Diffusion Processes in Biology with Special Reference to Insect Dispersal

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Abstract

Analysis of the movement patterns of animals using diffusion processes helps to understand and predict the dispersal rate, which is a key parameter in spatial population dynamics. Diffusion processes have been used to model many processes in biology, including dispersal of pest insects such as mosquitoes and tsetse flies. In this essay, we review the formal mathematical work on diffusion processes, including but not limited to stochastic processes, Markov processes, random walks, reflection and absorption boundaries, and first passage problems. The results are then applied to the dispersal of tsetse flies (Glossina spp), where simulations are used to evaluate their movement pattern.

Keywords: Diffusion equation, spatial dispersal, movement pattern, tsetse flies, survival and recapture probabilities, random walk, population dynamics.

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1. Introduction

Knowledge about the movement pattern of insects is significant in understanding and predicting population dynamics in space and time. The species and the environment being considered are major factors that determine the relative difficulty of studying the movement pattern of insects in their natural habitat without affecting their behaviour.

For unknown small-scale movement patterns of an organism, it is recommended to make the assumption that the animals move randomly, and to model their dispersal using diffusion techniques [Ske51]. Hence, the word diffusion in relation to insect movement has the same meaning as in other fields. The type of dispersal to be discussed in this essay deals with the diffusion of flying insects which are initially located at one central point.

Extensions to diffusion models have been made possible through the inclusion of additional population growth dynamics [Hol93, Mur93], and factors describing the tendency of animals to move to more conducive habitats [Shi80, SKT79]. The assumption that insect dispersal starts at one central point is just a necessary simplification for the derivation of the insect movement model, though it cannot depict the true situation of insects dispersing from a finite area.

There are a number of biological factors that catalyse dispersal, such as feeding and larvae laying requirements. Whatever the cause, the impact is that insects move in such a way that their population density[1], decreases with distance from the central point. There will usually be a random component, in that movement will not always necessarily be away from the centre, in contrast to a mass migratory type of flight, say, in which the whole population moves in the same direction. The principal purpose of this essay is to review the mathematical work on diffusion processes, and to then apply the results in the field of entomology[2]. The flight nature to be discussed in this essay occurs with several types of insects, but we particularly emphasise the dispersal of tsetse flies (Glossina spp).

1.1 Basic concepts

For one to understand the theory of Kolmogorov in relation to diffusion processes on a real line, it suffices to have an idea of what a stochastic process is. Considering X_n to be a value at the n^{th} unit of time, its generation can be represented by a group of random variables $\{X_0, X_1, \ldots\}$ indexed by the *discrete-time parameter* $n \in \mathbb{Z}_+$.

For example, the number X_t of insects in any given habitat during the time interval $[0, t]$ results into a collection of random variables $\{X_t : t \geq 0\}$ indexed by the *continuous-time parameter* t. In a more generalised form, the definition below holds:

Definition 1.1. *Given an index set I, a stochastic process (also known as a random process)*

[1] number of insects per unit area

[2] Entomology is the scientific study of insects. This definition is some times widened to include the study of terrestrial animals in other arthropod groups or other phyla, such as arachnids, myriapods, earthworms, and slugs.

indexed by I is a collection of random variables $\{X_\lambda : \lambda \in I\}$ on a probability space $(\Omega, \mathscr{F}, P)$ taking values in a set S. The set S is referred to as the state space of the process.

Therefore, we can respectively consider: (a) $I = \mathbb{Z}_+, S = \mathbb{R}_+$; (b) $I = [0, \infty), S = \mathbb{Z}_+$; or (c) $I = \mathbb{R}^3, S = \mathbb{R}^3$. The state space S is in most cases a set of real numbers, finite, countable (discrete) or uncountable. Notation wise, $\{X_n\}$ is used to mean $\{X_n : n = 0, 1, 2, \ldots\}$, and $\{X_t\}$ is used to mean $\{X_t : t \geq 0\}$.

For a stochastic process, the values of the random variables corresponding to the occurrence of a sample point $\omega \in \Omega$ gives rise to a sample realization of the process. In the general case of a discrete-time stochastic process with state space S and index set $I = \mathbb{Z}_+ = \{0, 1, 2, \ldots\}$, the sample realizations of the processes are of the form $(X_0(\omega), X_1(\omega), \ldots, X_n(\omega), \ldots), X_n(\omega) \in S$. In the case of a continuous-parameter stochastic process with state space S and index set $I = \mathbb{R}_+ = [0, \infty]$, the sample realizations are functions $t \to X_t(\omega) \in S$, $\omega \in \Omega$. Sample realizations of a stochastic process are sometimes called *sample paths*.

It is worth noting that when choosing Ω, the sample points of Ω represent sample paths. This means that Ω is some set of functions ω defined on I, taking values in S, and the value $X_t(\omega)$ of the process at time t corresponding to the outcome $\omega \in \Omega$ is simply the coordinate projection $X_t(\omega) = \omega_t$. Stochastic models are mostly specified by prescribing the probabilities of the events that depend only on the values of the process at either finitely or infinitely many time points for simple and complex events respectively.

Definition 1.2. *A process X_t is referred to as a Markov process (or process without memory) if for all n and $t_1 < t_2 < \ldots < t_n$, we get:*

$$f[X(t_n)|X(t_{n-1}); X(t_{n-2}); \ldots; X(t_1)] = f[X(t_n)|X(t_{n-1})] \tag{1.1}$$

Equation (1.1) is due to the fact that a Markov process is a stochastic process that has the Markov property, which states that the conditional distribution of the next future state $X(t_n)$, given the present and past states, is a function of the present state alone. In simple terms, Markov process is one having a *"time-homogeneous transition law"*, unless stated otherwise.

2. Diffusion Processes on a Real Line

This chapter focuses on the study of continuous Markov processes, also known as diffusions defined on a real line. The derivations of Kolmogorov's forward and backward diffusion equations, and the rest of the content in this section is based on [BW86, BZ99, Ric77].

2.1 Kolmogorov's equations for diffusion processes

Let $\{X_t : t \geq 0\}$ be a continuous stochastic process of the Markov type defined on a real line; that is, X_t is a Markovian random variable that depends on a continuous parameter t, which assumes values in the state space $\mathbb{R} = \{x : \infty < x < \infty\}$. The first derivation (backward equation) is satisfied by the transition probabilities of $\{X_t : t \geq 0\}$, whereas the forward equation is satisfied by probability density of the process. If we represent the transition probabilities[1] of the process $\{X_t : t \geq 0\}$ by;

$$F(t, x; \tau, y) = \mathcal{P}\left\{X_\tau < y | X_t = x\right\}, \quad \tau > t \tag{2.1}$$

then for t and x fixed, $F(t, x; \tau, y)$ is a continuous function of y satisfying the conditions:

$$\lim_{y \to -\infty} F(t, x; \tau, y) = 0 \quad \text{and} \quad \lim_{y \to +\infty} F(t, x; \tau, y) = 1. \tag{2.2}$$

$$\text{For} \quad x, y, t, \tau \quad \text{and} \quad S \in (t, \tau), \quad \text{we have} \quad F(t, x; \tau, y) = \int_{-\infty}^{\infty} F(s, z; \tau, y) d_z F(t, x; s, z), \tag{2.3}$$

which is the condition that caters for the Markov property. Expression (2.3) is known as the Chapman-Kolmogorov equation that describes Markov processes of a diffusion nature. We also assume continuity, that is;

$$\lim_{\tau \to t+0} F(t, x; \tau, y) = \lim_{\tau \to t-0} F(t, x; \tau, y) = \mathcal{X}(x, y) = \begin{cases} 0 & \text{if} \quad y \leq x \\ 1 & \text{if} \quad y > x \end{cases}. \tag{2.4}$$

Since we assume that $F(t, x; \tau, y)$ admits a density function $f(t, x; \tau, y)$, then $f(t, x; \tau, y) = \dfrac{\partial F(t, x; \tau, y)}{\partial y}$ must satisfy the conditions:

$$F(t, x; \tau, y) = \int_{-\infty}^{y} f(t, x; \tau, z) dz, \tag{2.5}$$

$$\int_{-\infty}^{\infty} f(t, x; \tau, z) dz = 1, \tag{2.6}$$

$$\text{and} \quad f(t, x; \tau, y) = \int_{-\infty}^{\infty} f(s, z; \tau, y) f(t, x; s, z) dz \tag{2.7}$$

For the Backward equation to be derived, we assume that;

[1] The conditional probability p_{ij} is called the probability of a transition (transition probability) from the state i to the state j, and the square matrix $\mathbf{P} = (p_{ij})$ is called the transition probability matrix or stochastic matrix.

