J. Appl. Prob. **40,** 557–580 (2003)
Printed in Israel

BIASED MOVEMENT AT A BOUNDARY AND CONDITIONAL OCCUPANCY TIMES FOR DIFFUSION PROCESSES

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Abstract

Motivated by edge behaviour reported for biological organisms, we show that random walks with a bias at a boundary lead to a discontinuous probability density across the boundary. We continue by studying more general diffusion processes with such a discontinuity across an interior boundary. We show how hitting probabilities, occupancy times and conditional occupancy times may be solved from problems that are adjoint to the original diffusion problem. We highlight our results with a biologically motivated example, where we analyze the movement behaviour of an individual in a network of habitat patches surrounded by dispersal habitat.

Keywords: Random walk; bias at boundary; diffusion approximation; hitting probability; exit time; conditional exit time; occupancy time; conditional occupancy time

AMS 2000 Subject Classification: Primary 60J60
Secondary 92D50

1. Introduction

Random walks and their diffusion approximations have become a standard tool for modelling the movement behaviour of a variety of biological organisms [9], [13]. One of the most challenging problems in such models is the response of individuals to habitat heterogeneity, which is often allowed in diffusion models in the form of smoothly varying diffusion coefficients. However, landscapes often consist of mosaics of patches of different habitat types with more or less well-defined patch boundaries. In such a case, the manner in which individuals respond to patch boundaries may be a major determinant of overall movement behaviour. As an example, Ries and Debinski [12] tracked the behaviour of two butterfly species at four edge types (ranging from low to high contrast) to determine the extent to which habitat boundaries act as a barrier to emigration. A habitat specialist (*Speyeria idalia*) responded strongly to all edge types, both by turning to avoid crossing them and by returning to the patch if they had crossed the edge. A habitat generalist (*Danaus plexippus*) responded strongly only to high-contrast (treeline) edges. It responded by seldom crossing edges, but rarely returned once it had crossed.

Random walks and their diffusion approximations incorporating individual behaviour at patch boundaries have been previously analysed in [3] and [4]. The boundary condition used in these studies was taken from the literature for skew Brownian motion [14], [7]. As pointed out in [2], skew Brownian motion predicts that the probability density may have a point mass at

Received 20 May 2002; revision received 26 February 2003.
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the boundary point, meaning that individuals accumulate at the boundary. Such accumulation has been observed in experimental studies [8].

In this paper, we analyze random walks with another type of biologically motivated biased movement at patch boundaries. We assume that in the vicinity of the boundary, the individual is able to perceive the presence of the two habitat types, and that it will bias its movement towards the preferred habitat type. We show in Section 2 that the diffusion approximation for the random walk shows a discontinuity in the probability density across the boundary where the bias occurs. The boundary conditions that are derived here are profoundly different from the condition used in [3] and [4].

We continue in Section 3 by studying more general diffusion processes with a discontinuity across an interior boundary. We show how hitting probabilities, occupancy times and conditional occupancy times may be solved from problems that are adjoint to the original diffusion problem. We illustrate our results in Section 4 with biologically motivated examples, where we analyze the movement behaviour of an individual in a network of habitat patches surrounded by dispersal habitat.

2. Biased movement at patch boundary

2.1. Bias at a single point

We start by considering random walks in a one-dimensional lattice. We assume that the negative and the positive sides of the x-axis represent different habitat types, which will be denoted by the subscripts $-$ and $+$ below. Two types of movement rules are considered.

Case A. (*Discrete time*.) Here we assume a discrete-time discrete-space process. At each time step (the length of which is denoted by τ), the individual attempts to make a move either to the left or to the right. The probability of death during the time step is denoted for $x < 0$ by $c_-\tau$ and for $x > 0$ by $c_+\tau$. If the individual does not die, it makes a move of length λ_- if $x < 0$ or λ_+ if $x > 0$. If the individual is not located at the origin, the probabilities of taking the move to the left or to the right are assumed to be equal. If the individual is located at the origin, it is assumed to have a preference in move direction. The probability of moving to the left (to habitat type $-$) is denoted by $(1 - z)/2$ and the probability for moving to the right (to habitat type $+$) is thus $(1 + z)/2$, where $-1 \le z \le 1$ measures the preference for the habitat at $x < 0$. If $z = 0$, then there is no preference in boundary behaviour.

Case B. (*Continuous time*.) Here we start with a continuous-time discrete-space process. We assume that during time $\mathrm{d}t$, an individual dies with probability $c_+\,\mathrm{d}t$ or $c_-\,\mathrm{d}t$ and moves with probability $p_+\,\mathrm{d}t$ or $p_-\,\mathrm{d}t$ depending on whether $x < 0$ or $x > 0$. If the individual is originally not at the origin, the probabilities of moving to the left or to the right are both $\frac{1}{2}$; at the origin they are $(1 - z)/2$ and $(1 + z)/2$ respectively. The length of the move is denoted by λ_+ or λ_-. If the individual is located at the origin, the death and movement rates are respectively denoted by c_0 and p_0.

In order to derive a diffusion equation approximating the movement behaviour described above, we assume that both the time step and the step lengths are small. To do this, we denote the spatial scale by λ, so that $\lambda_- = q_-\lambda$ and $\lambda_+ = q_+\lambda$, where q_- and q_+ are assumed to be constants. In Case B, we denote by $p = 1/\tau$ the rate at which the steps are taken, and let $p_\pm = r_\pm p$ and $p_0 = r_0 p$, where r_+, r_- and r_0 are constants. In Case A, where we did not allow the time step to be different for the two habitat types, we simply let $r_\pm = r_0 = 1$.

Assuming that $\lambda, \tau \to 0$ in such a manner that $a = \lambda^2/2\tau$ remains a fixed positive constant, the time evolution of the probability density $v(x, t)$ of the individual's location at time t is approximated by the diffusion equation

$$\partial_t v(x,t) = \begin{cases} a_- \partial_{xx} v(x,t) - c_- v(x,t) & \text{for } x < 0, \\ a_+ \partial_{xx} v(x,t) - c_+ v(x,t) & \text{for } x > 0, \end{cases}$$

where $a_- = r_- q_-^2 a$ and $a_+ = r_+ q_+^2 a$ represent the diffusivity [9], [13]. We use ∂_t as a shorthand for ∂/∂_t and ∂_{xx} for ∂^2/∂_x^2.

As shown in Appendix A, the assumption that $\lambda, \tau \to 0$ with $a = \lambda^2/2\tau$ constant leads to the boundary conditions

$$s_+(1-z)v(0^+, t) = s_-(1+z)v(0^-, t), \tag{2.1}$$

$$a_+ \partial_x v(0^+, t) = a_- \partial_x v(0^-, t), \tag{2.2}$$

where $s_+ = r_+ q_+$ and $s_- = r_- q_-$ denote the relative velocities at which individuals are moving at the positive and negative sides of the x-axis. The boundary condition (2.1) represents the effect of the bias at the boundary, whereas (2.2) expresses the fact that the diffusion flux to the left of the boundary must equal that to the right. Note that the density difference in (2.1) does not depend solely on the preference at the boundary, but also on the relative velocities by which individuals are moving at both sides of the boundary.

2.2. Bias in a boundary region

We now allow the walker's diffusivity and bias to vary within a narrow 'boundary region'. Consider a regular one-dimensional lattice on which a walker at position x can spontaneously move a distance $\pm\lambda$ at rate $p(x)(1 \pm z(x))/2$. We here assume that there is no mortality, though it is straightforward to show that the same boundary conditions would apply if there were. We assume that the hopping probability p and the bias z only vary within a region of width 2ε around the origin, so

$$(z(\pm x), p(\pm x)) = (0, p_\pm) \quad \text{for } x > \varepsilon.$$

We will then take the limit $\lambda \to 0$, $\varepsilon \to 0$, in such a way that there is a constant $c > 0$ for which $\varepsilon > c\lambda$ and $\lambda^2 p_\pm \to 2a_\pm$. The probability density of the individual's location at x will then satisfy

$$\partial_t v(x,t) = \begin{cases} a_- \partial_{xx} v(x,t) & \text{for } x < 0, \\ a_+ \partial_{xx} v(x,t) & \text{for } x > 0. \end{cases} \tag{2.3}$$

2.2.1. *Continuum limit.* We first consider the case where the bias and diffusivity change slowly in space relative to the step length λ. In that case, we can take a spatial continuum limit before taking $\varepsilon \to 0$. As shown in Appendix B, in the diffusion limit the fundamental solution $v(x, t)$ satisfies

$$\partial_t v(x,t) = \partial_{xx}(a(x)v(x,t)) - \partial_x(b(x)v(x,t)), \tag{2.4}$$

where $a(x) = \lim_{\lambda \to 0}(p(x)/2)\lambda^2$ and $b(x) = \lim_{\lambda \to 0} p(x)z(x)\lambda$. We assume that a and b take the forms

$$a(x) = \begin{cases} a_- & \text{for } x < -\varepsilon, \\ \tilde{a}\left(\dfrac{x}{\varepsilon}\right) & \text{for } -\varepsilon < x < \varepsilon, \\ a_+ & \text{for } x > \varepsilon, \end{cases}$$

and

$$b(x) = \begin{cases} \dfrac{1}{\varepsilon}\tilde{b}\Big(\dfrac{x}{\varepsilon}\Big) & \text{for } |x| < \varepsilon, \\ 0 & \text{for } |x| > \varepsilon, \end{cases}$$

where $\tilde{a}$ and $\tilde{b}$ are independent of ε. The choice $z \sim \lambda/\varepsilon$ is essential in order for the bias to produce a finite discontinuity across the boundary.

