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Partial differential equation techniques for analysing animal movement: a comparison of different methods

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Abstract

Recent advances in animal tracking have allowed us to uncover the drivers of movement in unprecedented detail. This has enabled modellers to construct ever more realistic models of animal movement, which aid in uncovering detailed patterns of space use in animal populations. Partial differential equations (PDEs) provide a popular tool for mathematically analysing such models. However, their construction often relies on simplifying assumptions which may greatly affect the model outcomes. Here, we analyse the effect of various PDE approximations on the analysis of some simple movement models, including a biased random walk, central-place foraging processes and movement in heterogeneous landscapes. Perhaps the most commonly-used PDE method dates back to a seminal paper of Patlak from 1953. However, our results show that this can be a very poor approximation in even quite simple models. On the other hand, more recent methods, based on transport equation formalisms, can provide more accurate results, as long as the kernel describing the animal's movement is sufficiently smooth. When the movement kernel is not smooth, we show that both the older and newer methods can lead to quantitatively misleading results. Our detailed analysis will aid future researchers in the appropriate choice of PDE approximation for analysing models of animal movement.

Keywords: transport equation; theoretical ecology; movement ecology; central-place foraging; home range

1 Introduction

Spatial considerations are relevant to many issues in animal ecology. Space use patterns emerge from individual movements and interactions both with each other and the environment. For example, home range and territory formation from individual behaviour processes has been studied extensively (Börger *et al.* 2008, Lewis and Murray 1993, Moorcroft *et al.* 1999, Potts and Lewis 2014*a*, 2014*b*, 2016), while resource selection in a heterogeneous space resulting from movement decisions is also a well-explored topic (Forester *et al.* 2009, Fortin *et al.* 2005, Potts *et al.* 2014, Thurfjell *et al.* 2014).

One of the main goals of current research is to predict population space use patterns from the rules of individual movement. Environmental change often impacts animal movement; for example, the alteration of the relationship between wolves and caribous resulting from industrial constructions (Latham *et al.* 2011), and the movement decisions of birds in fragmented landscapes (Gillies *et al.* 2011). This makes effective predictions especially critical to help assess the impact on animals and make appropriate policies to ensure the sustainability of species (Kays *et al.* 2015, Potts and Lewis 2014*a*, Thurfjell *et al.* 2014). To achieve the goal of constructing predictive models from individual behavioural mechanisms, it is essential to construct mathematical theories that derive population distributions from individual-level mechanisms.

However, making such theory analytically tractable often requires approximate techniques. Consequently, the various methods that enable spatial patterns to be derived from individual-level decisions can sometimes lead to quite different results. In this paper, we are interested in models that convert movement decisions into partial differential equation (PDE) models. We investigate three methods for deriving PDEs from descriptions of small-scale animal movements, which all give slightly different results (Potts *et al.* 2016). The first dates back to Patlak (1953), and the other two come from more recent analysis of transport equations (Hillen and Painter 2013. Othmer *et al.* 1988).

The aim of this paper is to investigate conditions under which each PDE method most accurately captures the emergent population distribution in a few example scenarios: a biased random walk, central-place foraging and movement in heterogeneous environments.

We focus in particular detail on the three central-place foraging models, each of which describes a biased movement to a fixed point in a one-dimensional space.

This paper is organised as follows. In Section 2, we introduce the three PDE approaches used in our study. Then we compare these PDE approaches in two stages. First, in Section 3, we examine the accuracy of the three approaches using a simple biased random walk model that can be solved exactly for all time. Here, we demonstrate that Patlak's (1953) approach fails to capture accurately even for some very basic movement rules, whereas the newer methods (Hillen and Painter 2013) correct the error. Next, we consider the long-term behaviour of these three approximations by comparing the steady-state distributions that they produce. Section 4 describes three central-place foraging models and presents their approximations using each of the three PDE methods. Section 5 compares the results of each PDE approach in Section 4 using numerical analysis. Section 6 briefly considers some examples beyond central-place foraging: namely examples of movement on heterogeneous landscapes, and analyses the emergent steady-state distributions using the same three PDE methods. Some discussion and concluding remarks are given in Section 7.

2 Movement kernel analysis

A *movement kernel* $k_\tau(z|x)$ is a function that describes the probability of an animal moving from its current position x to position z after a period of time τ. Movement kernels only represent movement over a small time-step, τ. Thus understanding long-term spatial patterns requires methods for projecting movement kernels forward in time. In this section, we describe three such methods, using the formalism of PDEs. These three methods are based on different assumptions. The first method, the *Hyperbolic Scaling* technique (Hillen and Painter 2013, Othmer et al. 1988), assumes that the drift component of movement dominates over the diffusion component. Another method, the *Moment Closure* approach, is based on the assumption that movement can be derived accurately using only the first and second moments of the movement kernel. The higher moments are assumed to be at equilibrium (Hillen and Painter 2013). Patlak's approach is the third method we use, which uses similar assumptions about higher moments, but also relies on the assumption that the movement kernel changes slowly across space (Patlak 1953). The results in this section are present in previous studies (e.g. Hillen and Painter 2013, Patlak 1953, Potts *et al.* 2016), but we summarise them here for the purpose of introducing both notation and some key results used in this paper.

2.1 Hyperbolic Scaling method

Given a movement kernel $k_\tau(z|x)$, the Hyperbolic Scaling method gives rise to a PDE describing the probability distribution $u_H(x,t)$ of the animal at time t (we use the subscript "H" to stand for "Hyperbolic Scaling"). In 1D, this PDE is given as (Potts *et al.* 2016)

$$\frac{\partial u_H}{\partial t}(x,t) = \frac{\tau}{2}\frac{\partial^2}{\partial x^2}[D(x)u_H(x,t)] - \frac{\partial}{\partial x}[c(x)u_H(x,t)] + \frac{\tau}{2}\frac{\partial}{\partial x}\left[c(x)\frac{\partial c(x)}{\partial x}u_H(x,t)\right], \quad (1)$$

where

$$c(x) = \frac{1}{\tau}\int_{-\infty}^{\infty}(z-x)k_\tau(z|x)\mathrm{d}z, \quad (2)$$

and

$$D(x) = \frac{1}{\tau^2}\int_{-\infty}^{\infty}(z-x)^2 k_\tau(z|x)\mathrm{d}z - c(x)^2. \quad (3)$$

Here, $c(x)$ is the mean drift velocity of the animal, while the diffusion coefficient, $D(x)$, is the variance of this velocity.

The long-term population distribution in which we are interested can be represented by the steady-state solution to PDE (1). To derive the steady-state distribution, the left-hand side of Equation (1), is set to 0, resulting in the following ordinary differential equation (ODE)

$$\frac{\tau}{2}\frac{\mathrm{d}^2}{\mathrm{d}x^2}[D(x)u_H^*(x)] - \frac{\mathrm{d}}{\mathrm{d}x}[c(x)u_H^*(x)] + \frac{\tau}{2}\frac{\mathrm{d}}{\mathrm{d}x}\left[c(x)\frac{\mathrm{d}c(x)}{\mathrm{d}x}u_H^*(x)\right] = 0, \quad (4)$$

where $u_H^*(x)$ is the steady-state distribution. Assuming that flux is zero at the steady state, the solution to Equation (4) is given by

$$u_H^*(x) = \frac{C_H}{D(x)} \exp\left(\frac{1}{\tau}\int_0^x \frac{2c(s) - \tau\frac{\mathrm{d}c}{\mathrm{d}s}c(s)}{D(s)}\mathrm{d}s\right), \tag{5}$$

where C_H is a normalising constant, ensuring that $u_H^*(x)$ integrates to 1 across its domain of definition.

2.2 Moment Closure method

When using the Moment Closure method, the PDE derived in 1D is (Potts *et al.* 2016)

$$\frac{\partial u_M}{\partial t}(x,t) = \frac{\tau}{2}\frac{\partial^2}{\partial x^2}[D(x)u_M(x,t)] - \frac{\partial}{\partial x}[c(x)u_M(x,t)] \tag{6}$$

with $c(x)$ and $D(x)$ defined by Equations (2) and (3). We use the subscript "M" here to refer to "Moment Closure". To obtain the steady-state distribution, we solve

$$\frac{\tau}{2}\frac{\mathrm{d}^2}{\mathrm{d}x^2}[D(x)u_M^*(x)] - \frac{\mathrm{d}}{\mathrm{d}x}[c(x)u_M^*(x)] = 0, \tag{7}$$

where $u_M^*(x)$ is the steady-state distribution. The solution to Equation (7) is

$$u_M^*(x) = \frac{C_M}{D(x)} \exp\left(\frac{2}{\tau}\int_0^x \frac{c(s)}{D(s)}\mathrm{d}s\right), \tag{8}$$

where C_M is a normalising constant ensuring that $u_M^*(x)$ integrates to 1 across its domain of definition.

