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Study of Wildebeest Foraging Processes Using Advection Diffusion Equation: Case of the Serengeti Ecosystem in Tanzania

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Abstract

We studied the foraging processes of wildebeest using an advection-diffusion equation. We equipped the model with data collected between 1999 and 2007 from the Serengeti ecosystem from 18 GPS-collared wildebeest. Results analysis show that wildebeest foraging behavior can be explained by advective and diffusive parameters in a heterogeneous habitat like the Serengeti ecosystem.

Keywords

Advection-Diffusion, Movement, Foraging, Random Walk

1. Introduction

Wildebeest with other ungulates usually migrate from the Serengeti National Park in northern Tanzania to the Masai Mara region in Kenya in search of high-quality plant forage [1]. This migration is an annual mass movement of millions of ungulates and other species in groups [2]. The great migration involves an estimated 1.3 million wildebeest, 200,000 zebra, and a multitude of gazelles, among various other hooved species [3]. The great migration is triggered by the flush of the green and nutritious pasture vegetation in the Serengeti plains following rains and green flushes of vegetation [2].

While the movement patterns have remained the same for centuries, the wildebeest population in the Serengeti ecosystem has been extremely variable in size, increasing from 263,000 in 1961 to fluctuating around 1.5 million [4]. In the early 1960s, the numbers of zebra and wildebeest in the Serengeti were similar while overtime, the population of zebra in Serengeti has not changed significantly in contrast to wildebeest [5], partly due to a rinderpest outbreak in the year 1960, which greatly affected wildebeest and buffalo (*Syncerus caffer*) but not zebra populations [5] [6].

In addition to the movement for food, wildebeest, as many other ungulate species, also select their habitat use based on the presence of predators [7] [8]. The main predators of wildebeest are lion (*Panthera leo*) and hyena (*Crocuta crocuta*) [4].

The advection-diffusion equation is considered to describe the transportation of different substances in moving fluids including the movements of animals [8] [9]. Diffusion describes how a group of individual particles spreads out due to the irregular motion of each particle [9]. For animal movements, diffusion is regarded as describing the distribution of a large population of animals or the expected location of an individual animal in space and time. The advection diffusion equation is viewed as an individual-based model [10].

In this study, a two-dimensional Fokker-Plank equation with diffusion and migration parameters was used to explain the foraging efficiency of wildebeest. The model was equipped with data from the Serengeti ecosystem from 18 GPS collared wildebeest. The advection and diffusion movement parameters were calculated in different seasons of the year to show how these components can be used to explain the foraging and migration of wildebeest.

Studying wildebeest foraging processes is partly rooted in animal behaviour. Therefore, the findings of this study could increase awareness of wildlife behaviour to ecologists and conservationists through understanding animals' dynamics such as animal movements and foraging patterns, predator-prey relations, and social behavior of these species, this study could be of great importance to increase awareness on how environmental variations affect the survival of different species. This is because the protection of animals is linked to the environmental conditions (such as rainfall), reproduction rates, predation pressure, and survival rates of the species [2]. Some of these dynamics are discussed in this study. The results, discussions and recommendations from this study could be helpful in management decisions for wildlife protection.

Furthermore, this study has shown how wildebeest can survive and adapt in different habitats and ecosystems. Conservation of wildlife species requires that we know enough about natural behaviour (migration patterns, foraging demands, interaction with other groups) in order to develop effective protection measures ([4] [11]). Such measures include detecting and taking measures on early clues of environmental degradation [12], changes in the reproductive outcomes of different species [7], and managing their population size, to offset illegal hunting and establish laws that protect the ecosystem [13].

2. Methods

The Advection-Diffusion Equation

The advection-diffusion equation is considered to describe the transportation of different substances in moving fluids including movements of animals [9]. Diffusion describes how a group of individual particles spreads out due to the irregular motion of each particle [10]. For animal movements, diffusion is regarded as describing the distribution of a large population of animals or the expected location of an individual animal in space and time. The advection diffusion equation is viewed as individual-based model [11].

In this study, we introduced the mathematical theory behind simple random walk that follows Brownian motion and diffusive processes in general. The model was extended to include drift by making the probability of moving in a certain direction greater thus creating a drift-diffusion (advection diffusion) equation [10] [14]. Wildebeest are foraging animals that move towards a certain preferred forage target, thus, such paths that contain a consistent bias in a preferred forage target are termed biased random walks (BRWs) [14]. The BRWs were used to explain the foraging process of wildebeest in two dimensions.

Consider the Brownian motion in two dimensions that include movements and probabilities that are spatially dependent [9].

Suppose that an individual moves on a two dimensional lattice. At each time step τ an individual can move a distance δ either up, down, left, or right with probabilities dependent on location given by $u(x,y), d(x,y), l(x,y)$ and $r(x,y)$ respectively with $u+d+l+r \le 1$, or remain at the same location with probability $1-u(x,y)-d(x,y)-l(x,y)-r(x,y)$.

To calculate the probability a walker jumps on a two dimensional lattice at one time step based on the previous time step at a time $(m+1)\tau$, Consider the probability of the walker in position n is equal to the probability that it was already there times the probability that it stayed there, plus the probability that it was one position to the left times the probability that it jumped to the right, plus the probability that it was one position to the right times the probability that it jumped to the left, plus the probability that it was one position up times the probability that it jumped down, plus the probability that it was one position down times the probability that it jumped up. This can be expressed as follows:

$$\begin{aligned} & p\left[n\delta,(m+1)\tau\right] \\ & =(1-r-l-u-d)\,p(n\delta,m\tau)+rp\left[(n-1)\delta,m\tau\right]+lp\left[(n+1)\delta,m\tau\right] \\ & \quad +up\left[(n-1)\delta,m\tau\right]+dp\left[(n+1)\delta,m\tau\right] \end{aligned} \tag{1}$$

where $p(0,0)=1$ and $p(n\delta,0)=0$ for $n \ne 0$.

Rewriting Equation (1), gives the following

$$\begin{aligned} & p\left[n\delta,(m+1)\tau\right]-p(n\delta,m\tau) \\ & =-(r+l+u+d)\,p(n\delta,m\tau)+rp\left[(n-1)\delta,m\tau\right]+lp\left[(n+1)\delta,m\tau\right] \\ & \quad +up\left[(n-1)\delta,m\tau\right]+dp\left[(n+1)\delta,m\tau\right] \end{aligned} \tag{2}$$

Using Taylor series expansion to calculate the probability function $p\left[n\delta,(m+1)\tau\right]$:

From
$$p\left[(n\pm1)\delta,m\tau\right]=p(n\delta,m\tau)\pm\delta\frac{\partial p}{\partial x}+\frac{1}{2}\delta^2\frac{\partial^2 p}{\partial x^2}\pm\frac{1}{6}\delta^3\frac{\partial^3 p}{\partial x^3}+O\left(\delta^4\right)$$
$$+p(n\delta,m\tau)\pm\delta\frac{\partial p}{\partial y}+\frac{1}{2}\delta^2\frac{\partial^2 p}{\partial y^2}\pm\frac{1}{6}\delta^3\frac{\partial^3 p}{\partial y^3}+O\left(\delta^4\right) \quad (3)$$

Then,
$$p\left[n\delta,(m+1)\tau\right]=p(n\delta,m\delta)+\tau\frac{\partial p}{\partial t}+O\left(\tau^2\right) \quad (4)$$

All the derivatives are taken at $(x=y=n\delta,t=m\tau)$.