1.
$$\lim_{\Delta t\to 0}\frac{1}{\Delta t}\int_{|y-x|\geq\delta} d_yF(t,x;t+\Delta t,y)=\lim_{\Delta t\to 0}\frac{1}{\Delta t}\int_{|y-x|\geq\delta} d_yF(t-\Delta t,x;t,y)=0, \quad (2.8)$$
where $\delta>0$. This condition states that the probability that $|X_\tau - X_t|\geq\delta$, given $X_t=x$, during an infinitesimal time interval Δt is small compared to Δt.

2. The first and second partial derivatives of $F(t,x;\tau,y)$ with respect to the backward state variable x exist and are continuous functions in x, namely;
$$\frac{\partial F(t,x;\tau,y)}{\partial x} \text{ and } \frac{\partial^2 F(t,x;\tau,y)}{\partial x^2} \text{ respectively.} \quad (2.9)$$

3. If at some time $t-\Delta t$, $X(t-\Delta t)=x$, then the mean and variance of the change in X_t due to the time interval of the duration Δt are
$$\int_{-\infty}^{\infty}(y-x)d_yF(t-\Delta t,x;t,y) \text{ and } \int_{-\infty}^{\infty}(y-x)^2 d_yF(t-\Delta t,x;t,y). \quad (2.10)$$

But the integrals in (2.10) may diverge, hence we define the *truncated moments*
$$\begin{aligned}\lim_{\Delta t\to 0}\frac{1}{\Delta t}\int_{|y-x|<\delta}(y-x)d_yF(t-\Delta t,x;t,y) &= \lim_{\Delta t\to 0}\frac{1}{\Delta t}\int_{|y-x|<\delta}(y-x)d_yF(t,x;t+\Delta t,y)\\ &= b(t,x). \quad (2.11)\\ \lim_{\Delta t\to 0}\frac{1}{\Delta t}\int_{|y-x|<\delta}(y-x)^2d_yF(t-\Delta t,x;t,y) &= \lim_{\Delta t\to 0}\frac{1}{\Delta t}\int_{|y-x|<\delta}(y-x)^2d_yF(t,x;t+\Delta t,y)\\ &= a(t,x)\geq 0. \quad (2.12)\end{aligned}$$

(2.11) and (2.12) are known as the *infinitesimal mean and variance in X_t*, respectively.

2.1.1 Derivation of Kolmogorov's Backward diffusion equation

Using the above assumptions, (2.3) becomes;
$$\begin{aligned}F(t-\Delta t,x;\tau,y) &= \int_{-\infty}^{\infty}F(t,z;\tau,y)d_zF(t-\Delta t,x;\tau,z), \quad (2.13)\\ \text{and } F(t,x;\tau,y) &= \int_{-\infty}^{\infty}F(t,z;\tau,y)d_zF(t-\Delta t,x;\tau,z). \quad (2.14)\end{aligned}$$

Combining (2.13) and (2.14) we get;
$$\begin{aligned}\frac{F(t-\Delta t,x;\tau,y)-F(t,x;\tau,y)}{\Delta t} &= \frac{1}{\Delta t}\int_{-\infty}^{\infty}[F(t,z;\tau,y)-F(t,x;\tau,y)]d_zF(t-\Delta t,x;\tau,z)\\ &= \frac{1}{\Delta t}\int_{|z-x|\geq\delta}[F(t,z;\tau,y)-F(t,x;\tau,y)]d_zF(t-\Delta t,x;\tau,z)\\ &\quad+\frac{1}{\Delta t}\int_{|z-x|<\delta}[F(t,z;\tau,y)-F(t,x;\tau,y)]d_zF(t-\Delta t,x;\tau,z)\end{aligned}$$
(2.15)

Using (2.8), the first integral of (2.15) approaches zero as $\Delta t \to 0$. Therefore (2.15) reduces to;

$$\frac{F(t-\Delta t, x; \tau, y) - F(t, x; \tau, y)}{\Delta t} = \frac{1}{\Delta t}\int_{|z-x|<\delta}[F(t, z; \tau, y) - F(t, x; \tau, y)]d_z F(t-\Delta t, x; \tau, z). \tag{2.16}$$

Using (2.9) and Taylor's formula we get;

$$F(t-\Delta t, x; \tau, y) - F(t, x; \tau, y) = (z-x)\frac{\partial}{\partial x}F(t, x; \tau, y) + \frac{1}{2}(z-x)^2\frac{\partial^2}{\partial x^2}F(t, x; \tau, y) + o[(z-x)^2]. \tag{2.17}$$

On substituting (2.17) into (2.16) we get;

$$\begin{aligned}\frac{F(t-\Delta t, x; \tau, y) - F(t, x; \tau, y)}{\Delta t} &= \frac{1}{\Delta t}\frac{\partial}{\partial x}F(t, x; \tau, y)\int_{|z-x|<\delta}(z-x)d_z F(t-\Delta t, x; \tau, z) \\ &+ \frac{1}{2\Delta t}\frac{\partial^2}{\partial x^2}\int_{|z-x|<\delta}\left\{(z-x)^2 + o[(z-x)^2]\right\}d_z F(t-\Delta t, x; \tau, z)\end{aligned} \tag{2.18}$$

Applying limits and using (2.11) and (2.12), reduces (2.18) to;

$$\frac{\partial}{\partial t}F(t, x; \tau, y) = \frac{1}{2}a(t, x)\frac{\partial^2}{\partial x^2}F(t, x; \tau, y) + b(t, x)\frac{\partial}{\partial x}F(t, x; \tau, y). \tag{2.19}$$

This is Kolmogorov's backward equation for a diffusion process. In terms of the density function $f(t, x; \tau, y)$, (2.19) becomes;

$$\frac{\partial}{\partial t}f(t, x; \tau, y) = \frac{1}{2}a(t, x)\frac{\partial^2}{\partial x^2}f(t, x; \tau, y) + b(t, x)\frac{\partial}{\partial x}f(t, x; \tau, y).$$

2.1.2 Derivation of Kolmogorov's Forward diffusion equation

Kolmogorov's Forward diffusion equation is sometimes referred to as the *"Fokker-Plank equation"*. In its derivation, we assume the existence of the following continuous partial derivatives.

$$\frac{\partial f(t, x; \tau, y)}{\partial \tau}; \qquad \frac{\partial[b(\tau, x)f(t, x; \tau, y)]}{\partial y}; \qquad \frac{\partial^2[a(\tau, x)f(t, x; \tau, y)]}{\partial y^2}. \tag{2.20}$$

Taking $G(y)$ to be a non-negative continuous function such that

$$G(y) = 0 \quad \text{for} \quad y < y_1 \quad \text{and} \quad y > y_2. \quad \Rightarrow y_1 < y_2 \quad \text{and} \tag{2.21}$$

$$G(y_1) = G(y_2) = G'(y_1) = G'(y_2) = G''(y_1) = G''(y_2) = 0 \tag{2.22}$$

Therefore, we get;

$$\begin{aligned}\lim_{\Delta\tau\to 0}\int_{-\infty}^{\infty}\frac{f(t, x; \tau+\Delta\tau, y) - f(t, x; \tau, y)}{\Delta\tau}G(y)dy &= \int_{y_1}^{y_2}\frac{\partial f(t, x; \tau, y)}{\partial \tau}G(y)dy \\ &= \frac{\partial}{\partial \tau}\int_{y_1}^{y_2}f(t, x; \tau, y)G(y)dy,\end{aligned} \tag{2.23}$$

Using the Markov Property in (2.7) we get;

$$f(t,x;\tau+\Delta\tau,y)=\int_{-\infty}^{\infty}f(t,x;\tau,y)f(\tau,z;\tau+\Delta\tau,y)dz. \tag{2.24}$$