After taking the limit $\varepsilon \to 0$, we recover (2.3) and the boundary conditions

$$\frac{v(0^+)}{v(0^-)} = \frac{a_-}{a_+} \exp\bigg(\int_{-\infty}^{\infty} \frac{b(x)}{a(x)}\, \mathrm{d}x\bigg), \tag{2.5}$$

$$a_- \partial_x v(0^-) = a_+ \partial_x v(0^+). \tag{2.6}$$

As before, (2.6) represents an equal flux of individuals across the origin. It is straightforward to show that these boundary conditions also apply if $\partial_x \tilde{a}$ and $\tilde{b}$ are of infinite support, provided that $\lim_{x\to\infty} \tilde{a}(\pm x) = a_\pm$ and that $\lim_{x\to\infty} x\tilde{b}(x) \to 0$. Moreover, (2.4) generalises to higher dimensions, with ∂_x being replaced by $\boldsymbol{\nabla}$, so these boundary conditions will also apply across a smooth boundary, whose radius of curvature is much larger than ε, where the integral in (2.5) is performed along a local normal to the boundary. Note also that, if the motion obey's Fick's law of diffusion, so that the underlying equation is

$$\partial_t v(x,t) = \partial_x (a(x)\partial_x v(x,t)) - \partial_x (b(x) v(x,t))$$

rather than (2.4), then the equal-flux condition (2.6) remains unchanged but the discontinuity condition becomes

$$\frac{v(0^+)}{v(0^-)} = \exp\bigg(\int_{-\infty}^{\infty} \frac{b(x)}{a(x)}\, \mathrm{d}x\bigg).$$

2.2.2. *General case.* Similar results can also be obtained without assuming that $\varepsilon \gg \lambda$; in that case the boundary conditions are (2.6) and

$$\frac{v(0^+)}{v(0^-)} = \frac{a_-}{a_+} \prod_{x'=-\varepsilon}^{\varepsilon} \frac{1 + z(x')}{1 - z(x')}. \tag{2.7}$$

Note that (2.7) reduces to (2.1) for the case where $z(x) = 0$ for $x \neq 0$ since when $\lambda_+ = \lambda_-$ we have $s_+/s_- = a_+/a_-$. The continuum limit (2.5) can also be obtained as a special case by noting that $2z(x) = \lambda b(x)/a(x)$, so

$$\log \frac{1+z}{1-z} \to 2\lambda \frac{b}{a} \quad \text{and} \quad \sum_{x=-\varepsilon,-\varepsilon+\lambda,\ldots}^{\varepsilon} 2z(x) \to \int_{-\varepsilon}^{\varepsilon} \frac{b(x)}{a(x)}\, \mathrm{d}x \quad \text{as } \lambda \to 0.$$

3. Hitting probabilities and (conditional) occupancy times

In this section we assume a d-dimensional diffusion process with possible discontinuities across interior boundaries. We derive adjoint problems from which hitting probabilities, occupancy times and conditional occupancy times may be derived. For an introduction to these concepts, we refer the reader to [10].

We assume that an open, connected set $\Omega \subset \mathbb{R}^d$ is composed of a finite number of disjoint open sets Ω_i so that $\bar{\Omega} = \bar{\Omega}^0$, where $\Omega^0 = \bigcup_i \Omega_i$. We let Γ_i be the boundary of Ω_i and

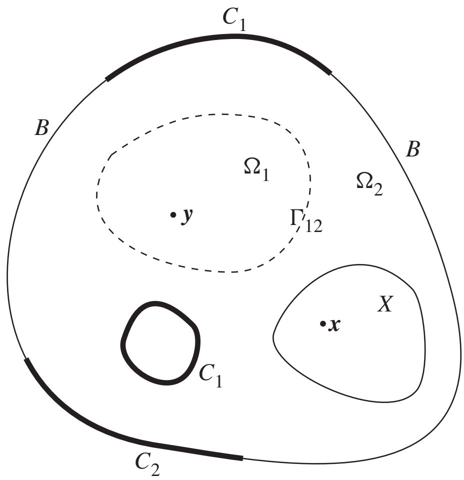

FIGURE 1: The domain Ω.

let $\Gamma_{ij} = \Gamma_i \cap \Gamma_j$ be the common boundary of Ω_i and Ω_j. We assume that the boundary $\partial\Omega$ of Ω is composed of three disjoint parts: $\partial\Omega = B \cup C_1 \cup C_2$. We will refer to $\Gamma = \bigcup_{i \neq j} \Gamma_{ij}$ as the interior boundary of Ω, whereas $\partial\Omega = \bigcup_i \Gamma_i \setminus \Gamma$ is called the exterior boundary of Ω. An example of the domain Ω is illustrated in Figure 1.

We consider a general diffusion problem with drift and mortality with a reflecting boundary condition on B and an absorbing boundary condition on $C = C_1 \cup C_2$. We assume that the diffusion, drift and mortality coefficients vary smoothly within each subdomain, but they may be discontinuous between the subdomains. Motivated by the results of Section 2, we allow the solution to the diffusion problem to be discontinuous through the interior boundary Γ, but assume that its flux is continuous through Γ.

We denote by $v = v(\boldsymbol{x}, t; \boldsymbol{y})$ the fundamental solution giving the probability density that an individual is at $\boldsymbol{x}$ at time t if it is given that it was located at $\boldsymbol{y} \in \Omega$ at time $t = 0$. In other words, the probability that the individual is located in the region $X \subset \Omega$ at time t is given by $\int_X v(\boldsymbol{x}, t; \boldsymbol{y})\,\mathrm{d}\boldsymbol{x}$.

The aim of this section is to address the following four questions.

1. What is the mean time that the individual is expected to spend in a region $X \subset \Omega$ before it hits C or dies? The density for the mean time will be denoted by $u(\boldsymbol{x}; \boldsymbol{y})$, so that $T_X(\boldsymbol{y})$, the mean time spent in X, is given by $T_X(\boldsymbol{y}) = \int_X u(\boldsymbol{x}; \boldsymbol{y})\,\mathrm{d}\boldsymbol{x}$. The exit time, defined as the mean time before the individual hits C or dies, is denoted by $T(\boldsymbol{y}) = T_\Omega(\boldsymbol{y})$.

2. What is the probability that the individual hits C_1 before it hits C_2 or dies? The solution to this problem will be denoted by $p^{C_1}(\boldsymbol{y})$.

3. What is the conditional probability density that the individual will be at a point $\boldsymbol{x} \in \Omega$ at time t if it is given that it will hit C_1 before it hits C_2 or dies? The solution to this problem will be denoted by $v^{C_1} = v^{C_1}(\boldsymbol{x}, t; \boldsymbol{y})$,

4. What is the conditional mean time that the individual is expected to spend in a region $X \subset \Omega$ before it hits C_1 if it is given that it will hit C_1 before it hits C_2 or dies? The density for the conditional mean time will be denoted by $u^{C_1}(\boldsymbol{x}; \boldsymbol{y})$, so that $T_X^{C_1}(\boldsymbol{y})$,

the conditional mean time spent in X, is given by $T_X^{C_1}(\boldsymbol{y}) = \int_X u^{C_1}(\boldsymbol{x}; \boldsymbol{y})\,\mathrm{d}\boldsymbol{x}$. The conditional exit time, defined as the conditional mean time before the individual hits C_1 if it is given that it will hit C_1 before it hits C_2 or dies, is denoted by $T^{C_1}(\boldsymbol{y}) = T_\Omega^{C_1}(\boldsymbol{y})$.

3.1. Preliminaries

We consider an elliptic partial differential operator $\mathcal{L}$ defined by

$$\mathcal{L}f(\boldsymbol{x}) = \sum_{i,j=1}^{d} \partial_{ij}[a_{ij}(\boldsymbol{x})f(\boldsymbol{x})] + \sum_{i=1}^{d} \partial_i[b_i(\boldsymbol{x})f(\boldsymbol{x})] - c(\boldsymbol{x})f(\boldsymbol{x}).$$

The functions a_{ij}, b_i and c represent diffusion, drift and mortality respectively, and ∂_i is used as a shorthand for $\partial/\partial x_i$ and ∂_{ij} for $\partial^2/(\partial x_i \partial x_j)$. The reason for multiplying by the functions a_{ij} and b_i before differentiation is that this form is natural for most biological applications [9], [13]. The adjoint operator $\mathcal{L}^*$ is defined by

$$\mathcal{L}^* g(\boldsymbol{x}) = \sum_{i,j=1}^{d} a_{ij}(\boldsymbol{x})\partial_{ij} g(\boldsymbol{x}) - \sum_{i=1}^{d} b_i(\boldsymbol{x})\partial_i g(\boldsymbol{x}) - c(\boldsymbol{x})g(\boldsymbol{x}).$$

Formal integration by parts gives

$$\int_\Omega g(\boldsymbol{x})\mathcal{L}f(\boldsymbol{x})\,\mathrm{d}\boldsymbol{x} = \int_\Omega f(\boldsymbol{x})\mathcal{L}^* g(\boldsymbol{x})\,\mathrm{d}\boldsymbol{x} + \sum_k \int_{\Gamma_k} (g(\boldsymbol{x})\mathcal{F}_k f(\boldsymbol{x}) + f(\boldsymbol{x})\mathcal{F}_k^* g(\boldsymbol{x}))\,\mathrm{d}\mathcal{S}, \tag{3.1}$$

where $\mathrm{d}\mathcal{S}$ denotes integration along a curve with respect to the variable $\boldsymbol{x}$,

$$\mathcal{F}_k f(\boldsymbol{x}) = \sum_i f(\boldsymbol{x}) b_i(\boldsymbol{x}) n_i^k(\boldsymbol{x}) + \sum_{i,j} \partial_j[a_{ij}(\boldsymbol{x})f(\boldsymbol{x})] n_i^k(\boldsymbol{x}) \tag{3.2}$$

is the flux of individuals at the boundary Γ_k and

$$\mathcal{F}_k^*(g)(\boldsymbol{x}) = -\sum_{i,j} a_{ij}(\boldsymbol{x})\partial_i g(\boldsymbol{x}) n_j^k(\boldsymbol{x}). \tag{3.3}$$

Here $\boldsymbol{n}^k(\boldsymbol{x}) = \{n_i^k(\boldsymbol{x})\}_{i=1}^d$ denotes the exterior normal to the set Ω^k at $\boldsymbol{x} \in \Gamma_k$.

The formula (3.1) will play a central part in the derivation of the adjoint problems. We note that a rigorous application of (3.1) would require that Ω and the functions a_{ij}, b_i, c, f and g are known to be sufficiently smooth. As the rigorous validation of such conditions is beyond the scope of the present paper, we will take the liberty of simply assuming that these conditions apply whenever (3.1) is applied. This will certainly be the case for the examples considered in Section 4.

3.1.1. *Interior boundary conditions.* We define the space $\mathcal{A}(\Omega)$ as the space of functions f which satisfy the interior boundary condition

$$k_j(\boldsymbol{x}_0) f(\boldsymbol{x}_i) \to k_i(\boldsymbol{x}_0) f(\boldsymbol{x}_j)$$

for $\boldsymbol{x}_i, \boldsymbol{x}_j \to \boldsymbol{x}_0 \in \Gamma_{ij}$ with $\boldsymbol{x}_i \in \Omega_i, \boldsymbol{x}_j \in \Omega_j$, and for which the flux $\mathcal{F} f(\boldsymbol{x})$ is continuous through the interior boundaries Γ_{ij}. In other words, it is assumed that the relative value of the function $f \in \mathcal{A}(\Omega)$ jumps from $k_i(\boldsymbol{x}_0)$ to $k_j(\boldsymbol{x}_0)$ as the boundary Γ_{ij} is crossed from Ω_i through the point $\boldsymbol{x}_0$ to Ω_j.