Therefore, the left-hand side of Equation (2) becomes
$$p(n\delta,m\tau)+\tau\frac{\partial p}{\partial t}+O\left(\delta^2\right)-p(n\delta,m\tau)=\tau\frac{\partial p}{\partial t}+O\left(\tau^2\right) \quad (5)$$

The right-hand side of Equation (2) can be rewritten in the following ways
$$\frac{1}{2}(r+l)right-hand\left(p\left[(n-1)\delta,m\tau\right]-2p(n\delta,m\tau)+p\left[(n+1)\delta,m\tau\right]\right)$$
$$-\frac{1}{2}(r-l)\left(p\left[(n+1)\delta,m\tau\right]-p\left[(n-1)\delta,m\tau\right]\right)$$
$$+\frac{1}{2}(u+d)\left(p\left[(n-1)\delta,m\tau\right]-2p(n\delta,m\tau)+p\left[(n+1)\delta,m\tau\right]\right)$$
$$-\frac{1}{2}(u-d)\left(p\left[(n+1)\delta,m\tau\right]-p\left[(n-1)\delta,m\tau\right]\right) \quad (6)$$

The first term of the right hand side of Equation (6) can be expanded by the Taylor series as follows
$$\frac{1}{2}(r+l)\left(p(n\delta,m\tau)-\delta\frac{\partial p}{\partial x}+\frac{1}{2}\delta^2\frac{\partial^2 p}{\partial x^2}-\frac{1}{6}\delta^3\frac{\partial^3 p}{\partial x^3}+O\left(\delta^4\right)\right.$$
$$\left.-2p(n\delta,m\tau)+p(n\delta,m\tau)+\delta\frac{\partial p}{\partial x}+\frac{1}{2}\delta^2\frac{\partial^2 p}{\partial x^2}+\frac{1}{6}\delta^3\frac{\partial^3 p}{\partial x^3}+O\left(\delta^4\right)\right)$$
$$+\frac{1}{2}(u+d)\left(p(n\delta,m\tau)-\delta\frac{\partial p}{\partial y}+\frac{1}{2}\delta^2\frac{\partial^2 p}{\partial y^2}-\frac{1}{6}\delta^3\frac{\partial^3 p}{\partial y^3}+O\left(\delta^4\right)\right.$$
$$\left.-2p(n\delta,m\tau)+p(n\delta,m\tau)+\delta\frac{\partial p}{\partial y}+\frac{1}{2}\delta^2\frac{\partial^2 p}{\partial y^2}+\frac{1}{6}\delta^3\frac{\partial^3 p}{\partial y^3}+O\left(\delta^4\right)\right) \quad (7)$$

Simplifying gives
$$(r+l)\left(\frac{\delta^2}{2}\frac{\partial^2 p}{\partial x^2}+O\left(\delta^4\right)\right)+(u+d)\left(\frac{\delta^2}{2}\frac{\partial^2 p}{\partial y^2}+O\left(\delta^4\right)\right) \quad (8)$$

And the last term of the right hand side of Equation (6) can be expanded by Taylor series to give
$$-\frac{1}{2}(r-l)\left(p(n\delta,m\tau)+\delta\frac{\partial p}{\partial x}+\frac{1}{2}\delta^2\frac{\partial^2 p}{\partial x^2}+\frac{1}{6}\delta^3\frac{\partial^3 p}{\partial x^3}+O\left(\delta^4\right)\right.$$
$$\left.-p(n\delta,m\tau)+\delta\frac{\partial p}{\partial x}-\frac{1}{2}\delta^2\frac{\partial^2 p}{\partial x^2}+\frac{1}{6}\delta^3\frac{\partial^3 p}{\partial x^3}-O\left(\delta^4\right)\right)$$
$$-\frac{1}{2}(u-d)\left(p(n\delta,m\tau)+\delta\frac{\partial p}{\partial y}+\frac{1}{2}\delta^2\frac{\partial^2 p}{\partial y^2}+\frac{1}{6}\delta^3\frac{\partial^3 p}{\partial y^3}+O\left(\delta^4\right)\right.$$

$$-p(n\delta, m\tau) + \delta\frac{\partial p}{\partial y} - \frac{1}{2}\delta^2\frac{\partial^2 p}{\partial y^2} + \frac{1}{6}\delta^3\frac{\partial^3 p}{\partial y^3} - O(\delta^4)\Bigg) \tag{9}$$

Simplifying and ignoring higher order terms gives

$$-(r-l)\left(\delta\frac{\partial p}{\partial x}\right) - (u-d)\left(\delta\frac{\partial p}{\partial y}\right) \tag{10}$$

Combining Equations (5), (8) and (10) gives

$$\begin{aligned}\tau\frac{\partial p}{\partial t} &= (r+l)\left(\frac{\delta^2}{2}\frac{\partial^2 p}{\partial x^2}\right) + (u+d)\left(\frac{\delta^2}{2}\frac{\partial^2 p}{\partial y^2}\right) - (r-l)\left(\delta\frac{\partial p}{\partial x}\right) \\ &\quad - (u-d)\left(\delta\frac{\partial p}{\partial y}\right) + O(\delta^4) + O(\tau^2)\end{aligned} \tag{11}$$

Divide by τ, gives

$$\begin{aligned}\frac{\partial p}{\partial t} &= (r+l)\left(\frac{\delta^2}{2\tau}\frac{\partial^2 p}{\partial x^2}\right) - (r-l)\left(\frac{\delta}{\tau}\frac{\partial p}{\partial x}\right) + O\left(\frac{\delta^4}{\tau}\right) + O(\tau) \\ &\quad + (u+d)\left(\frac{\delta^2}{2\tau}\frac{\partial^2 p}{\partial y^2}\right) - (u-d)\left(\frac{\delta}{\tau}\frac{\partial p}{\partial y}\right) + O\left(\frac{\delta^4}{\tau}\right) + O(\tau)\end{aligned} \tag{12}$$

Let $k_1 = r+l; k_2 = u+d; \epsilon_1 = r-l; \epsilon_2 = u-d$, it can be defined that

$$\frac{\partial p}{\partial t} = \frac{k_1\delta^2}{2\tau}\frac{\partial^2 p}{\partial x^2} - \frac{\epsilon_1\delta}{\tau}\frac{\partial p}{\partial x} - \frac{k_2\delta^2}{2\tau}\frac{\partial^2 p}{\partial y^2} - \frac{\epsilon_2\delta}{\tau}\frac{\partial p}{\partial y} + O\left(\frac{\delta^4}{\tau}\right) + O(\tau) \tag{13}$$

Taking limits as $\tau \to 0$ and $\delta \to 0$, such that the following limits are positive and definite $D_x = \lim_{\delta,\tau\to 0}\frac{k_1\delta^2}{2\tau}$, $D_y = \lim_{\delta,\tau\to 0}\frac{k_2\delta^2}{2\tau}$, $u_x = \lim_{\delta,\tau,\epsilon_1\to 0}\frac{\epsilon_1\delta}{\tau}$ and $u_y = \lim_{\delta,\tau,\epsilon_2\to 0}\frac{\epsilon_2\delta}{\tau}$.

