage distributions were more widespread and homogeneous than observed ones. In the simulation, animals were quickly captured by local peaks in the preference function $h(x)$ close to their trips' origin whereas, in the model, animals would cross over less preferred habitat in order to perform an overall, more profitable path. Real animals explore (as well as exploit) their environment and remember (and repeat) profitable paths. Therefore (Farnsworth and Beecham, 1999), the behaviour

of real animals is likely to be between the two extremes defined by the 'short-sighted' automata of the simulation and the 'omniscient' individuals implied by assumption (i). The rules of movement in the simulated animals were selected specifically in order to create a conservative environment for validating the model. The fact that, under such conditions, prediction and observation were in relative agreement (Figs. 7–9) is therefore promising for the successful application of the framework to real systems.

With reference to assumption (ii), the multiplicative relationship between internal and external preference for modes of movement would be incorrect if the realization of internal preference depends on environmental attributes. Orientation by environmental cues (e.g. Hölldobler, 1980) could, for example, cause this. In the most difficult case, orientation and the spatial distribution of conspecifics would be coupled. Although internal preference for movement modes can still exist in isolation from environmental characteristics (Séguinot et al., 1998; Scharstein, 1990), representing its interaction with the environment will require a more elaborate formulation.

7.4. Important issues addressed by this work

The central question in spatial ecology is how the interaction between the behaviour of individuals and their environment gives rise to the observed patterns in the spatial distribution of populations (Bernstein et al., 1988; Turchin, 1991; Farnsworth and Beecham, 1999; Wiengand et al., 1999). The problem can be approached either by empirical or by process modelling. The different types of empirical models (reviewed in Guisan and Zimmermann, 2000) place emphasis on generality in the model formulation. In, turn this facilitates model fitting and selection (Pearce and Ferrier, 2000). Process models in spatial ecology place emphasis on animal behaviour and, as a result, often take the form of individual-based simulations (e.g. Carter and Finn, 1999; Moorcroft et al., 1999; South, 1999; Benhamou et al., 1995; Roese et al., 1991; Ollason, 1983 and reviews by Judson, 1994; Uchmanski and Grimm, 1996).

Unarguably, there is a gap between the empirical and process approaches. Although both aim to model the distribution of animals in space, they differ in the detail with which they treat the closely related topic of animal movement. In their majority, empirical models make the equivalent of a 'perfect mixing' assumption, where all points in space (or an arbitrarily delineated region of space) are freely and equally accessible by all animals.

Recent papers (Rosenberg and McKelvey, 1999; Huettmann and Diamond, 2001) have pointed out that this is not a suitable assumption for central-place foragers. The results of this paper agree with those of previous authors in that ignoring the effect of accessibility on usage can seriously bias the conclusions of an empirical study of habitat preference. However, the model presented here goes one step further by acknowledging that accessibility is not simply a function of distance from the central place but, also, a function of the duration, speed and overall sinuosity of movement. The rationale behind a more detailed model of accessibility is twofold. Firstly, the type of data relating to accessibility are relatively easy to obtain. Secondly, given the structural limitations of empirical models, their input needs to be as biologically accurate as it can possibly be. For example, even though it is undoubtedly true that for a central-place forager accessibility will decrease with distance from the central-place (e.g. Fryxell, 1992; Rosenberg and McKelvey, 1999) it is not clear whether it does so in the manner allowed for by the structure of (say) a logistic regression model.

At the other extreme, individual-based simulations, being an entirely mechanistic approach, need to incorporate greater detail about the physiology, mechanics and behaviour of movement. Although it is becoming evident that analyses of habitat preference must incorporate some measure of accessibility, detailed assumptions about individual movement may be difficult to quantify with the available data, or simply not required for the derivation of a large-scale, distribution of expected usage. Such models run the risk of being over-specific and over-parameterised.