The space $\mathcal{A}^*(\Omega)$ is defined as the space of functions g which are continuous through the interior boundaries Γ_{ij} and which satisfy the interior boundary condition

$$k_i(\boldsymbol{x}_0)\mathcal{F}^*g(\boldsymbol{x}_i) \to k_j(\boldsymbol{x}_0)\mathcal{F}^*g(\boldsymbol{x}_j).$$

for $\boldsymbol{x}_i, \boldsymbol{x}_j \to \boldsymbol{x}_0 \in \Gamma_{ij}$ with $\boldsymbol{x}_i \in \Omega_i, \boldsymbol{x}_j \in \Omega_j$.

We note that, if $f \in \mathcal{A}(\Omega)$ and $g \in \mathcal{A}^*(\Omega)$, the boundary terms in (3.1) cancel for the interior boundary Γ and thus

$$\int_\Omega g(\boldsymbol{x})\mathcal{L}f(\boldsymbol{x})\,\mathrm{d}\boldsymbol{x} = \int_\Omega f(\boldsymbol{x})\mathcal{L}^*g(\boldsymbol{x})\,\mathrm{d}\boldsymbol{x} + \int_{\partial\Omega}(g(\boldsymbol{x})\mathcal{F}f(\boldsymbol{x}) + f(\boldsymbol{x})\mathcal{F}^*g(\boldsymbol{x}))\,\mathrm{d}\mathcal{S}, \tag{3.4}$$

where $\mathcal{F}$ and $\mathcal{F}^*$ are defined as in (3.2) and (3.3) but using $\boldsymbol{n}$, the exterior normal to Ω, instead of $\boldsymbol{n}^k$.

When deriving occupancy times for a set X, partial integration will include terms integrated over the boundary ∂X. However, we remark that (3.4) remains valid for this case also as we will assume that, for any $f \in \mathcal{A}(\Omega)$, f and $\mathcal{F}f$ are continuous through $\partial X \setminus (\partial\Omega \cup \Gamma)$, and that, for any $g \in \mathcal{A}^*(\Omega)$, g and $\mathcal{F}^*g$ are continuous through $\partial X \setminus (\partial\Omega \cup \Gamma)$.

3.1.2. *Exterior boundary conditions.* We will need three types of boundary conditions. We say that f satisfies the boundary condition $\mathcal{B}$ if $\mathcal{F}f(\boldsymbol{x}) = 0$ on B and $f(\boldsymbol{x}) = 0$ on C. We say that g satisfies the boundary condition $\mathcal{B}^*$ if $\mathcal{F}^*g(\boldsymbol{x}) = 0$ on B and $g(\boldsymbol{x}) = 0$ on C. We say that g satisfies the boundary condition $\mathcal{B}^{C_1*}$ if $\mathcal{F}^*g(\boldsymbol{x}) = 0$ on B, $g(\boldsymbol{x}) = 1$ on C_1 and $g(\boldsymbol{x}) = 0$ on C_2.

3.2. The unconditional process

Definition 3.1. (*Fundamental solution.*) We denote by $v = v(\boldsymbol{x}, t; \boldsymbol{y})$ the fundamental solution to the diffusion problem with drift and mortality, the parameter $\boldsymbol{y}$ denoting the initial state. More precisely, we assume that $v(\boldsymbol{x}, t; \boldsymbol{y}) \in \mathcal{A}(\Omega)$ for all $t \in (0, \infty)$, $\boldsymbol{y} \in \Omega$, and that $v(\boldsymbol{x}, t; \boldsymbol{y})$ satisfies the equation

$$\partial_t v(\boldsymbol{x}, t; \boldsymbol{y}) = \mathcal{L}v(\boldsymbol{x}, t; \boldsymbol{y}), \tag{3.5}$$

the initial condition

$$v(\boldsymbol{x}, 0; \boldsymbol{y}) = \delta(\boldsymbol{x} - \boldsymbol{y})$$

and the boundary condition $\mathcal{B}$.

Definition 3.2. (*Occupancy time density.*) We denote by $u = u(\boldsymbol{x}; \boldsymbol{y})$ the time integral of the fundamental solution, defined by

$$u(\boldsymbol{x}; \boldsymbol{y}) = \int_0^\infty v(\boldsymbol{x}, t; \boldsymbol{y})\,\mathrm{d}t.$$

Integrating (3.5) with respect to time shows that $u(\boldsymbol{x}; \boldsymbol{y}) \in \mathcal{A}(\Omega)$ for all $\boldsymbol{y} \in \Omega$ and that u satisfies the equation

$$\mathcal{L}u(\boldsymbol{x}; \boldsymbol{y}) = -\delta(\boldsymbol{x} - \boldsymbol{y}) \tag{3.6}$$

and the boundary condition $\mathcal{B}$.

Definition 3.3. (*Occupancy time.*) We denote by $T_X = T_X(\boldsymbol{y})$ the mean time that an individual located initially at $\boldsymbol{y} \in \Omega$ spends in area X before it hits C or dies, defined by

$$T_X(\boldsymbol{y}) = \int_X u(\boldsymbol{x}; \boldsymbol{y}) \, \mathrm{d}\boldsymbol{x}.$$

The following theorem shows that the occupancy time may be solved from an adjoint problem.

Theorem 3.1. *The occupancy time $T_X(\boldsymbol{x})$ is the solution to the following problem: find a $T_X \in \mathcal{A}^*(\Omega)$ that satisfies the equation*

$$\mathcal{L}^* T_X(\boldsymbol{x}) = \begin{cases} -1 & \text{for } x \in X, \\ 0 & \text{for } x \in \Omega \setminus X, \end{cases}$$

and the boundary condition $\mathcal{B}^*$.

Proof. Assume that $T_X(\boldsymbol{x})$ is the function defined in the theorem. Multiplying both sides of (3.6) by $T_X(\boldsymbol{x})$ and integrating $\boldsymbol{x}$ over Ω yields

$$\int_\Omega T_X(\boldsymbol{x}) \mathcal{L} u(\boldsymbol{x}; \boldsymbol{y}) \, \mathrm{d}\boldsymbol{x} = -T_X(\boldsymbol{y}).$$

Utilizing (3.4) and the boundary conditions for u and T gives

$$T_X(\boldsymbol{y}) = -\int_\Omega u(\boldsymbol{x}; \boldsymbol{y}) \mathcal{L}^* T_X(\boldsymbol{x}) \, \mathrm{d}\boldsymbol{x} = \int_X u(\boldsymbol{x}; \boldsymbol{y}) \, \mathrm{d}\boldsymbol{x}.$$

As the exit time T is a special case of the occupancy time, $T(\boldsymbol{x}) = T_\Omega(\boldsymbol{x})$, Theorem 3.1 shows that the exit time T may be solved from the equation $\mathcal{L}^* T(\boldsymbol{x}) + 1 = 0$ with suitable boundary conditions. We will next show the exit time T is related to a survival probability S and a passage probability F.

Definition 3.4. We denote by $S = S(t; \boldsymbol{y})$ the survival probability that the individual has neither died nor hit C at time t, defined by

$$S(t; \boldsymbol{y}) = \int_\Omega v(\boldsymbol{x}, t; \boldsymbol{y}) \, \mathrm{d}\boldsymbol{x}.$$

We assume that the individual will eventually either die or hit the boundary C in such a manner that $S(t; \boldsymbol{y})t \to 0$. This assumption should be satisfied for most applications, as for example $c(\boldsymbol{x}) \geq c_0 > 0$ for all $\boldsymbol{x} \in \Omega$ ensures that $S(t; \boldsymbol{y})$ decays exponentially fast.

Definition 3.5. We denote by $F = F(t; \boldsymbol{y})$ the probability density that the individual will hit the part C of the boundary or die at time t, defined by

$$F(t; \boldsymbol{y}) = -\partial_t S(t; \boldsymbol{y}).$$

Utilizing (3.5) and (3.4) with $f = v$ and $g = 1$ shows that

$$F(t; \boldsymbol{y}) = \int_\Omega v(\boldsymbol{x}, t; \boldsymbol{y}) c(\boldsymbol{x}) \, \mathrm{d}\boldsymbol{x} - \int_C \mathcal{F} v(\boldsymbol{x}, t; \boldsymbol{y}) \, \mathrm{d}\mathcal{S}. \tag{3.7}$$

The first term on the right-hand side of (3.7) represents the possibility that the individual will die, whereas the second term represents the possibility that the individual will hit C. The second term motivates us to call $\mathcal{F} v(\boldsymbol{x}, t;\, \boldsymbol{y})$ the flux of individuals through a boundary.

The following lemma ensures that the exit time T is connected to the passage probability F in an intuitive way.

Lemma 3.1. *We have*

$$T(\boldsymbol{y}) = \int_0^\infty t F(t;\, \boldsymbol{y})\, \mathrm{d}t.$$

Proof. The assumption that $S(t)t \to 0$ as $t \to \infty$ yields

$$\begin{aligned} T(\boldsymbol{y}) &= \int_\Omega u(\boldsymbol{x};\, \boldsymbol{y})\, \mathrm{d}\boldsymbol{x} \\ &= \int_\Omega \int_0^\infty v(\boldsymbol{x}, t;\, \boldsymbol{y})\, \mathrm{d}t\, \mathrm{d}\boldsymbol{x} \\ &= \int_0^\infty S(t)\, \mathrm{d}t \\ &= \int_0^\infty t F(t;\, \boldsymbol{y})\, \mathrm{d}t. \end{aligned}$$

In order to consider the probability p^{C_1} that the individual will hit C_1 before it hits C_2 or dies, we need to consider a single component of the survival probability S separately.

