Bulletin of Mathematical Biology (2009) 71: 107–129
DOI 10.1007/s11538-008-9354-x

ORIGINAL ARTICLE

First Passage Time Analysis of Animal Movement and Insights into the Functional Response

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Received: 23 January 2008 / Accepted: 28 August 2008 /

Abstract Movement plays a role in structuring the interactions between individuals, their environment, and other species. Although movement models coupled with empirical data are widely used to study animal distribution, they have seldom been used to study search time. This paper proposes first passage time as a novel approach for understanding the effect of the landscape on animal movement and search time. In the context of animal movement, first passage time is the time taken for an animal to reach a specified site for the first time. We synthesize current first passage time theory and derive a general first passage time equation for animal movement. This equation is related to the Fokker–Planck equation, which is used to describe the distribution of animals in the landscape. We illustrate the first passage time method by analyzing the effect of territorial behavior on the time required for a red fox to locate prey throughout its home range. Using first passage time to compute search times, we consider the effect of two different searching modes on a functional response. We show that random searching leads to a Holling type III functional response. First passage time analysis provides a new tool for studying how animal movement may influence ecological processes.

Keywords First passage time · Animal movement · Search time · Predation

1. Introduction

Movement is a central theme in ecology, determining in part what animals eat, where they live, their survival, and their reproductive output. The movement patterns we observe may depend upon the distribution of resources and other species in the landscape. Therefore, movement data can be used to interpret species interactions with each other and their environment. To date, mechanistic movement models coupled to empirical data have been used to explain the distribution of animals in space (Turchin, 1991; Okubo and Levin,

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2001). Despite the widespread use of movement models to understand animal distribution, their full potential remains unexploited. Besides animal distribution, search time plays an essential role in predator-prey dynamics. Search time is the time required for the predator to find a prey (Holling, 1959). Models of search time as a function of the interaction between animal movement and the environment are uncommon (but see McCauley et al., 1993).

This paper describes a method for modeling search time as a function of animal movement using theory from the physical and mathematical literature on first passage time. First passage time is the time required for a random variable, such as an animal's location in space, to go from a given starting point to a predefined endpoint (Redner, 2001). Search time, the time taken for a predator to find a prey, is an example of a first passage time where the prey location is the endpoint. Though much of the first passage time theory has been previously developed (Gardiner, 1985; Redner, 2001; Condamine et al., 2007; Ovaskainen, 2008), it has not been widely placed in the context of animal movement. We do so here by synthesizing first passage time theory using examples from animal movement, deriving a general equation for first passage time from a random walk in a heterogeneous environment, and discussing the connection to the backward Fokker–Planck equation.

Using first passage time, we analyzed red fox (*Vulpes vulpes*) movement data to understand the effect of prey distance from den site on search time for prey within a red fox home range. The idea of a home range was first proposed by Burt (1943) and subsequent analysis of animal locations support Burt's suggestion that movement of nonmigratory animals is not random in the landscape, but focused within a home range (Siniff and Jessen, 1969). A simple model for animal movement within a home range was first proposed by Holgate (1971) and further described by Okubo and Levin (2001). The Holgate–Okubo model assumes a centralizing tendency in the animal's movement directions because of the need to care for young located at the den site. During denning, many canids, including the red fox, display the central foraging behavior that is well described by this model (Siniff and Jessen, 1969; Mech and Boitani, 2003), which we use as the basis for our first passage time model.

In addition to understanding how search time varies with animal movement, we can incorporate this variation into the functional response. The shape of the functional response, which describes the number of prey consumed by a single predator as a function of prey density and predator behavior (Solomon, 1949; Holling, 1959) depends heavily on search time. In the derivation of the Holling disk equation, Holling (1959) assumed that predators moved at a constant speed and searched a constant area per unit time. This directed predator movement resulted in a linear (type I) functional response. When handling time was included, the functional response become concave asymptotic (type II). Holling also suggested the existence of a sigmoidal functional response (type III). Prey switching and prey refuges have been evoked as potential biological mechanisms explaining the type III functional response. In this paper, we demonstrate that random predator searching offers an alternate explanation for the type III functional response. Because first passage time is derived from individual movement behavior, it can be used to derive a functional response that accounts for different types of searching behaviors. We derive functional responses without and including handling time for pure advection and simple diffusion in a one-dimensional homogeneous landscape, and discuss their biological interpretations.

2. First passage time and animal movement

Though widely discussed in the physical literature, first passage time has received minimal attention from ecologists. This is perhaps because of its highly theoretical treatment to date. First passage time was first discussed in an ecological context by Berg (1993) who calculated the mean time to capture of a randomly moving bacteria by a sticky disk at the center of a homogeneous Petri dish. First passage time was also proposed as an alternative to mean squared displacement to characterize diffusion behavior (Johnson et al., 1992) and used to identify optimal search strategies (Benichou et al., 2005). In the above examples, the mean first passage time is calculated from diffusion-type equations based on description of movement as a random walk. Empirically calculated first passage times have been used as a measure of search time along a path (Fauchauld and Tveraa, 2003) and to distinguish between movement behaviors at different scales (Frair et al., 2005). We show that a general equation for first passage time, which incorporates empirical data, can be widely applied to ecological questions related to animal movement.

Diffusion describes how a group of individual particles spreads out due to the irregular motion of each particle (Okubo and Levin, 2001). When applied to animals, diffusion may alternatively be viewed as describing the distribution of a large population of animals or the expected location of an individual animal in space and time. General diffusion models are appropriate for describing the distribution of animals in time and space for many ecological systems (Turchin, 1991; Holmes et al., 1994; Okubo and Levin, 2001). To date, ecologists have used diffusion to describe the expected location of an animal after a certain amount of time. We turn this question on its head and ask how long, on average, it takes an animal to reach a particular location for the first time. In the first case, it is the animal location at a fixed time that is of interest, whereas in the second case, we are concerned with time taken to reach a fixed location. The equation for mean first passage time can be interpreted as the average time taken by many animals beginning at the same start location to reach the fixed location or endpoint. Commonly, the endpoint (e.g., the prey) is assumed to be stationary, while the animals (e.g., the predators) are mobile. Indeed this assumption is necessary to solve the advection-diffusion formulation of the mean first passage time problem proposed here (see Redner and Krapivsky, 1999; Moreau et al., 2004; Dushek and Coombs, 2008 for examples where mobile endpoints are considered). However, there are many biological examples where it is reasonable to consider stationary prey. Imagine the case where the mobility of the predator is much greater than that of the prey, for example, red foxes preying on duck nests (Sovada et al., 1995). In addition, models predict that the best strategy for prey in the presence of diffusing predators is to remain stationary (Moreau et al., 2003, 2004). Therefore, it is of interest to consider the case of stationary prey in the context of first passage time. An equation for mean first passage time is obtained by reformulating the random walk and applying the diffusion approximation (Skellam, 1991; Berg, 1993). To demonstrate this method, we review the formulation of the mean first passage time equation for an unbiased random walk with constant diffusion (Berg, 1993). More complex movement behaviors, including spatially variable diffusion and attraction toward a bias, are considered in the Section 3.5.