Substituting (2.24) into (2.23) we get;

$$\begin{aligned}
&\int_{y_1}^{y_2}\frac{\partial f(t,x;\tau,y)}{\partial\tau}G(y)dy\\
=&\lim_{\Delta\tau\to 0}\frac{1}{\Delta\tau}\left\{\int_{-\infty}^{\infty}\int_{-\infty}^{\infty}f(t,x;\tau,y)f(\tau,z;\tau+\Delta\tau,y)G(y)dzdy\right.\\
&\left.-\int_{-\infty}^{\infty}f(t,x;\tau,y)G(y)dy\right\}\\
=&\lim_{\Delta\tau\to 0}\frac{1}{\Delta\tau}\left\{\int_{-\infty}^{\infty}f(t,x;\tau,y)\int_{-\infty}^{\infty}f(\tau,z;\tau+\Delta\tau,y)G(y)dzdy\right.\\
&\left.-\int_{-\infty}^{\infty}f(t,x;\tau,y)G(y)dy\right\}\\
=&\lim_{\Delta\tau\to 0}\frac{1}{\Delta\tau}\int_{-\infty}^{\infty}f(t,x;\tau,y)\left\{\int_{-\infty}^{\infty}f(\tau,y;\tau+\Delta\tau,z)G(z)dz-G(y)\right\}dy
\end{aligned} \tag{2.25}$$

Taylor's expansion for $G(z)$ about y is:

$$G(z)=G(y)+(z-y)G'(y)+\frac{1}{2}(z-y)^2G''(y)+o[(z-y)^2]. \tag{2.26}$$

But $G(z)$ is bounded because of (2.8). Hence,

$$\int_{|y-z|\geq\delta}f(\tau,y;\tau+\Delta\tau,z)G(z)dz = o(\Delta\tau),\quad\text{and} \tag{2.27}$$

$$\int_{|y-z|<\delta}f(\tau,y;\tau+\Delta\tau,z)dz = 1+o(\Delta\tau) \tag{2.28}$$

Using (2.26), (2.27) and (2.28), the expression in the braces of (2.25) becomes;

$$\begin{aligned}
\int_{-\infty}^{\infty}f(\tau,y;\tau+\Delta\tau,z)G(z)dz-G(y)=G'(y)\int_{|y-z|<\delta}(z-y)f(\tau,y;\tau+\Delta\tau,z)dz\\
+\frac{1}{2}G''(y)\int_{|y-z|<\delta}\left\{(z-y)^2+o[(z-y)^2]\right\}f(\tau,y;\tau+\Delta\tau,z)dz+o(\delta\tau).
\end{aligned} \tag{2.29}$$

Substituting (2.29) into (2.25) gives;

$$\begin{aligned}
&\int_{y_1}^{y_2}\frac{\partial f(t,x;\tau,y)}{\partial\tau}G(y)dy\\
=&\lim_{\Delta\tau\to 0}\int_{-\infty}^{\infty}f(t,x;\tau,y)\left\{G'(y)\int_{|y-z|<\delta}(z-y)f(\tau,y;\tau+\Delta\tau,z)dz\right.\\
&\left.+\frac{1}{2}G''(y)\int_{|y-z|<\delta}\left\{(z-y)^2+o[(z-y)^2]\right\}f(\tau,y;\tau+\Delta\tau,z)dz+o(\delta\tau)\right\}dy
\end{aligned} \tag{2.30}$$

Taking limits, and using assumptions (2.11) and (2.12), reduces (2.30) to;

$$\int_{y_1}^{y_2} \frac{\partial f(t,x;\tau,y)}{\partial \tau} G(y)dy = \int_{-\infty}^{\infty} f(t,x;\tau,y) \left\{ b(\tau,y)G'(y) + \frac{1}{2}a(\tau,y)G''(y) \right\} dy, \tag{2.31}$$

but $G'(y) = G''(y) = 0$ in the region $y \leq y_1$, $y \geq y_2$. Therefore,

$$\int_{y_1}^{y_2} \frac{\partial f(t,x;\tau,y)}{\partial \tau} G(y)dy = \int_{y_1}^{y_2} f(t,x;\tau,y) \left\{ b(\tau,y)G'(y) + \frac{1}{2}a(\tau,y)G''(y) \right\} dy. \tag{2.32}$$

Using integration by parts, (2.31) splits into the relations below:

$$\int_{y_1}^{y_2} f(t,x;\tau,y)b(\tau,y)G'(y)dy = \int_{y_1}^{y_2} G(y)\frac{\partial[b(\tau,y)f(t,x;\tau,y)]}{\partial y}dy, \quad \text{and} \tag{2.33}$$

$$\int_{y_1}^{y_2} f(t,x;\tau,y)a(\tau,y)G''(y)dy = \int_{y_1}^{y_2} G(y)\frac{\partial^2[a(\tau,y)f(t,x;\tau,y)]}{\partial y^2}dy. \tag{2.34}$$

Substituting (2.33) and (2.34) into (2.32) gives;

$$\int_{y_1}^{y_2} \frac{\partial f(t,x;\tau,y)}{\partial \tau} G(y)dy = \int_{y_1}^{y_2} \left\{ -\frac{\partial[b(\tau,y)f(t,x;\tau,y)]}{\partial y} + \frac{1}{2}\frac{\partial^2[a(\tau,y)f(t,x;\tau,y)]}{\partial y^2} \right\} G(y)dy. \tag{2.35}$$

Re-arranging (2.35) gives;

$$\int_{y_1}^{y_2} \left\{ -\frac{\partial f(t,x;\tau,y)}{\partial \tau} - \frac{\partial[b(\tau,y)f(t,x;\tau,y)]}{\partial y} + \frac{1}{2}\frac{\partial^2[a(\tau,y)f(t,x;\tau,y)]}{\partial y^2} \right\} G(y)dy = 0. \tag{2.36}$$

Since the function $G(y)$ is arbitrary, then the expression in the braces of (2.36) must be zero. That is;

$$-\frac{\partial f(t,x;\tau,y)}{\partial \tau} - \frac{\partial[b(\tau,y)f(t,x;\tau,y)]}{\partial y} + \frac{1}{2}\frac{\partial^2[a(\tau,y)f(t,x;\tau,y)]}{\partial y^2} = 0,$$

$$\text{implying that} \quad \frac{\partial f(t,x;\tau,y)}{\partial \tau} = \frac{1}{2}\frac{\partial^2[a(\tau,y)f(t,x;\tau,y)]}{\partial y^2} - \frac{\partial[b(\tau,y)f(t,x;\tau,y)]}{\partial y}. \tag{2.37}$$

Equation (2.37) is known as the *Fokker-Planck equation*, which is Kolmogorov's forward equation of a diffusion process.

2.2 Singular Diffusion Equations

The coefficient $a(x)$ is essentially positive in most physical applications of Kolmogorov's diffusion equations, but in some applications, we consider equations in such away that $a(x)$ vanishes at one (or perhaps both) of the boundaries or one of the coefficients has no finite limit. Equations whose coefficients have the same description as the one above are called *"Singular diffusion equations"*. For example, if we consider a diffusion process on the interval $I = \{x|0 < x < 1\}$ with $a(x) = \beta x(1-x)$, $\beta > 0$, and $b(x) = 0$, then it is clear that $a(x)$ will vanish at both boundaries.

Remark 2.1.

There is no treatment for the existence and uniqueness theory for the Kolmogorov's diffusion equation as it is in the case of Kolmogorov's differential equations for discontinuous processes.

2.3 The Theory of Feller

A diffusion process of the Markovian type on the interval $I = (r_1, r_2)$ where $-\infty \leq r_1 < r_2 \leq \infty$ is going to be considered. It is necessary to specify the boundary conditions in addition to an initial condition for the differential equation, whenever the interval I is finite, or semi-infinite.

2.3.1 Classification of Boundaries

In the previous section, that is (2.1), we realised that the coefficients $a(x)$ and $b(x)$ define a particular Markov process of the diffusion type. Hence, if we consider a pair $(a(x), b(x))$, then it is likely that the process will show different types of behaviours at the boundaries r_1 and r_2. The classification of the boundaries is as follows.

1. If the coefficients are in such away that the random variable X_t never takes on the value $x = r_1$ or $x = r_2$, then it means that no boundary conditions have to be imposed, and the boundaries are called *"natural"*

2. If the coefficients are in such away that X_t never takes on the values r_1 or r_2, then two possible cases arise, that is;

   - The drift towards the boundaries can be such that the boundaries automatically act as absorbing barriers and no boundary conditions can be imposed. These types of boundaries are referred to as *"exit"* boundaries.
   - The other case is one in which the process behaves like the classical diffusion process on a finite interval, where several boundary conditions can be imposed, These are categorised as *"regular"* boundaries.