2.3 Patlak's approach

The third method we use dates back to Patlak (1953), but was popularised in the ecology literature by Turchin (1991). In one dimension, the PDE that Patlak (1953) uses to approximate the movement kernel is (Potts *et al.* 2016)

$$\frac{\partial u_P}{\partial t}(x,t) = \frac{\partial^2}{\partial x^2}\left[\frac{M_2(x)}{2\tau}u_P(x,t)\right] - \frac{\partial}{\partial x}\left[\frac{M_1(x)}{\tau}u_P(x,t)\right] \tag{9}$$

with

$$M_1(x) = \int_{-\infty}^{\infty} (z - x) k_\tau(z|x) \mathrm{d}z, \tag{10}$$

and

$$M_2(x) = \int_{-\infty}^{\infty} (z - x)^2 k_\tau(z|x) \mathrm{d}z, \tag{11}$$

where $M_1(x)$ and $M_2(x)$ are the first and second moments of the distance moved respectively. Here, the subscript "P" refers to the fact that we are using Patlak's formalism.

Note that this differs from the Hyperbolic Scaling and Moment Closure approaches, where the diffusion function is proportional to the variance of the velocity, rather than the second moment. To obtain the steady-state distribution, $u_P^*(x)$, requires solving the following ODE

$$\frac{\mathrm{d}^2}{\mathrm{d}x^2}\left[\frac{M_2(x)}{2\tau} u_P^*(x)\right] - \frac{\mathrm{d}}{\mathrm{d}x}\left[\frac{M_1(x)}{\tau} u_P^*(x)\right] = 0. \tag{12}$$

The solution to (12) is

$$u_P^*(x) = \frac{C_P}{M_2(x)} \exp\left(\int_0^x \frac{2M_1(s)}{M_2(s)} \mathrm{d}s\right) \tag{13}$$

with C_P a normalising constant ensuring that $u_P^*(x)$ integrates to 1 across its domain of definition.

3 A simple analytic example

Having built three models of population density distributions by using different PDE approximation methods, the next goal is to determine which method is the best at representing the space use pattern. To examine this analytically, note that the movement kernel, $k_\tau(z|x)$, is the probability density of an animal being at location z in time τ given it is now at x. On the other hand, the distributions $u_H(x,t)$, $u_M(x,t)$ or $u_P(x,t)$ all attempt to describe the animal's probability density at position x at time t. Therefore, the population density distributions at time τ - $u_H(x,\tau)$, $u_M(x,\tau)$ or $u_P(x,\tau)$ - should each equal the movement kernel $k_\tau(x|x_0)$ when given initial condition $u(x,0) = \delta(x_0)$, where $\delta(\cdot)$ is the Dirac delta function.

Here, we show that, even for a very simple movement kernel, Patlak's model, $u_P(x,t)$, fails to give the correct result when evaluated at $t = \tau$. Moreover, the Hyperbolic Scaling and Moment Closure models succeed in this regard. The movement kernel we use is a Normal distribution, with mean μ and variance σ^2, so that

$$k_\tau(z|x) = \frac{1}{\sqrt{2\pi}\sigma} \exp\left(\frac{-(z-x-\mu)^2}{2\sigma^2}\right). \tag{14}$$

This represents a biased random walk.

To calculate the various steady state distributions in Equations (5), (8), and (13), we need to calculate the mean and variance of the velocity (Equations 2 and 3), as well as the first and second moments of the distance moved in one time step (Equations 10 and 11), using the movement kernel from Equation (14). This leads to the following expressions

$$c(x) = \frac{\mu}{\tau}, \tag{15}$$

$$D(x) = \frac{\sigma^2}{\tau^2}, \tag{16}$$

$$M_1(x) = \mu, \tag{17}$$

$$M_2(x) = \sigma^2 + \mu^2. \tag{18}$$

Since $c(x)$ is constant, the term with the derivative of $c(x)$ in the PDE (1) from the Hyperbolic Scaling method is 0 and so Equation (1) is equal to the PDE in Equation (6) obtained by using the Moment Closure technique. Consequently, both the Hyperbolic Scaling and Moment Closure methods leads to the following PDE

$$\frac{\partial u_M}{\partial t}(x,t) = \frac{\sigma^2}{2\tau}\frac{\partial^2}{\partial x^2}u_M(x,t) - \frac{\mu}{\tau}\frac{\partial}{\partial x}u_M(x,t). \tag{19}$$

This is an advection-diffusion equation with constant coefficients.

For Patlak's approach, we substitute Equations (17) and (18) into Equation (9), to

(a) (b)

Figure 1: Errors arising from Patlak's approximation are corrected by the (more recent) Moment Closure approach. Here, we show the movement kernel from Equation (14) with values of mean, μ, and standard deviation, σ, as given in the panels, together with solutions of the PDEs for Patlak's approximation ($u_P(x,\tau)$; Equation 22) and the Moment Closure method ($u_M(x,\tau)$; Equation 21), given at time τ. Progressing from the left panel to the right, we see that a higher μ leads to a greater difference between the two methods, but the Moment Closure method always gives the correct result.

obtain the following PDE

$$\frac{\partial u_P}{\partial t}(x,t) = \frac{\partial^2}{\partial x^2}\left[\frac{\sigma^2+\mu^2}{2\tau}u_P(x,t)\right] - \frac{\partial}{\partial x}\left[\frac{\mu}{\tau}u_P(x,t)\right]. \qquad (20)$$

With the assumption that $u_M(x,0) = \delta(x_0)$, the solution to Equation (19) at time $t=\tau$ is the density distribution (Grimmett and Stirzaker 2001, Montroll and Shlesinger 1984)

$$u_M(x,\tau) = \frac{1}{\sqrt{2\pi\sigma^2}}\exp\left(\frac{-(x-x_0-\mu)^2}{2\sigma^2}\right). \qquad (21)$$

Similarly, with $u_P(x,0) = \delta(x_0)$, the solution to Equation (20) at time $t=\tau$ is

$$u_P(x,\tau) = \frac{1}{\sqrt{2\pi(\sigma^2+\mu^2)}}\exp\left(\frac{-(x-x_0-\mu)^2}{2(\sigma^2+\mu^2)}\right). \qquad (22)$$

We immediately see that $u_M(x,\tau) = k_\tau(x|x_0)$, as required. Since $u_H = u_M$, we also have $u_H(x,\tau) = k_\tau(x|x_0)$. However, comparing Equation (22) with Equation (14) reveals that $u_P(x,\tau) \neq k_\tau(x|x_0)$. Thus Patlak's approach fails to represent the probability distribution correctly even in this simple case, whereas the other PDE methods succeed in this regard.

The difference between Patlak's approach and the others arises because the diffusion coefficient of Equation (19) is proportional to the variance of velocity, whereas the diffusion coefficient of Equation (20) is proportional to the second moment of velocity. This causes Patlak's approximation to predict a transient probability distribution with an overly-high variance (see Figure 1).

In general, it would be inaccurate to use the second moment for the diffusion coefficient unless the drift term is very small compared to the diffusion term. This is because the diffusion term in any advection-diffusion equation with constant coefficients describes the variance over time. If this is significantly different to the second moment then inaccuracies will arise in Patlak's formulation (Figure 1). This analytical example suggests that the Hyperbolic Scaling and Moment Closure methods may tend to be better, in general, at representing the population distribution than Patlak's approach.

4 Three models of home-ranging movement

Having shown that Patlak's PDE approach can give an inaccurate picture of transient dynamics in certain situations, we now explore the effect of using the three different PDE techniques for understanding steady-state distributions. In practice, the PDEs we study here are useful tools for steady-state analysis, since they admit exact analytic solutions (given in Equations 5, 8, and 13). Furthermore, from a biological perspective, steady-state analysis is useful for understanding broad-scale population patterns that might emerge from movement decisions. We proceed by examining three models of a simple, yet classical, biological phenomenon: that of central-place foraging. These models have broad ecological interest, as many animals exhibit home-ranging or site-fidelity behaviour (Börger *et al.* 2008).

4.1 Discontinuous mean velocity model

Our first model is a version of the classical Hogate-Okubo localising tendency model (Holgate 1971, Okubo 1980). Here, we assume animals have a constant-velocity bias towards the central place, which for convenience is located at the origin $x = 0$. A movement kernel that describes this movement, using a Normal distribution, is given by

$$k_\tau^1(z|x) = \begin{cases} \dfrac{1}{\sqrt{2\pi}\sigma} \exp\left(\dfrac{-(z-x-\mu)^2}{2\sigma^2}\right) & \text{if } x < 0, \\ \dfrac{1}{\sqrt{2\pi}\sigma} \exp\left(\dfrac{-(z-x+\mu)^2}{2\sigma^2}\right) & \text{if } x > 0, \\ \dfrac{1}{\sqrt{2\pi}\sigma} \exp\left(\dfrac{-(z-x)^2}{2\sigma^2}\right) & \text{if } x = 0, \end{cases} \tag{23}$$

where μ is the average distance the animal moves over a time τ, and σ^2 is the variance of displacement. In the following, we use the three PDE methods defined in Section 2 to calculate the steady-state probability distribution derived from this movement kernel.