Let the mean first passage time from location x be denoted $T(x)$. An animal undergoing an unbiased random walk located at x has equal probability of jumping a step δ to the left or right. The mean first passage time from the current location x is equal to the sum of the mean first passage times from all possible next locations multiplied by the probability of moving to those locations, plus the time taken to move, τ. This is summarized by the equation,

$$T(x) = \tau + \frac{1}{2}T(x-\delta) + \frac{1}{2}T(x+\delta). \tag{1}$$

Using Taylor series expansion and applying the diffusion approximation (Appendix A), we obtain the differential equation

$$d\frac{d^2}{dx^2}T(x) + 1 = 0 \tag{2}$$

where d is the diffusion coefficient. The diffusion approximation relates movement in discrete and continuous space (Skellam, 1991) and requires the assumption that the animal takes shorter and shorter steps in shorter and shorter time intervals, so that the step length and time interval both approach zero (see Holmes et al., 1994 for a discussion of this assumption). To solve Eq. (2), we must define an appropriate domain and boundary conditions. The domain must be finite to ensure that $T(x)$ is well defined. Further, we assume the animal remains in the domain. Therefore, because the animal is reflected at the edges of the domain, the mean first passage time does not change with space and we use a Neumann condition, $\frac{d}{dx}T(x) = 0$. Islands, lakes, home ranges, or habitat patches with impermeable boundaries are all examples of ecologically reasonable domains. At the endpoint, the animal is absorbed and the random walk ends. Therefore, the mean first passage time for an animal beginning at the endpoint, x_e, is zero, because the animal is immediately absorbed and we use a Dirichlet boundary condition, $T(x_e) = 0$. In the following examples, we use the one-dimensional domain of length L with Dirichlet and Neumann boundary conditions at 0 and L, respectively. Biologically, this domain might be an example of a corridor with a good habitat patch at 0 and a bad habitat patch at L. Then Eq. (2) has solution

$$T(x) = \frac{1}{2d}\left(2Lx - x^2\right). \tag{3}$$

It may also be of interest to ask how long until an animal leaves the domain. For example, to model the length of time spent foraging in a particular habitat patch. In this case, both 0 and L are subject to Dirichlet conditions and the solution to Eq. (2) becomes

$$T(x) = \frac{1}{2d}\left(Lx - x^2\right). \tag{4}$$

The mean first passage time for these two scenarios is shown in (Fig. 1a). The solutions show that on average animals beginning further from the endpoint take longer to reach it than animals that start closer to the endpoint. Therefore, first passage time will always be monotonically decreasing in the neighborhood of the endpoint.

3. First passage time in spatially heterogeneous landscapes

Most animals do not move according to an unbiased random walk. Movement occurs on a complex landscape template, where many landscape features may affect animal movement. Therefore, first passage time based on an unbiased random walk usually will not

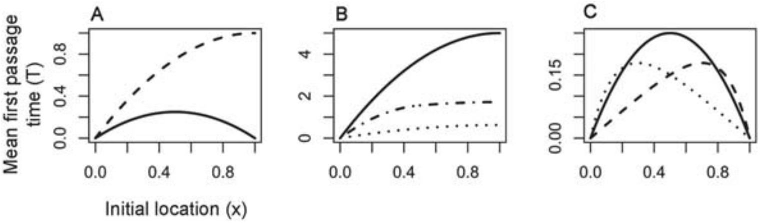

Fig. 1 Example solutions to mean first passage time equations. (A) Mean first passage time for diffusion walk with homogeneous Dirichlet (solid line) and mixed Dirichlet and Neumann (dashed line) boundary conditions at 0 and 1, respectively. The diffusion coefficient is $d = 0.5$. (B) Mean first passage time for simple diffusion with spatially variable diffusion coefficient in a two-patch environment divided at $a = 0.5$ with mixed boundary conditions. The solid and dotted lines represent the solution in homogeneous environments with slow ($d = 0.1$) and fast ($d = 0.8$) diffusion. The dash-dotted line is the solution for the heterogeneous environment. (C) Mean first passage time for diffusion and advection with homogeneous Dirichlet boundary conditions. The solid line is the solution for simple diffusion with $c = 0$ and $d = 0.5$. The dotted and dashed lines are solutions for diffusion and advection with $d = 0.5$ and $c = \pm 3$, respectively.

be a good approximation of search time. In this section, we use the random walk framework to derive the more general equation for first passage time for animal movement. We divide the influence of landscape heterogeneity on animal movement into two parts: movement rate and movement direction (Weins, 2001). Habitat structure may vary, resulting in varying movement rates between different habitats in the landscape. For example, wolves are observed to move greater than two times faster on linear features than in the forest (James, 1999) and prairie butterflies move faster between habitat patches than within them (Schultz and Crone, 2001). Spatial variability in movement speed is incorporated into the model by allowing the diffusion coefficient to vary in space. Animals may also bias their movement directions relative to landscape features. For example, red fox movements are directionally biased toward den site (Siniff and Jessen, 1969) and male checkerspot butterflies bias their movement in the uphill direction when searching for mates (Turchin, 1991). Directional bias is introduced into the model with an advection term describing the directed component of movement. This more complex movement can still be treated using the same approach illustrated for the simple case above. Before giving some examples of models for more complex movement behavior, we consider how empirical data is incorporated into the first passage time model.

3.1. Spatially variable movement rates

Following Moorcroft and Lewis (2006), we generalize the first passage time model by deriving advection and diffusion coefficients which are functions of animal movement data. To do this, we summarize the movement data in the form of a redistribution kernel, which is a density function describing the probability that an animal jumps from its current location to a new location (Moorcroft and Lewis, 2006) and we allow the animal to move steps of different lengths in any one time step. The end result is an equation where the advection and diffusion coefficients are functions of the animals redistribution kernel.

Consider the lattice $\{-L, -L+\delta, -L+2\delta, \ldots, -\delta, 0, \delta, \ldots, L-2\delta, L-\delta, L\}$ and suppose the animal is located at x. In the next time step, the animal can make a jump of size $n\delta$, where $n > 0$ is a movement to the right, $n < 0$ is a movement to the left, and $n = 0$ represents the event the animal stays still. Then the redistribution kernel $k(x, x + n\delta, \tau)$ gives the probability the animal jumps from x to $x + n\delta$ in time τ. Because k incorporates all possible jumps, $\sum_{n=-\infty}^{\infty} k(x, x + n\delta, \tau) = 1$. Using the redistribution kernel, we can rewrite the master equation for the mean first passage time as

$$T(x) = \tau + \sum_{n=-\infty}^{\infty} k(x, x + n\delta, \tau)T(x + n\delta). \tag{5}$$

Taking the limit as the step size and using the definition of the integral, Eq. (5) becomes

$$T(x) = \tau + \int_{-\infty}^{\infty} k(x, x', \tau)T(x')\,dx' \tag{6}$$

where x is the current location and x' is the next location. We define a new variable $a = x' - x$ for the distance between x and x'. Then the redistribution kernel can be rewritten as $K(x, a, \tau)$ where x is the current location and a is the jump distance in time τ. After applying the diffusion approximation to Eq. (6) (Appendix C), we obtain the mean first passage time equation

$$c(x)\frac{\partial T}{\partial x} + d(x)\frac{\partial^2 T}{\partial x^2} + 1 = 0 \tag{7}$$

where now the advection and diffusion coefficients are the first and second infinitesimal moments of the redistribution kernel (Moorcroft and Lewis, 2006)

$$c(x) = \lim_{\tau\to 0} \frac{1}{\tau} \int_{-\infty}^{\infty} aK(x, a, \tau)\,da \tag{8}$$

and

$$d(x) = \lim_{\tau\to 0} \frac{1}{2\tau} \int_{-\infty}^{\infty} a^2 K(x, a, \tau)\,da. \tag{9}$$

Therefore, animal movement data is incorporated into the coefficients of the mean first passage time equation through the redistribution kernel.