Previous authors have recognized that to study the macroscopic consequences of individual movement, one needs to quantify 'the distance covered, the convolutedness or directionality of the track, and any systematic relationships of the track with properties of the environment it passes through' (Marsh and Jones, 1988). In this paper, I have attempted to describe movement using such a limited set of variables and assumptions. Consequently, the fundamental assumptions used in the model are somewhat idealised and can be violated by specific biological processes or circumstances. If these are known, then the model can be modified to incorporate them. For a particular biological system this gradual increase in specificity will make the model similar to an individual-based simulation. Until that occurs however, the generality of the present model will allow it to generate plausible predictions and use observed patterns to extract information about processes.

7.5. Further applications

The framework can be used to model usage of space by animals whose movement is restricted by time, speed or obstacles. The application to populations of central-place foragers or colonial breeders is immediately obvious. Additionally, the nature of its state variable (usage) means that it can also be used to generate probabilistic predictions for the position of a single individual. Hence, if the framework is initialized with two endpoints and a travel duration, it can be used as a biologically realistic way of interpolating over gaps in the observed path of an individual animal.
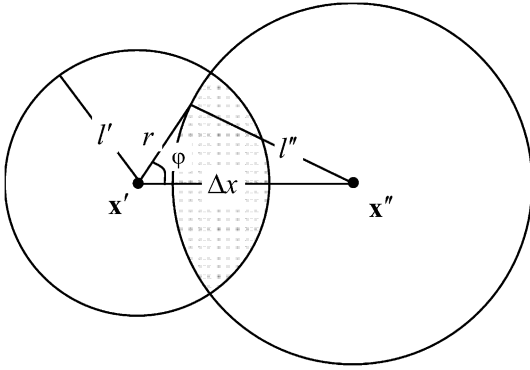
Fig. 11. Algorithm 1 generates a path by placing a fixed number of arbitrarily-ordered points on the plane of movement. Points that have already been placed during previous iterations of the algorithm and the pre-determined path length between any two points in the path restrict the possible positions for points that are yet to be placed. The feasible region (shaded area) for a new path point (x) is determined by the positions of the two already-positioned points x' and x'' immediately before and after the new point and the path lengths l' and l'' between the three path points.

Appendix A: Calculating the feasible region for placing the next point in the path generation algorithm

The situation is summarised in Fig. 11. Given the positions (x' and x'') of the two path points immediately preceding and following the point to be placed in space (say, at x) and, also, given the lengths (l' and l'') of the two path segments between these three points, we need to determine the boundaries of the feasible region (the shaded region in Fig. 11) for the new point, i.e. the region that satisfies the conditions

$$\|x' - x\| \leqslant l' \tag{A.1}$$
$$\|x'' - x\| \leqslant l'' \tag{A.2}$$

I consider the straight line segment between the points x' and x''. This has length Δx and forms an angle θ with a fixed frame of reference. I base the description of the feasible region on the pair of polar coordinates (r, $\theta + \phi$) where r is the distance of x from x' and θ is the angle formed between r and Δx (Fig. 11(a)).

Firstly, note that if $l'' \geqslant l' + \Delta x$ then the feasible region is the entire disc (x', l'). Conversely, if $l'' \geqslant l' + \Delta x$ then the feasible region is the disc (x'', l'').

In all other cases,

$$|\Delta x - l''| \leqslant r \leqslant l' \tag{A.3}$$

I distinguish two cases, $\Delta x \geqslant l''$ and $\Delta x < l''$. It is straightforward to find the range of angles that, for a given value of r, give a point within the feasible region

$$\varphi \in [\varphi_1(r), \ \varphi_2(r)]$$

where $\varphi_1(r), \ \varphi_2(r)$

$$= \left\{ \pm \tan^{-1} \left(\frac{4r^2 \Delta x^2}{(r^2 - l''^2 + \Delta x^2)^2} - 1 \right)^{1/2} \right.$$

if $\Delta x \geqslant l''$

$$\pm \left(\pi - \tan^{-1} \left(\frac{4r^2 \Delta x^2}{(l''^2 - r^2 - \Delta x^2)^2} - 1 \right)^{1/2} \right) \tag{A.4}$$

if $\Delta x < l''$

In order to choose a point uniformly randomly from the feasible region a value for r must be chosen at random from the range given by Eq. (A.3) according to the probability distribution $f(r) \propto \varphi_1(r)$. This ensures that all points in the feasible region (rather than all values of r) have the same probability of being selected. Then, a value for φ can be chosen uniformly randomly from the range given by Eq. (A.4). A quicker approach is to choose points at random from within the smallest rectangle bounding the feasible region and then reject those that do not fall within the feasible region.