Definition 3.6. We denote by $S^{C_1} = S^{C_1}(t;\, \boldsymbol{y})$ the probability that the individual has not hit C_1 before time t, defined by

$$S^{C_1}(t;\, \boldsymbol{y}) = 1 + \int_0^t \int_{C_1} \mathcal{F} v(\boldsymbol{x}, t';\, \boldsymbol{y})\, \mathrm{d}\mathcal{S}\, \mathrm{d}t'. \tag{3.8}$$

Definition 3.7. We denote by $F^{C_1} = F^{C_1}(t;\, \boldsymbol{y})$ the probability density that the individual will hit C_1 at time t, defined by

$$F^{C_1}(t;\, \boldsymbol{y}) = -\partial_t S^{C_1}(t;\, \boldsymbol{y}).$$

Definition 3.8. We denote by $p^{C_1}(\boldsymbol{y})$ the probability that the individual located initially in $\boldsymbol{y} \in \Omega$ will hit C_1 before it hits C_2 or dies, defined by

$$p^{C_1}(\boldsymbol{y}) = 1 - S^{C_1}(\infty;\, \boldsymbol{y}).$$

Theorem 3.2. *The hitting probability $p^{C_1}(\boldsymbol{x})$ is the solution to the following problem: find a $p^{C_1} \in \mathcal{A}^*(\Omega)$ that satisfies the equation*

$$\mathcal{L}^* p^{C_1}(\boldsymbol{x}) = 0$$

and the boundary condition $\mathcal{B}^{C_1 *}$.

Proof. Let us first note that changing the order of integration in (3.8) shows that

$$p^{C_1}(\boldsymbol{y}) = -\int_{C_1} \mathcal{F} u(\boldsymbol{x};\, \boldsymbol{y})\, \mathrm{d}\mathcal{S}.$$

Assume then that $p^{C_1}(\boldsymbol{x})$ is the function defined in the theorem. Multiplying both sides of (3.6) by $p^{C_1}(\boldsymbol{x})$ and integrating $\boldsymbol{x}$ over Ω yields

$$\int_\Omega p^{C_1}(\boldsymbol{x})\mathcal{L}u(\boldsymbol{x};\,\boldsymbol{y})\,\mathrm{d}\boldsymbol{x} = -p^{C_1}(\boldsymbol{y}).$$

Utilizing (3.4) and the boundary conditions for u and p^{C_1} gives

$$p^{C_1}(\boldsymbol{y}) = -\int_\Omega u(\boldsymbol{x};\,\boldsymbol{y})\mathcal{L}^* p^{C_1}(\boldsymbol{x})\,\mathrm{d}\boldsymbol{x} - \int_{C_1} \mathcal{F}u(\boldsymbol{x};\,\boldsymbol{y})\,\mathrm{d}\mathcal{S}.$$

3.3. The conditional process

We let $v^{C_1} = v^{C_1}(\boldsymbol{x}, t;\,\boldsymbol{y})$ denote the conditional probability density for finding the individual which is initially at point $\boldsymbol{y}$ at point $\boldsymbol{x}$ at time t if it is given that the individual will eventually hit C_1 before it hits C_2 or dies. An elementary probabilistic consideration suggests the following definition.

Definition 3.9. We define $v^{C_1}(\boldsymbol{x}, t;\,\boldsymbol{y})$ by the relation

$$v^{C_1}(\boldsymbol{x}, t;\,\boldsymbol{y}) = v(\boldsymbol{x}, t;\,\boldsymbol{y})\frac{p^{C_1}(\boldsymbol{x})}{p^{C_1}(\boldsymbol{y})}.$$

We note that substituting

$$v(\boldsymbol{x}, t;\,\boldsymbol{y}) = v^{C_1}(\boldsymbol{x}, t;\,\boldsymbol{y})\frac{p^{C_1}(\boldsymbol{y})}{p^{C_1}(\boldsymbol{x})}$$

into (3.5) would lead to a partial differential equation for v^{C_1}, from which various quantities for the conditional process could be derived directly. We will, however, proceed indirectly without explicitly referring to the partial differential equation for v^{C_1}.

The conditional process suggests the following redefinitions of S^{C_1} and F^{C_1}.

Definition 3.10. We denote by $\tilde{S}^{C_1} = \tilde{S}^{C_1}(t;\,\boldsymbol{y})$ the probability that the individual has not hit C_1 before time t, defined by

$$\tilde{S}^{C_1}(t;\,\boldsymbol{y}) = 1 - p^{C_1}(\boldsymbol{y})\left[1 - \int_\Omega v^{C_1}(\boldsymbol{x}, t;\,\boldsymbol{y})\,\mathrm{d}\boldsymbol{x}\right].$$

Definition 3.11. We denote by $\tilde{F}^{C_1} = \tilde{F}^{C_1}(t;\,\boldsymbol{y})$ the probability density that the individual will hit C_1 at time t, defined by

$$\tilde{F}^{C_1}(t;\,\boldsymbol{y}) = -\partial_t \tilde{S}^{C_1}(t;\,\boldsymbol{y}).$$

The following lemma ensures that these redefinitions are consistent with the original ones.

Lemma 3.2. *We have* $\tilde{S}^{C_1}(t;\,\boldsymbol{y}) = S^{C_1}(t;\,\boldsymbol{y})$ *and* $\tilde{F}^{C_1}(t;\,\boldsymbol{y}) = F^{C_1}(t;\,\boldsymbol{y})$.

Proof. Multiplying both sides of (3.5) by $p^{C_1}(\boldsymbol{x})$ and integrating over Ω gives

$$\begin{aligned}\tilde{F}^{C_1}(t;\,\boldsymbol{y}) &= -p^{C_1}(\boldsymbol{y})\int_\Omega \partial_t v^{C_1}(\boldsymbol{x},t;\,\boldsymbol{y})\,\mathrm{d}\boldsymbol{x}\\ &= -\int_\Omega \partial_t v(\boldsymbol{x},t;\,\boldsymbol{y})p^{C_1}(\boldsymbol{x})\,\mathrm{d}\boldsymbol{x}\\ &= -\int_\Omega \mathcal{L}v(\boldsymbol{x},t;\,\boldsymbol{y})p^{C_1}(\boldsymbol{x})\,\mathrm{d}\boldsymbol{x}\\ &= -\int_{C_1} \mathcal{F}v(\boldsymbol{x},t;\,\boldsymbol{y})\,\mathrm{d}\mathcal{S}\\ &= F^{C_1}(t;\,\boldsymbol{y}),\end{aligned}$$

where the fourth equality is based on (3.4). It now easily follows that $\tilde{S}(t;\,\boldsymbol{y}) = S(t;\,\boldsymbol{y})$, as, for example, $\tilde{S}(0;\,\boldsymbol{y}) = S(0;\,\boldsymbol{y}) = 1$.

In analogy with the occupancy time density u, we let the function u^{C_1} denote the conditional density for the mean time that an individual located initially in $\boldsymbol{y}\in\Omega$ spends at a point $\boldsymbol{x}$ before it hits C_1, conditioned on it eventually hitting C_1 before it hits C_2 or dies.

Definition 3.12. (*Conditional occupancy time density.*) We denote by $u^{C_1} = u^{C_1}(\boldsymbol{x};\,\boldsymbol{y})$ the time integral of the function v^{C_1}, defined by

$$u^{C_1}(\boldsymbol{x};\,\boldsymbol{y}) = \int_0^\infty v^{C_1}(\boldsymbol{x},t;\,\boldsymbol{y})\,\mathrm{d}t.$$

It is clear that u^{C_1} is given by

$$u^{C_1}(\boldsymbol{x};\,\boldsymbol{y}) = u(\boldsymbol{x};\,\boldsymbol{y})\frac{p^{C_1}(\boldsymbol{x})}{p^{C_1}(\boldsymbol{y})}.$$

Definition 3.13. (*Conditional occupancy time.*) We denote by $T_X^{C_1} = T_X^{C_1}(\boldsymbol{y})$ the mean time that an individual located initially at $\boldsymbol{y}\in\Omega$ spends in area X before it hits C_1 if it is given that it will hit C_1 before it hits C_2 or dies. Thus, $T_X^{C_1}$ is defined by

$$T_X^{C_1}(\boldsymbol{y}) = \int_X u^{C_1}(\boldsymbol{x};\,\boldsymbol{y})\,\mathrm{d}\boldsymbol{x}.$$

Theorem 3.3. *The conditional occupancy time $T_X^{C_1}(\boldsymbol{x})$ is given by*

$$T_X^{C_1}(\boldsymbol{y}) = \frac{G_X^{C_1}(\boldsymbol{y})}{p^{C_1}(\boldsymbol{y})},$$

where $G_X^{C_1}$ is the solution to the following problem: find a $G_X \in \mathcal{A}^*(\Omega)$ that satisfies the equation

$$\mathcal{L}^*G_X(\boldsymbol{x}) = \begin{cases} -p^{C_1}(\boldsymbol{x}) & \text{for } x\in X,\\ 0 & \text{for } x\in\Omega\setminus X,\end{cases}$$

and the boundary condition $\mathcal{B}^*$.

Proof. Assume that $G_X^{C_1}(x)$ is the function defined in the theorem. Multiplying both sides of (3.6) by $G_X^{C_1}(x)$, integrating x over Ω and applying (3.4) gives

$$G_X^{C_1}(\boldsymbol{y}) = \int_X p^{C_1}(\boldsymbol{x})u(\boldsymbol{x};\, \boldsymbol{y})\, \mathrm{d}\boldsymbol{x} = p^{C_1}(\boldsymbol{y}) \int_X u^{C_1}(\boldsymbol{x};\, \boldsymbol{y})\, \mathrm{d}\boldsymbol{x}.$$

In analogy with Lemma 3.1, we note that

$$G^{C_1}(\boldsymbol{y}) = \int_0^\infty t F^{C_1}(t;\, \boldsymbol{y})\, \mathrm{d}t,$$

where $G^{C_1}(\boldsymbol{y}) = G_\Omega^{C_1}(\boldsymbol{y})$.

4. Examples

We will illustrate the results of Sections 2 and 3 with three examples.

4.1. A one-dimensional example

We start by illustrating the boundary condition derived for Case A in Section 2.1 with a simple numerical example (Case B would behave similarly). We assume that $1 < x < 2$ represents a habitat patch which the individuals prefer, and that the rest of the x-axis consists of dispersal habitat. We assume that the strength of the bias at the boundary is $z = 0.8$, and that the individuals have the same mortality and movement parameters in the habitat patch and in the dispersal habitat. Figure 2 illustrates the quantities p^C, u, u^C, T and T^C, both according to simulations of the discrete process and according to the analytical solution to the diffusion approximation.