The steady-state distribution derived by using the Hyperbolic Scaling method is (see Equation 5 and Appendix A.1)

$$u_H^1(x) = \begin{cases} \dfrac{\mu}{\sigma^2} \exp\left(\dfrac{2\mu}{\sigma^2}x\right) & \text{if } x < 0, \\ \dfrac{\mu}{\sigma^2} \exp\left(-\dfrac{2\mu}{\sigma^2}x\right) & \text{if } x \geq 0. \end{cases} \tag{24}$$

As the corresponding mean velocity function, $c_1(x)$, is constant (see Appendix A.1), the Moment Closure method leads to the same steady-state distribution as the Hyperbolic Scaling method, that is, $u_M^1(x) = u_H^1(x)$.

Next, using Patlak's approach (see Equation 13) leads to the following steady-state distribution for objects moving in accordance with the movement kernel in Equation (23) (see Appendix A.2):

$$u_P^1(x) = \begin{cases} \dfrac{\mu}{\sigma^2+\mu^2} \exp\left(\dfrac{2\mu}{\sigma^2+\mu^2}x\right) & \text{if } x < 0, \\ \dfrac{\mu}{\sigma^2+\mu^2} \exp\left(-\dfrac{2\mu}{\sigma^2+\mu^2}x\right) & \text{if } x \geq 0. \end{cases} \tag{25}$$

Note that because the PDEs are not defined at $x = 0$ in this case, we solve them piecewise on the assumption that the solutions are continuous. In addition, Equations (24) and (25) are examples of the well-known Holgate-Okubo model (Holgate 1971, Okubo 1980).

4.2 Continuous mean velocity model

The movement kernel defined by Equation (23) implies that the animal tends to move in the direction towards the central place with a fixed average velocity. As such, the mean velocity is discontinuous at the central point, so PDE solutions can only be defined weakly. Therefore we analyse two further models of central-place foraging, one where the mean velocity is continuous (this section) and another where the mean velocity is continuously differentiable (Section 4.3). The first model is given as follows

$$k_\tau^2(z|x) = \begin{cases} \dfrac{1}{\sqrt{2\pi}\sigma} \exp\left(\dfrac{-(z-x-\mu)^2}{2\sigma^2}\right) & \text{if } x < -\mu, \\ \dfrac{1}{\sqrt{2\pi}\sigma} \exp\left(\dfrac{-z^2}{2\sigma^2}\right) & \text{if } -\mu \le x \le \mu, \\ \dfrac{1}{\sqrt{2\pi}\sigma} \exp\left(\dfrac{-(z-x+\mu)^2}{2\sigma^2}\right) & \text{if } x > \mu. \end{cases} \tag{26}$$

By using the Hyperbolic Scaling method, the steady-state distribution for the movement kernel in Equation (26) is (Appendix B.1)

$$u_H^2(x) = \begin{cases} C_H^2 \exp\left(\dfrac{2\mu}{\sigma^2}x + \dfrac{\mu^2}{2\sigma^2}\right) & \text{if } x < -\mu, \\ C_H^2 \exp\left(-\dfrac{3}{2\sigma^2}x^2\right) & \text{if } -\mu \le x \le \mu, \\ C_H^2 \exp\left(-\dfrac{2\mu}{\sigma^2}x + \dfrac{\mu^2}{2\sigma^2}\right) & \text{if } x > \mu, \end{cases} \tag{27}$$

where C_H^2 is a constant ensuring the distribution integrates to 1 (see Appendix B.1).

When applying the Moment Closure method, the steady-state distribution obtained for the movement kernel in Equation (26) is (Appendix B.2)

$$u_M^2(x) = \begin{cases} C_M^2 \exp\left(\dfrac{2\mu}{\sigma^2}x + \dfrac{\mu^2}{\sigma^2}\right) & \text{if } x < -\mu, \\ C_M^2 \exp\left(-\dfrac{x^2}{\sigma^2}\right) & \text{if } -\mu \le x \le \mu, \\ C_M^2 \exp\left(-\dfrac{2\mu}{\sigma^2}x + \dfrac{\mu^2}{\sigma^2}\right) & \text{if } x > \mu, \end{cases} \tag{28}$$

where C_M^2 is a normalising constant (see Appendix B.2).

The steady-state distribution arising from Patlak's approach is (Appendix B.3)

$$u_P^2(x) = \begin{cases} \dfrac{C_P^2}{(\sigma^2+\mu^2)^2}\exp\left(\dfrac{2\mu}{\sigma^2+\mu^2}x + \dfrac{2\mu^2}{\sigma^2+\mu^2}\right) & \text{if } x < -\mu, \\ \dfrac{C_P^2}{(\sigma^2+x^2)^2} & \text{if } -\mu \le x \le \mu, \\ \dfrac{C_P^2}{(\sigma^2+\mu^2)^2}\exp\left(\dfrac{-2\mu}{\sigma^2+\mu^2}x + \dfrac{2\mu^2}{\sigma^2+\mu^2}\right) & \text{if } x > \mu, \end{cases} \tag{29}$$

where C_P^2 is a normalising term (see Appendix B.3).

Note that the solutions in Equations (27), (28) and (29) are all defined weakly, since the PDE is undefined at $x = \pm\mu$. As in Section 4.1, we have implicitly assumed that the solutions are continuous.

4.3 Differentiable mean velocity model

As a third example, we introduce a movement kernel where the mean displacement of a step decreases as the animal proceeds toward the central place. Here, the mean velocity function $c_3(x)$ is continuously differentiable (see Appendix C.1). The movement kernel we use is

$$k_\tau^3(z|x) = \begin{cases} \dfrac{1}{\sqrt{2\pi}\sigma}\exp\left(\dfrac{-(z-x-\mu x^2)^2}{2\sigma^2}\right) & \text{if } x < 0, \\ \dfrac{1}{\sqrt{2\pi}\sigma}\exp\left(\dfrac{-(z-x+\mu x^2)^2}{2\sigma^2}\right) & \text{if } x \ge 0. \end{cases} \tag{30}$$

The steady-state distribution obtained by the Hyperbolic Scaling method is (see Appendix C.1)

$$u_H^3(x) = \begin{cases} C_H^3 \exp\left(\dfrac{2\mu}{3\sigma^2}x^3 - \dfrac{\mu^2}{2\sigma^2}x^4\right) & \text{if } x < 0, \\ C_H^3 \exp\left(-\dfrac{2\mu}{3\sigma^2}x^3 - \dfrac{\mu^2}{2\sigma^2}x^4\right) & \text{if } x \ge 0, \end{cases} \tag{31}$$

where C_H^3 is a constant ensuring the distribution integrates to 1 over the domain (see Appendix C.1).

The Moment Closure method gives (see Appendix C.2)

$$u_M^3(x) = \begin{cases} C_M^3 \exp\left(\frac{2\mu}{3\sigma^2}x^3\right) & \text{if } x < 0, \\ C_M^3 \exp\left(-\frac{2\mu}{3\sigma^2}x^3\right) & \text{if } x \geq 0, \end{cases} \tag{32}$$

where C_M^3 is a normalising constant (see Appendix C.2).

The steady-state distribution obtained using Patlak's approach is (see Appendix C.3)

$$u_P^3(x) = \begin{cases} \frac{C_P^3}{\sigma^2+\mu^2x^4} \exp\left(-\sqrt{\frac{1}{\mu\sigma}}\left[2^{-\frac{3}{2}} \ln\left(\frac{|\frac{\mu}{\sigma}x^2 + \sqrt{\frac{2\mu}{\sigma}}x+1|}{|\frac{\mu}{\sigma}x^2 - \sqrt{\frac{2\mu}{\sigma}}x+1|}\right)\right.\right. \\ \left.\left. + \frac{1}{\sqrt{2}}\arctan\left(-\sqrt{\frac{2\mu}{\sigma}}x+1\right) + \frac{1}{\sqrt{2}}\arctan\left(-\sqrt{\frac{2\mu}{\sigma}}x-1\right)\right]\right) \\ \qquad\qquad \text{if } x < 0, \\ \frac{C_P^3}{\sigma^2+\mu^2x^4} \exp\left(-\sqrt{\frac{1}{\mu\sigma}}\left[2^{-\frac{3}{2}} \ln\left(\frac{|\frac{\mu}{\sigma}x^2 - \sqrt{\frac{2\mu}{\sigma}}x+1|}{|\frac{\mu}{\sigma}x^2 + \sqrt{\frac{2\mu}{\sigma}}x+1|}\right)\right.\right. \\ \left.\left. + \frac{1}{\sqrt{2}}\arctan\left(\sqrt{\frac{2\mu}{\sigma}}x+1\right) + \frac{1}{\sqrt{2}}\arctan\left(\sqrt{\frac{2\mu}{\sigma}}x-1\right)\right]\right) \\ \qquad\qquad \text{if } x \geq 0, \end{cases} \tag{33}$$

where C_P^3 is a normalising constant, ensuring that the probability distribution integrates to 1 over the real line.