Taking the limits as $\delta, \tau, \epsilon_1, \epsilon_2 \to 0$ such that D_x, D_y, u_x, u_y all tend to constants gives

$$\frac{\partial p}{\partial t} = -\nabla\cdot(up) + \nabla\cdot(D\nabla p) \tag{14}$$

Equation (14) is the same as

$$\frac{\partial p}{\partial t} = \frac{\partial}{\partial x}\left(D_x\frac{\partial p}{\partial x}\right) + \frac{\partial}{\partial y}\left(D_y\frac{\partial p}{\partial y}\right) - \frac{\partial}{\partial x}(u_x p) - \frac{\partial}{\partial y}(u_y p) \tag{15}$$

Solving Equation (15) gives the following probability mass function

$$P(x,y,t) = \frac{1}{4\pi t\sqrt{D_x D_y}}\mathrm{e}^{-\left(\frac{(x-u_x t)^2}{4D_x t} + \frac{(y-u_y t)^2}{4D_y t}\right)} \tag{16}$$

This study used GPS data from the Serengeti ecosystem from 18 collared wildebeest. The GPS data for collared wildebeest on a 2D lattice was fitted to show random walk trajectories for each wildebeest. The positions (*x* and *y*) show how different animals walk randomly in the Serengeti ecosystem. Random walk trajectories for 5 wildebeest were plotted to visualize the movement trends (**Figure**

1), and then all 18 wildebeest trajectories were plotted (Figure 2). The movement of wildebeest from Southern Serengeti to the western part and continues to the northern part heading towards Masai Mara in Kenya was observed. There is a consistent movement of animals in a specified direction (biased random walk).

The average position and distance of each walker were calculated from the recorded data. The GPS data used in this study were recorded after each time step τ (6 hours) where an individual animal can move following the advection-diffusion Equation (15). Each animal generated its jump probabilities depending on its movement patterns and foraging needs as recorded by the GPS data.

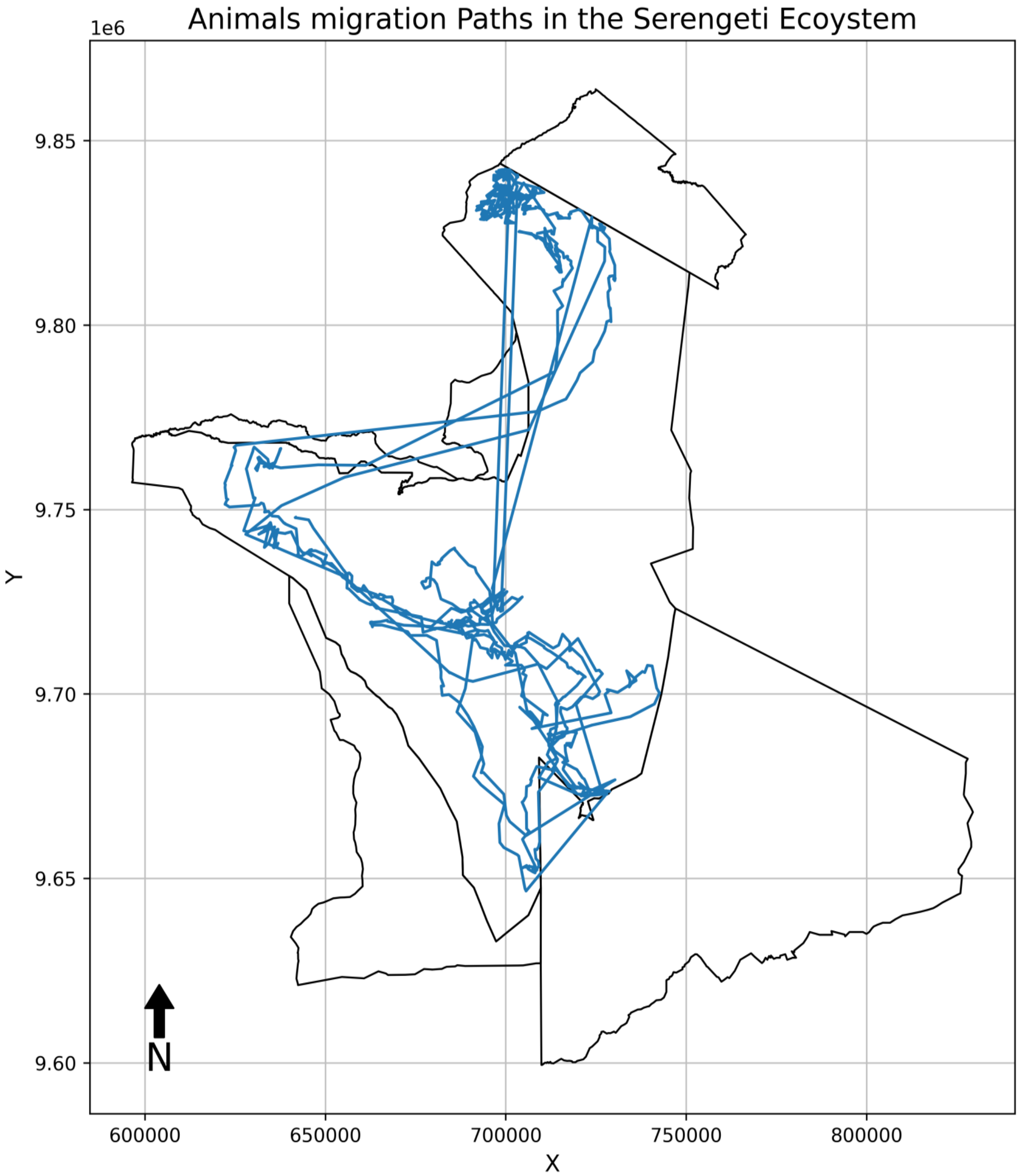

Figure 1. Individual random walk trajectories of 5 wildebeest on a 2D lattice (units of the grid are in UTM).