3. If boundaries are exit or regular, they are termed as *"accessible"* boundaries, else, they are *"inaccessible"*, and these include the natural and *"entrance"* boundaries.

3. The Diffusion Equation in Two Spatial Dimensions

This type of diffusion equation has three independent variables, that is; the two spatial variables x and y, and the time t. Since the second-order partial derivative with respect to the spatial variable x can be considered as the first term of the Laplacian operator, then it can be shown that the diffusion phenomena in two dimensions based on a rectangular coordinate system follows a nonhomogeneous partial differential equation

$$\frac{\partial}{\partial t}u(x,y,t) = \mathcal{D}\left(\frac{\partial^2}{\partial x^2}u(x,y,t) + \frac{\partial^2}{\partial y^2}u(x,y,t)\right), \tag{3.1}$$

where $\mathcal{D}$ is the diffusion coefficient that measures the dispersal rate that has a dimension of $distance^2/time$, $u(x,y,t)$ is the spatial-time-dependent position of the diffusing particle and the expression in the parentheses is called the Laplacian, oftenly denoted by either $\nabla^2 u$ or by Δu.

3.1 Solution of the Two-dimensional spatial diffusion equation

To find the position of the diffusing particle in time and space, that is $u(x,y,t)$, we consider (3.1) to be over a finite two-dimensional rectangular domain $\mathfrak{R} = \{(x,y)|0 < x < l_1, 0 < y < l_2\}$ subject to the nonhomogeneous boundary conditions

$$\left.\begin{array}{lll} u(x,0) = f_1(x), & u(x,l_2) = f_2(x) & (0 < x < l_1) \\ u(0,y) = g_1(y), & u(l_1,y) = g_2(y) & (0 < y < l_2) \end{array}\right\}, \tag{3.2}$$

and the initial condition

$$u(x,y,0) = f(x,y), \tag{3.3}$$

as shown in the figure below.

Note 3.1. *A problem with boundary conditions such as those in figure 3.1 is called a Dirichlet problem. Since all the boundary conditions are nonhomogeneous, this problem is not directly susceptible to the method of separation.*

3.2 Method of separation of variables

In this method, we assume a solution in form of a product, and because they are three variables involved, we write it as:

$$u(x,y,t) = X(x)Y(y)T(t). \tag{3.4}$$

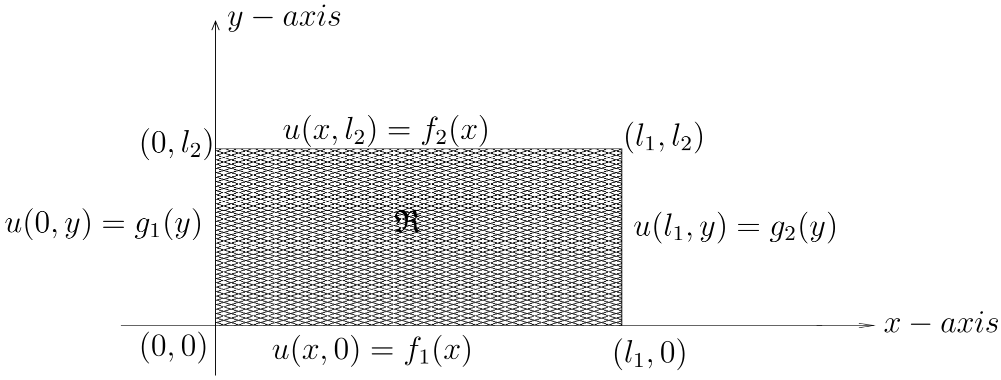


Figure 3.1: A rectangular plate with given boundary values

Substituting (3.4) into (3.1) gives;

$$\begin{aligned} X(x)Y(y)\left(\frac{dT(t)}{dt}\right) &= \mathcal{D}\left\{\left(\frac{d^2X(x)}{dx^2}\right)Y(y)T(t) + X(x)\left(\frac{d^2Y(y)}{dy^2}\right)T(t)\right\}, \\ \text{which implies} \quad \frac{1}{T(t)}\frac{dT(t)}{dt} &= \mathcal{D}\left\{\frac{1}{X(x)}\frac{d^2X(x)}{dx^2} + \frac{1}{Y(y)}\frac{d^2Y(y)}{dy^2}\right\}. \end{aligned} \tag{3.5}$$

If (3.5) is to hold for any arbitrary (x, y, t), then each term must be constant. This leads to three single-variable ordinary differential equations, and these are:

$$\frac{1}{T(t)}\frac{dT(t)}{dt} = -\alpha, \qquad \frac{1}{X(x)}\frac{d^2X(x)}{dx^2} = -\beta^2, \qquad \frac{1}{Y(y)}\frac{d^2Y(y)}{dy^2} = -\gamma^2. \tag{3.6}$$

Substituting (3.6) into (3.5) gives;

$$\alpha = \mathcal{D}[\beta^2 + \gamma^2]. \tag{3.7}$$

From (3.6) we get;

$$\left.\begin{aligned} X''(x) + \beta^2 X(x) &= 0 \\ Y''(y) + \gamma^2 Y(y) &= 0 \\ T'(t) + \alpha T(t) &= 0 \end{aligned}\right\} \quad \text{Homogeneous equations.} \tag{3.8}$$

3.3 Solving the Homogeneous equations

Using characteristic equations to solve (3.8), we get;

$$X(x) = C_1\cos\beta x + C_2\sin\beta x, \tag{3.9}$$

$$Y(y) = C_3\cos\gamma y + C_2\sin\gamma y, \tag{3.10}$$

$$T(t) = C_5 e^{-\alpha t}. \tag{3.11}$$

For homogeneous boundary conditions, (3.2) changes and becomes:

$$\left.\begin{aligned} f_(x) = f_2(x) = g_(y) = g_2(y) = 0 \\ \text{implying that} \quad u(x,0) = u(x,l_2) = u(0,y) = u(l_1,y) = 0 \end{aligned}\right\}. \tag{3.12}$$

From (3.12), applying $X(0) = 0$ on (3.9) we get

$$C_1 = 0 \quad \Longrightarrow X(x) \;=\; C_2\text{sin}\beta x, \tag{3.13}$$

and when $X(l_1) = 0$ is applied on (3.13), we get: $X(l_1) = C_2\text{sin}\beta l_1 = 0$. But $C_2 \neq 0$, as it will provide a trivial solution. Hence to obtain a nontrivial solution, we set sin$\beta l_1 = 0$.

$$\therefore \beta l_1 = m\pi \quad \Longrightarrow \beta = \frac{m\pi}{l_1}, \quad \text{where} \quad m = 1, 2, 3, \ldots \tag{3.14}$$

Substituting (3.14) into (3.13) gives

$$X(x) \;=\; C_2\text{sin}\frac{m\pi}{l_1}x, \quad m = 1, 2, 3, \ldots \tag{3.15}$$

Similarly, applying the conditions $Y(0) = 0$ and $Y(l_2) = 0$ got from (3.12), on to (3.10), we get

$$\gamma l_2 = n\Pi \quad \Longrightarrow \gamma = \frac{n\pi}{l_2}, \quad \text{where} \quad n = 1, 2, 3, \ldots \tag{3.16}$$

$$\therefore \quad Y(y) \;=\; C_4\text{sin}\frac{n\pi}{l_2}y. \tag{3.17}$$

β and γ constitute the eigenvalues whereas $X(x)$ and $Y(y)$ yields the eigenfunctions due to β and γ respectively. Substituting (3.14) and (3.16) into (3.7) gives

$$\alpha = \mathcal{D}\pi^2\left[\frac{m^2}{l_1^2} + \frac{n^2}{l_2^2}\right], \quad \text{where} \quad m, n = 1, 2, 3, \ldots \tag{3.18}$$

Substituting (3.18) into (3.11) gives;

$$T(t) = e^{-\mathcal{D}\pi^2\left[\frac{m^2}{l_1^2} + \frac{n^2}{l_2^2}\right]t}. \tag{3.19}$$