5 Numerical analysis

We now examine which of the PDE formalisms is most accurate at capturing the long-term behaviour of an animal moving in accordance with a given movement kernel $k_\tau(z|x)$. Doing this requires an exact technique for propagating the movement kernel forward in time. Such a technique is given by the *Master Equation* as follows

$$u_I(x, t+\tau) = \int_{-\infty}^{\infty} k_\tau(x|y)u_I(y,t)\mathrm{d}y, \tag{34}$$

where $u_I(x,t)$ is the probability density of the animal's position at time t. As $t \to \infty$, Equation (34) becomes

$$u_I^*(x) = \int_{-\infty}^{\infty} k_\tau(x|y) u_I^*(y) \mathrm{d}y, \tag{35}$$

where $u_I^*(x) = \lim_{t\to\infty} u_I(x,t)$. In general, it is difficult to find the analytic solution to Equation (35), thus numerical computation is required to obtain $u_I^*(x)$. (For a special case which can be solved analytically, see Barnett and Moorcroft 2008.)

We do this by iterating Equation (34), then setting $u_I^*(x) = u_I(x, t + n\tau)$ when the Kullback-Leibler divergence (Kullback and Leibler 1951) between $u_I(x, t + n\tau)$ and $u_I(x, t+(n-1)\tau)$ is less than 10^{-6}. Having found $u_I^*(x)$, we compare the three approximate PDE methods given in Section 2 by calculating the KL-divergence of $u_I^*(x)$ from the steady-state distributions derived by the approximation PDEs. The PDE method with the lowest KL-divergence from $u_I^*(x)$ is deemed to be the best model for understanding the long-term distribution of an animal moving in accordance with the kernel $k_\tau(z|x)$. Note that our results are essentially unchanged when Euclidean distance is used instead of KL-divergence (see Supplementary Material), indicating that they are not sensitive to the metric used.

In the following sections, the long-term distributions derived using the Master Equation (34) with the movement kernels from Equations (23), (26), and (30), are denoted by $u_I^1(x)$, $u_I^2(x)$, and $u_I^3(x)$ respectively.

5.1 Numerical analysis of the discontinuous mean velocity model

To understand how μ and σ influence the KL-divergence between $u_I^1(x)$ and the distributions derived by PDE methods, we plot contour lines of the KL-divergence on the μ-σ plane (Figures 2a,b). The contour lines indicate that both the KL-divergence of $u_I^1(x)$ from $u_M^1(x)$, which equals $u_H^1(x)$ (see Section 4.1), and the KL-divergence of $u_I^1(x)$ from $u_P^1(x)$ increase with growing μ/σ.

Figure 2 shows that the KL-divergence of $u_I^1(x)$ from $u_M^1(x)$ is greater than the KL-divergence of $u_I^1(x)$ from $u_P^1(x)$. This is in contrast with the analytical analysis, from which one might guess that $u_I^1(x)$ should be closer to $u_M^1(x)$ than $u_P^1(x)$. However,

(a) Moment Closure

(b) Patlak's method

(c) $0.05 \leq \mu \leq 0.2$, $\sigma = 0.05$

(d) $\mu = 0.05$, $0.05 \leq \sigma \leq 0.2$

(e) $\mu = 0.01$, $\sigma = 0.05$

(f) $\mu = 0.1$, $\sigma = 0.05$

Figure 2: Discontinuous mean velocity movement kernel $k_\tau^1(z|x)$ with μ the mean move length in one step and σ the standard deviation of move length: (a) The contours of the KL-divergence of the numerical solution, $u_I^1(x)$, from the analytic solution, $u_M^1(x)$ (Equation 24), derived using a moment closure technique, $\mu, \sigma \in [0.05, 0.2]$. (b) The contours of the KL-divergence of $u_I^1(x)$ from the analytic solution, $u_P^1(x)$ (Equation 25), derived using Patlak's method, $\mu, \sigma \in [0.05, 0.2]$. (c) KL-divergence between $u_M^1(x)$ and $u_I^1(x)$ (▲), and $u_P^1(x)$ and $u_I^1(x)$ ($\star$) with $0.05 \leq \mu \leq 0.2$ and $\sigma = 0.05$. (d) KL-divergence between $u_M^1(x)$ and $u_I^1(x)$ (▲), and $u_P^1(x)$ and $u_I^1(x)$ ($\star$) with $0.05 \leq \sigma \leq 0.2$ and $\mu = 0.05$. (e) steady-state distributions with $\mu = 0.01$ and $\sigma = 0.05$. (f) steady-state distributions with $\mu = 0.1$ and $\sigma = 0.05$.

note that both methods – Patlak's and the Moment Closure – are bad at capturing the dynamics of this movement kernel. Figures 2e and 2f show that $u_M^1(x)$ and $u_P^1(x)$ have sharp peaks at $x = 0$, whereas $u_I^1(x)$ is relatively smooth. Both $u_P^1(0)$ and $u_M^1(0)$ are larger than $u_I^1(0)$, but since $\mu/\sigma^2 > \mu/(\sigma^2 + \mu^2)$, we see from Equations (24) and (25) that $u_M^1(x)$ has lower variance than $u_P^1(x)$ so $u_P^1(0) < u_M^1(0)$. (Note that this lower variance concords with the analytic observations of Section 3.) Hence the KL-divergence between $u_P^1(x)$ and $u_I^1(x)$ is less than that between $u_M^1(x)$ and $u_I^1(x)$. In summary, the apparent improved performance of Patlak's model appears to be an artefact of the discontinuous advection terms used in these models.

5.2 Numerical analysis of the continuous mean velocity model

Numerical comparison between the three steady-state distributions for the second movement kernel reveals more interesting patterns. The contour lines of KL-divergence show similar patterns to those with the first movement kernel (Figures 3a-c), but the μ-σ plane is split into two regions, one where $u_P^2(x)$ is closer to $u_I^2(x)$ than $u_M^2(x)$, and another where $u_M^2(x)$ is closer (Figure 3d). The latter occurs for higher and lower values of μ/σ. In the region where $u_P^2(x)$ is nearer to $u_I^2(x)$, $u_M^2(x)$ and $u_P^2(x)$ are in fact quite close, which indicates that both the Moment Closure method and Patlak's approach work well in that region (Figures 3e-g). For larger μ, although the Moment Closure method seems to perform best, all three methods diverge visibly from the real long-term pattern (Figures 3e,h). As in Section 5.1, Patlak's approach leads to a higher variance in the steady-state pattern, which is in agreement with the analytic observations of Section 3.

In summary, either the Moment Closure method works a lot better than the others (for high μ/σ) or all three methods are very similar in which case sometimes Patlak's approach slightly outperforms the others. Nonetheless, as for the first movement kernel, the PDE approximations often perform poorly, and this might be due to the non-differentiable point at $x = 0$.

(a) Hyperbolic Scaling

(b) Moment Closure

(c) Patlak's method

(d)

(e) $0.05 \leq \mu \leq 0.3$, $\sigma = 0.2$.

(f) $\mu = 0.2$, $0.05 \leq \sigma \leq 0.3$.

(g) $\mu = 0.05$, $\sigma = 0.2$

(h) $\mu = 0.2$, $\sigma = 0.2$

Figure 3: Continuous mean velocity movement kernel $k_\tau^2(z|x)$ with μ (resp. $|x|$) the mean move length in one step for $|x| > \mu$ (resp. $|x| \leq \mu$) and σ the standard deviation of move length: (a) The contours of the KL-divergence of the numerical solution, $u_I^2(x)$, from the analytic solution, $u_H^2(x)$ (Equation 27), derived from a Hyperbolic Scaling method. (b) The contours of the KL-divergence of $u_I^2(x)$ from the analytic solution, $u_M^2(x)$ (Equation 28), derived from a moment closure technique. (c) The contours of the KL-divergence of $u_I^2(x)$ from the analytic solution, $u_P^2(x)$ (Equation 29), derived from Patlak's method. (d) Turquoise region: the KL-divergence of $u_I^2(x)$ from $u_P^2(x)$ is smaller than from $u_M^2(x)$ or $u_H^2(x)$. Blue region: the KL-divergence of $u_I^2(x)$ from $u_M^2(x)$ is the smallest. (e) KL-divergence between $u_H^2(x)$ and $u_I^2(x)$ ($\bullet$), $u_M^2(x)$ and $u_I^2(x)$ ($\blacktriangle$), and $u_P^2(x)$ and $u_I^2(x)$ ($\star$) with $0.05 \leq \mu \leq 0.3$ and $\sigma = 0.2$. (f) KL-divergence between $u_H^2(x)$ and $u_I^2(x)$ ($\bullet$), $u_M^2(x)$ and $u_I^2(x)$ ($\blacktriangle$), and $u_P^2(x)$ and $u_I^2(x)$ ($\star$) for $\mu = 0.2$, $0.05 \leq \sigma \leq 0.3$. (g) steady-state distributions with $\mu = 0.05$ and $\sigma = 0.2$. (h) steady-state distributions with $\mu = 0.2$ and $\sigma = 0.2$.