3.2. Examples of complex movement behaviour

Consider first spatially varying diffusion and no advection ($c(x) = 0$). Dividing the domain of length L into patches of fast and slow diffusion, subject to boundary conditions $T(0) = 0$ (Dirichlet, absorbing) and $\frac{d}{dx}T(L) = 0$ (Neumann, reflecting), the solution to Eq. (7) found by integrating is

$$T(x) = \begin{cases} \frac{1}{2d_1}(2ax - x^2) + \frac{1}{2d_2}(x - xa), & x \in (0, a), \\ \frac{a^2}{2d_1} - \frac{a^2}{2d_2} + \frac{1}{2d_2}(2Lx - x^2), & x \in (a, L). \end{cases} \tag{10}$$

If $d_1 = d_2$, Eq. (10) reduces to the solution of the unbiased random walk equation Eq. (3) (Berg, 1993). From the solution to the two-patch example, we see that spatial variation in the diffusion coefficient is reflected in the mean first passage time (Fig. 1b). For all starting locations, animals moving in the patchy landscape arrive at the endpoint later on average than animals moving in the fast landscape, but earlier than animals moving in a slow landscape.

Alternatively, we consider movement with both advection and diffusion. It is possible to solve Eq. (7) analytically if c and d are constant. On a domain of length L with homogeneous Dirichlet boundary conditions $T(x) = T(L) = 0$, Eq. (7) has solution

$$T(x) = \frac{L(\exp[-c/d(x)] - 1)}{c(\exp[-c/d(L)] - 1)} - \frac{x}{c}. \tag{11}$$

The effect of the movement bias is to skew the mean first passage time away from the bias point (Fig. 1c). The relation between the magnitudes of the directed and random components of movement will determine the shape of the mean first passage time curve. The larger the advection coefficient with respect to the diffusion coefficient, the more linear the mean first passage time curve will be.

3.3. *Mean first passage time in two-dimensions*

Extending the model to two-dimensions is straightforward. Let be the mean first passage time for an animal located at $\mathbf{x} = (x, y)$ and $\mathbf{a} = \mathbf{x}' - \mathbf{x}$ the distance between the current and next location. In two-dimensions, the redistribution kernel is a two-dimensional probability density function $k(\mathbf{x}, \mathbf{x}', \tau)$ describing the probability of moving from a small rectangle $[\mathbf{x}, \mathbf{x} + d\mathbf{x})$ at time t to another small rectangle $[\mathbf{x}', \mathbf{x}' + d\mathbf{x}')$ at time $t + \tau$. In vector notation, the master equation becomes

$$T(\mathbf{x}) = \tau + \int k(\mathbf{x}, \mathbf{x}', \tau)\, T(\mathbf{x}')\, d\mathbf{x}'. \tag{12}$$

Redefining the redistribution kernel as before to be where and applying the diffusion approximation yields the mean first passage time in two-dimensions (Appendix D)

$$\begin{aligned} \mathbf{c}(\mathbf{x}) \cdot \nabla T(\mathbf{x}) + d_{xx}(\mathbf{x}) \frac{\partial^2}{\partial x^2} T(\mathbf{x}) + d_{xy}(\mathbf{x}) \frac{\partial^2}{\partial x \partial y} T(\mathbf{x}) + d_{yx}(\mathbf{x}) \frac{\partial^2}{\partial y \partial x} T(\mathbf{x}) \\ + d_{yy}(\mathbf{x}) \frac{\partial^2}{\partial y^2} T(\mathbf{x}) + 1 = 0 \end{aligned} \tag{13}$$

where the spatially dependent advection and diffusion coefficients are given by

$$\mathbf{c}(\mathbf{x}) = \lim_{\tau \to 0} \frac{1}{\tau} \int \mathbf{a} K(\mathbf{x}, \mathbf{a}, \tau)\, d\mathbf{a}, \tag{14}$$

$$d_{xx}(\mathbf{x}) = \lim_{\tau \to 0} \frac{1}{2\tau} \int a_1^2 K(\mathbf{x}, \mathbf{a}, \tau)\, d\mathbf{a}, \tag{15}$$

$$d_{xy}(\mathbf{x}) = \lim_{\tau \to 0} \frac{1}{2\tau} \int a_1 a_2 K(\mathbf{x}, \mathbf{a}, \tau)\, d\mathbf{a}, \tag{16}$$

$$d_{yx}(\mathbf{x}) = d_{xy}(\mathbf{x}), \tag{17}$$

$$d_{yy}(\mathbf{x}) = \lim_{\tau\to 0} \frac{1}{2\tau} \int a_2^2\, K(\mathbf{x}, \mathbf{a}, \tau)\, d\mathbf{a}. \tag{18}$$

Solutions to Eq. (13) with coefficients defined by Eqs. (14)–(18) exist for continuous functions $K(\mathbf{x}, \mathbf{a}, \tau) > 0$ for all $\mathbf{x}, \mathbf{a}$, and τ. To see this, define an inner product $\langle f(\mathbf{a}), g(\mathbf{a})\rangle = \int f(\mathbf{a})g(\mathbf{a})K(\mathbf{x}, \mathbf{a}, \tau)\, d\mathbf{a}$ where $f(\mathbf{a})$ and $g(\mathbf{a})$ are continuous functions of **a**. It is then possible to show by using the Cauchy–Schwarz inequality for the resulting weighted Hilbert space, that the coefficient matrix associated with the second order operator is symmetric positive definite and, therefore, has only positive eigenvalues, meaning the equation is elliptic and solutions exist. The requirement that the redistribution kernel is positive everywhere means that any move is likely to occur with some nonzero probability. This is the case for biologically relevant redistribution kernels.

3.4. Interpreting mean first passage time

The solution to the mean first passage time equation is a curve (for movement in one-dimension) or surface (for movement in two-dimensions) whose value is the mean time to arrive at a specified location for the first time as a function of the starting location **x**. The solution gives the mean first passage time for every possible starting location in the domain. While the curve or surface gives a qualitative picture of how the mean first passage time changes throughout the landscape, it may be difficult to use this information without a summary statistic. This is particularly true if mean first passage time is being compared across different landscapes. One possible summary statistic is the spatial average of the mean first passage time over the landscape

$$T_{\text{avg}} = \int_{\mathbf{x}\in\Omega} u_0(\mathbf{x})T(\mathbf{x})\, d\mathbf{x} \tag{19}$$

where $u_0(\mathbf{x})$ is the initial probability distribution of the animals in space. If $u_0(\mathbf{x})$ is assumed to be a uniform distribution, T_{avg} is equivalent to the expected mean first passage time from a random starting location (Benichou et al., 2005). If the initial distribution of animals in space is known, T_{avg} is interpreted as the expected mean first passage time conditional on the initial distribution of animals. Therefore, the mean first passage time solution provides a map of how long on average it would take to arrive at the specified endpoint given different starting locations and can be summarized into a metric that facilitates comparisons among landscapes or searching strategies.