4.2. A circle

We continue with a two-dimensional example, which will be used as a prerequisite for the more comprehensive example of the next subsection. We assume that a disc $\Omega_\mathrm{h} \subset \mathbb{R}^2$ of radius r is centred at the origin. We call the disc the habitat patch, and the area Ω_d outside the disc the dispersal habitat. We denote the boundary between the habitat patch and the dispersal habitat by Γ. We assume that the operator $\mathcal{L}$ is given by $\mathcal{L}u(\boldsymbol{x}) = \Delta[a(\boldsymbol{x})u(\boldsymbol{x})] - c(\boldsymbol{x})u(\boldsymbol{x})$, where $a(\boldsymbol{x}) = a_\mathrm{h}$ and $c(\boldsymbol{x}) = c_\mathrm{h} > 0$ in Ω_h and $a(\boldsymbol{x}) = a_\mathrm{d}$ and $c(\boldsymbol{x}) = c_\mathrm{d} > 0$ in Ω_d. We assume that the discontinuity of the probability density v across Γ is quantified by functions $k_\mathrm{h}(\boldsymbol{x}) = k_\mathrm{h} > 0$ and $k_\mathrm{d}(\boldsymbol{x}) = k_\mathrm{d} > 0$, which are assumed to be constants within Γ. We let Γ^s denote a circle of radius $r + s$ (with $s > 0$) centred at the origin. We denote by I_ν and K_ν modified Bessel functions of the first and the second kind respectively [1]. Using the techniques of Section 3, it is straightforward to derive the following results (see Appendix C).

1. Assume that an individual is initially on Γ^s. Then the probability $P_1(r, s)$ that the individual will hit Γ before it dies is given by

$$P_1(r, s) = \frac{K_0(\alpha_\mathrm{d}(r + s))}{K_0(\alpha_\mathrm{d} r)} = 1 - s p_1(r) + \mathcal{O}(s^2), \tag{4.1}$$

where

$$\alpha_\mathrm{d} = \sqrt{\frac{c_\mathrm{d}}{a_\mathrm{d}}} \quad \text{and} \quad p_1(r) = \frac{\alpha_\mathrm{d} K_1(\alpha_\mathrm{d} r)}{K_0(\alpha_\mathrm{d} r)}.$$

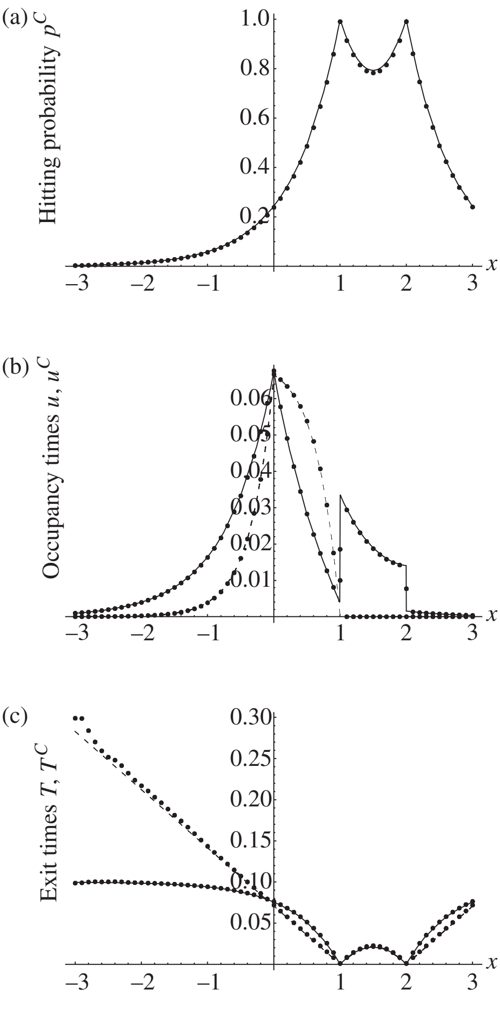

FIGURE 2: An illustration of boundary conditions derived for Case A in Section 2.1. The region $1 < x < 2$ represents a habitat patch with boundary $C = \{1, 2\}$. The individuals are assumed to prefer the patch as expressed by the bias $z = 0.8$ at the boundary. The dots refer to simulation results, which are based on simple bookkeeping of movements of 10^6 individuals that were initiated at $y = 0$, $y = 1.5$ and $y = 2.5$ and simulated until death occurred. The lines refer to analytical results based on the diffusion approximation derived in Section 2.1 and its elaborations derived in Section 3. Panel (a) depicts $p^C(x)$, the probability of hitting the boundary of the patch. Panel (b) depicts $u(x; 0)$, the occupancy time density for an individual starting at $y = 0$ (continuous line), and $u^C(x; 0)$, the conditional occupancy time density for an individual starting at $y = 0$ (dashed line). Panel (c) depicts $T(x)$, the mean exit time (continuous line), and $T^C(x)$, the conditional mean exit time (dashed line). The parameters $c = 10$, $\lambda = \frac{1}{10}$ and $\tau = 10^{-3}$ are assumed to be the same for the habitat patch and for the dispersal habitat.

2. Assume that an individual is initially on Γ. Then the probability $P_2(r, s)$ that it will hit Γ^s before it dies is given by

$$P_2(r, s) = \left[\alpha_d r\left(\beta_1 + \frac{\delta_h I_1(\alpha_h r)\beta_2}{\delta_d I_0(\alpha_h r)}\right)\right]^{-1} = 1 - sp_2(r) + O(s^2), \tag{4.2}$$

where

$$\beta_1 = I_1(\alpha_d r)K_0(\alpha_d(r+s)) + I_0(\alpha_d(r+s))K_1(\alpha_d r),$$
$$\beta_2 = I_0(\alpha_d(r+s))K_0(\alpha_d r) - I_0(\alpha_d r)K_0(\alpha_d(r+s)),$$
$$\alpha_h = \sqrt{\frac{c_h}{a_h}}, \qquad \delta_h = k_h\alpha_h a_h, \qquad \delta_d = k_d\alpha_d a_d,$$

and

$$p_2(r) = \frac{\delta_h I_1(\alpha_h r)}{a_d k_d I_0(\alpha_h r)}.$$

3. Assume that an individual is initially on Γ. Then the mean time $T_1(r, s)$ that the individual is expected to spend in the habitat patch before it hits Γ^s or dies is given by

$$T_1(r, s) = \left[c_h\left(1 + \frac{\delta_d I_0(\alpha_h r)\beta_1}{\delta_h I_1(\alpha_h r)\beta_2}\right)\right]^{-1} = st_1(r) + O(s^2), \tag{4.3}$$

where

$$t_1(r) = \frac{k_h I_1(\alpha_h r)}{k_d a_d \alpha_h I_0(\alpha_h r)}.$$

4. Assume that an individual is initially on Γ. Then the mean time $T_2(r, s)$ that the individual is expected to spend in the habitat patch before it hits Γ^s if it is given that it will hit Γ^s before it dies is given by

$$T_2(r, s) = \frac{\delta_h\alpha_h r[I_0^2(\alpha_h r) - I_1^2(\alpha_h r)]}{2c_h I_0(\alpha_h r)[\delta_h I_1(\alpha_h r) + \delta_d I_0(\alpha_h r)(\beta_1/\beta_2)]} = st_2(r) + O(s^2), \tag{4.4}$$

where

$$t_2(r) = \frac{k_h r}{2a_d k_d}\left[1 - \frac{I_1^2(\alpha_h r)}{I_0^2(\alpha_h r)}\right].$$

5. Assume that an individual is initially on Γ. Then the mean time $T_3(r, s)$ that the individual is expected to spend in the habitat patch before it hits Γ^s if it is given that it will die before it hits Γ^s, is given by

$$T_3(r, s) = \frac{T_1(r, s) - P_2(r, s)T_2(r, s)}{1 - P_2(r, s)} = t_3(r) + O(s),$$

where

$$t_3(r) = \frac{1}{c_h}\left\{1 - \frac{\alpha_h r[I_0^2(\alpha_h r) - I_1^2(\alpha_h r)]}{2I_0(\alpha_h r)I_1(\alpha_h r)}\right\}.$$

Note that, for $s \to 0$, any path that returns from Ω_h to Γ will hit Γ^s almost surely. This means that the condition that the individual dies before hitting Γ^s is synonymous with the

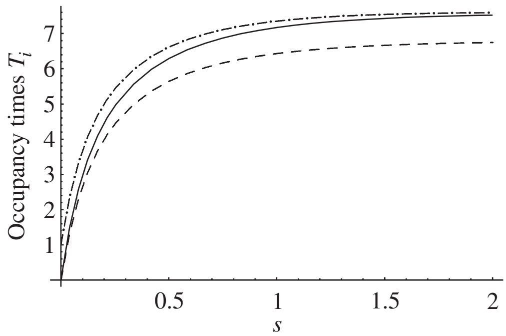

FIGURE 3: A comparison of the occupancy time T_1 (continuous line) with the conditional occupancy times T_2 (dashed line) and T_3 (dot-dashed line). The parameter values are $a_\mathrm{h} = a_\mathrm{d} = c_\mathrm{h} = c_\mathrm{d} = \frac{1}{10}$, $k_\mathrm{d} = 1$, $k_\mathrm{h} = 10$ and $r = 1$.

individual never leaving Ω_h, which is reflected by the fact that $\lim_{s\to 0} T_3(r, s)$ is independent of the properties of Ω_d. Figure 3 illustrates how the quantities T_1, T_2 and T_3 differ from each other.

4.3. A highly fragmented landscape

We will finally consider the problem of 'a highly fragmented landscape', which gave the original motivation for this paper. We assume that the plane $\mathbb{R}^2$ contains a finite number n of disjoint habitat patches Ω_i $(i = 1, \dots, n)$ surrounded by dispersal habitat $\Omega_\mathrm{d} = \mathbb{R}^2 \backslash \bigcup_i \Omega_i$. The notion of a 'highly fragmented landscape' comes from the assumption that the habitat patches are small. Due to habitat loss and habitat fragmentation, such landscapes are increasingly relevant in biological applications [5]. For technical simplicity, we assume here that the habitat patches Ω_i are discs with radii $r_i = \varepsilon R_i$, where the R_i are fixed and $0 < \varepsilon < 1$, and we will be concerned with the limit $\varepsilon \to 0$. The centroid-to-centroid distance between patches i and j is denoted by d_{ij}, and the boundary of patch i is denoted by Γ_i. Utilizing the asymptotic results derived in the previous section, we will solve the following three problems.

1. What is the probability P_{ij} that an individual initially on Γ_i will hit Γ_j before it dies and before it hits Γ_k with $k \neq i, j$? We will use the convention $P_{ii} = 0$, so that the probability that the individual will die before hitting any of the Γ_j for $j \neq i$ is $\mu_i = 1 - \Sigma_j P_{ij}$. We note that the above definition for the probability P_{ij} is not well posed, as the individual's location within Γ_i may have an effect. However, as $\varepsilon \to 0$, the inconsistency disappears, and our results (which will contain an error term of order $\mathcal{O}(\varepsilon)$) will hold for any initial location.