Appendix B: Correcting for bias in sampling the paths from a given event space Ω_m

For fixed endpoint trips and especially for return trips, the procedure for path generation described in Algorithm 1 is computationally less wasteful than a random walk approach. However, it does not give an unbiased sample of the paths contained in a given event space Ω_m. This is because, unlike a random walk approach, not all lattice paths of a given type have the same probability of been generated. Below I discuss how to correct for this by using a weighting term
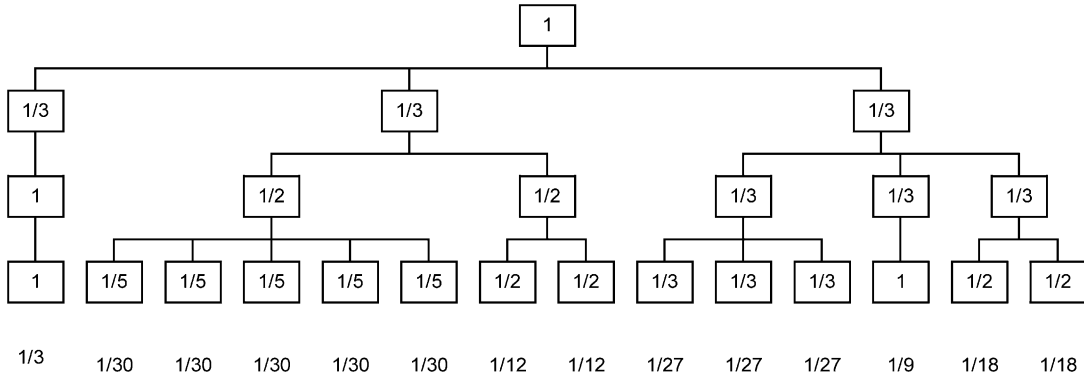
Fig. 12. A decision tree of three levels. Each node branches down to a variable number of decisions, each with equal probability (shown inside the boxes) of being made. The different routes through the tree can have different probabilities (shown at the bottom) of being followed.

for each $U \in \Omega_m$ derived from combinatorial arguments.

Consider a decision tree similar to that of Fig. 12. Each level in the tree represents a single decision. At each node there is a variable number of options each with equal probability of being selected. Hence, different routes through the decision tree can have different probabilities of being followed. If it is given that routes, rather than individual decisions, are equiprobable then the bias caused by the decision process can be corrected by multiplying each route by the weight

$$w \propto \prod_{i=1}^{k} w_i \qquad \text{(B.1)}$$

where w_i is the total number of options available for the ith decision and k is the total number of decisions made.

The path generation algorithm (Algorithm 1) introduces bias in the selection of paths in exactly the same way. The number of options available at each decision is proportional to the area of the feasible region. Hence, once it has been generated, the contribution of a particular path to the spatial usage resulting from the mode of movement to which it belongs must first be weighted by

$$w = \prod_{i=1}^{n-2} a_i \qquad \text{(B.2)}$$

Where a_i is the area of the feasible region for the ith point placed by the algorithm. The area of the feasible region can be calculated from the results in Appendix A. Alternatively, it can be approximated by the area of the smallest rectangle bounding the feasible region.

Appendix C: Minimum time ($t_{\min}(l)$) required to do a path of length l

I begin with a path of length l. By writing the equation of average speed (V) as a function of path length and time $V(l, t) = l/t$, it is possible to examine average speed in terms of scale (either length or time). The simplest model, assumes that the animals move at a constant speed ($V(l, t) = V$). In that case, the minimum time required to do a path of given length would be $t_{\min}(l) = l/V$. While this idealised situation offers analytical and computational convenience, it is rarely biologically realistic.