(a) Hyperbolic Scaling

(b) Moment Closure

(c) Patlak's method

(d) $0.05 \leq \mu \leq 0.5$, $\sigma = 0.1$

(e) $\mu = 0.05$, $\sigma = 0.05$

(f) $\mu = 0.8$, $\sigma = 0.5$

Figure 4: Differentiable mean velocity movement kernel $k^3_\tau(z|x)$ with μx^2 the mean move length in one step and σ the standard deviation of the move length: (a) The contours of the KL-divergence of the numerical solution, $u^3_I(x)$, from the analytic approximation, $u^3_H(x)$ (Equation 31), obtained using a Hyperbolic Scaling method, $\mu, \sigma \in [0.05, 0.5]$. (b) The contours of the KL-divergence of $u^3_I(x)$ from the analytic approximation, $u^3_M(x)$ (Equation 32), obtained using a moment closure technique, $\mu, \sigma \in [0.05, 0.5]$. (c) The contours of the KL-divergence of $u^3_I(x)$ from the analytic approximation, $u^3_P(x)$ (Equation 33), obtained using Patlak's method, $\mu, \sigma \in [0.05, 0.5]$. (d) KL-divergence between $u^3_H(x)$ and $u^3_I(x)$ ($\bullet$), $u^3_M(x)$ and $u^3_I(x)$ ($\blacktriangle$), and $u^3_P(x)$ and $u^3_I(x)$ ($\star$) with $0.05 \leq \mu \leq 0.5$ and $\sigma = 0.1$. (e) steady-state distribution with $\mu = 0.05$ and $\sigma = 0.05$. (f) steady-state distribution with $\mu = 0.8$ and $\sigma = 0.5$.

5.3 Numerical analysis of the differentiable mean velocity model

For the third model in Equation (30), the movement kernel is differentiable. The contour lines of KL-divergence illustrate substantially different patterns from the previous cases in Sections 5.1 and 5.2. For small μ and σ, the KL-divergence is very low, and all PDE methods perform well (Figure 4e). As μ and σ are increased, the PDE methods become increasingly worse, but the Moment Closure method outperforms the others (Figure 4a-d).

This trend is rather different to the trends observed in the non-differentiable models (Figures 2a-b and 3a-c). There, the inaccuracy came about from having a sharp peak at the origin in the PDE models. This peak is sharper if the drift term (μ) is large compared to the diffusion term (σ), leading to aggregation near the origin. Hence inaccuracies increase as μ/σ increases.

However, for the differentiable mean velocity model, the main cause of error is that the PDE approaches underestimate the width of the steady-state "home range". As σ is increased, the home range width increases. Yet, this increase in width is greater for $u_I^3(x)$ than for the PDE approximations (Figure 4f), so the disparity between $u_I^3(x)$ and the PDE steady-states increases with σ. Likewise, an increase in μ causes an increase in the overestimation of the probability distribution near the peak, so a greater KL distance between $u_I^3(x)$ and each of $u_P^3(x)$, $u_M^3(x)$, and $u_H^3(x)$.

This overestimation is larger for the Hyperbolic Scaling and Patlak's method. The Moment Closure method appears to give a better estimator of the height of the steady-state distribution's peak, but it gives a "flatter" peak, so overestimating the height of the probability distribution near (but not at) the peak (Figure 4f). The slightly fatter tails in Patlak's approximation from Figure 4f, as compared with the other approximations, is a result of the overestimation of the variance observed in Figure 1.

(a) $w_t(x) = \begin{cases} 1 & \text{if } x \in [0, 1/3] \cup (2/3, 1] \\ 2 & \text{if } x \in (1/3, 2/3] \end{cases}$

(b) $w_s(x) = \sin(3\pi x) + 2$

(c)

(d)

(e)

(f)

Figure 5: Steady-state distributions emerging from movement on heterogeneous landscapes. (a) The weighting function $w_t(x)$ (Equation 39). (b) The weighting function $w_s(x)$ (Equation 40). (c) Movement according to kernel $k_\tau^4(z|x)$ (Equation 41) based on a Normal distribution with $w_t(x)$ as the weighting function. (d) Movement according to kernel $k_\tau^5(z|x)$ (Equation 42) based on a Normal distribution with $w_s(x)$ as the weighting function. (e) Movement according to kernel $k_\tau^6(z|x)$ (Equation 43) based on a Laplace distribution with $w_t(x)$ as the weighting function. (f) Movement according to kernel $k_\tau^7(z|x)$ (Equation 44) based on a Laplace distribution with $w_s(x)$ as the weighting function.

6 Models of movement on heterogeneous landscapes

Finally, we examine a few situations beyond central-place foraging. In particular, we consider some models describing movement on a heterogeneous landscape, based on the type of step selection functions described in Potts *et al.* (2014). The general form of the movement kernels we will study, which describe the probability of moving to position z from position x in time τ, is as follows:

$$k_\tau(z|x) = \frac{\phi_\tau(z|x)w(z)}{\int_\Omega \phi_\tau(y|x)w(y)\mathrm{d}y}. \tag{36}$$

The function $\phi_\tau(z|x)$ represents the probability of changing location from x to z on a homogeneous landscape in a time-interval τ, while $w(z)$ is a weighting function taking account of environmental factors (such as resources) at position z.

Here, we use Normal and Laplace distributions as examples to describe the probability of an animal moving from x to z without considering habitat conditions. The superscripts "n" and "l" stand for Normal and Laplace distributions respectively:

$$\phi^n_\tau(z|x) = \frac{1}{\sqrt{2\pi}\sigma}\exp\left(\frac{-(z-x)^2}{2\sigma^2}\right), \tag{37}$$

$$\phi^l_\tau(z|x) = \begin{cases} \dfrac{1}{2b}\exp\left(\dfrac{z-x}{b}\right) & \text{if } z < x, \\ \dfrac{1}{2b}\exp\left(\dfrac{x-z}{b}\right) & \text{if } z \geq x, \end{cases} \tag{38}$$

where σ^2 and $2b^2$ are the variance of move length.

As for the landscapes, we assume that the resources are uneven across the land and we use two types of weighting functions to describe the quality of resources. The first weighting function for resources, which we call a "top hat" function, is (Figure 5a)

$$w_t(x) = \begin{cases} 1 & \text{if } x \in [0, 1/3] \cup (2/3, 1], \\ 2 & \text{if } x \in (1/3, 2/3], \end{cases} \tag{39}$$

where the subscript "t" stands for "top hat". For example, such a function was used by

Moorcroft and Barnett (2008) to model resource heterogeneity.

As well as a top-hat function, it is worth investigating environments that change smoothly over space (a similar strategy to using both smooth and non-smooth central-place foraging models in Section 4). Therefore we also use a sine function, indicated by a subscript "s", to describe the resource distribution (Figure 5b):

$$w_s(x) = \sin(3\pi x) + 2. \tag{40}$$

We investigate the four possible movement kernels constructed by substituting either Equations (37) or (38) in place of $\phi_\tau(z|x)$ in Equation (36), and either Equations (39) or (40) in place of $w(z)$ in Equation (36). These movement kernels are as follows:

$$k_\tau^4(z|x) = \frac{\phi_\tau^n(z|x)w_t(z)}{\int_0^1 \phi_\tau^n(y|x)w_t(y)\mathrm{d}y}, \tag{41}$$

$$k_\tau^5(z|x) = \frac{\phi_\tau^n(z|x)w_s(z)}{\int_0^1 \phi_\tau^n(y|x)w_s(y)\mathrm{d}y}, \tag{42}$$

$$k_\tau^6(z|x) = \frac{\phi_\tau^l(z|x)w_t(z)}{\int_0^1 \phi_\tau^l(y|x)w_t(y)\mathrm{d}y}, \tag{43}$$

$$k_\tau^7(z|x) = \frac{\phi_\tau^l(z|x)w_s(z)}{\int_0^1 \phi_\tau^l(y|x)w_s(y)\mathrm{d}y}. \tag{44}$$

Exact formulae for $k_\tau^4(z|x)$, $k_\tau^5(z|x)$, $k_\tau^6(z|x)$, and $k_\tau^7(z|x)$ are given in Appendix D.

We use the three PDE approximating methods – the Hyperbolic Scaling (Equation 5) and Moment Closure (Equation 8) methods, and Patlak's approach (Equation 13) – to derive steady-state distributions, which represent the long-term space use patterns. Unlike the examples discussed in Sections 3 and 4, it is not possible to solve analytically the PDEs for approximating space use using the models in this section (Equation 41-44). Therefore, in this section, the steady-state distributions are obtained numerically.