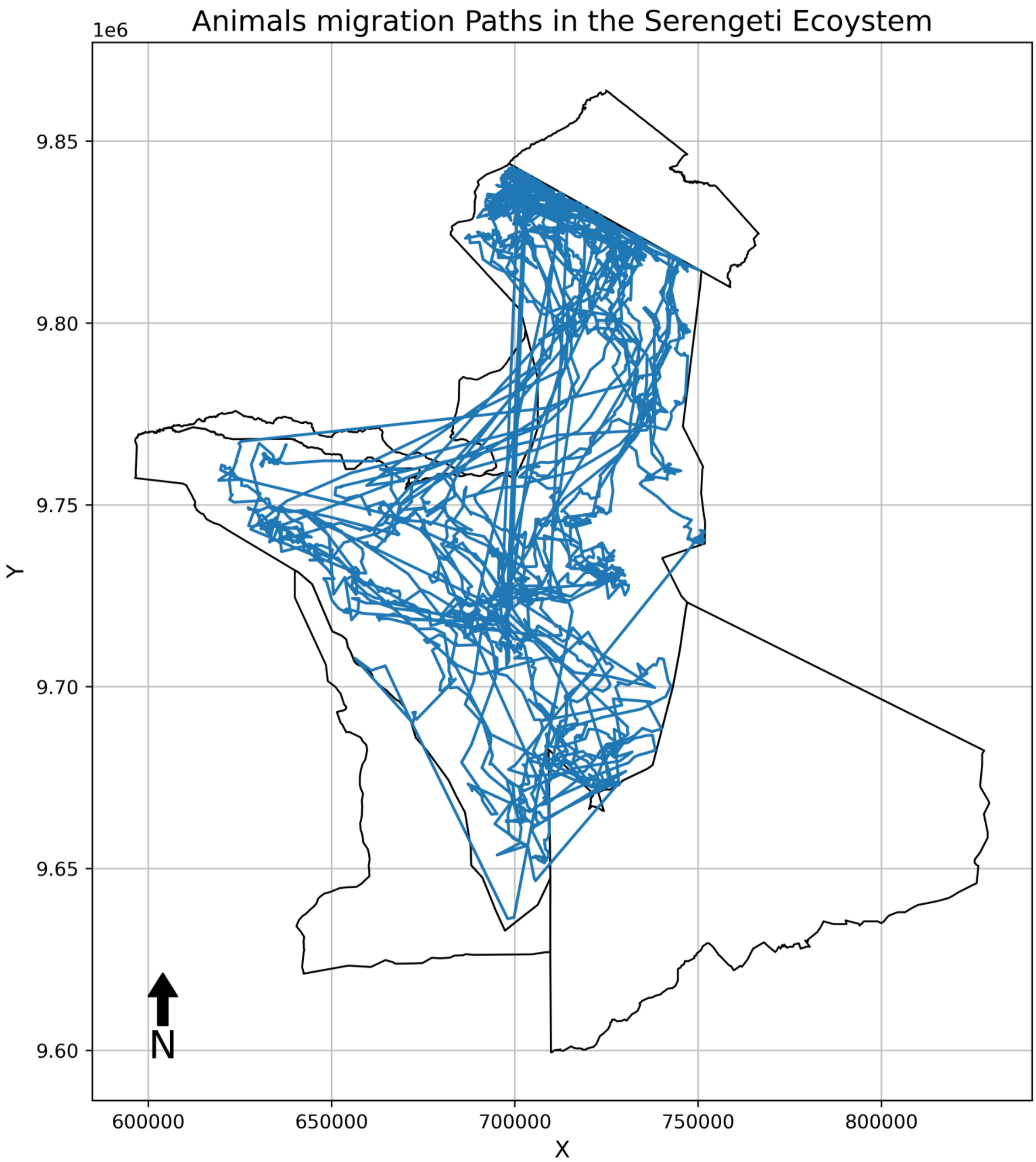

Figure 2. Individual random walk trajectories of 18 wildebeest on a 2D lattice (units of the grid are in UTM).

The random walk was motivated by diffusion and advection movement parameters in two dimensions (from equation 15). The diffusion (rate of spread) parameters were D_x and D_y in x and y directions respectively while the advective (migration) parameters were u_x and u_y in x and y directions respectively. These movement parameters were calculated by fitting the GPS data to the mathematical model (Equation (15)) for each year. The movement parameters were calculated with the help of the python computer software. Mathematical model (15) was translated into python code, and the GPS data was fitted into the model to produce diffusion and advection (migration) movement parameters. The calculated movement parameters are shown in **Table 1**.

Table 1. Calculated hourly average diffusion and advection movement parameters from the advection diffusion equation for each year.

Year	D_x (M^2/Hour)	D_y (M^2/Hour)	u_x (M/Hour)	u_y (M/Hour)
1999	112,429.80	102,578.94	12.74	19.47
2000	113,845.89	101,548.44	−8.33	−14.96
2003	116,051.93	104,569.41	−12.95	5.24
2004	116,139.19	104,336.58	22.80	6.76
2005	115,445.82	104,335.65	2.38	12.66
2006	116,139.19	104,648.03	11.87	23.79
2007	113,988.47	102,710.10	14.78	23.84

There is large variability between directed (u_x and u_y) and dispersive (D_x and D_y) components of the movement in different years. The dispersive components seem to be larger than the directed components (**Table 1**). But it must be understood that the unit for D_x and D_y is M^2 while the unit of u_x and u_y is M. There is a small variability in diffusion parameters for different years. This shows that the annual rate at which animals spread to search for forage resources at different seasons of the year is constant. The migration parameters (advection) seem to be changing over years. In the following section wildebeest seasonal movement patterns was analysed.

3. Results

3.1. Wildebeest Movement Patterns in the Dry Season

Usually, the dry season starts in June where most columns of wildebeest in Serengeti seem to be moving north migrating to seek fresh grazing and water [7]. Wildebeest slowly start their movements (in May) from southern Serengeti following fresh grass in central Serengeti [7]. Large wildebeest movements are observed heading to seek forage refuge in northern woodlands of Serengeti national park and Masai Mara National Reserve in Kenya when the southern highlands (south Serengeti ecosystem) go dry (**Figure 3** and **Figure 4**). When the dry season starts to hit in June, large concentrations of wildebeest are observed in the west of Serengeti and on the southern banks of Grumeti River [12]. Wildebeest congregate around this area forming large herds before crossing dangerous rivers. This is the toughest moment of their journey as each wildebeest must face the challenge of crossing the crocodile-infested-rivers. Late June and July, large herds of wildebeest continue to head north crossing the Mara River in the north of Serengeti to Masai Mara National Reserve in Kenya. By July most wildebeest herds are foraging around the northern woodlands of Serengeti National Park and Masai Mara National Reserve in Kenya. This area is characterized by short diffusion movements with little migration from place to place (**Figure 3** and **Table 2**).