Substituting (3.15), (3.17) and (3.19) into (3.4), and applying the superposition principle gives

$$u(x, y, t) = \sum_{m,n=1}^{\infty} A_{mn}e^{-\mathcal{D}\pi^2\left[\frac{m^2}{l_1^2} + \frac{n^2}{l_2^2}\right]t}\text{sin}\frac{m\pi x}{l_1}\text{sin}\frac{n\pi y}{l_2}, \tag{3.20}$$

where A_{mn} has replaced the constants C_2C_4 and can be determined by the initial condition (3.3). But the orthogonality of the sine functions states that:

$$\int_0^1 \text{sin}\frac{k'\pi y}{l}\text{sin}\frac{k\pi x}{l}dx = \frac{1}{2}\delta_{kk'}.$$

Hence the expression for the dispersal coefficient is:

$$A_{mn} = \frac{4}{l_1 l_2}\int_0^{l_1} dx \int_0^{l_2} f(x, y)\;\text{sin}\frac{m\pi x}{l_1}\text{sin}\frac{n\pi y}{l_2}dy. \tag{3.21}$$

Assuming the simplest initial condition, that is $f(x, y) = U_0$, (3.21) is integrated, thus yielding

$$A_{mn} = \frac{4U_0}{l_1 l_2} \cdot \frac{-l_2}{n\pi} \cdot \frac{-l_1}{m\pi} \left[(-1)^n - 1\right]\left[(-1)^m - 1\right],$$

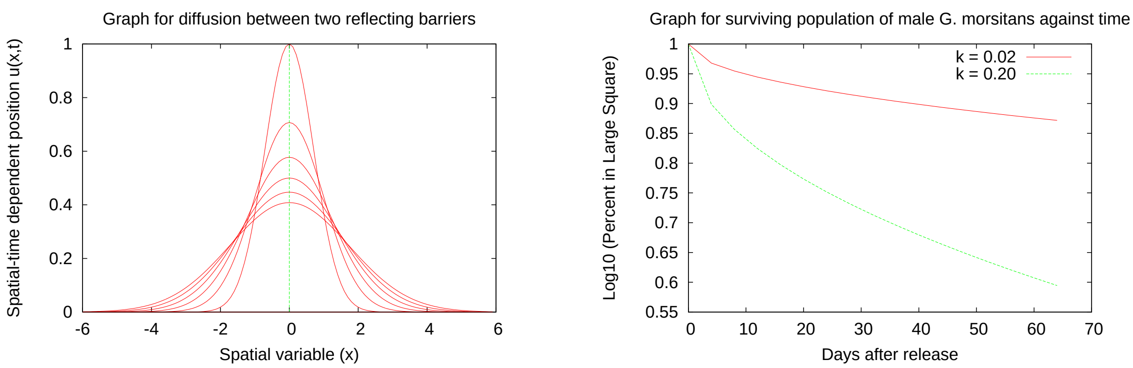
which implies that

$$A_{mn} = \begin{cases} \frac{16}{\pi^2} \cdot \frac{U_0}{mn} & m, n \text{ odd} \\ 0 & \text{otherwise} \end{cases} . \tag{3.22}$$

Substituting (3.22) into (3.20) gives;

$$u(x, y, t) = \frac{16}{\pi^2} \sum_{m,n \ odd} \frac{1}{mn} e^{-\mathcal{D}\pi^2\left[\frac{m^2}{l_1^2} + \frac{n^2}{l_2^2}\right]t} \sin\frac{m\pi x}{l_1} \sin\frac{n\pi y}{l_2}, \tag{3.23}$$

(3.23) is the exact solution for the diffusion equation in two spatial dimensions based on a rectangular coordinate system with $u = 0$ boundary conditions along the edges of the rectangular plate and taking $u(x, y, 0) = f(x, y) = U_0$.



(a) (b)

Figure 3.2: A one-dimensional diffusion process between two reflecting boundaries (Fig: 3.2(a)), constitutes a normal distribution. This simulation is obtained from equation equation (5.1), when the variable y is fixed, that is: $u(x, t) = \frac{1}{2\pi\nu}\text{exp}\left(-\frac{x^2}{2\nu}\right)$. Fig: 3.2(b), shows the fraction of the surviving population of male G. morsitans remaining within a square, plotted against time after their release from randomly selected points within the square. Equation (5.68) produces this simulation with two different values of k, that is: $k = 0.02$ (yards $\times 10^3)^2$ and $k = 0.20$ (yards $\times$ $10^3)^2$.

4. Diffusions with Reflecting Boundaries

For unrestricted diffusions on $\mathfrak{X} = (-\infty, \infty)$, or on open intervals, the end points of the state space of a diffusion can not be reached from the interior hence *inaccessible*. The diffusions to be considered in this section are restricted to subintervals of $\mathfrak{X}$ with one or more end points that can be reached from the interior. In simple words, the boundaries must be *accessible*.

When a process hits a boundary point, it can not continue unless a boundary condition or behaviour consistent with the requirement that the process is Markovian is specified. The *reflecting boundary condition*, some times referred to as the *Neumann boundary condition* is the one to be accounted for in this section. Since $\mathfrak{X} = (-\infty, \infty)$, then the transition probability distribution $p(t; x, y)$ of $Y_{\mathfrak{r}+t}$ given $Y_{\mathfrak{r}} = x$ will have a density given by:

$$p(t; x, y) = \frac{1}{(2\pi\sigma^2 t)^{\frac{1}{2}}} \text{exp} \left\{ -\frac{(y - x - \mu t)^2}{2\sigma^2 t} \right\}, \tag{4.1}$$

where μ is the drift coefficient and $\sigma^2 > 0$ is the diffusion coefficient.

4.1 One-Point Boundary Case

Let $\mu(x)$ and $\sigma^2(x)$ be defined on $\mathfrak{X} = [0, \infty)$, and satisfy equation (4.1) where "0" is considered to be the reflecting boundary. Taking $\mu(0) = 0$, the coefficients $\mu(\cdot)$ and $\sigma^2(\cdot)$ on $\mathbb{R}^1$ can be extended by setting

$$\mu(-x) = -\mu(x), \quad \text{and} \quad \sigma^2(-x) = \sigma^2(x), \quad \text{for} \quad (x > 0). \tag{4.2}$$

If $\{X_t\}$ is a diffusion on $\mathbb{R}^1$ with the extended coefficients $\mu(\cdot)$,$\sigma^2(\cdot)$ defined above, then $\{|X_t|\}$ is a Markov process on the state space $\mathfrak{X} = [0, \infty)$ with transition probability density given as:

$$q(t; x, y) = p(t; x, y) + p(t; x, -y) \quad \text{for all} \quad x, y \in [0, \infty), \tag{4.3}$$

where $p(t; x, y)$ is the transition probability density of $\{X_t\}$.

Note 4.1. *Two Markov processes $\{X_t\}$ and $\{-X_t\}$ have the same drift and diffusion coefficients. This means that the conditional density $p(t; x, y)$ of X_t at y given $X_0 = x$ is the same as the conditional density of $-X_t$ at y given $-X_0 = x$.*

$$\textit{Therefore,} \quad p(t; x, y) = p(t; -x, -y). \tag{4.4}$$

Definition 4.1. *A Markov process on $\mathfrak{X} = [\alpha, \infty]$, that has continuous sample paths and whose transition probability density satisfies the backward diffusion equation (2.19) and condition (4.3), with 0 substituted by α is known as a "reflecting diffusion" on $[\alpha, \infty]$ having $\mu(x)$, $\sigma^2(x)$ as the drift and diffusion coefficients respectively. α is called the "reflecting boundary point".*

As an example, if we have a reflecting diffusion on $\mathfrak{X} = [0, \infty)$, with $\mu(\cdot) = 0$ and $\sigma^2(x) = \sigma^2 > 0$, then the transition probability density will be given by;

$$\begin{aligned} q(t;x,y) &= p(t;x,y) + p(t;-x,y), \\ &= \frac{1}{(2\pi\sigma^2 t)^{\frac{1}{2}}}\exp\left\{-\frac{(y-x)^2}{2\sigma^2 t}\right\} + \frac{1}{(2\pi\sigma^2 t)^{\frac{1}{2}}}\exp\left\{-\frac{(y+x)^2}{2\sigma^2 t}\right\}, \\ &= \frac{1}{(2\pi\sigma^2 t)^{\frac{1}{2}}}\left[\exp\left\{-\frac{(y-x)^2}{2\sigma^2 t}\right\} + \exp\left\{-\frac{(y+x)^2}{2\sigma^2 t}\right\}\right] \quad (t > 0; x, y \geq 0). \end{aligned}$$