In Figure 5, we show an example of the steady-state distributions for the models derived above when the variance of the function $\phi_\tau(z|x)$ is fixed at 10^{-4}. We use subscripts "H", "M", "P" and "I" to refer to the steady-state distributions obtained from the

Hyperbolic Scaling method, the Moment Closure method, Patlak's approach, and the integration of the Master Equation (34) respectively, and superscript numbers 4-7 to refer to the movement kernels number 4-7 in Equations (41)-(44) (cf. Sections 4 and 5). For example, $u_H^4(x)$ is the steady-state distribution of the Hyperbolic Scaling PDE (given in Equation 5), using movement kernel number 4 in Equation (41).

The steady-state distributions derived from the three PDE methods are not significantly different, but are all quite inaccurate at discontinuous points (Figures 5c, 5e). Among all these four examples in this section, only the Normal-sine model $k_\tau^5(z|x)$ (Equation 42) is based on a smooth movement rule and a smooth landscape. In this case, the Moment Closure method gives the best approximation. These qualitative observations mirror those which we saw for the central-place foraging models in Section 5.

7 Discussion

The PDE approximation methods illustrated in this paper are efficient tools to derive population-level distribution from underlying movement rules, particularly when the movement rules vary over space - i.e. when the animal is moving in a heterogeneous environment. They have been applied in a wide range of studies of animal movement (e.g., Hillen and Painter 2013, Painter 2014, Potts *et al.* 2016, Turchin 1991, 1998). However, our work suggests that the accuracy of the approximate distributions depends on the movement kernel used and which PDE method is applied.

By investigating analytically a simple movement kernel, representing a biased random walk, Patlak's approach is shown to be unable to capture the movement process. The main reason for this is that it leads to use of the second moment of the movement kernel for the diffusion coefficient, rather than the variance. This leads, in even the simplest case of a normally distributed movement kernel, to transient distributions that have an overestimated variance (Figure 1). In contrast, the Hyperbolic Scaling and Moment Closure methods describe the movement process correctly. Numerical results of central-place foraging models indicate that when the mean velocity of the movement is differentiable, then the Moment Closure methods outperforms the other methods (Figure 4).

We have focussed here on three simple movement kernels for central-place foraging models. Although more complicated movement kernels could be investigated (e.g., Forester *et al.* 2009, Potts *et al.* 2014, Rhodes *et al.* 2005), our analysis of these simple cases allows us to gain concrete insight into the capability of each PDE method for giving a correct representation of long-term behaviour. In addition, we have shown that qualitatively similar results also hold for some simple models of movement in heterogeneous environments – i.e. PDE methods work poorly with non-smooth models, but the Moment Closure method outperforms the other methods for smooth models, although often only marginally better for the cases we studied.

In general, our results show that when there is a significant disparity between the second moment and the variance of a movement kernel, the choice of PDE formalism can cause large differences in the resulting distributions. These appear to be more apparent at transient times, where Patlak's approach can fail drastically (Figure 1) but can also be observed at steady state (Figures 2-5).

Patlak's approach will tend to lead to solutions with larger variances than the other approaches. When the movement kernel is sufficiently smooth – so that the Moment Closure method works reasonably well – this can cause Patlak's approximation to predict broader distributions than the other approaches. That said, for a wide variety of examples of differentiable movement kernels (e.g. Figures 4e, 5d, and 5f), we found Patlak's approach to give a relatively reasonable approximation in the steady state, which is somewhat surprising due to its analytic shortcomings. This perhaps goes some way to explaining why it has remained popular for many decades.

For non-smooth kernels, we see that all three PDE approaches can cause very unrealistic spikes in the steady-state distribution – predicting probability densities that peak at a point many times higher than the real distribution in certain cases (e.g. Figure 3h). Since Patlak's approach overestimates the variance of the distribution, this error can end up dampening the effect of the high peaks, leading to Patlak's approach giving estimations that are closer to the real distribution than the other approaches. However, this is merely a serendipitous cancelling of two opposing inaccuracies. In general, one should be very wary of using any of the PDE approximations studied here when the movement kernels are non-smooth. They may give results with a vague qualitative similarity to reality, but quantitatively they can be wildly wrong.

In summary, when applying PDE methods for approximating movement kernels, we suggest two things. First, be careful if the movement kernel leads to advection terms that are not differentiable: the PDEs will require weak analysis that may give quantitatively misleading results. Second, we generally recommend using the Moment Closure method over Patlak's approach.

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Appendix A Discontinuous mean velocity model

A.1 Movement kernel $k_\tau^1(z|x)$ with the Hyperbolic Scaling method

Here, we use the Hyperbolic Scaling method to analyse the movement kernel $k_\tau^1(z|x)$ given by Equation (23). To use the Hyperbolic Scaling method, we place Equation (23) into Equations (2) and (3) in Section 2.1 to give

$$c_1(x) = \begin{cases} \dfrac{\mu}{\tau} & \text{if } x < 0, \\ -\dfrac{\mu}{\tau} & \text{if } x > 0, \\ 0 & \text{if } x = 0, \end{cases} \tag{A.1.1}$$

and

$$D_1(x) = \frac{\sigma^2}{\tau^2}. \tag{A.1.2}$$

The mean velocity function, $c_1(x)$, is discontinuous at $x = 0$. Thus the resulting PDEs, and steady-state ODEs, can only be defined piecewise. We thus solve Equation (4) in the two cases where $x < 0$ and $x > 0$, and make an assumption that the solution is continuous. The resulting solution is a weak solution on the real line (similar to that in Potts *et al.* 2016, Appendix B). Substituting expressions (A.1.1) and (A.1.2) into Equation (5) gives:

$$u_H^1(x) = \begin{cases} C_{H1}^1 \dfrac{\tau^2}{\sigma^2} \exp\left(\dfrac{2\mu}{\sigma^2} x\right) & \text{if } x < 0, \\ C_{H2}^1 \dfrac{\tau^2}{\sigma^2} \exp\left(-\dfrac{2\mu}{\sigma^2} x\right) & \text{if } x > 0, \end{cases} \tag{A.1.3}$$

where C_{H1}^1 and C_{H2}^1 are arbitrary constants, and $u_H^1(x)$ is the steady-state distribution. Our continuity assumption means we must have $C_{H1}^1 = C_{H2}^1$. To ensure $u_H^1(x)$ integrates to 1, we calculate

$$\begin{aligned} C_{H1}^1 &= \left[\int_{-\infty}^0 \frac{\tau^2}{\sigma^2} \exp\left(\frac{2\mu}{\sigma^2} x\right) \mathrm{d}x + \int_0^\infty \frac{\tau^2}{\sigma^2} \exp\left(-\frac{2\mu}{\sigma^2} x\right) \mathrm{d}x\right]^{-1} \\ &= \frac{\mu}{\tau^2}. \end{aligned} \tag{A.1.4}$$

Inserting Equation (A.1.4) into Equation (A.1.3) and setting $u_H^1(0) = \lim_{x\to 0} u_H^1(x) = \mu/\sigma^2$ yields

$$u_H^1(x) = \begin{cases} \dfrac{\mu}{\sigma^2} \exp\left(\dfrac{2\mu}{\sigma^2} x\right) & \text{if } x < 0, \\ \dfrac{\mu}{\sigma^2} \exp\left(-\dfrac{2\mu}{\sigma^2} x\right) & \text{if } x \geq 0, \end{cases} \tag{A.1.5}$$

which is Equation (24) in Section 4.1.

Note that $c_1(x)$ is piecewise constant, therefore the derivative of $c_1(x)$ is 0 for $x \neq 0$ and the steady-state distribution obtained using the Hyperbolic Scaling method is the same as using the Moment Closure method (compare Equations (5) and (8) in Sections 2.1 and 2.2). That is, $u_H^1(x) = u_M^1(x)$.