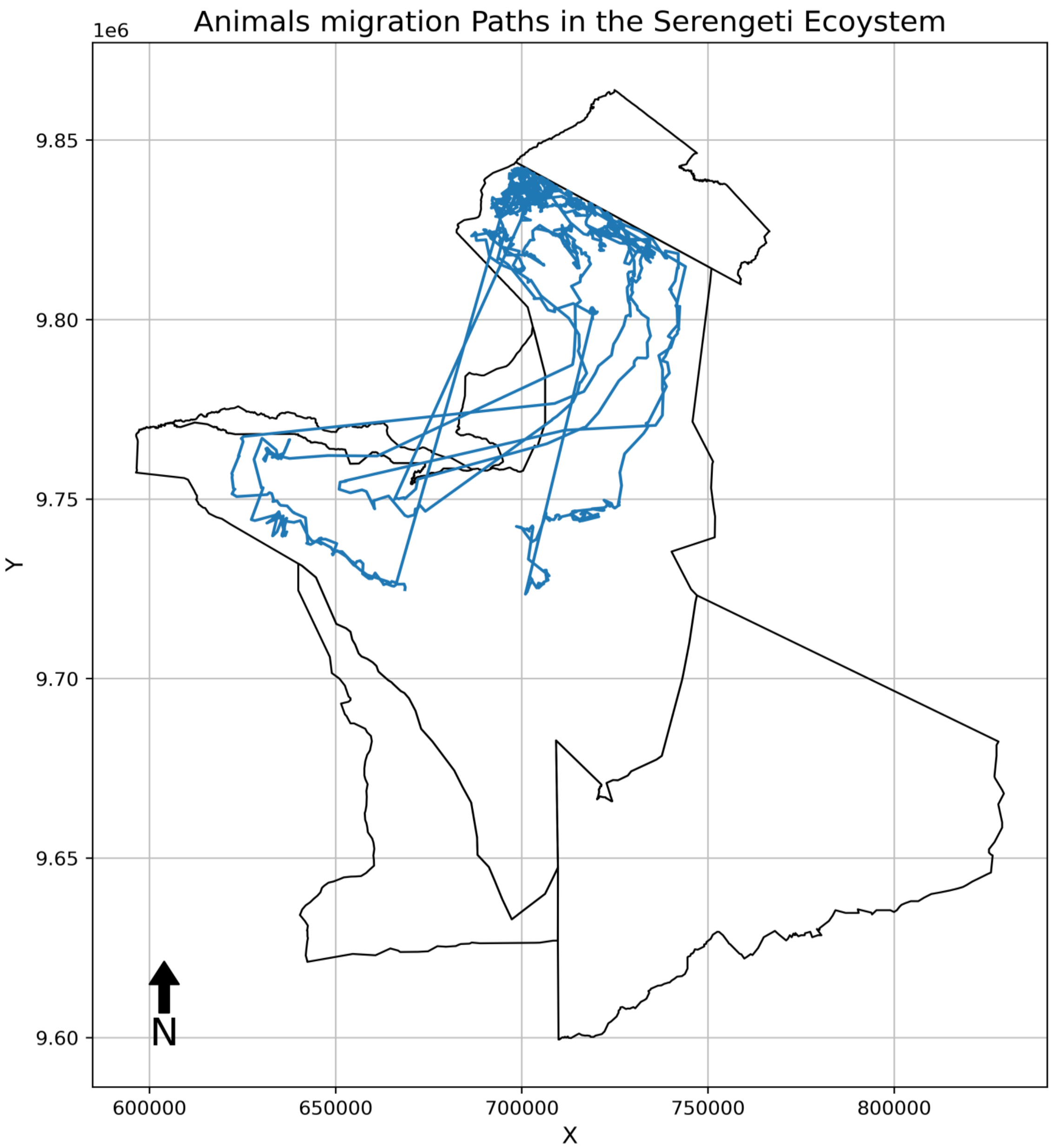

Figure 3. Individual random walk trajectories for 5 wildebeest on a 2D plane in the dry season (the units of the grid are in UTM).

The trajectories show the migration from the central Serengeti towards the western part of the ecosystem. Wildebeest arrive in the northern woodlands of Serengeti national park and Masai Mara in Kenya. Figure 3 and Figure 4 show the northern part of the Serengeti ecosystem where most of the movements take place in the dry season.

The average advection and diffusion movement parameters for the dry season are summarized in the following Table 2.

3.2. Wildebeest Movement Patterns in Wet Season

The wet season starts in November to May. Short rains start in early November

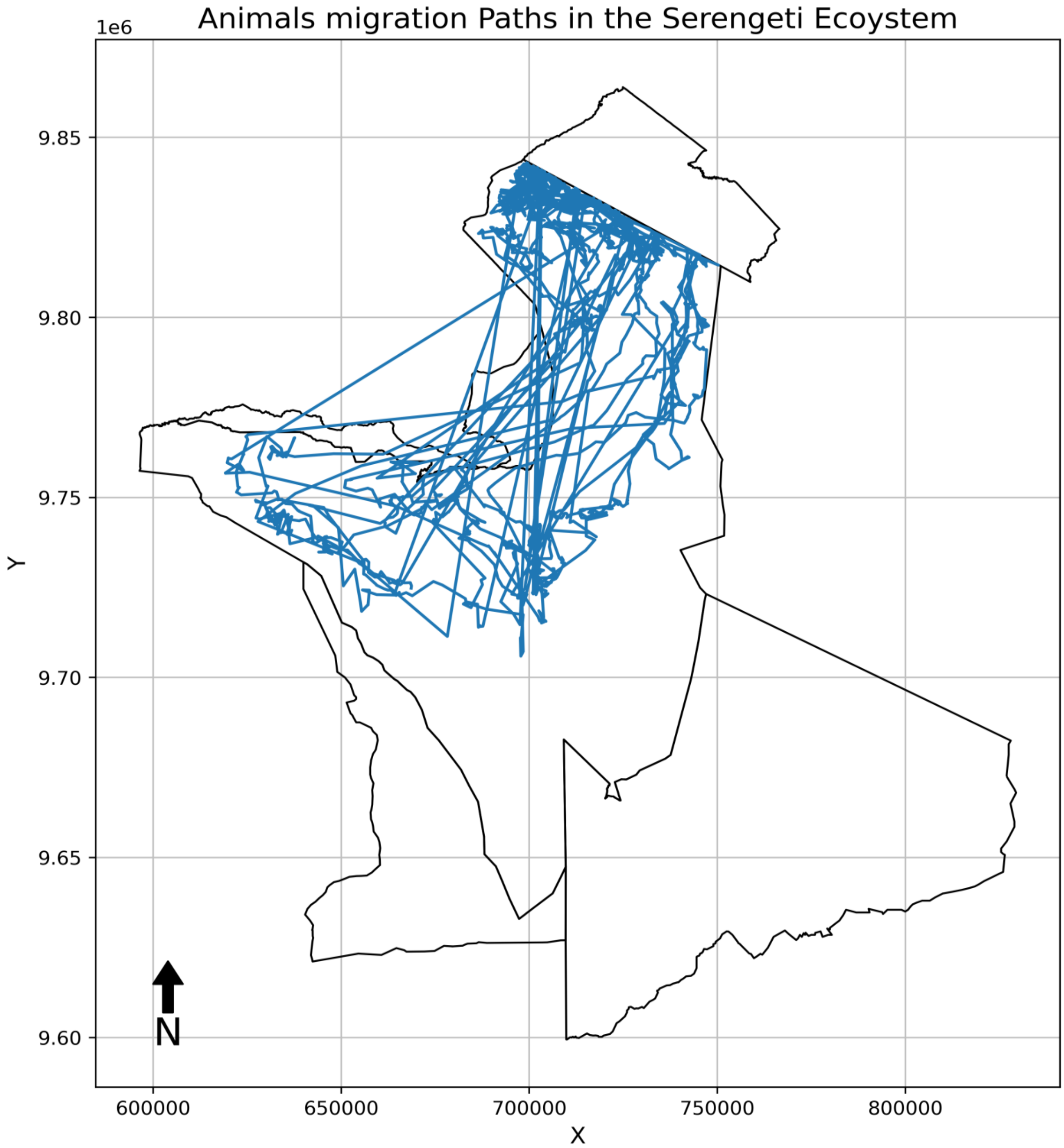

Figure 4. Individual random walk trajectories for 18 wildebeest on a 2D lattice in dry season (the units of the grid are in UTM).