A more plausible model admits that speed varies with scale and assumes that the scale-independent constant is the maximum average speed ($V_{\max}$). In that case, the minimum time required to do a path of given length would be $t_{\min}(l) = l/V_{\max}$. In many cases however, maximum average speed is a non-constant function of scale. Many animals can maintain higher-than-average speed at small scales, but at greater scales, their maximum average speed approaches their overall average speed. I therefore examine a third model in which maximum average speed ($V_{\max}(l, t)$) is a mono-
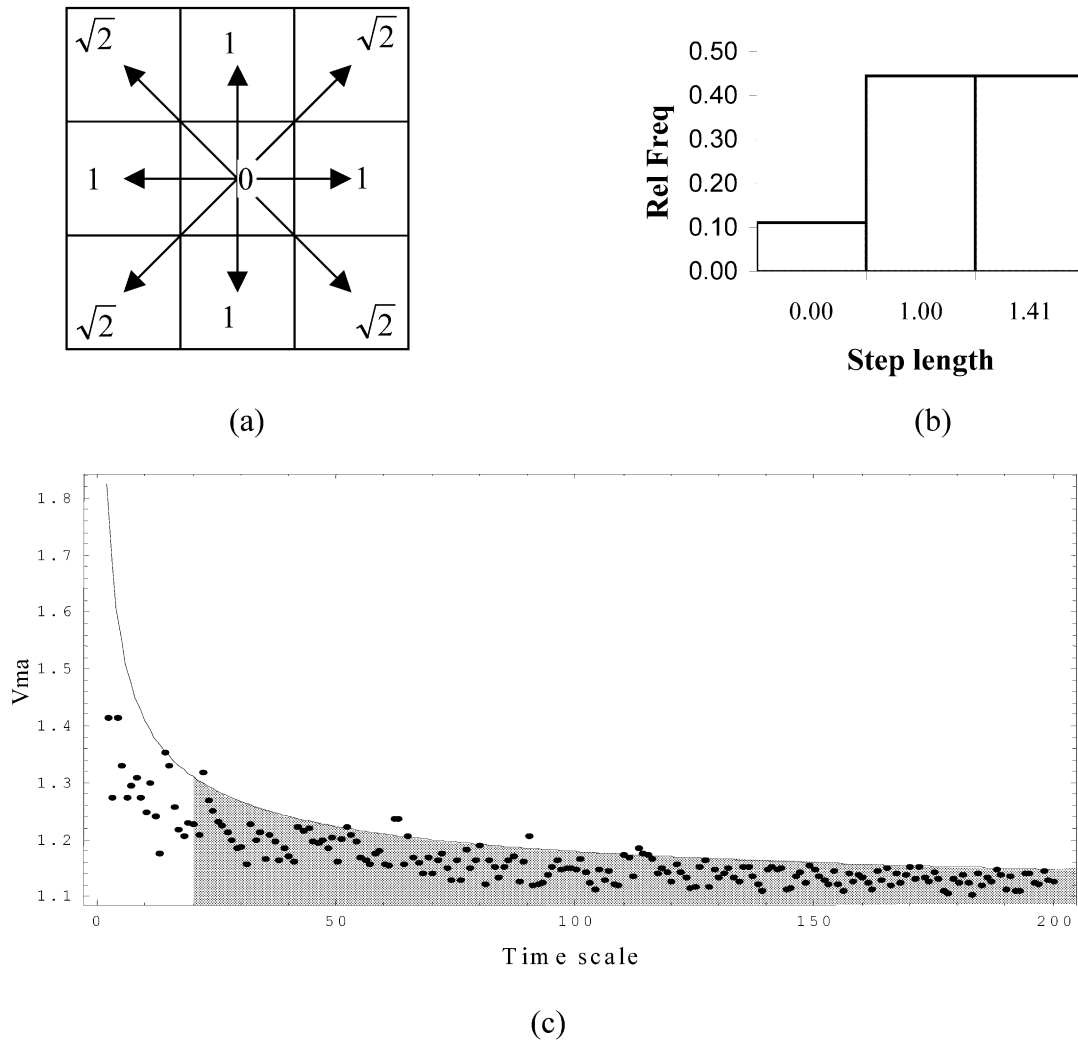
Fig. 13. For the simulated animals, the nine possible transitions in the grid (a) give a simple probability distribution for step length (b). I used 20 paths, each consisting of 20 steps, to obtain an observed sequence of $V_{\max}(\kappa)$ $(1 < \kappa \leqslant 20)$. I then fitted the model $V_{\max}(\kappa) = \mu + \eta\sigma/\sqrt{\kappa}$ to this sequence of values to obtain $\eta = 1.45$ (un-shaded region in (c)). This was then used to extrapolate for the value of the maximum average speed at greater time scales (shaded region in (c)).