2. What is the mean time F_j that an individual initially on Γ_j will spend in the patch Ω_j before it dies or hits any of the other patches?

3. What is the mean time T_{ij} that an individual initially on Γ_i will spend in patch Ω_j before it dies?

The first hitting probabilities P_{ij} are relevant, for example, for species which disperse as juveniles from their natal habitat patch and search for a new patch to colonize. The mean times F_j and T_{ij} are relevant, for example, for species which may leave propagules in several patches, if it is assumed that the expected number of propagules left in a patch is proportional to the time spent in the patch.

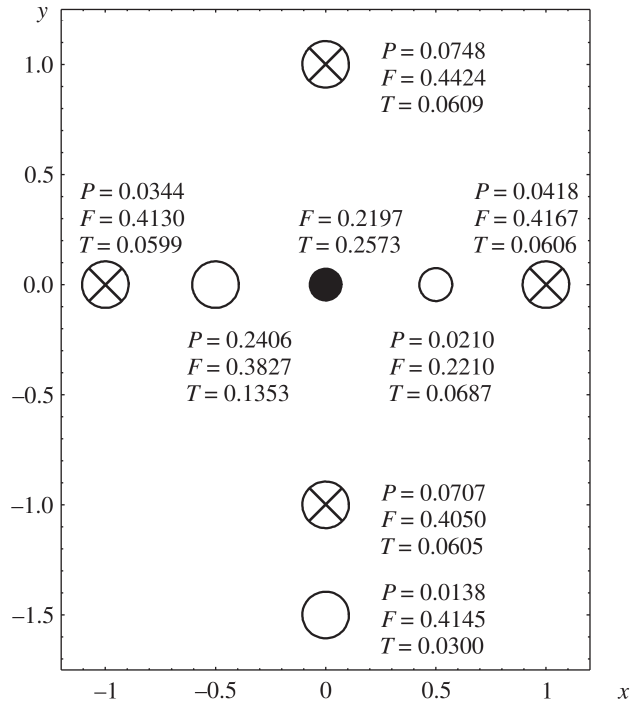

FIGURE 4: An illustration of the quantities $P = P_{ij}$, $F = F_j$ and $T = T_{ij}$ in a hypothetical network of habitat patches. The spatial scale may be considered to be kilometers, and the sizes of the patches are 1 hectare (the six large patches) or 0.5 hectares (the two small patches). The sizes of the discs have been enlarged in the figure. Parameter values as in Figure 3.

In order to derive P_{ij}, we denote by $\boldsymbol{Z}$ the matrix with entries

$$Z_{ij} = \frac{K_0(\alpha_{\mathrm{d}} d_{ij})}{K_0(\alpha_{\mathrm{d}} r_j)}$$

for $i \neq j$ and $Z_{ii} = 1$. We let $\boldsymbol{D}(p_1)$ denote the diagonal matrix with entries $D(p_1)_{ii} = p_1(r_i)$, and we let $\boldsymbol{S} = \boldsymbol{D}(p_1)\boldsymbol{Z}^{-1}$. As shown in Appendix D,

$$P_{ij} = \frac{-S_{ij}}{S_{ii} + p_2(r_i)}[1 + \mathcal{O}(\varepsilon)]. \tag{4.5}$$

In order to derive the mean times F_j and T_{ij}, we let $\boldsymbol{X} = \boldsymbol{S} + \boldsymbol{D}(p_2)$, where $\boldsymbol{D}(p_2)$ is a diagonal matrix with entries $D(p_2)_{ii} = p_2(r_i)$, and we let $\boldsymbol{D}(t_1)$ denote a diagonal matrix with entries $D(t_1)_{ii} = t_1(r_i)$. As shown in Appendix D,

$$F_j = \frac{t_1(r_j)}{X_{jj}}[1 + \mathcal{O}(\varepsilon)], \tag{4.6}$$

$$\boldsymbol{T} = \boldsymbol{X}^{-1}\boldsymbol{D}(t_1)[1 + \mathcal{O}(\varepsilon)]. \tag{4.7}$$

Figure 4 illustrates the quantities P_{ij}, F_j and T_{ij} in a hypothetical network of habitat patches, where both the parameter values and the properties of the landscape have been chosen to correspond roughly with some butterfly metapopulations [5]. We show the first hitting probabilities and the mean times spent in the habitat patches, assuming that an individual is initially in the black patch (patch i). The four patches marked with crosses are identical with respect to their size and distance from the filled patch, and thus the differences in their P, F and T values are solely due to fact that the other habitat patches are in a sense competing for the migrating individual.

5. Discussion

We have derived boundary conditions for the diffusion approximation of a random walk with preference in movement direction at a single point, and for a random walk with biased movement in a narrow boundary region. The boundary conditions (Sections 2.1 and 2.2) imply that the probability density of an individual's location is expected to be discontinuous across the boundary. The present result is contrary to the results of earlier analyses [3], [4], which have used the boundary conditions

$$\alpha a_+ \partial_x v(0+, t) = (1 - \alpha) a_- \partial_x v(0-, t), \tag{5.1}$$

$$a_+ \partial_{xx} v(0+, t) + c_+ v(0+, t) = a_- \partial v_{xx}(0-, t) + c_- v(0-, t), \tag{5.2}$$

where the parameter α quantifies the bias at the boundary. These conditions follow from skew Brownian motion, which is obtained as a limit of a random walk in a one-dimensional lattice where at one point there is a directional bias in the probability of reversing directions. The condition (5.1) represents a discontinuous flux, which implies that individuals accumulate at or emanate from the boundary.

We expect that the present result should find a number of constructive applications in studies attempting to quantify movement in landscapes consisting of mosaics of patches of different habitat types. For example, diffusion approximations of random walks with appropriate boundary conditions at patch boundaries would provide a natural framework for analysing mark-recapture studies conducted in heterogeneous landscapes. So far, such studies have been analysed using more phenomenological models without reference to mechanistic assumptions about movement behaviour [6], [11].

Appendix A. Derivation relating to bias at a single point

As illustrated in Figure 5, we shorten the notation by writing $v_{\pm i}(t) = v(\pm\lambda_\pm i, t)$ for the probability density of the individual's location. The length of the interval around v_0 is denoted by $\lambda_0 = k_0\lambda$.

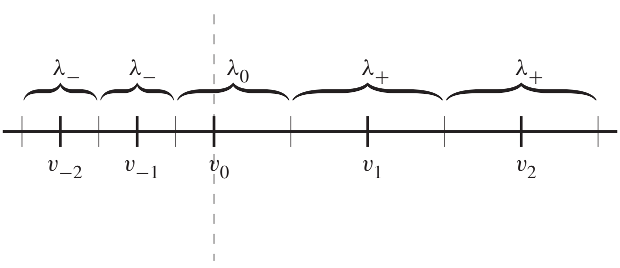

FIGURE 5: An illustration of the one-dimensional grid.

A.1. Case A

The mechanistic description of the random walk gives the following equations for the time evolution of the probability density v around the origin:

$$\lambda_- v_{-1}(t+\tau) = \frac{(1+c_-\tau)[\lambda_- v_{-2}(t) + (1-z)\lambda_0 v_0(t)]}{2}, \tag{A.1}$$

$$\lambda_0 v_0(t+\tau) = \frac{[(1+c_-\tau)\lambda_- v_{-1}(t) + (1+c_+\tau)\lambda_+ v_1(t)]}{2}, \tag{A.2}$$

$$\lambda_+ v_1(t+\tau) = \frac{(1+c_+\tau)[(1+z)\lambda_0 v_0(t) + \lambda_+ v_2(t)]}{2}. \tag{A.3}$$

We assume that the function $v(x,t)$ may be approximated by a first-order Taylor series at both sides of the boundary. In this case, we have

$$v_{-1}(t+\tau) = v_{-1}(t) + \tau\partial_t v(-\lambda_-, t) + \mathcal{O}(\tau^2), \tag{A.4}$$

$$v_1(t+\tau) = v_1(t) + \tau\partial_t v(\lambda_+, t) + \mathcal{O}(\tau^2), \tag{A.5}$$

$$v_{-2}(t) = v_{-1}(t) - \lambda_-\partial_x v(-\lambda_-, t) + \mathcal{O}(\lambda^2), \tag{A.6}$$

$$v_2(t) = v_1(t) + \lambda_+\partial_x v(\lambda_+, t) + \mathcal{O}(\lambda^2). \tag{A.7}$$

In order to derive the boundary condition (2.1), we start by noting that (A.1), (A.3), (A.6) and (A.7) give

$$\begin{aligned} &q_+(1-z)v_1(t+\tau) - q_-(1+z)v_{-1}(t+\tau) \\ &\quad = \frac{q_+(1-z)v_1(t) - q_-(1+z)v_{-1}(t)}{2} + \mathcal{O}(\tau+\lambda). \end{aligned} \tag{A.8}$$

On the other hand, by (A.4) and (A.5),

$$\begin{aligned} &q_+(1-z)v_1(t+\tau) - q_-(1+z)v_{-1}(t+\tau) \\ &\quad = q_+(1-z)v_1(t) - q_-(1+z)v_{-1}(t) + \mathcal{O}(\tau). \end{aligned} \tag{A.9}$$

Combining (A.8) and (A.9), we obtain

$$q_+(1-z)v_1(t) - (1+z)q_- v_{-1}(t) = \mathcal{O}(\tau+\lambda),$$

Thus, assuming that $\tau \to 0$ and $\lambda \to 0$ (without assumptions about the way this happens), we obtain the condition (2.1).

In order to derive the boundary condition (2.2), we note that, by (A.1) and (A.3),

$$v_{-2}(t) - v_{-1}(t) = v_{-1}(t) - (1-z)\frac{q_0}{q_-}v_0(t) + \mathcal{O}(\tau), \tag{A.10}$$

$$v_2(t) - v_1(t) = v_1(t) - (1+z)\frac{q_0}{q_+}v_0(t) + \mathcal{O}(\tau). \tag{A.11}$$

Thus,

$$\begin{aligned} aq_+^2\partial_x v(\lambda_+, t) - aq_-^2\partial_x v(-\lambda_-, t) &= aq_+\frac{v_2(t) - v_1(t)}{\lambda} + aq_-\frac{v_{-2}(t) - v_{-1}(t)}{\lambda} + \mathcal{O}(\lambda) \\ &= a\frac{q_+v_1 + q_-v_{-1} - 2q_0v_0}{\lambda} + \mathcal{O}\Big(\frac{\tau}{\lambda} + \lambda\Big) \\ &= \mathcal{O}\Big(\frac{\tau}{\lambda} + \lambda\Big). \end{aligned}$$

In the above derivation, the first equality is based on (A.6) and (A.7), the second equality is based on (A.11) and (A.10), and the third equality is based on (A.2). Assuming that $\lambda, \tau \to 0$ in such a way that $\tau = \mathcal{O}(\lambda^2)$, we obtain the condition (2.2).