Table 2. Dry season hourly average diffusion and advection movement parameters calculated from the advection diffusion equation for each year.

Year	D_x (M^2/Hour)	D_y (M^2/Hour)	u_x (M/Hour)	u_y (M/Hour)
1999	88,243.43	84,281.22	11.32	24.89
2000	89,815.63	82,734.75	−5.12	−1.10
2003	91,633.66	85,883.85	−15.50	12.82
2005	91,070.901	85,671.36	0.50	20.18
2006	91,743.01	85,986.33	11.43	26.86
2007	90,965.52	85,257.63	−8.04	10.00

[1] and wildebeest start their journey back to the Serengeti ecosystem. By December most of wildebeest herds arrive on the short glass plains of the southern Serengeti from the north. Large wildebeest movements (both advection and diffusion) are observed during this season (**Figure 5** and **Table 3**). During the wet season wildebeest spread around south and east of Seronera, Ndutu and around the Ngorongoro conservation area. They disperse across these plains feeding on fresh and nutritious grass [12]. Most wildebeest calve late January or early February [7]. They stay there around January, February and March and gradually, they spread west across these plains. In the wet season, there is high average

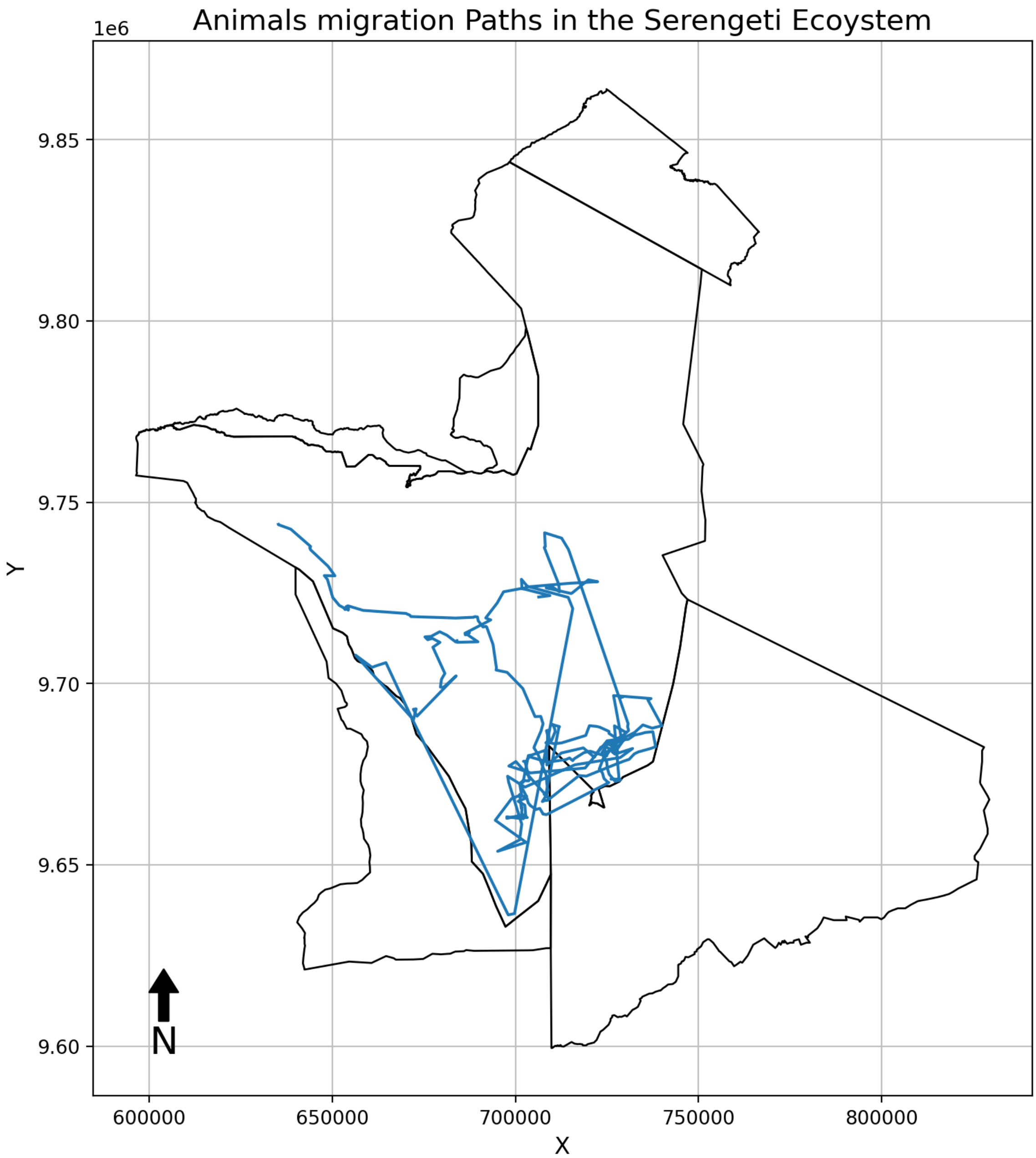

Figure 5. Individual random walk trajectories for 5 wildebeest on a 2D lattice in wet season (the units of the grid are in UTM).

distances travelled by wildebeest in the wet season compared to the dry season (see Table 3). The rate of spread (diffusion) is the highest and compared to other seasons of the year.

Around April, wildebeest start to drift north-west towards the fresh grass of the central Serengeti, drawing with them thousands of zebra, Thomson's Gazelles and other ungulates [2]. Therefore, the annual wildebeest migration is a response to local cues when they search especially following rainfall, nutritious grass and water.