3.5. Connecting animal distribution and search time

The mean first passage time equation is related to the Kolmogorov equations (Gardiner, 1985). The forward and backward Kolmogorov equations describe the time evolution of stochastic processes. Gardiner (1985) elegantly describes the relationship between the backward and forward Kolmogorov equations, as well as their relationship to first passage time. We briefly summarize this description here. In one dimension, the forward

Kolmogorov equation, also known as the Fokker–Planck equation,

$$\frac{\partial}{\partial s}u(x,s) = -\frac{\partial}{\partial x}\big[c(x)\,u(x,s)\big] + \frac{\partial^2}{\partial x^2}\big[d(x)\,u(x,s)\big] \tag{20}$$

describes how the probability density function for the location of an animal in space $u(x,s)$, changes over time (Turchin, 1998; Okubo and Levin, 2001). The initial probability density function for the initial location of the animal, $u_t(x)$, is an initial condition and the expected location is integrated forward in time for the solution at time $s > t$. The backward Kolmogorov equation

$$-\frac{\partial}{\partial t}v(x,t) = c(x)\frac{\partial}{\partial x}\big[v(x,t)\big] + d(x)\frac{\partial^2}{\partial x^2}\big[v(x,t)\big] \tag{21}$$

is the adjoint of Eq. (20) and describes the probability that the animal arrives in some set of final locations at a future time s, for all initial locations at the current time t. Therefore, the set of final locations, $v_s(x)$, is a final condition and $v(x,t)$ is integrated backward in time.

The first passage time equation arises from the backward Kolmogorov equation, as we are interested in the length of time taken for the animal starting at a current position to arrive in the set of final locations at some later time. While we derived the first passage time equation directly from a random walk formulation, the backward Kolmogorov equation provides an alternate derivation of the first passage time equation based on moments (for details, see Appendix E).

4. First passage time analysis of animal movement

We have proposed first passage time as an alternate method for quantifying animal movement rates in heterogeneous landscapes. For example, it can be used to determine the effect of different movement behaviors on search time. To illustrate the method, we apply first passage time analysis to understand how central-place foraging behavior of the red fox affects search time for prey. Red fox movement data was collected by Siniff and Jessen (1969) at the Minnesota Creek Long-Term Ecological Research Site in the spring of 1969 using an automated tracking system that relocated the animal at 10 minute intervals (see Siniff and Jessen, 1969). The animals movement path can be broken down into distances moved and direction of move relative to den site that characterize the animals movement (Fig. 2). The overall pattern of space use suggests the red fox is confining its movement within a finite area. In addition, there is a higher occurrence of moves toward the den site than in any other direction, suggesting a bias toward the den site. These observations raise the question: How might the observed bias toward the den site affect the search time of the red fox for prey throughout its territory? Mean first passage time is an appropriate metric for answering this question because it enables us to translate the observed random walk of the red fox into an equation for mean first passage time where the advection and diffusion coefficients are computed directly from empirical movement data.

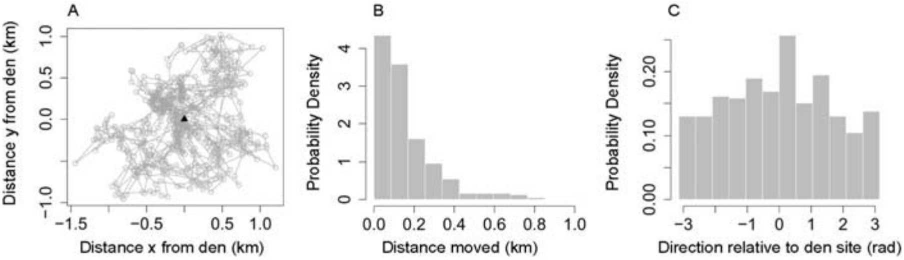

Fig. 2 Movement data of a red fox (Siniff and Jessen, 1969). (A) Observed path of an individual red fox recorded by the Minnesota Cedar Creek tracking system over a 30-day period. The black triangle represents the assumed den site location. (B) Observed distribution of distances between successive relocations for the individuals path shown in A. (C) Observed distribution of movement directions relative to the location of the den site for the individuals path shown in A.

4.1. Influence of central place foraging behavior on first passage time to prey

The Holgate–Okubo model was mechanistically derived and parameterized by Moorcroft and Lewis (2006) using the red fox location data (Siniff and Jessen, 1969). The expected location of the red fox $u(x,s)$, is described by the forward Fokker–Planck equation

$$\frac{\partial u}{\partial s} = -\nabla \cdot \big[\mathbf{c}(\mathbf{x})u\big] + \nabla^2[du], \tag{22}$$

with constant diffusion coefficient $d = 0.41$ km^2/h and advection vector $\mathbf{c}(\mathbf{x}) = -c\,\mathbf{x}/\|\mathbf{x}\|$ pointing in the direction of the home range centre with magnitude $c = 0.085$ km/h. The details for calculating the advection and diffusion coefficients from the red fox movement data are found in Appendix D. The steady state solution to this equation, which describes the long-term pattern of space use of the red fox is given by

$$u(x,y) = \frac{c^2}{d^2\pi} E_1\left[\frac{c}{d}\sqrt{x^2+y^2}\right] \tag{23}$$

where E_1 is the exponential integral $\int_u^\infty \frac{\exp[-t]}{t}\,dt$. Figure 3 shows that the expected pattern of space use is radially symmetric around the home range center and the individual is more likely to be found close to the home range center. The fit of the model to the data is further analyzed and discussed in Moorcroft and Lewis (2006).

We are now ready to address the question of how the central foraging behavior affects the search time of a red fox for prey throughout its territory. Using mean first passage time, we compare the search times for prey of a red fox moving according to the Holgate–Okubo centralizing tendency model (biased random walk) to that of one moving randomly (unbiased random walk). From Eq. (13) and the assumption of isotropic diffusion, the mean first passage time equation for the Holgate–Okubo model is

$$\mathbf{c}(\mathbf{x}) \cdot \nabla T(\mathbf{x}) + d\,\nabla^2 T(\mathbf{x}) + 1 = 0, \tag{24}$$

with advection and diffusion coefficients as described above. If there is no centralizing tendency ($c = 0$), then $\mathbf{c}(\mathbf{x}) = \mathbf{0}$ and Eq. (24) describes the mean first passage time to

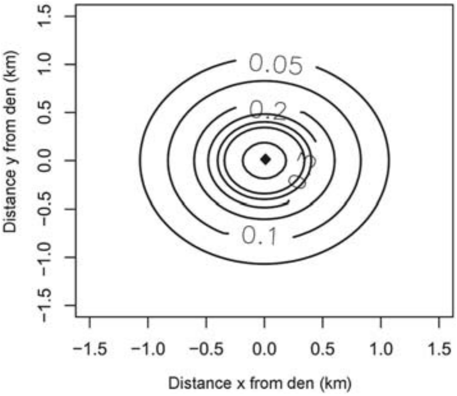

Fig. 3 Steady state solution to the centralizing tendency model for the Cedar Creek red fox. The assumed location of the den site is shown (black diamond).

prey when the fox is moving without the centralizing tendency (random walk). To obtain mean first passage time to prey for a red fox moving with and without the centralizing tendency, Eq. (24) was solved for $c = 0.085$ km/h and $c = 0$ km/h on a circular domain similar in area to the 95% minimum convex polygon for the expected location of the red fox (radius of 1.5 km, Moorcroft and Lewis, 2006). The edges of the domain were subject to Neumann (reflecting) conditions. Ecologically, this corresponds to the red fox remaining within its home range. Prey were specified at distances of 0, 0.25, 0.5, 0.75, 1, 1.25, and 1.5 km due south of the den site as a disk of radius 10 m with Dirichlet (absorbing) boundary conditions. Solutions were found numerically (Appendix F) and summarized using T_{avg}, where the initial distribution of expected starting locations for the red fox $u_0(\mathbf{x})$ in Eq. (19) was assumed to be the uniform distribution for randomly moving foxes and the steady state solution to the forward Fokker–Planck equation given by Eq. (23) for foxes moving with a centralizing tendency.