A.2. Case B

In this case, the mechanistic rules give the following equations for the time evolution of the probability density v:

$$\lambda_0 v_0(t + \mathrm{d}t) = [1 - (p_0 - c_0)\,\mathrm{d}t]\lambda_0 v_0(t) + \frac{p_- \lambda_- v_{-1}(t) + p_+ \lambda_+ v_1(t)}{2}\,\mathrm{d}t.$$

Writing similar equations for v_1 and v_{-1} and rearranging leads to the equations

$$\begin{aligned}
\lambda_- \partial_t v_{-1}(t) &= -\lambda_-(p_- - c_-)v_{-1}(t) + \frac{[p_- \lambda_- v_{-2}(t) + (1 - z)p_0 \lambda_0 v_0(t)]}{2},\\
\lambda_0 \partial_t v_0(t) &= -\lambda_0(p_0 - c_0)v_0(t) + \frac{[p_- \lambda_- v_{-1}(t) + p_+ \lambda_+ v_1(t)]}{2},\\
\lambda_+ \partial_t v_1(t) &= -\lambda_+(p_+ - c_+)v_1(t) + \frac{[p_+ \lambda_+ v_2(t) + (1 + z)p_0 \lambda_0 v_0(t)]}{2}.
\end{aligned}$$

The boundary conditions follow as in Case A.

Appendix B. Derivation relating to bias in a boundary region

Starting from the model defined in Section 2.2, the probability $P(x, t+\mathrm{d}t)$ that the individual is at position x at time $t + \mathrm{d}t$ satisfies

$$\begin{aligned}
P(x, t + \mathrm{d}t) = (1 - p(x)\,\mathrm{d}t)P(x, t) &+ \tfrac{1}{2}p(x - \lambda)(1 + z(x - \lambda))P(x - \lambda, t)\\
&+ \tfrac{1}{2}p(x + \lambda)(1 - z(x + \lambda))P(x + \lambda, t).
\end{aligned}$$

Performing a Taylor expansion in time, the probability density of the individual's location $v(x, t) = P(x, t)/\lambda$ satisfies

$$\partial_t v(x, t) = J(x, t) - J(x + \lambda, t), \tag{B.1}$$

where

$$J(x) = \tfrac{1}{2}p(x - \lambda)(1 + z(x - \lambda))v(x - \lambda, t) - \tfrac{1}{2}p(x)(1 - z(x))v(x, t).$$

For $|x| > \varepsilon$, $z(x) = 0$ and $p(x) = p_\pm$, and (2.3) follow in the usual way [13].

B.1. Continuum limit

Assuming that p and z vary slowly, we can perform a Taylor expansion of J in (B.1) to give

$$\partial_t v(x, t) = \lambda^2 \partial_{xx}(p(x)v(x, t)) - \lambda \partial_x(p(x)z(x)v(x, t)) + O(\lambda^4 p + \lambda^3 pz).$$

Letting now $\lambda \to 0$, $1/p \to 0$, $1/z \to 0$ in such a way that $\lambda^2 p \to 2a(x)$, $\lambda pz \to b(x)$, we obtain (2.4).

Integrating (2.4) over x yields

$$\int_{x_1}^{x_2} \partial_t v(x', t)\,\mathrm{d}x' = \partial_x w(x_2) - \partial_x w(x_1, t) - b(x_2)v(x_2, t) + b(x_1)v(x_1, t), \qquad \text{(B.2)}$$

where $w(x) = a(x)v(x)$. Setting $x_1 = -\delta = -x_2$, where $\varepsilon < \delta < 1$ so that $b(\pm\delta) = 0$, we find that

$$\partial_x w(-\delta) - \partial_x w(\delta) = a_- \partial_x v(-\delta) - a_+ \partial_x v(\delta) = O(\delta).$$

Taking $\varepsilon \to 0$, $\delta \to 0$ leads to (2.6).

Setting $x_1 = 0$, writing $C = b(0)v(0, t) - \partial_x w(0, t)$, multiplying (B.2) by the integrating factor

$$I(x) = \exp\biggl(-\int_0^{x_2} \frac{b(x')}{a(x')}\,\mathrm{d}x'\biggr)$$

and integrating leads to

$$\int_0^x \int_0^{x'} I(x')\partial_t v(x'', t)\,\mathrm{d}x''\,\mathrm{d}x' = I(x)w(x, t) - w(0, t) + C\int_0^x I(x')\,\mathrm{d}x'. \qquad \text{(B.3)}$$

We now set $x = \pm\delta$, with $\varepsilon < \delta < 1$, and note that the left-hand side of (B.3) is $O(\delta^2)$, and the integral on the right-hand side of (B.3) is $O(\delta)$. Rearranging,

$$w(\pm\delta) = (w(0, t) + O(\delta))\exp\biggl(\int_0^{\pm\delta} \frac{\tilde{b}(y)}{\tilde{a}(y)}\,\mathrm{d}y\biggr),$$

Taking $\varepsilon \to 0$ and then $\delta \to 0$ as before, we obtain the discontinuity boundary condition (2.5).

B.2. General case

Summing (B.1) from $x = -\delta$ to $x = x_1 - \lambda$, where $\delta > \varepsilon$, gives

$$J(-\delta) - J(x_1) = \sum_{x=-\delta, -\delta+\lambda, \ldots}^{x_1-\lambda} \partial_t v(x, t). \qquad \text{(B.4)}$$

First set $x_1 = \delta$ and $\delta > \varepsilon$. We express J in terms of v and perform a Taylor expansion, to give $J(\pm\delta) = \lambda p_\pm \partial_x v(x, t)|_{x=\pm\delta} + O(\lambda^2 p)$. As there are $2(\delta/\lambda)$ terms in the sum on the right-hand side of (B.4), the sum is $O(\delta/\lambda)$. We multiply (B.4) by λ and let $\lambda \to 0$, to get $a_- v(-\delta, t) - a_+ v(\delta, t) = O(\delta)$, leading to (2.6) when $\delta \to 0$.

Rewriting J in terms of v in (B.4),

$$\begin{aligned}&\tfrac{1}{2}p(x_1)(1 + z(x_1))v(x_1, t) - \tfrac{1}{2}p(x_1 + \lambda)(1 - z(x_1 + \lambda))v(x_1 + \lambda, t)\\ &\quad = J(-\delta, t) - \sum_{x'=-\delta, -\delta+\lambda, \ldots}^{x_1} \partial_t v(x', t).\end{aligned}$$

Multiplying by $Z(x_1) = \prod_{x'=-\delta}^{x_1}(1 - z(x'))/(1 + z(x'))$ and summing up to $x_1 = \delta - \lambda$,

$$p(-\delta)v(-\delta, t) - p(\delta)v(\delta, t)Z(\delta) = 2\sum_{x'=-\delta}^{\delta-\lambda} Z(x')\biggl\{J(-\delta, t) - \sum_{x''=0}^{x'} \partial_t v(x'', t)\biggr\}.$$

We multiply by λ^2 and consider the dominant behaviour of J and $\sum_x v$ to get

$$a_- v(-\delta, t) - Z(\delta) a_+ v(\delta t) = \sum_{x'=-\delta}^{\delta-\lambda} Z(x') O(\lambda + \lambda^2 \delta). \tag{B.5}$$

Since $Z(x) = \exp \sum_{x'=-\delta}^{x} \log[(1-z)/(1+z)]$ and the sum contains $(x+\delta)/\lambda$ terms, it is possible for $Z(x)$ to diverge or vanish when $\lambda \to 0$. Assuming first that $\lim_{\lambda\to 0} Z(\delta)$ is finite and nonzero, we see that the right-hand side of (B.5) is $O(\delta + \delta^2/\lambda)$, so in the limit $\lambda \to 0$ followed by $\delta \to 0$ we obtain the discontinuity boundary condition (2.7). Alternatively, if $Z \to \infty$ or $Z \to 0$ as $\lambda \to 0$, (B.5) suggests that $v(0^+) \to 0$ and $v(0^-) \to 0$ respectively, and we note that (2.7) is correct for these limits too.

Appendix C. Derivations relating to the circle

Since the system has circular symmetry, the Laplacian may be written in the form

$$\nabla^2 = \frac{1}{x} \frac{\mathrm{d}}{\mathrm{d}x} \left(x \frac{\mathrm{d}}{\mathrm{d}x} \right),$$

where x is the distance from the centre of the circle. The quantities in Section 4.2 are all obtained by solving an equation of the form

$$a_i \frac{\mathrm{d}^2}{\mathrm{d}x^2} F^{(j)}(x) + \frac{a_i}{x} \frac{\mathrm{d}}{\mathrm{d}x} F^{(j)}(x) - c_i F^{(j)}(x) + c_i G_i^{(j)}(x) = 0, \tag{C.1}$$

where $i = h$ for $0 \le x < r$, $i = d$ for $x > r$ and the superscript (j) denotes the particular quantity under consideration. The general solution to (C.1), subject to $F^{(j)}(0)$ being finite, may be written in the form

$$F^{(j)} = \begin{cases} I_0(\alpha_\mathrm{h} x)\{A^{(j)} + L_\mathrm{h}^{(j)}(x, r)\} + K_0(\alpha_\mathrm{h} x) M_\mathrm{h}^{(j)}(0, x) & \text{for } 0 \le x < r, \\ I_0(\alpha_\mathrm{d} x)\{B^{(j)} + L_\mathrm{d}^{(j)}(x, \infty)\} + K_0(\alpha_\mathrm{d} x)\{C^{(j)} + M_\mathrm{d}^{(j)}(r, x)\} & \text{for } x > r, \end{cases}$$

where $A^{(j)}$, $B^{(j)}$ and $C^{(j)}$ are constants, $\alpha_i = \sqrt{c_i/a_i}$, I_ν and K_ν are modified Bessel functions of the first and second kind respectively (see [11, Section 9.6—in particular, 9.6.14, 9.6.27, and 11.3.31]), and

$$L_i^{(j)}(x_1, x_2) = \int_{x_1}^{x_2} y K_0(\alpha_i y) G_i^{(j)}(y)\, \mathrm{d}y,$$
$$M_i^{(j)}(x_1, x_2) = \int_{x_1}^{x_2} y I_0(\alpha_i y) G_i^{(j)}(y)\, \mathrm{d}y.$$