A.2 Movement kernel $k_\tau^1(z|x)$ with Patlak's approach

Here, we apply Patlak's approach to derive the steady-state distribution from movement kernel $k_\tau^1(z|x)$ defined by Equation (23). This requires that we place the movement kernel in Equation (23) into Equations (10) and (11) to give

$$M_1^1(x) = \begin{cases} \mu & \text{if } x < 0, \\ -\mu & \text{if } x > 0, \\ 0 & \text{if } x = 0, \end{cases} \tag{A.2.1}$$

and

$$M_2^1(x) = \sigma^2 + \mu^2. \tag{A.2.2}$$

Placing these expressions for $M_1^1(x)$ and $M_2^1(x)$ into Equation (13) and making the continuity assumption $\lim_{x\to 0^+} u_P^1(x) = \lim_{x\to 0^-} u_P^1(x)$, as in Section A.1, leads to the following solution as Equation (25) in Section 4.1:

$$u_P^1(x) = \begin{cases} \frac{\mu}{\sigma^2+\mu^2} \exp\left(\frac{2\mu}{\sigma^2+\mu^2}x\right) & \text{if } x < 0, \\ \frac{\mu}{\sigma^2+\mu^2} \exp\left(-\frac{2\mu}{\sigma^2+\mu^2}x\right) & \text{if } x \geq 0. \end{cases} \tag{A.2.3}$$

Appendix B Continuous mean velocity model

B.1 Movement kernel $k_\tau^2(z|x)$ with the Hyperbolic Scaling method

Here, we consider the movement kernel $k_\tau^2(z|x)$ defined by Equation (26) in Section 4.2. To use the Hyperbolic Scaling method, $c_2(x)$ and $D_2(x)$ are computed, using Equations (2) and (3), to give:

$$c_2(x) = \begin{cases} \frac{\mu}{\tau} & \text{if } x < -\mu, \\ -\frac{x}{\tau} & \text{if } -\mu \leq x \leq \mu, \\ -\frac{\mu}{\tau} & \text{if } x > \mu, \end{cases} \tag{B.1.1}$$

and

$$D_2(x) = \frac{\sigma^2}{\tau^2}. \tag{B.1.2}$$

In this case, the mean velocity, $c_2(x)$, is continuous and decreases to 0 as the animal approaches the central place.

By solving the ODE (4) given in Section 2.1, the Hyperbolic Scaling steady-state distribution for the movement kernel in Equation (26) is (Equation 27)

$$u_H^2(x) = \begin{cases} C_H^2 \exp\left(\frac{2\mu}{\sigma^2}x + \frac{\mu^2}{2\sigma^2}\right) & \text{if } x < -\mu, \\ C_H^2 \exp\left(-\frac{3}{2\sigma^2}x^2\right) & \text{if } -\mu \le x \le \mu, \\ C_H^2 \exp\left(-\frac{2\mu}{\sigma^2}x + \frac{\mu^2}{2\sigma^2}\right) & \text{if } x > \mu, \end{cases} \tag{B.1.3}$$

where

$$C_H^2 = \left[\frac{\sigma^2}{\mu}\exp\left(-\frac{3\mu^2}{2\sigma^2}\right) + \frac{\sqrt{2\pi}\sigma}{\sqrt{3}}\text{erf}\left(\frac{\sqrt{3}\mu}{\sqrt{2}\sigma}\right)\right]^{-1}. \tag{B.1.4}$$

B.2 Movement kernel $k_\tau^2(z|x)$ with the Moment Closure method

To apply the Moment Closure method when analysing movement kernel $k_\tau^2(z|x)$ given by Equation (26) in Section 4.2, we place Equations (B.1.1) and (B.1.2) into Equation (7) in Section 2.2 to give the steady-state distribution in Equation (28):

$$u_M^2(x) = \begin{cases} C_M^2 \exp\left(\frac{2\mu}{\sigma^2}x + \frac{\mu^2}{\sigma^2}\right) & \text{if } x < -\mu, \\ C_M^2 \exp\left(-\frac{x^2}{\sigma^2}\right) & \text{if } -\mu \le x \le \mu, \\ C_M^2 \exp\left(-\frac{2\mu}{\sigma^2}x + \frac{\mu^2}{\sigma^2}\right) & \text{if } x > \mu, \end{cases} \tag{B.2.1}$$

where

$$C_M^2 = \left[\frac{\sigma^2}{\mu}\exp\left(-\frac{\mu^2}{\sigma^2}\right) + \sqrt{\pi}\sigma\text{erf}\left(\frac{\mu}{\sigma}\right)\right]^{-1}. \tag{B.2.2}$$

B.3 Movement kernel $k_\tau^2(z|x)$ with Patlak's approach

For using Patlak's approach to analyse the movement kernel $k_\tau^2(x)$ in Equation (26), we use Equations (10) and (11) to compute $M_1^2(x)$ and $M_2^2(x)$, so that

$$M_1^2(x) = \begin{cases} \mu & \text{if } x < -\mu, \\ -x & \text{if } -\mu \le x \le \mu, \\ -\mu & \text{if } x > \mu, \end{cases} \tag{B.3.1}$$

and

$$M_2^2(x) = \begin{cases} \sigma^2 + \mu^2 & \text{if } x < -\mu \text{ or } x > \mu, \\ \sigma^2 + x^2 & \text{if } -\mu \le x \le \mu. \end{cases} \tag{B.3.2}$$

The steady-state distribution arising from Patlak's approach is obtained by placing Equations (B.3.1) and (B.3.2) into Equation (13), giving Equation (29):

$$u_P^2(x) = \begin{cases} \dfrac{C_P^2}{(\sigma^2+\mu^2)^2} \exp\left(\dfrac{2\mu}{\sigma^2+\mu^2}x + \dfrac{2\mu^2}{\sigma^2+\mu^2}\right) & \text{if } x < -\mu, \\ \dfrac{C_P^2}{(\sigma^2+x^2)^2} & \text{if } -\mu \le x \le \mu, \\ \dfrac{C_P^2}{(\sigma^2+\mu^2)^2} \exp\left(\dfrac{-2\mu}{\sigma^2+\mu^2}x + \dfrac{2\mu^2}{\sigma^2+\mu^2}\right) & \text{if } x > \mu, \end{cases} \tag{B.3.3}$$

where

$$C_P^2 = \left[\frac{1}{\mu(\sigma^2+\mu^2)} + \frac{\arctan(\mu/\sigma)}{\sigma^3} + \frac{\mu}{\sigma^2(\sigma^2+\mu^2)}\right]^{-1}. \tag{B.3.4}$$

Appendix C Differentiable mean velocity model

C.1 Movement kernel $k_\tau^3(z|x)$ with the Hyperbolic Scaling method

Here, we use PDE methods introduced in Section 2 to obtain the long-term population distributions from the underlying movement kernel $k_\tau^3(z|x)$ given by Equation (30). To apply the Hyperbolic Scaling and Moment Closure methods, the corresponding mean and variance of the velocity are calculated, using Equations (2) and (3):

$$c_3(x) = \begin{cases} \dfrac{\mu x^2}{\tau} & \text{if } x < 0, \\ -\dfrac{\mu x^2}{\tau} & \text{if } x \geq 0, \end{cases} \tag{C.1.1}$$

and

$$D_3(x) = \frac{\sigma^2}{\tau^2}. \tag{C.1.2}$$

The steady-state distribution obtained by the Hyperbolic Scaling method is obtained by placing Equations (C.1.1) and (C.1.2) into Equation (5) to give

$$u_H^3(x) = \begin{cases} C_H^3 \exp\left(\dfrac{2\mu}{3\sigma^2}x^3 - \dfrac{\mu^2}{2\sigma^2}x^4\right) & \text{if } x < 0, \\ C_H^3 \exp\left(-\dfrac{2\mu}{3\sigma^2}x^3 - \dfrac{\mu^2}{2\sigma^2}x^4\right) & \text{if } x \geq 0, \end{cases} \tag{C.1.3}$$

where

$$C_H^3 = \left[\int_{-\infty}^{0} \exp\left(\frac{2\mu}{3\sigma^2}x^3 - \frac{\mu^2}{2\sigma^2}x^4\right) \mathrm{d}x + \int_{0}^{\infty} \exp\left(-\frac{2\mu}{3\sigma^2}x^3 - \frac{\mu^2}{2\sigma^2}x^4\right) \mathrm{d}x\right]^{-1}. \tag{C.1.4}$$

C.2 Movement kernel $k_\tau^3(z|x)$ with the Moment Closure method

To use the Moment Closure method when analysing movement kernel $k_\tau^3(z|x)$ given by Equation (30) in Section 4.3, we place Equations (C.1.1) and (C.1.2) into Equation (7) to give

$$u_M^3(x) = \begin{cases} C_M^3 \exp\left(\dfrac{2\mu}{3\sigma^2}x^3\right) & \text{if } x < 0, \\ C_M^3 \exp\left(-\dfrac{2\mu}{3\sigma^2}x^3\right) & \text{if } x \geq 0, \end{cases} \tag{C.2.1}$$

where

$$C_M^3 = \left[\int_{-\infty}^{0} \exp\left(\frac{2\mu}{3\sigma^2}x^3\right) \mathrm{d}x + \int_{0}^{\infty} \exp\left(-\frac{2\mu}{3\sigma^2}x^3\right) \mathrm{d}x\right]^{-1}. \tag{C.2.2}$$