4.2 Two-Point Boundary Case

In this section, we consider a diffusion on $\mathfrak{X} = [\alpha, \beta]$ with two reflecting boundary points α and β. Let $\{X_t\}$ be an unrestricted diffusion with zero drift starting at $x \in [0, 1]$.

$$\text{Let us define} \quad Z_t^{(1)} = X_t(\text{mod } 2). \tag{4.5}$$

If $\{Z_t\} = \{X_t(\text{mod } d)\}$, then $\{Z_t\}$ is a Markov process on $[0, d)$ with a transition probability density function given by;

$$q(t;z,z') = \sum_{m=-\infty}^{\infty} p(t;z,z'+md) \quad (t > 0; z, z' \in [0,d)). \tag{4.6}$$

Thus using (4.5), $\left\{Z_t^{(1)}\right\}$ is a diffusion on $[0, 2]$. This implies that;

$$Z_t^{(2)} = \left\{|Z_t^{(1)} - 1|\right\} \quad \text{is a diffusion on} \quad [-1, 1]. \tag{4.7}$$

Using (4.1) and (4.6) gives the transition probability density of (4.7) as:

$$q^{(2)}(t;z,z') = \sum_{m=-\infty}^{\infty} \frac{1}{(2\pi\sigma^2 t)^{\frac{1}{2}}}\exp\left\{-\frac{(2m+z'-z)^2}{2\sigma^2 t}\right\} \quad \text{for} \quad -1 \leq z', z \leq 1. \tag{4.8}$$

From (4.4), we can say that;

$$\begin{aligned} q^{(2)}(t;z,z') &= q^{(2)}(t;-z,-z'), \\ \text{implying that} \quad q(t;x,y) &= q^{(2)}(t;-x,y) + q^{(2)}(t;x,y). \end{aligned} \tag{4.9}$$

Substituting (4.8) into (4.9) gives

$$q(t;x,y) = \sum_{m=-\infty}^{\infty} \frac{1}{(2\pi\sigma^2 t)^{\frac{1}{2}}}\left[\exp\left\{-\frac{(2m+y-x)^2}{2\sigma^2 t}\right\} + \exp\left\{-\frac{(2m+y+x)^2}{2\sigma^2 t}\right\}\right], \quad \text{for } x, y \in [0,1]. \tag{4.10}$$

as the transition probability density of the Markov process on $[0, 1]$, having reflecting boundary points $0, 1$. For a generalised case, let the coefficients $\mu(\cdot)$ and $\sigma^2(\cdot)$ satisfy condition (4.1) on

$[0,1]$. Let $\mu(0) = 0 = \mu(1)$, then the coefficients $\mu(\cdot)$ and $\sigma^2(\cdot)$ can be extended to $(-\infty, \infty)$ by setting

$$\mu(-x) = -\mu(x), \quad \sigma^2(-x) = \sigma^2(x) \quad \text{for} \quad x \in [0,1],$$

and also

$$\mu(x+2m) = \mu(x), \quad \sigma^2(x+2m) = \sigma^2(x) \quad \text{for} \quad x \in [-1,1] \quad \text{where} \quad m = 0, \pm 1, \pm 2, \ldots.$$

4.3 Mixed Two-Point Boundary Case

In this case we consider two boundary points, where one of them is reflecting and the other absorbing. Let $\{X_t\}$ be a diffusion on $[m,\infty)$ with a reflecting boundary m, having $\mu(\cdot)$ and $\sigma^2(\cdot)$ as the drift and diffusion coefficients respectively. If $n > m$, then we define

$$\widetilde{X}_t = \begin{cases} X_t & \text{if} \quad t < \tau_n \\ n = X_{\tau_n} & \text{if} \quad t \geq \tau_n \end{cases}, \tag{4.11}$$

where τ_n is the *first passage time*[1] to n defined by;

$$\tau_n = \inf\{t \geq 0 : X_t = m\}.$$

Therefore, if $\{X_t\}$ starts at $x \in [m,n]$, then $\left\{\widetilde{X}_t\right\}$ is a Markov process on $[m,n]$, starting at x, which is called a diffusion on $[m,n]$, with a reflecting boundary point m and an absorbing boundary point n, having coefficients $\mu(\cdot)$ and $\sigma^2(\cdot)$.

4.4 Probability of reaching one boundary point before another

In this section, We consider a diffusion between two boundary points, and then discuss the probability of it hitting one of the boundary points before the other.

Theorem 4.1. *Let $\{X_t\}$ be a one dimensional Brownian motion with zero drift and diffusion coefficient $\sigma^2 > 0$. Let $m < n$ be the two boundary points.*

$$\textit{Let us define} \quad \eta(x) = P_x(\{X_t\} \ \textit{hits} \ m \ \textit{before} \ n), \quad (m \leq x \leq n). \tag{4.12}$$

$$\textit{For} \ x \in [m,n] \ \textit{and} \ h > 0, \quad \textit{then} \ [x-h, x+h] \subset (m,n). \tag{4.13}$$

Therefore, taking $\tau = \tau_{x-h} \wedge \tau_{x+h}$ to be the first time $\{X_t\}$ reaches $x-h$ or $x+h$, then $P_x(\tau < \infty) = 1$.

[1] First passage time can be defined as a random variable $T_i = T_i^0$ representing the first time a simple random walk starting at zero reaches the state i, where the distribution of T_i can be computed through the analysis of the sample paths of the simple random walk. Therefore, if we let $Q_{N,i} = \{T_i = N\}$ denote the event that the particle reaches state i for the first time at the N^{th} step, then $Q_{N,i} = \{S_n \neq i \ \text{for} \ n = 0, 1, \ldots, N-1, S_N = i\}$, where $S_N = i$ means that there are $\frac{N+i}{2}$ plus 1's and $\frac{N-i}{2}$ minus 1's among $X_1, X_2, \ldots, X_N$.

Proof:

$$P_x(\tau > t) \leq P_x(x-h < X_t < x+h) = \frac{1}{(2\pi\sigma^2 t)^{\frac{1}{2}}} \int_{x-h}^{x+h} \exp\left\{-\frac{(y-x)^2}{2\sigma^2 t}\right\} dy. \quad (4.14)$$

Changing variables gives;

$$z = \frac{y-x}{\sigma\sqrt{t}}; \quad x+h = \frac{h}{\sigma\sqrt{t}}; \quad x-h = -\frac{h}{\sigma\sqrt{t}}; \quad dy = \sigma\sqrt{t}\, dz. \quad (4.15)$$

Substituting (4.15) into (4.14) gives;

$$P_x(\tau > t) \leq P_x(x-h < X_t < x+h) = \frac{1}{(2\pi)^{\frac{1}{2}}} \int_{-\frac{h}{\sigma\sqrt{t}}}^{\frac{h}{\sigma\sqrt{t}}} \exp\left\{-\frac{z^2}{2}\right\} dz. \quad (4.16)$$

$$\text{But} \quad \lim_{t\to\infty} \frac{1}{(2\pi)^{\frac{1}{2}}} \int_{-\frac{h}{\sigma\sqrt{t}}}^{\frac{h}{\sigma\sqrt{t}}} \exp\left\{-\frac{z^2}{2}\right\} dz = 0, \quad (4.17)$$

now, from (4.12), we get:

$$\begin{aligned} \eta(x) &= P_x(\{X_t\} \text{ hits } m \text{ before } n), \\ &= P_x(\{(X_\tau^+)_t\} \text{ hits } m \text{ before } n), \\ &= E_x\left[P_x(\{(X_\tau^+)_t\} \text{ hits } m \text{ before } n) | \{X_{t\wedge\tau}; t \geq 0\}\right]. \quad (4.18) \end{aligned}$$

But the *"strong Markov property"* states that if τ is a *stopping time*[2] on $\{\tau < \infty\}$, the conditional distribution of X_τ^+ given the past up to the time τ is the same as the distribution of the diffusion $\{X_t\}$ starting at X_τ. In simple terms, the conditional distribution is P_{X_τ} on $\{\tau < \infty\}$.
Now, applying the strong Markov property on (4.18) we get;

$$\eta(x) = E_x(\eta(X_\tau)). \quad (4.19)$$

Using the symmetry of normal distribution, (4.19) becomes;

$$\begin{aligned} \eta(x) &= \eta(x-h)P_x(X_\tau = x-h) + \eta(x+h)P_x(X_\tau = x+h), \\ &= \frac{1}{2}\eta(x-h) + \frac{1}{2}\eta(x+h), \quad (4.20) \\ \text{implying that} \quad 2\eta(x) &= \eta(x-h) + \eta(x+h). \quad (4.21) \end{aligned}$$

Rearranging (4.21) and splitting the term on the right into two yields;

$$\begin{aligned} \eta(x-h) + \eta(x+h) - 2\eta(x) &= 0, \\ \eta(x+h) - \eta(x) - \eta(x) + \eta(x-h) &= 0, \\ \text{and} \quad [\eta(x+h) - \eta(x)] - [\eta(x) - \eta(x-h)] &= 0. \quad (4.22) \end{aligned}$$

[2] A stopping time τ (sometimes also called a Markov time) for the process $\{X_t\}$ is a random variable taking non-negative integer values, including possibly the value $+\infty$, such that $\{\tau \leq n\} \in \mathscr{F}_n$ for $n = 0, 1, 2, \ldots$ where $\mathscr{F}_n$ is an increasing sequence of sigmafields, that is: $\mathscr{F}_n \subset \mathscr{F}_{n+1}$.