Wildebeest arrive in the Serengeti national park from the Masai Mara in Kenya. Figure 5 and Figure 6 show the southern part of Serengeti plains. Most

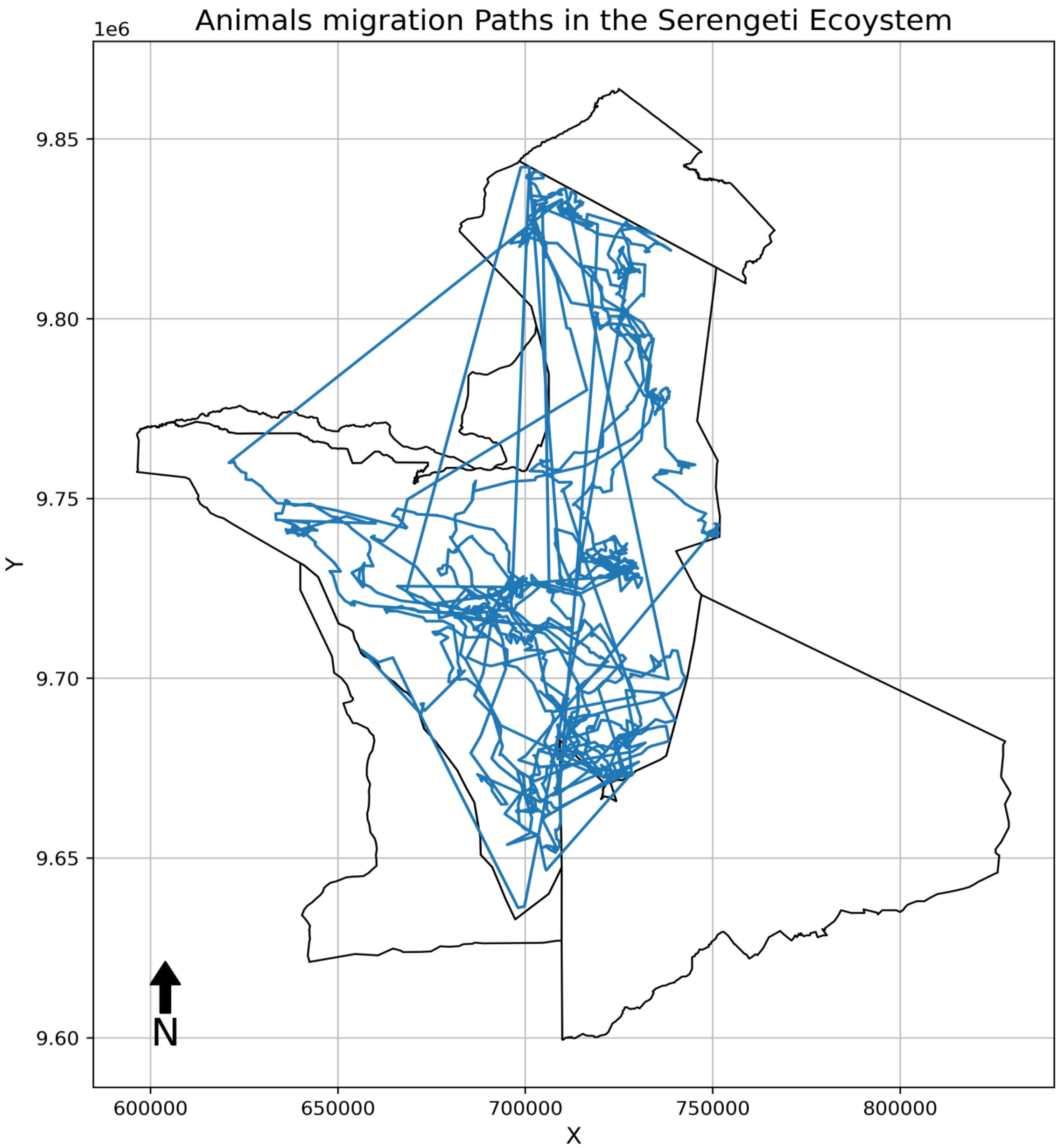

Figure 6. Individual random walk trajectories for 18 wildebeest on a 2D lattice in wet season (the units of the grid are in UTM).

of the movements take place in this area during the wet season with little migration towards the central Serengeti.

The average advection and diffusion movement parameters for the dry season are summarized in the following **Table 3**.

4. Discussion

A consistent movement of wildebeest towards specific directions was observed (**Figure 3** to **Figure 6**). Thus, such paths that contain a consistent movement in a preferred direction are termed biased random walks (BRWs) [14]. Therefore, the central question was to address the biased random walk in relation to foraging efficiency. The key idea of movement ecology is that animals move in response to internal needs such as hunger and thirst and external needs such as avoidance of predators and responding to local landscape variables such as looking for favorable forage targets [15] [16]. Forage resources in the Serengeti ecosystem are heterogeneously distributed in space. Wildebeest (in their herds) take advantage of this spatial distribution of resources by selecting patches of high resource abundance or traveling to locate them in order to inhabit. The wet season, when resources are plentiful wildebeest travel longer distances through both advection and diffusion (**Table 3**) compared to dry seasons (**Table 2**) [1] [8]. This is because during the dry season forage resources are low; hence they spend more time in areas of low resource abundance to maximize their intake [17]. Therefore, the movement trajectories depicted in **Figure 3** to **Figure 6** are a result of wildebeest responding to their forage needs. This wildebeest movement pattern was expected as it has been explained in different literature.

Wildebeest in the Serengeti ecosystem are migratory species that exhibit consistent large-scale directed movements that lead to a net displacement in a unique direction as evident in **Figure 3** to **Figure 6**. This is a characteristic of animal migration [15]. Wildebeest travel across different habitats through directed movement parameters and they spread across different habitats through diffusive parameters. Therefore, the great migration of wildebeest to different habitats is the result of directed movements (searching for forage resources) and

Table 3. Wet season hourly average diffusion and advection movement parameters calculated from the advection diffusion equation for each year.

Year	D_x (M^2/Hour)	D_y (M^2/Hour)	u_x (M/Hour)	u_y (M/Hour)
1999	169,107.17	18,125.18	16.01	10.41
2000	170,390.74	159,220.77	−16.48	−57.39
2003	173,406.51	161,325.01	−4.74	13.70
2004	173,406.51	160,844.88	30.08	9.07
2005	173,406.51	161,325.01	10.35	−49.94
2006	173,406.51	161,325.01	−15.04	−87.03
2007	168,043.42	156,335.58	56.43	54.43

they spread across different habitats to utilize the resources through diffusive trends.

The extent to which wildebeest can be random or dispersive depends on habitat selection, socialization, and avoidance of predators ([18] [19]). Wildebeest are foraging animals and usually travel in groups making movement decisions that depend on forage availability but also their social interactions [18]. Therefore, the stability and direction of their group largely depend on the knowledge about the quality and location of the food source, avoidance of predators and the ability of the informed individuals to influence group decisions to move to a desired direction [16].

As observed in this study, during the dry seasons or when resources are scarce, wildebeest prefer to move further away from each other (increased repulsion) to reduce competition while grazing [17]. In such cases, they spread making short movements to maximize their daily grass intake.

Predation pressure is another factor that affects foraging efficiency of wildebeest. This occurs when an animal makes a choice between choosing a patch with good forage while reducing predation risks [7]. The fear for predation determines the patch an animal may select and how long it may stay in that area [17].