The quantity $P_1(r, a) = F^{(1)}(r + s)$ in (4.1) is obtained from $G_\mathrm{h}^{(1)} = G_\mathrm{d}^{(1)} = 0$, and applying the boundary conditions $F^{(1)}(r) = 1$, $\lim_{x\to\infty} F^{(1)}(x) = 0$, whence $B^{(1)} = 0$, $C^{(1)} = 1/K_0(\alpha_\mathrm{d} r)$. The other quantities in Section 4.2 are obtained by considering $x < r + s$ only, and choosing $A^{(j)}$, $B^{(j)}$ and $C^{(j)}$ such that $F^{(j)}$ satisfies the boundary conditions

$$\lim_{x\to r^-} F^{(j)}(x) = \lim_{x\to r^+} F^{(j)}(x),$$
$$k_\mathrm{h} a_\mathrm{h} \lim_{x\to r^-} \frac{\mathrm{d}}{\mathrm{d}x} F^{(j)}(x) = k_\mathrm{d} a_\mathrm{d} \lim_{x\to r^+} \frac{\mathrm{d}}{\mathrm{d}x} F^{(j)}(x),$$
$$F^{(j)}(r + s) = f^{(j)},$$

that is, the constants satisfy the following linear system of equations:

$$A^{(j)}I_0(\alpha_\mathrm{h}r) + K_0(\alpha_\mathrm{h}r)M_\mathrm{h}^{(j)}(0,r) = B^{(j)}I_0(\alpha_\mathrm{d}r)B + C^{(j)}K_0(\alpha_\mathrm{d}r),$$
$$\alpha_\mathrm{h}k_\mathrm{h}a_\mathrm{h}[A^{(j)}I_1(\alpha_\mathrm{h}r) - K_1(\alpha_\mathrm{h}r)M_\mathrm{h}^{(j)}(0,r)] = \alpha_\mathrm{d}k_\mathrm{d}a_\mathrm{d}[B^{(j)}I_1(\alpha_\mathrm{d}r) - C^{(j)}K_1(\alpha_\mathrm{d}r)],$$
$$f^{(j)} = B^{(j)}I_0(\alpha_\mathrm{d}(r+s)) + C^{(j)}K_0(\alpha_\mathrm{d}(r+s)),$$

where for simplicity we have assumed that $G_\mathrm{d}^{(j)} = 0$, which is the case for the examples considered here.

Using the results in Section 3, the specific values of $G_i^{(j)}$ and $f^{(j)}$ are:

$$G_\mathrm{d}^{(2)} = G_\mathrm{h}^{(2)} = 0, \qquad f^{(2)} = 1,$$

Equation (4.2) is obtained with $P_2(r,s) = F^{(2)}(r)$;

$$G_\mathrm{h}^{(3)}(x) = \frac{1}{c_\mathrm{h}}, \qquad G_\mathrm{d}^{(3)} = 0, \qquad f^{(3)} = 0,$$

Equation (4.3) is obtained with $T_1(r,s) = F^{(3)}(r)$;

$$G_\mathrm{h}^{(4)}(x) = \frac{F^{(2)}(x)}{c_\mathrm{h}}, \qquad G_\mathrm{d}^{(4)}(x) = 0, \qquad f^{(4)} = 0,$$

Equation (4.4) is obtained with $T_2(r,s) = F^{(4)}(r)/F^{(2)}(r)$.

Appendix D. Derivations relating to the highly fragmented landscape

D.1. Derivation of (4.5)

In order to derive the probability P_{ij}, we first draw a circle Γ_i^s around each patch i, so that the distance between the patch boundary Γ_i and the circle Γ_i^s is $s > 0$. We will eventually consider the limit $s \to 0$, so we may assume that s is so small that the circles Γ_i^s are disjoint.

We start by deriving an expression for $P_{ij}(s)$, which is defined to be the probability that an individual initially on Γ_i^s will hit Γ_j before it dies or hits any other of the patch boundaries. As the probability $P_{ij}(s)$ does not depend on the diffusion parameters inside the habitat patches, we may assume for a moment that there is no difference between the habitat patches and the dispersal habitat, and thus the boundaries Γ_i are solely technical. We let $H_{ij}(s)$ denote the probability that an individual which is initially on Γ_i^s will hit Γ_j before it dies, but not necessarily before it hits any other habitat patches. From (4.1) we obtain $H_{ii}(s) = 1 - sD(p_1)_{ii} + \mathcal{O}(s^2)$ and $H_{ij}(s) = Z_{ij}[1 + \mathcal{O}(s+\varepsilon)]$, where the error term $\mathcal{O}(s+\varepsilon)$ for $i \neq j$ is due to the fact that the individual may be on Γ_i in any direction from patch i. We let $\tilde{E}_i(s)$ be the probability that the individual on Γ_i will hit Γ_i^s before it dies. By (4.2) and the assumption that the patch is indistinguishable from dispersal habitat, $\tilde{E}_i(s)$ is given by $\tilde{E}_i(s) = 1 + \mathcal{O}(s\varepsilon) + \mathcal{O}(s^2)$. Next, we let $\boldsymbol{Z}(s)$ denote the matrix with entries $Z_{ij}(s) = \tilde{E}_i(s)H_{ij}(s)$ for $j \neq i$ and $Z_{ii}(s) = 1$. Then

$$\boldsymbol{H}(s) = \boldsymbol{P}(s)\boldsymbol{Z}(s) \tag{D.1}$$

and thus $\boldsymbol{P}(s) = \boldsymbol{H}(s)\boldsymbol{Z}^{-1}(s)$. To illustrate, we write the $(1, 2)$th entry of (D.1) as

$$H_{12}(s) = P_{11}(s)\tilde{E}_1(s)H_{12}(s) + P_{12}(s) + \cdots + P_{1n}(s)\tilde{E}_n(s)H_{n2}(s). \tag{D.2}$$

The left-hand side of (D.2) gives the probability that an individual on Γ_1^s will hit Γ_2 before it dies. For example, the last term in the right-hand side of (D.2) is the probability that an individual on Γ_1^s will hit Γ_n before it dies or hits any other patches, multiplied by the probability that the individual on Γ_n will hit Γ_n^s before it dies and by the probability that the individual on Γ_n^s will hit Γ_2 before it dies. As $\boldsymbol{H}(s) = (\boldsymbol{Z}(s) - s\boldsymbol{D}(p_1))[1 + \mathcal{O}(s\varepsilon + s^2)]$ and $\boldsymbol{Z}(s) = \boldsymbol{Z}[1 + \mathcal{O}(s\varepsilon + s^2)]$, it follows that $\boldsymbol{P}(s) = (\boldsymbol{I} - s\boldsymbol{S})[1 + \mathcal{O}(s\varepsilon + s^2)]$.

Finally, we retain the assumption that patches are different from dispersal habitat, and let $E_i(s)$ be the probability that an individual on Γ_i will hit Γ_i^s before it dies. By (4.2), $E_i(s)$ is given by $E_i(s) = (1 - p_2(r_i)s)[1 + \mathcal{O}(s^2)] = 1 + \mathcal{O}(s\varepsilon + s^2)$. As $P_{ij} = E_i(s)[P_{ij}(s) + P_{ii}(s)P_{ij}]$ and as $E_i(s)P_{ii}(s) = 1 - s(p_2(r_i) + S_{ii}) + \mathcal{O}(\varepsilon s + s^2)$, it follows that

$$P_{ij} = \lim_{s \to 0} \frac{E_i(s)P_{ij}(s)}{1 - E_i(s)P_{ii}(s)} = \frac{-S_{ij}}{S_{ii} + p_2(r_i)}[1 + \mathcal{O}(\varepsilon)].$$

D.2. Derivation of (4.6) and (4.7)

Assume that an individual is initially on Γ_i. The probability that the individual will die before it hits Γ_i^s is $1 - P_2(r_i, s)$. If it is known to die, then it will spend on average the time $T_3(r_i, s)$ in the patch before it dies. If it hits the boundary first, which happens with probability $P_2(r_i, s)$, then it will spend on average the time $T_2(r_i, s)$ in the patch before it hits Γ_i^s. If the individual is on Γ_i^s, it will hit Γ^i next with probability $P_{ij}(s)$ and die before hitting any of the patches with probability $1 - \Sigma_j P_{ij}(s)$. By the above reasoning,

$$T_{ij} = [1 - P_2(r_i, s)]\delta_{ij}T_3(r_i, s) + P_2(r_i, s)\left[\delta_{ij}T_2(r_i, s) + \sum_k P_{ik}(s)T_{kj}\right].$$

In matrix form, we have $\boldsymbol{T} = \boldsymbol{Y}(s) + \boldsymbol{X}(s)\boldsymbol{T}$, where $\boldsymbol{Y}(s)$ is a diagonal matrix with entries $Y_{ii}(s) = [1 - P_2(r_i, s)]T_3(r_i, s) + P_2(r_i, s)T_2(r_i, s) = T_1(r_i, s) = st_1(r_i) + \mathcal{O}(s^2)$, and the entries of the matrix $\boldsymbol{X}(s)$ are defined by $X_{ij}(s) = P_2(r_i, s)P_{ij}(s)$. As $\delta_{ij} - X_{ij}(s) = sX_{ij} + \mathcal{O}(s\varepsilon + s^2)$, it follows that $\boldsymbol{T} = \lim_{s\to 0}(\boldsymbol{I} - \boldsymbol{X}(s))^{-1}\boldsymbol{Y}(s) = \boldsymbol{X}^{-1}\boldsymbol{D}(t_1)[1 + \mathcal{O}(\varepsilon)]$. In order to derive (4.6), we note that

$$\begin{aligned} F_i &= [1 - P_2(r_i, s)]T_3(r_i, s) + P_2(r_i, s)[T_2(r_i, s) + P_{ii}(s)F_i] \\ &= T_1(r_i, s) + P_2(r_i, s)P_{ii}(s)F_i. \end{aligned}$$

Thus, $F_i = T_1(r_i, s)/(1 - P_2(r_i, s)P_{ii}(s))$, from which (4.6) follows by letting $s \to 0$.

Acknowledgements

We thank Benjamin Bolker, Chris Cosner, Ilkka Hanski and Hans Othmer for valuable comments. OO thanks the Academy of Finland (grant 50165 and the Finnish Centre of Excellence Programme (2000-2005), grant 44887) and the Royal Society for funding. OO is grateful to the Isaac Newton Institute for Mathematical Sciences, Cambridge, for financial support and intellectual stimulus during the programme 'From Individual to Collective Behaviour in Biological Systems'. SJC is grateful to the Wellcome Trust for financial support.

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