The mean first passage time surfaces differ for movement with and without a centralizing tendency (Fig. 4). The T_{avg} for both models increased with prey distance from the den site (Fig. 5). As would be expected, prey near the den site were located faster by animals with the centralizing tendency, whereas prey farther from the den site were located more quickly by randomly searching animals. For the parameters used here, the switch occurred approximately when the prey was located 1 km from the home range center. The degree to which central place foraging ($c = 0.085$ km/h) improved the rate of prey location near the den site over random foraging ($c = 0$ km/h) was striking: Prey near the den site were, on average, located 4 times faster by central place foraging (comparing the average of the no-bias/bias search times for the first 4 prey locations). This is due to the combined effects of the central place foragers starting closer to the den site on average (see $u_0(\mathbf{x})$, Fig. 3), the additional speed with which the central place foragers moved (due to the contribution from the advection term: $c = 0.085$ km/h versus $c = 0$ km/h), and their tendency to return to the den site.

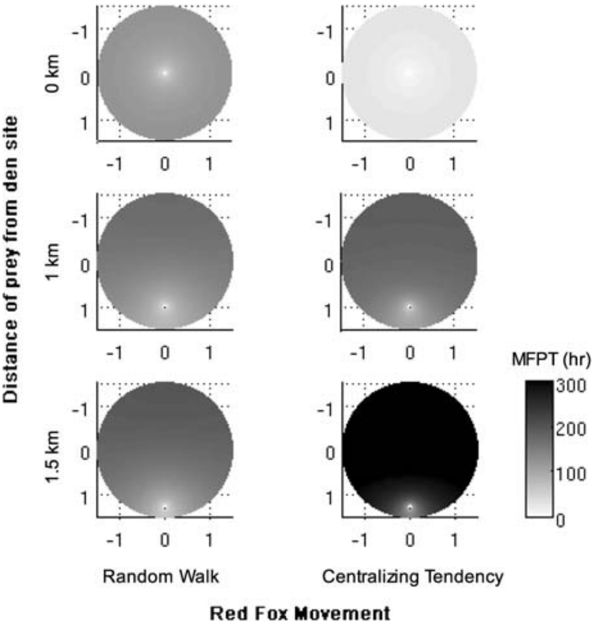

Fig. 4 Mean first passage time of the Cedar Creek red fox to prey predicted by the model.

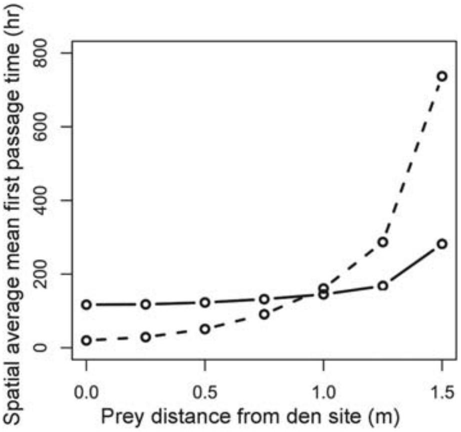

Fig. 5 Spatial average of the mean first passage time for the Cedar Creek red fox to prey predicted by the model, assuming movement without ($c = 0$ km/h, solid line) and with ($c = 0.085$ km/h, dotted line) a centralizing tendency.

5. Incorporating movement into the functional response

We now apply first passage time methods to the mechanistic derivation of functional responses. The Holling disk equation for the functional response assumes a constant area is searched for new prey per unit time (Holling, 1959). This is consistent with pure directed motion (advection), where displacement of an individual increases linearly with time. Here, the size of the region searched scales linearly with the time elapsed. However, for random motion (diffusion), it is the mean squared displacement that increases linearly with time. In this case, the size of the area searched scales with the square root of the time elapsed. In other words, to search an area of twice the size requires four times longer. This scaling arises from the fact that Brownian motion allows individuals to move back and forth over regions recently searched, via random switching of direction. In this section, we deduce the effect of random versus directed movement behavior on the functional response. We consider only the case where prey are stationary and located randomly in space.

Consider an infinite one-dimensional landscape where prey are distributed according to a Poisson process with intensity λ per unit length (λ is equivalent to N, the expected density of prey). The waiting times or times between consecutive events of a Poisson process are exponentially distributed (Karlin and Taylor, 1998). Denote the locations of prey as $\{\ldots, x_{-3}, x_{-2}, x_{-1}, 0, x_1, x_2, x_3, \ldots\}$. Translating this to a Poisson process for prey locations in space indicates the distances between prey, x_i, are exponentially distributed,

$$g(x_i) = \lambda\, e^{-\lambda x_i}. \tag{25}$$

Without loss of generality, we consider the subdomain $[0, x_1]$ to be representative, where prey are located at 0 and x_1. Suppose $T(x)$ is the solution to the mean first passage time equation on $[0, x_1]$, given some underlying movement and homogeneous Dirichlet boundary conditions at $x = 0$ and $x = x_1$. Then the expected mean first passage time on $[0, x_1]$, assuming a uniform distribution of starting locations of the predator, is

$$E\left[T(x)|x_1\right] = \frac{1}{x_1}\int_0^{x_1} T(x)\, dx. \tag{26}$$

Now, the expected mean first passage time over all possible subdomains $[0, x_1]$ is

$$E\left[T(x)\right] = \int_0^{\infty} E\left[T(x)|x_1\right] g(x_1)\, dx_1. \tag{27}$$

Then an estimate for the rate at which predators encounter prey as a function of prey density is given by $E[T(x)]^{-1}$. We used this method to derive functional responses for predators undergoing pure advection and simple diffusion.

5.1. Pure advection

The mean first passage time equation for pure advection is given by Eq. (7), where $d = 0$ and c is constant. For this case, the solution is

$$T(x) = \frac{L - x}{c}. \tag{28}$$

Substituting Eq. (28) into Eq. (26), the expected mean first passage time for a fixed x_1 is

$$E\left[T(x)|x_1\right] = \frac{1}{x_1}\int_0^{x_1} \frac{x_1 - x}{c} = \frac{x_1}{2c} \tag{29}$$

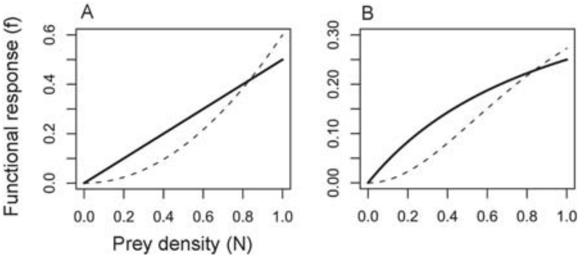

Fig. 6 The functional response derived assuming an underlying movement mechanism. (A) Functional response without handling time for pure advection (solid line) and pure diffusion (dashed line). (B) Functional response including handling time for pure advection (solid line) and pure diffusion (dashed line). The parameters are $c = 0.25$ km/h, $d = 0.1$ km^2/h, and $T_h = 2$ h.

and the expected mean first passage time is

$$E\left[T(x)\right] = \int_0^\infty \lambda\, e^{-\lambda x_1} \frac{x_1}{2c}\, dx_1 = \frac{1}{2c\lambda}. \tag{30}$$

Therefore, the encounter rate is $2c\lambda$. This is equivalent to the Holling Type I functional response where $a = 2c$, $f_c(N) = 2cN$ (Fig. 6a, solid line).