Dividing (4.22) by h^2 gives;

$$\frac{\frac{\eta(x+h)-\eta(x)}{h} - \frac{\eta(x)-\eta(x-h)}{h}}{h} = 0. \tag{4.23}$$

If we let $h \downarrow 0$, (4.23) yields;

$$\eta''(x) = 0, \quad \eta(m) = 1, \quad \text{and} \quad \eta(n) = 0. \tag{4.24}$$

Since $\eta''(x) = 0$, then $\eta(x)$ takes the form of a linear equation, that is;

$$\eta(x) = ax + b. \tag{4.25}$$

Applying the conditions in (4.24) onto equation (4.25) we get;

$$a = -\frac{1}{n-m} \quad \text{and} \quad b = \frac{n}{n-m}. \tag{4.26}$$

Substituting (4.26) into (4.25) gives;

$$\eta(x) = \frac{n-x}{n-m}. \tag{4.27}$$

This means that: $P_x(\{X_t\} \text{ hits } m \text{ before } n) = \dfrac{n-x}{n-m}$.
But from (4.16), (4.17) and (4.27), we get;

$$P_x(\{X_t\} \text{ hits } n \text{ before } m) = 1 - \eta(x) = \frac{x-m}{n-m} \text{ for } m \leq x \leq n. \tag{4.28}$$

Hence, if we let $n \uparrow \infty$ in (4.27) and $m \downarrow -\infty$ in (4.28), then we get the required proof to the stated theorem as;

$$P_x(\tau_y < \infty) = 1 \quad \text{for all } x, y. \tag{4.29}$$

5. Application of Diffusion Processes to Insect Dispersal

Most models for describing the dispersal of organisms have been developed by using diffusion equations with a diffusion coefficient that measures the rate of dispersal. They have proposed that the dispersal in tsetse flies (Glossina spp) can be viewed as a series of discrete daily steps each considered to be in a random direction [HL89]. A proposed elaboration to this model states that the step length may be varied depending on the age and physiological state of the fly [HL89]. According to [Ske51], several results that define the spatio-temporal distribution of a diffusing particle are hardly available via the discrete method. This justifies the preference of diffusion models in the estimation of the rates of several insect movements. This approach has an advantage of being sufficiently accurate and providing easier statistical techniques for the measurement of the dispersal rates, despite being an initial approximation to the exact situation, and lacking the interaction of individuals which is biologically implausible.

5.1 Theoretical development

The model to be discussed in this section focuses on a diffusion coefficient which may keep changing with time, though it does not depend on the position of the particle. The spatial-time-dependent position of a particle that moves by diffusion in a plane, starting at the origin when time $t = 0$, having coefficient of diffusion $\sigma^2(t)$, is defined by a normally distributed random variable with density function

$$u(x,y,t) = \frac{1}{2\pi\nu}\text{exp}\left\{-\frac{(x^2+y^2)}{2\nu}\right\}, \quad \text{where} \quad \nu = \nu(t) = \int_0^t \sigma^2(s)ds. \tag{5.1}$$

proof follows:

Consider the diffusion equation $\dfrac{\partial u}{\partial t} = \sigma^2(t)\left(\dfrac{\partial^2 u}{\partial x^2} + \dfrac{\partial^2 u}{\partial y^2}\right)$. Expressing this equation in terms of a Fourier space, we get:

$$\begin{aligned}\frac{\partial}{\partial t}F(u) &= \sigma^2(t)\left(\frac{\partial^2}{\partial x^2}F(u) + \frac{\partial^2}{\partial y^2}F(u)\right)\\ &= \sigma^2(t)\left[(-ix)^2F(u) + (-iy)^2F(u)\right]\\ &= \sigma^2(t)(x^2+y^2)F(u).\end{aligned} \tag{5.2}$$

Separating variables, changing variables and integrating gives:

$$F(u)(k_1,k_2,t) = \lambda\text{exp}\left\{-(k_1^2+k_2^2)\int_0^t \sigma^2(s)ds\right\}.$$

Let $\nu = \nu(t) = \int_0^t \sigma^2(s)ds.$ This means that;

$$F(u)(k_1, k_2, t) = \lambda \text{exp}\left\{-(k_1^2 + k_2^2)\nu\right\}. \tag{5.3}$$

For (5.3) to be converted from Fourier space back to normal space, it suffices to compute the inverse of the Fourier transform as follows.

$$u(x, y, t) = \frac{1}{2\pi}\int_{-\infty}^{\infty}\int_{-\infty}^{\infty} \text{exp}(-ik_1x - ik_2y) \cdot F(u)(k_1, k_2, t)dk_1dk_2. \tag{5.4}$$

Substituting (5.3) into (5.4) gives;

$$\begin{aligned} u(x, y, t) &= \frac{1}{2\pi}\int_{-\infty}^{\infty}\int_{-\infty}^{\infty} \text{exp}(-ik_1x - ik_2y) \cdot \lambda\text{exp}\left\{-(k_1^2 + k_2^2)\nu\right\} dk_1dk_2 \\ &= \frac{\lambda}{2\pi}\int_{-\infty}^{\infty}\int_{-\infty}^{\infty} \text{exp}(-ik_1x - \nu k_1^2) \cdot \text{exp}(-ik_2y - \nu k_2^2)dk_1dk_2 \\ &= \frac{\lambda}{2\pi}\int_{-\infty}^{\infty} \text{exp}(-ik_1x - \nu k_1^2)dk_1 \int_{-\infty}^{\infty} \text{exp}(-ik_1y - \nu k_2^2)dk_2 \\ &= \frac{\lambda}{2\pi}\int_{-\infty}^{\infty} \text{exp}\left\{-\nu\left(k_1^2 + \frac{ik_1x}{\nu}\right)\right\} dk_1 \int_{-\infty}^{\infty} \text{exp}\left\{-\nu\left(k_2^2 + \frac{ik_2y}{\nu}\right)\right\} dk_2 \end{aligned} \tag{5.5}$$

Using the method of completing squares we get,

$$\begin{aligned} \int_{-\infty}^{\infty} \text{exp}\left\{-\nu\left(k_1^2 + \frac{ik_1x}{\nu}\right)\right\} dk_1 &= \int_{-\infty}^{\infty} \text{exp}\left\{-\nu\left(k_1 + \frac{ix}{2\nu}\right)^2 + \nu\left(\frac{ix}{2\nu}\right)^2\right\} dk_1 \\ &= \int_{-\infty}^{\infty} \text{exp}(-\nu k_1^2)dk_1 \cdot \text{exp}\left(-\frac{x^2}{4\nu}\right) \\ &= \frac{\sqrt{\pi}}{\nu}\text{exp}\left(-\frac{x^2}{4\nu}\right). \end{aligned} \tag{5.6}$$

$$\text{Similarly,} \quad \int_{-\infty}^{\infty} \text{exp}\left\{-\nu\left(k_2^2 + \frac{ik_2y}{\nu}\right)\right\} dk_2 = \frac{\sqrt{\pi}}{\nu}\text{exp}\left(-\frac{y^2}{4\nu}\right). \tag{5.7}$$