C.3 Movement kernel $k^3_\tau(z|x)$ with Patlak's approach

For Patlak's approach, $M^3_1(x)$ and $M^3_2(x)$ are computed by placing Equation (30) into Equations (10) and (11), to give:

$$M^3_1(x) = \begin{cases} \mu x^2 & \text{if } x < 0, \\ -\mu x^2 & \text{if } x \geq 0, \end{cases} \tag{C.3.1}$$

and

$$M^3_2(x) = \sigma^2 + \mu^2 x^4. \tag{C.3.2}$$

The steady-state distribution is then given by placing Equations (C.3.1) and (C.3.2) into Equation (12) to give

$$u^3_P(x) = \begin{cases} \dfrac{C^3_P}{\sigma^2 + \mu^2 x^4} \exp\left(-\sqrt{\dfrac{1}{\mu\sigma}} \left[2^{-\frac{3}{2}} \ln \left(\dfrac{|\frac{\mu}{\sigma}x^2 + \sqrt{\frac{2\mu}{\sigma}}x + 1|}{|\frac{\mu}{\sigma}x^2 - \sqrt{\frac{2\mu}{\sigma}}x + 1|} \right) \right.\right. \\ \quad \left.\left. + \dfrac{1}{\sqrt{2}} \arctan\left(-\sqrt{\dfrac{2\mu}{\sigma}}x + 1 \right) + \dfrac{1}{\sqrt{2}} \arctan\left(-\sqrt{\dfrac{2\mu}{\sigma}}x - 1 \right) \right] \right) \\ \qquad\qquad\qquad\qquad\qquad\qquad\qquad\qquad \text{if } x < 0, \\ \dfrac{C^3_P}{\sigma^2 + \mu^2 x^4} \exp\left(-\sqrt{\dfrac{1}{\mu\sigma}} \left[2^{-\frac{3}{2}} \ln \left(\dfrac{|\frac{\mu}{\sigma}x^2 - \sqrt{\frac{2\mu}{\sigma}}x + 1|}{|\frac{\mu}{\sigma}x^2 + \sqrt{\frac{2\mu}{\sigma}}x + 1|} \right) \right.\right. \\ \quad \left.\left. + \dfrac{1}{\sqrt{2}} \arctan\left(\sqrt{\dfrac{2\mu}{\sigma}}x + 1 \right) + \dfrac{1}{\sqrt{2}} \arctan\left(\sqrt{\dfrac{2\mu}{\sigma}}x - 1 \right) \right] \right) \\ \qquad\qquad\qquad\qquad\qquad\qquad\qquad\qquad \text{if } x \geq 0, \end{cases} \tag{C.3.3}$$

where C^3_P is a normalising constant, ensuring that the probability distribution integrates to 1 over the real line.

Appendix D Movement on heterogeneous landscapes

Here we give exact expressions for the functions $k_\tau^4(z|x)$, $k_\tau^5(z|x)$, $k_\tau^6(z|x)$, and $k_\tau^7(z|x)$ in Equations (41-44). These are as follows.

$$\begin{aligned} k_\tau^4(z|x) &= \frac{\phi_\tau^n(z|x)w_t(z)}{\int_0^1 \phi_\tau^n(y|x)w_t(y)\mathrm{d}y} \\ &= \begin{cases} \dfrac{1}{g_4(x)\sqrt{2\pi}\sigma}\exp\left(\dfrac{-(z-x)^2}{2\sigma^2}\right) & \text{if } z\in[0,1/3]\cup(2/3,1], \\ \dfrac{2}{g_4(x)\sqrt{2\pi}\sigma}\exp\left(\dfrac{-(z-x)^2}{2\sigma^2}\right) & \text{if } z\in(1/3,2/3], \end{cases} \end{aligned} \tag{D.1}$$

where

$$g_4(x) = \frac{1}{2}\left[\mathrm{erf}\left(\frac{x}{\sqrt{2}\sigma}\right) + \mathrm{erf}\left(\frac{x-1/3}{\sqrt{2}\sigma}\right) - \mathrm{erf}\left(\frac{x-2/3}{\sqrt{2}\sigma}\right) - \mathrm{erf}\left(\frac{x-1}{\sqrt{2}\sigma}\right)\right] \tag{D.2}$$

is a normalising function used to ensure that the probability distribution (D.1) integrates to 1.

$$\begin{aligned} k_\tau^5(z|x) &= \frac{\phi_\tau^n(z|x)w_s(z)}{\int_0^1 \phi_\tau^n(y|x)w_s(y)\mathrm{d}y} \\ &= \frac{1}{g_5(x)\sqrt{2\pi}\sigma}\exp\left(\frac{-(z-x)^2}{2\sigma^2}\right)(\sin(3\pi z)+2), \end{aligned} \tag{D.3}$$

where

$$g_5(x) = \int_0^1 \frac{1}{\sqrt{2\pi}\sigma}\exp\left(\frac{-(z-x)^2}{2\sigma^2}\right)(\sin(3\pi z)+2)\mathrm{d}z. \tag{D.4}$$

$$
\begin{aligned}
k_\tau^6(z|x) &= \frac{\phi_\tau^l(z|x)w_t(z)}{\int_0^1 \phi_\tau^l(y|x)w_t(y)\mathrm{d}y} \\
&= \begin{cases}
\frac{1}{2bg_{61}(x)}\exp\left(\frac{z-x}{b}\right) & \text{if } x\in[0,1/3] \text{ and } z\in[0,x], \\
\frac{1}{2bg_{61}(x)}\exp\left(\frac{x-z}{b}\right) & \text{if } x\in[0,1/3] \text{ and } z\in[x,1/3]\cup(2/3,1], \\
\frac{1}{bg_{61}(x)}\exp\left(\frac{x-z}{b}\right) & \text{if } x\in[0,1/3] \text{ and } z\in(1/3,2/3], \\
\frac{1}{2bg_{62}(x)}\exp\left(\frac{z-x}{b}\right) & \text{if } x\in(1/3,2/3] \text{ and } z\in[0,1/3], \\
\frac{1}{bg_{62}(x)}\exp\left(\frac{z-x}{b}\right) & \text{if } x\in(1/3,2/3] \text{ and } z\in(1/3,x], \\
\frac{1}{bg_{62}(x)}\exp\left(\frac{x-z}{b}\right) & \text{if } x\in(1/3,2/3] \text{ and } z\in(x,2/3], \\
\frac{1}{2bg_{62}(x)}\exp\left(\frac{x-z}{b}\right) & \text{if } x\in(1/3,2/3] \text{ and } z\in(2/3,1], \\
\frac{1}{2bg_{63}(x)}\exp\left(\frac{z-x}{b}\right) & \text{if } x\in(2/3,1] \text{ and } z\in[0,1/3]\cup(2/3,x], \\
\frac{1}{bg_{63}(x)}\exp\left(\frac{z-x}{b}\right) & \text{if } x\in(2/3,1] \text{ and } z\in(1/3,2/3], \\
\frac{1}{2bg_{63}(x)}\exp\left(\frac{x-z}{b}\right) & \text{if } x\in(2/3,1] \text{ and } z\in(x,1],
\end{cases}
\end{aligned}
\tag{D.5}
$$

where

$$
g_{61}(x) = 1 - \frac{1}{2}\left[\exp\left(\frac{-x}{b}\right) - \exp\left(\frac{x-1/3}{b}\right) + \exp\left(\frac{x-2/3}{b}\right) + \exp\left(\frac{x-1}{b}\right)\right], \tag{D.6}
$$

$$
g_{62}(x) = 2 - \frac{1}{2}\left[\exp\left(\frac{-x}{b}\right) + \exp\left(\frac{1/3-x}{b}\right) + \exp\left(\frac{x-2/3}{b}\right) + \exp\left(\frac{x-1}{b}\right)\right], \tag{D.7}
$$

$$
g_{63}(x) = 1 - \frac{1}{2}\left[\exp\left(\frac{-x}{b}\right) + \exp\left(\frac{1/3-x}{b}\right) - \exp\left(\frac{2/3-x}{b}\right) + \exp\left(\frac{x-1}{b}\right)\right]. \tag{D.8}
$$

$$
\begin{aligned}
k^7_\tau(z|x) &= \frac{\phi^l_\tau(z|x)w_s(z)}{\int_0^1 \phi^l_\tau(y|x)w_s(y)\mathrm{d}y} \\
&= \begin{cases} \dfrac{1}{2bg_7(x)}\exp\left(\dfrac{z-x}{b}\right)(\sin 3\pi z + 2) & \text{if } z < x, \\ \dfrac{1}{2bg_7(x)}\exp\left(\dfrac{x-z}{b}\right)(\sin 3\pi z + 2) & \text{if } z \geq x, \end{cases}
\end{aligned} \tag{D.9}
$$

where

$$
\begin{aligned}
g_7(x) = 2 &- \frac{4}{(18\pi^2b^2)^2-4}\sin(3\pi x) - \frac{108\pi^3b^3}{(18\pi^2b^2)^2-4}\cos(3\pi x) \\
&+ \left(\frac{3\pi b}{18\pi^2b^2+2}-1\right)\exp\left(\frac{-x}{b}\right) - \left(\frac{3\pi b}{18\pi^2b^2-2}+1\right)\exp\left(\frac{x-1}{b}\right).
\end{aligned} \tag{D.10}
$$

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