5.2. *Simple diffusion*

Now consider a predator moving according to simple diffusion. Then $T(x) = \frac{1}{2d}(2x_1x - x^2)$ and the expected mean first passage time for a fixed x_1 is

$$E\left[T(x)|x_1\right] = \frac{1}{x_1}\int_0^{x_1} \frac{x(x_1 - x)}{2d} = \frac{x_1^2}{12d}, \tag{31}$$

and the expected mean first passage time is

$$E\left[T(x)\right] = \int_0^\infty \lambda\, e^{-\lambda x_1} \frac{x_1^2}{12d}\, dx_1 = \frac{1}{6d\lambda^2}. \tag{32}$$

The rate that a single predator encounters prey as a function of prey density, λ, is $6d\lambda^2$, leading to the functional response $f_d(N) = 6fN^2$ (Fig. 6a, dotted line).

5.3. *Including handling time in the functional response*

We extend the results from the above encounter rate calculations to include handling time, T_h. Following the argument of Gurney and Nisbet (1998), the average number of prey items ingested by an individual predator per unit time is given by

$$f(N) = \frac{R}{1 + T_h R} \tag{33}$$

where predators capture prey at an average rate R per unit time. For each underlying movement mechanism (i.e., pure advection or simple diffusion), R can be obtained from the encounter rates above. Therefore, the functional responses with handling time assuming pure advection and simple diffusion are

$$f_c(N) = \frac{2cN}{1 + T_h 2cN} \tag{34}$$

and

$$f_d(N) = \frac{6cN^2}{1 + T_h 6cN^2}, \tag{35}$$

respectively (Fig. 6b, solid and dotted lines).

The directed searching originally described by Holling (1959) is consistent with advective movement. However, predators display a wide range of movement behaviors during searching ranging from random (diffusive) to directed (advective) movement, and including alternation of these (Bell, 1991). We answered the question as to how the underlying predator movement during searching changes the form of the functional response, using a mechanistic biased random walk model for predator searching. This outcome is an alternate derivation for the Type III functional response which is based on random predator searching.

6. Discussion

Advection and diffusion models are widely applied in ecology to understand how landscape animal movement and landscape heterogeneity effect animal distribution (Turchin, 1991; Holmes et al., 1994; Okubo and Levin, 2001). The forward Fokker–Planck equation relates animal movement to the probability of the animal occurring at a particular point in time and space and time. However, it is often important to know when the animal first arrived at a given location. This is relevant, for example, when animals must gain control of a territory or obtain a limited resource. Drawing on established physical literature, we derived from first principles, an equation for the mean first passage time of an animal in a two-dimensional heterogeneous landscape that incorporated directed (advection) and random (diffusion) components of movement and can be coupled with empirical movement data. Similarly, the mean first passage time equation can be derived directly from the backward Fokker–Planck equation (Gardiner, 1985). The equation is then solved either analytically or numerically, depending on the complexity of the movement behavior and landscape structure. The solutions to the mean first passage time equation provide insight into the effect of the interaction between the landscape and animal movement behavior on the search time. They can be interpreted graphically by examining the mean first passage time surface and quantitatively by using mean first passage time from particular starting locations or a summary statistic, such as the average mean first passage time over space. We view the description of animal distribution and mean first passage time analysis as complimentary, providing tools to answer different but related questions. We focused on the interpretation of first passage time as the search time of a predator for prey, but recognize that search time may also be interpreted more broadly as the time taken by an animal to find food, refuge, or mates. Additionally, search time could refer to the time needed for a parasite or disease to come into contact with a new host.

One application of mean first passage time is to study the effect of landscape heterogeneity and animal search strategies on search times. In this paper, we considered the effect of territoriality on search time of a red fox for prey. Mean first passage time analysis indicated that foxes with a centralizing tendency found prey near their den site more quickly than randomly moving foxes. This was true up to a certain distance of the prey from the den site, after which point the randomly moving foxes found the prey more quickly. This result has implications for prey, as it suggests that predation risk for prey of territorial predators is related to prey distance from the den site. However, additional factors such as neighboring foxes, resource distribution, and topography, were not included in the model, but may influence red fox movement. Interested readers should refer to Moorcroft and Lewis (2006) for examples of how to include more complex movement behavior into animal movement models. Mean first passage time could also be used to understand the effect of landscape change on search time. For example, wolves move faster on seismic lines and trails than in the forest (James, 1999). A mean first passage time analysis would give insight as to how increasing seismic line density can affect search time of a wolf for prey (McKenzie et al., in preparation). In this case, understanding how search time will change is important for predicting potential consequences of increased industrial development for predator-prey dynamics.

The mean first passage time equation is a general formulation for searching time that models the random and directed movement of animals (Turchin, 1991). It is an approximation that uses the advection and diffusion coefficients as summary statistics for complex spatial movement patterns (Holmes et al., 1994). Individual based simulations provide an alternate method for computing first passage times. We highlight some advantages and disadvantages of each method here. The general formulation for mean first passage time yields an equation that need only be solved once either by analytical or numerical methods, although solving the Poisson-type equation on an inhomogeneous domain is not always trivial. This contrasts with individual based simulations of the same process. Obtaining a mean first passage time surface by simulation requires that n realizations of well-defined animal movement be simulated from each possible initial starting location, where n is large enough to provide a reasonable estimate of the mean. Whereas this simulation process may be possible for simple problems, it becomes computationally intensive for complex animal movement behavior in large heterogeneous landscapes (Grimm, 1999). However, individual based simulations lead to the full distribution of first passage times that is not available from the advection-diffusion approximation (see Gardiner, 1985, for details on deriving partial differential equation models for higher order moments of the first passage time).

The mean first passage time equation has the ability to model animal movement, using summary statistics for animal movement (i.e., means and variances, as given in Eqs. 14–18), even when the underlying detailed movement rules are unknown. This is often beneficial, as detailed behavioral rules are rarely known for ecological processes (Lima and Zollner, 1996; Belisle, 2005). Instead empirical movement data, such as move distance and direction, can be used to calculate the summary statistics for animal movement (Turchin, 1991). However, if more complex movement behavior is of interest, individual based simulations are able to incorporate it. These could include, for example, complex decision-making processes in response to environmental cues or temporally varying environments. Thus, in general, the best approach will depend on the data available and the desired information about the first passage time.

Mean first passage time finds another application in investigating the effect of including different animal movement mechanisms into the functional response. We found that the functional responses of predators moving according to pure advection and diffusion in one-dimension were qualitatively different. When we included handling time, we found that the functional response of diffusing animals was sigmoidal, not concave asymptotic as found by Holling (1959). Therefore, random searching behavior could be an alternate biological mechanism to prey refuges or prey switching, which gives rise to the Holling Type III functional response. However it is important to recognize that the analysis in higher dimensions remains to be done. In addition, for the functional response including handling time, it would be interesting to consider what would happen if the expected functional response was evaluated directly instead of the function of the expectation of the first passage time random variable. The effect on search time of switching between advective and diffusive movement has further been investigated by Moreau et al. (2007) using a similar approach involving averaging over the length of subdomains. They found that the optimal duration of phases in an intermittent searching strategy (i.e., where searchers alternate between purely advective motion during which they are not able to detect prey, and purely diffusive motion during which they have a nonzero probability of detecting prey within a certain radius) differ depending on the prey distribution.