tonically decreasing function of scale (either length or time) that asymptotically approaches the animal's average speed.

It is then necessary to determine the rate, with respect to scale, at which this decrease occurs using a limited amount of fine-scale, movement data. Typically, such data will consist of sets of positional observations (sets of coordinates) recorded at an arbitrary time scale Δt. If the time scale Δt is fine enough, the displacement between successive observations (the step length) can be used as an approximation of the length of the intervening path segment. Collating all of these measurements leads to the observed frequency distribution of step lengths $f_{\mathrm{L}}(l|\Delta t)$, at the time scale of data collection Δt. Estimates of the mean μ and standard deviation σ of the true step length distribution can thus be obtained.

To derive a model for the rate of decrease of $V_{\max}(l, t)$ I firstly fix the time scale to a value $t =$

$\kappa \Delta t$ ($\kappa = 2,3,\ldots$) and define as unfeasible all the path lengths that cannot be performed given the animal's maximum average speed at that time scale. Repeatedly generating larger path lengths by randomly selecting samples of size κ from the observed frequency distribution $f_L(l|\Delta t)$ gives a PDF $f_L(l|t)$ of path lengths at the time scale $t = \kappa \Delta t$. The probability density thus allocated to each value of l is purely a result of combinatorics. The fact that there is a maximum to the animal's average speed at the time scale t means that a proportion of these path lengths will be unfeasible. For this model, I assume that, this proportion is a constant, independent of scale.

The PDF $f_L(l|\Delta t)$ at a time scale $t = \kappa \Delta t$ ($\kappa \gg 1$), can, using the central limit theorem, be approximated by $N(\mu\kappa, \sigma\sqrt{\kappa})$. Then, the maximum path length that can be performed at a time scale t is

$$l_{\max}(\kappa) = \mu\kappa + \eta\sigma\sqrt{\kappa} \qquad \text{(C.1)}$$

In other words, the minimum time required to perform a path of length l will be given by solving

$$l = \mu t_{\min}(l)/\Delta t + \eta\sigma\sqrt{t_{\min}(l)/\Delta t} \qquad \text{(C.2)}$$

The required value for $t_{\min}(l)$ will be the smallest non-negative solution of Eq. (C.2). It is straightforward to show that this is

$$t_{\min}(l) = \Delta t \frac{2l\mu + \eta^2\sigma^2 - \eta\sigma\sqrt{4l\mu + \eta^2\sigma^2}}{2\mu^2} \qquad \text{(C.3)}$$

To parameterise (Eq. (C.3)), the average and sample standard deviation of the step length data collected at the time scale Δt can be used as estimates of μ and σ. The value of η can be obtained by fitting $V_{\max}(\kappa) = l_{\max}(\kappa)/\kappa$ (from Eq. (C.1)) as the ceiling of a set of fine-scale data. To illustrate this, I use the example of the random walkers employed in the simulations of this paper. The nine possible transitions in the grid (Fig. 13a) give a simple probability distribution for step length (Fig. 13b). I used 20 paths, each consisting of 20 steps, to obtain an observed sequence of $V_{\max}(\kappa)$ ($1 < \kappa \leqslant 20$). I then fitted the model $V_{\max}(\kappa) = \mu + \eta\sigma/\sqrt{\kappa}$ as the ceiling of this sequence of values to obtain a value for η. This was then used to extrapolate for the value of the maximum average speed at greater time scales (Fig. 13c).

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