The nature of the habitat may determine how advective and diffusive factors may determine wildebeest forage. Usually wildebeest avoid dangerous habitats such as along rivers or water sources where predators may hide [17]. Wildebeest cross such habitats through drift (higher advective) forces and they avoid spreading to reduce chances that prevent herd formation. Therefore dispersive and advective components of wildebeest movements are useful for searching and acquiring of forage resources and avoidance of predators.

This observation on foraging efficiency has certainly been described by other authors for various herbivore species. For instance [18] explained the spatial distribution of African savannah herbivores. They urge that, wildebeest were positively associated with normalized difference vegetation index (NDVI) while foraging. This shows that wildebeest make movement decisions depending on the environmental gradients and responses to conspecifics.

It can be concluded that, wildebeest foraging behavior can be explained by the advection-diffusion equation. The random walk trajectories are responses to different habitats, seasons and responses to conspecifics [7]. Such changes in behaviour could be a result of changes in the nutritional requirements of the animals at different times of the year as a result of meeting different needs such as calving [7].

5. Conclusions

We have shown how the movement patterns of wildebeest can be described by the advection-diffusion equation when they respond to environmental variables like water and grass.

Theoretical predictions point out that partial differential equations (PDEs) are useful for examining the interaction between habitat geometry and competitive coexistence [20]. The PDEs models developed in this study have successfully captured the theoretical predictions that the movement and diffusion of the two species' populations are motivated by a search for better forage availability and by avoiding predators. Researchers conclude that the survival of the two prey species is primarily affected by climate and predation, particularly from lions and hyenas.

Conflicts of Interest

The authors declare no conflicts of interest regarding the publication of this paper.

References

[1] Torney, C. *et al.* (2018) From Single Steps to Mass Migration: The Problem of Scale in the Movement Ecology of the Serengeti Wildebeest. *Philosophical Transactions of the Royal Society B*: *Biological Sciences*, **373**, Article ID: 20170012. https://doi.org/10.1098/rstb.2017.0012

[2] Holdo, R. M., *et al.* (2011) Predicted Impact of Barriers to Migration on the Serengeti Wildebeest Population. *PLOS ONE*, **6**, e16370. https://doi.org/10.1371/journal.pone.0016370

[3] Grange, S., Duncan, P., Gaillard, J.M., Sinclair, A. R. E., Gogan, P. J. P., Packer, C., Hofer, H. and East, M. (2004) What Limits the Serengeti Zebra Population? *Oecologia*, **140**, 523-532. https://doi.org/10.1007/s00442-004-1567-6

[4] Mduma, S.A.R., Sinclair, A.R.E. and Hilborn, R. (1999) Food Regulates the Serengeti Wildebeest: A 40-Year Record. *Journal of Animal Ecology*, **68**, 1101-1122. https://doi.org/10.1046/j.1365-2656.1999.00352.x

[5] Duncan, P.T. *et al.* (1990) Comparative Nutrient Extraction from Forages by Grazing Bovids and Equids: A Test of the Nutritional Model of Equid/Bovid Competition and Coexistence. *Oecologia*, **84**, 411-418. https://doi.org/10.1007/BF00329768

[6] Menard, C., Duncan, P., Fleurance, G., Georges, J. Y. and Lila, M. (2002) Comparative Foraging and Nutrition of Horses and Cattle in European Wetlands. *Journal of Applied Ecology*, **39**, 120-133. https://doi.org/10.1046/j.1365-2664.2002.00693.x

[7] Hopcraft, J.G.C. (2010) Ecological Implications of Food and Predation Risk for Herbivores in the Serengeti. Groningen. https://research.rug.nl/en/publications/ecological-implications-of-food-and-predation-risk-for-herbivores

[8] Hopcraft, J.G.C., Morales, J.M., Beyer, H.L., Borner, M., Mwangomo, E., Sinclair, A. R.E., Olff, H. and Haydon, D.T. (2014) Competition, Predation and Migration: Individual Choice Patterns of Serengeti Migratnts Catured by Hierarchical Models. *Ecological Monographs*, **84**, 355-372. https://doi.org/10.1890/13-1446.1

[9] Okubo, A. and Levin, S.A. (2001) Diffusion and Ecological Problems Modern Perspectives. Springer, New York.

[10] Sibert, J.R. *et al.* (1999) An Advection-Diffusion-Reaction Model for the Estimation of Fish Movement Parameters from Tagging Data, with Application to Skipjack Tuna (*Katsuwonus pelamis*). *Canadian Journal of Fisheries and Aquatic Sciences*,

56, 925-938. https://doi.org/10.1139/f99-017

[11] Sagamiko, T., Shaban, N., Nahonyo, C. and Makinde, O. (2015) Optimal Control of a Threatened Wildebeest-Lion Prey-Predator System in the Serengeti Ecosystem. *Open Journal of Ecology*, **5**, 110-119. https://doi.org/10.4236/oje.2015.54010

[12] Codling, E.A., Plank, M.J. and Benhamou, S. (2008) Random Walk Models in Biology. *Journal of the Royal Society Interface*, **5**, 813-834. https://doi.org/10.1098/rsif.2008.0014

[13] Mduma, S.A.R. (1996) Serengeti Wildebeest Population Dynamics: Regulation, Limitation and Implication for Harvesting. PhD Thesis, University of British Columbia, Vancouver.

[14] Kideghesho, J. (2010) 'Serengeti Shall Not Die': Transforming an Ambition into a Reality. *Tropical Conservation Science*, **3**, 228-248. https://doi.org/10.1177/194008291000300301

[15] Fagan, W.F. (2019) Improved Foraging by Switching between Diffusion and Advection : Benefits from Movement that Depends on Spatial Context. *Theoretical Ecology*, **13**, 127-136. https://doi.org/10.1007/s12080-019-00434-w

[16] Couzin, I, *et al*. (2002) Collective Memory and Spatial Sorting in Animal Groups. *Journal of Theoretical Biology*, **218**, 1-11. https://doi.org/10.1006/jtbi.2002.3065

[17] Ferguson, E.A., Matthiopoulos, J. and Insall, R.H. (2017) Statistical Inference of the Mechanisms Driving Collective Cell Movement. *Journal of the Royal Statistical Society Series C: Applied Statistics*, 66, 869-890. https://doi.org/10.1111/rssc.12203

[18] Anderson, T.M., *et al*. (2016) The Spatial Distribution of African Savannah Herbivores: Species Associations and Habitat Occupancy in a Landscape Context. *Philosophical Transactions of the Royal Society B: Biological Sciences*, **371**, Article ID: 20150314. https://doi.org/10.1098/rstb.2015.0314

[19] Ma, Q., Johansson, A. and Sumpter, D.J.T. (2011) A First-Principle Derivation of Animal Group Size Distributions. *Journal of Theoretical Biology*, **283**, 35-43. https://doi.org/10.1016/j.jtbi.2011.04.031

[20] Holmes, E.E., *et al*. (1994) Partial Differential Equations in Ecology: Spatial Interactions and Population Dynamics. *Ecology*, **75**, 17-29. https://doi.org/10.2307/1939378