In summary, mean first passage time is a theoretical approach for modeling animal movement. It contributes an equation for animal movement in heterogeneous landscapes and opens up the potential for further research on the interaction between animal movement and other ecological processes, such as predation, mate-finding, and disease transmission. Future applications of mean first passage time could include interactions between adjacent territory holders, dispersal, and mate finding in heterogeneous landscapes, the effect of environmental heterogeneity on predator search time, or time to first contact in spatial disease models.

Acknowledgements

HWM acknowledges NSERC, Alberta Ingenuity and the University of Alberta for funding support. MAL is supported by a NSERC Discovery Grant and a Canada Research Chair in Mathematical Biology. EHM is supported by a NSERC CRO grant. Thanks to Odo Diekmann and Thomas Hillen for helpful feedback on aspects of the modeling.

Appendix A: Unbiased random walk to mean first passage time equation

Using the random walk framework following Berg (1993), the first passage time is written as

$$T(x) = \tau + \frac{1}{2}T(x-\delta) + \frac{1}{2}T(x+\delta). \tag{A.1}$$

Using Taylor series expansion, rewriting the above equation leads to

$$T(x) = \tau + \frac{1}{2}\left(T(x) - \delta\frac{dT}{dx} + \frac{\delta^2}{2}\frac{d^2T}{dx^2}\right) + \frac{1}{2}\left(T(x) + \delta\frac{dT}{dx} + \frac{\delta^2}{2}\frac{d^2T}{dx^2}\right) + \text{h.o.t.} \tag{A.2}$$

Divide through by τ and rearrange to obtain

$$\frac{\delta^2}{2\tau}\frac{d^2T}{dx^2} + 1 + \text{h.o.t.} = 0. \tag{A.3}$$

Take the limit as $\delta, \tau \to 0$ to arrive at the equation for mean first passage time

$$d\frac{d^2T}{dx^2} + 1 = 0 \tag{A.4}$$

where $d = \lim_{\delta,\tau\to 0} \frac{\delta^2}{2\tau}$ is the diffusion coefficient.

Appendix B: Unbiased random walk with variable diffusion to mean first passage time equation

The master equation describing the first passage time as a random walk is

$$T(x) = \tau + \frac{1-N(x)}{2}T(x-\delta) + N(x)T(x) + \frac{1-N(x)}{2}T(x+\delta). \tag{B.1}$$

Simplifying and collecting terms,

$$\begin{aligned} T(x) = \tau + \frac{1}{2}\big[&T(x-\delta) - N(x)T(x-\delta) + N(x)T(x) + T(x+\delta) \\ &- N(x)T(x+\delta)\big]. \end{aligned} \tag{B.2}$$

Expand $T(x-\delta)$ and $T(x+\delta)$ using Taylor series, divide by τ, and take the limit as $\tau, \delta \to 0$ to obtain the mean first passage time equation

$$d(x)\frac{d^2T}{dx^2} + 1 = 0 \tag{B.3}$$

where $d(x) = \lim_{\delta,\tau\to 0} \frac{\delta^2[1-N(x)]}{2\tau}$ is the spatially variable diffusion coefficient.

Appendix C: Incorporating movement data into the first passage time equation

Begin with the master equation

$$T(x) = \tau + \int_{-\infty}^{\infty} k(x, x', \tau)\, T(x')\, dx'. \tag{C.1}$$

Let $x' = x + a$ and define a new redistribution kernel as $K(x, a, \tau)$ where a is the directed length of the move and (C.1) becomes

$$T(x) = \tau + \int_{-\infty}^{\infty} K(x, a, \tau)\, T(x+a)\, da. \tag{C.2}$$

Expand $x + a$ using Taylor series,

$$T(x) = \tau + \int_{-\infty}^{\infty} K(x, a, \tau)\left(T(x) + a\frac{\partial}{\partial x}T(x) + \frac{a^2}{2}\frac{\partial^2}{\partial x^2}T(x) + \text{h.o.t.}\right) da. \quad \text{(C.3)}$$

Divide by τ and use the fact that $\int_{-\infty}^{\infty} K(x, a, \tau)\, da = 1$ to obtain

$$\int_{-\infty}^{\infty} K(x, a, \tau)\left(T(x) + a\frac{\partial}{\partial x}T(x) + a^2\frac{\partial^2}{\partial x^2}T(x) + \text{h.o.t.}\right) da + 1 = 0. \quad \text{(C.4)}$$

Because the derivatives are independent of a it is possible to remove them from the integral. Take the limit as $\delta, \tau \to 0$ and the equation becomes

$$c(x)\frac{\partial}{\partial x}T(x) + d(x)\frac{\partial^2}{\partial x^2}T(x) + 1 = 0 \quad \text{(C.5)}$$

where

$$c(x) = \lim_{\tau \to 0}\frac{1}{\tau}\int_{-\infty}^{\infty} a\, K(x, a, \tau)\, da \quad \text{(C.6)}$$

and

$$d(x) = \lim_{\tau \to 0}\frac{1}{2\tau}\int_{-\infty}^{\infty} a^2\, K(x, a, \tau)\, da. \quad \text{(C.7)}$$

Appendix D: Extension of the mean first passage time equation for one- to two-dimensions

From the random walk in two-dimensions, the master equation is

$$T(\mathbf{x}) = \tau + \int k(\mathbf{x}, \mathbf{x}', \tau)T(\mathbf{x}')\, d\mathbf{x}'. \quad \text{(D.1)}$$

Rewrite $\mathbf{x}' = \mathbf{x} + \mathbf{a}$ and define a new redistribution kernel $K(\mathbf{x}, \mathbf{a}, \tau)$, where $\mathbf{a}$ is the vector representing the move. The equation becomes

$$T(\mathbf{x}) = \tau + \int K(\mathbf{x}, \mathbf{a}, \tau)\, T(\mathbf{x} + \mathbf{a})\, d\mathbf{a}. \quad \text{(D.2)}$$

Expand $T(\mathbf{x} + \mathbf{a})$ using a two-dimensional Taylor series to obtain the equation

$$\begin{aligned} T(\mathbf{x}) = \tau + \int K(\mathbf{x}, \mathbf{a}, \tau)\Bigg(& T(\mathbf{x}) + a_1\frac{\partial}{\partial x}T(\mathbf{x}) + a_2\frac{\partial}{\partial y}T(\mathbf{x}) + \frac{a_1^2}{2}\frac{\partial^2}{\partial x^2}T(\mathbf{x}) \\ & + \frac{a_1 a_2}{2}\frac{\partial^2}{\partial x \partial y}T(\mathbf{x}) + \frac{a_2 a_1}{2}\frac{\partial^2}{\partial y \partial x}T(\mathbf{x}) + \frac{a_2^2}{2}\frac{\partial^2}{\partial y^2}T(\mathbf{x}) + \text{h.o.t.}\Bigg). \quad \text{(D.3)} \end{aligned}$$

Divide by τ, and using the fact that $\int K(\mathbf{x}, \mathbf{a}, \tau)\, d\mathbf{a} = 1$, rearrange and take the limit as $\tau \to 0$ to obtain the mean first passage time equation

$$\mathbf{c}(\mathbf{x}) \cdot \nabla T(\mathbf{x}) + d_{xx}(\mathbf{x}) \frac{\partial^2}{\partial x^2} T(\mathbf{x}) + d_{xy}(\mathbf{x}) \frac{\partial^2}{\partial x \partial y} T(\mathbf{x}) + d_{yx}(\mathbf{x}) \frac{\partial^2}{\partial y \partial x} T(\mathbf{x})$$
$$+ d_{yy}(\mathbf{x}) \frac{\partial^2}{\partial y^2} T(\mathbf{x}) + 1 = 0 \tag{D.4}$$

where

$$\mathbf{c}(\mathbf{x}) = \lim_{\tau \to 0} \frac{1}{\tau} \int \mathbf{a}\, K(\mathbf{x}, \mathbf{a}, \tau)\, d\mathbf{a}, \tag{D.5}$$

$$d_{xx}(\mathbf{x}) = \lim_{\tau \to 0} \frac{1}{2\tau} \int a_1^2\, K(\mathbf{x}, \mathbf{a}, \tau)\, d\mathbf{a}, \tag{D.6}$$

$$d_{xy}(\mathbf{x}) = \lim_{\tau \to 0} \frac{1}{2\tau} \int a_1 a_2\, K(\mathbf{x}, \mathbf{a}, \tau)\, d\mathbf{a}, \tag{D.7}$$

$$d_{yx}(\mathbf{x}) = d_{xy}(\mathbf{x}), \tag{D.8}$$

$$d_{yy}(\mathbf{x}) = \lim_{\tau \to 0} \frac{1}{2\tau} \int a_2^2\, K(\mathbf{x}, \mathbf{a}, \tau)\, d\mathbf{a}. \tag{D.9}$$

In the case of isotropic diffusion and constant bias toward the point $\mathbf{x} = \mathbf{0}$ (such as in the centralizing tendency model), (D.4) simplifies to (24), where the advection coefficient is $\mathbf{c}(\mathbf{x}) = -c\,\mathbf{x}/\|\mathbf{x}\|$ ($\mathbf{x}$ is a unit vector pointing in the direction of the den site and c is the advection speed) and the diffusion coefficient is a constant, d. We now show explicitly how to obtain these coefficients from movement data. The methods used here are taken directly from Moorcroft and Lewis (2006). We assume the movement kernel K can be expressed as the product the distribution of distances moved ($\rho = \|\mathbf{a}\|$) and the distribution of movement directions ($\phi = \tan^{-1}(a_2/a_1)$),

$$K(\mathbf{x}, \mathbf{a}, \tau) = \frac{1}{\rho} f_\tau(\rho)\, K_\tau(\phi, \hat{\phi}) \tag{D.10}$$

where the distribution of movement distances is exponential with mean $\bar{\rho}_\tau$

$$f_\tau(\rho) = \bar{\rho}_\tau \exp[-\bar{\rho}_\tau\, \rho] \tag{D.11}$$

and the movement directions follows the von Mises distribution

$$K_\tau(\phi, \hat{\phi}) = \frac{1}{2\pi I_0(\kappa_\tau)} \exp\bigl[\kappa_\tau \cos(\phi - \hat{\phi})\bigr] \tag{D.12}$$

with mean direction $\hat{\phi}$ ($-\pi \le \hat{\phi} \le \pi$) and concentration parameter κ_τ ($\kappa_\tau \ge 0$). Here, $\hat{\phi} = \tan^{-1}(y/x)$ is the direction of the individuals den site from its current location (x, y).

Using trigonometric identities as given in Appendix E of Moorcroft and Lewis (2006) yields the following formulae for the coefficients,

$$c = \lim_{\tau \to 0} \frac{\bar{\rho}_\tau \, \kappa_\tau}{2\tau}, \tag{D.13}$$

$$d = \lim_{\tau \to 0} \frac{(\bar{\rho})^2}{4\tau}. \tag{D.14}$$

Therefore, the advection speed c and the diffusion coefficient d can be estimated directly from the mean distance moved and the von Mises concentration parameter, which are estimated by fitting the exponential and von Mises distributions to the observed move distances and directions, respectively (see Fig. 3.6 of Moorcroft and Lewis, 2006).

Appendix E: Alternate derivation of the mean first passage time equation

We follow closely the derivation in Gardiner (1985). Consider an animal moving in the one-dimensional domain $[a, b]$, with absorbing boundary conditions at a and b. The probability the particle is still in the interval at time t is given by

$$\int_a^b p(x', t|x, 0)\, dx' \equiv G(x, t) \tag{E.1}$$

where $p(x', t|x, 0)$ is the probability the animal is at location x' at time t given it was at location x at time 0. If the animal leaves the interval at time T, we obtain the relationship

$$\Pr(T \geq t) = \int_a^b p(x', t|x, 0)\, dx' = G(x, t). \tag{E.2}$$

Because the system is homogeneous in time $p(x', t|x, 0) = p(x', 0|x, -t)$ and the backward Kolmogorov equation becomes (as we are differentiating with respect to t, which now has a negative sign in front),

$$\frac{\partial}{\partial t} p(x', t|x, 0) = c(x) \frac{\partial}{\partial x} p(x', t|x, 0) + d(x) \frac{\partial^2}{\partial x^2} p(x', t|x, 0). \tag{E.3}$$

Integrating both sides of (E.3) over x', taking the integral sign inside the derivative, and applying the definition of $G(x, t)$,

$$\frac{\partial}{\partial t} G(x, t) = c(x) \frac{\partial}{\partial x} G(x, t) + d(x) \frac{\partial^2}{\partial x^2} G(x, t) \tag{E.4}$$

where $G(x, 0) = 1,\ x \in (a, b)$ and 0 elsewhere, from the initial condition on (E.3), and $p(x', 0|x, 0) = \delta(x - x')$. In addition, if $x = a$ or b, $G(a, t) = G(b, t) = 0$ since the particle is absorbed immediately, and so $\Pr(T \geq t) = 0$. Now, T is a random variable with distribution function $1 - G(x, t)$. Therefore, using the definition of expectation of a random variable, the mean first passage time $T(x)$ is given by

$$T(x) = -\int_0^\infty t \frac{\partial}{\partial t} G(x, t). \tag{E.5}$$

After applying integration by parts,

$$T(x) = \int_0^\infty G(x,t)\,dt. \tag{E.6}$$

To obtain the familiar differential equation for mean first passage time (Eq. (7)), integrate Eq. (E.4) over $t \in (0, \infty)$, and again take the integrals inside the derivative.

Appendix F: Numerical methods

The spatially heterogeneous mean first passage time problem was solved using COMSOL Multiphysics. The landscape was defined in COMSOL using the draw tools. The model was defined using the PDE, coefficient form (stationary analysis) application mode. The general pde, adapted for the red fox example is

$$\begin{cases} d\nabla^2 T - \mathbf{c}(\mathbf{x}) \cdot \nabla T + 1 = 0 & \text{in } \partial\Omega, \\ \mathbf{n} \cdot d\nabla T = 0 & \text{on } \partial\Omega_{\text{ext}}, \\ T = 0 & \text{on } \partial\Omega_{\text{int}}, \end{cases} \tag{F.1}$$

where $\mathbf{c}(\mathbf{x}) = (CX, CY)^T$ are MATLAB functions that compute the spatially dependent advection coefficients, d is the constant diffusion coefficient, Ω is the computational domain, $\partial\Omega_{\text{ext}}$ is the boundary of the home range with outward pointing normal $\mathbf{n}$, and $\partial\Omega_{\text{int}}$ is the boundary of the detection region around the prey.

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