Substituting (5.6) and (5.7) into (5.5) gives;

$$\begin{aligned} u(x, y, t) &= \frac{\lambda}{2\pi}\left[\frac{\sqrt{\pi}}{\nu}\text{exp}\left(-\frac{x^2}{4\nu}\right) \cdot \frac{\sqrt{\pi}}{\nu}\text{exp}\left(-\frac{y^2}{4\nu}\right)\right] \\ &= \frac{\lambda}{2\nu}\text{exp}\left\{-\frac{(x^2 + y^2)}{4\nu}\right\}. \end{aligned} \tag{5.8}$$

Since the summation of all the probabilities over any given domain is 1, then;

$$\frac{\lambda}{2\nu}\int_{-\infty}^{\infty}\int_{-\infty}^{\infty} \text{exp}\left\{-\frac{(x^2 + y^2)}{4\nu}\right\} dxdy = 1, \tag{5.9}$$

$$\begin{aligned} \int_{-\infty}^{\infty}\int_{-\infty}^{\infty} \text{exp}\left\{-\frac{(x^2 + y^2)}{4\nu}\right\} dxdy &= \int_{-\infty}^{\infty} \text{exp}\left(-\frac{x^2}{4\nu}\right) dx \int_{-\infty}^{\infty} \text{exp}\left(-\frac{y^2}{4\nu}\right) dy \\ &= (\sqrt{4\nu}\sqrt{\pi}) \cdot (\sqrt{4\nu}\sqrt{\pi}) \\ &= 4\pi\nu. \end{aligned} \tag{5.10}$$

Substituting (5.10) into (5.11) gives;

$$\frac{4\pi\nu\lambda}{2\nu} = 1, \quad \text{this implies that:} \quad \lambda = \frac{1}{2\pi}. \tag{5.11}$$

Substituting (5.10) into (5.11) gives;

$$u(x, y, t) = \frac{1}{4\pi\nu}\text{exp}\left\{-\frac{(x^2 + y^2)}{4\nu}\right\}. \tag{5.12}$$

Equation (5.1) gives the probability per unit area that the dispersing insects will be located around a point (x, y) at time t, though equation (5.12) shows that it is not quite correct as stated in [HL89], because of the missing factor of 2 in the denominator. However, the impact of this inaccuracy is too insignificant to the obtained results. The probability (5.1) yields can be determined by integrating $u(x, y, t)$ over the region, though it is quite hard for a general case. To make it easier, we consider particular shapes like circles and rectangles, and the results yielded from this approach are quite satisfactory in practice [HL89].

5.1.1 Diffusion in a circular domain

For a circular domain, diffusion is firstly considered to originate from the centre. Due to symmetry, the mean displacement of a diffusing particle from its initial point is zero for all time. Since the equation of a circle is $x^2 + y^2 = R^2$, where R is the radius of the circular domain, then the random distance $R = \sqrt{x^2 + y^2}$ of a particle moving from the origin as a function of time can be studied. Considering a finite domain, the moments of the truncated distance T_d can be defined for all $d > 0$, that is:

$$T_d = \begin{cases} R & \text{for} \quad 0 \le R \le d \\ 0 & \text{otherwise} \end{cases} \tag{5.13}$$

Converting the cartesian coordinates to polar coordinates gives;

$$x = r\text{cos}\theta \ \text{ and } \ y = r\text{sin}\theta \ \text{ implying that } \ x^2 + y^2 = R^2 \tag{5.14}$$

$$\text{Also, since} \quad (x, y) \to (r, \theta), \quad \text{then} \quad dxdy = rdrd\theta. \tag{5.15}$$

But the n^{th} moment of the probability distribution is given by the Riemann-Stieltjes integral

$$E(X^n) = \int_{-\infty}^{\infty} x^n dF(x), \tag{5.16}$$

where X is the random variable that has this distribution. Using (5.14), equation (5.1) can be written in polar coordinates as;

$$u(r, \theta, t) = \frac{1}{2\pi\nu}\text{exp}\left\{-\frac{r^2}{2\nu}\right\}. \tag{5.17}$$

Using (5.13), (5.15) and (5.16), the moments of R can be generated from equation (5.17) and they are expressed as;

$$\begin{aligned} E(T_d^n) &= \frac{1}{2\pi\nu}\int_0^d\int_0^{2\pi} r^n \text{exp}\left\{-\frac{r^2}{2\nu}\right\} r dr d\theta \\ &= \frac{1}{2\pi\nu}\int_0^d\int_0^{2\pi} r^{n+1} \text{exp}\left\{-\frac{r^2}{2\nu}\right\} dr d\theta. \end{aligned} \tag{5.18}$$

$$\text{But} \quad \int_0^{2\pi} d\theta = 2\pi, \tag{5.19}$$

hence combining (5.18) and (5.19) generates;

$$E(T_d^n) = \frac{1}{\nu}\int_0^d r^{n+1} \text{exp}\left\{-\frac{r^2}{2\nu}\right\} dr, \quad \text{for} \;\; n = 0, 1, 2, \ldots \tag{5.20}$$

when $n = 0$, equation (5.20) becomes;

$$\begin{aligned} E(T_d^0) &= \int_0^d \frac{r}{\nu} \text{exp}\left\{-\frac{r^2}{2\nu}\right\} dr \\ &= \left[-\text{exp}\left\{-\frac{r^2}{2\nu}\right\}\right]_0^d = -\left(\text{exp}\left\{-\frac{d^2}{2\nu}\right\} - 1\right) \\ &= 1 - \text{exp}\left\{-\frac{d^2}{2\nu}\right\}. \end{aligned} \tag{5.21}$$

Equation (5.21) gives the probability $\mathscr{P}(R \leq d)$ that the diffusing particle is within a distance d from the origin at time t. When $n = 1$, equation (5.20) becomes

$$E(T_d^1) = \frac{1}{\nu}\int_0^d r^2 \text{exp}\left\{-\frac{r^2}{2\nu}\right\} dr. \tag{5.22}$$

To apply integration by parts on (5.22), the integral I will be defined as;

$$I = uv - \int_0^d v\frac{du}{dr} dr. \tag{5.23}$$

From the integral in (5.22), let

$$\left.\begin{aligned} \frac{dv}{dr} = r\ \text{exp}\left\{-\frac{r^2}{2\nu}\right\}, \quad \text{implying that} \quad v = -\frac{1}{2}\cdot 2\nu\ \text{exp}\left\{-\frac{r^2}{2\nu}\right\} \\ u = r, \quad \text{implying that} \quad \frac{du}{dr} = 1 \end{aligned}\right\} \tag{5.24}$$

Substituting (5.24) into (5.23) gives;

$$\begin{aligned} \int_0^d r^2 \text{exp}\left\{-\frac{r^2}{2\nu}\right\} dr &= \left[-\nu r\ \text{exp}\left\{-\frac{r^2}{2\nu}\right\}\right]_0^d + \nu\int_0^d \text{exp}\left\{-\frac{r^2}{2\nu}\right\} dr \\ &= \nu\left(-d\text{exp}\left\{-\frac{d^2}{2\nu}\right\} + \int_0^d \text{exp}\left\{-\frac{r^2}{2\nu}\right\} dr\right). \end{aligned} \tag{5.25}$$

Substituting (5.25) into (5.22) gives;

$$E(T_d^1) = -d\text{exp}\left\{-\frac{d^2}{2\nu}\right\} + \int_0^d \text{exp}\left\{-\frac{r^2}{2\nu}\right\} dr.$$

To integrate equation (5.20) by parts, let

$$\left.\begin{aligned} \frac{dv}{dr} = r\ \text{exp}\left\{-\frac{r^2}{2\nu}\right\}, \quad \text{implying that} \quad v = -\nu\ \text{exp}\left\{-\frac{r^2}{2\nu}\right\} \\ u = r^n, \quad \text{implying that} \quad \frac{du}{dr} = nr^{n-1} \end{aligned}\right\} \tag{5.26}$$

Using (5.23) and (5.26) we get;

$$\begin{aligned} \int_0^d r^{n+1}\text{exp}\left\{-\frac{r^2}{2\nu}\right\} dr &= \left[-\nu r^n \text{exp}\left\{-\frac{r^2}{2\nu}\right\}\right]_0^d + \nu \int_0^d nr^{n-1}\text{exp}\left\{-\frac{r^2}{2\nu}\right\} dr \\ &= \nu\left(-d^n\text{exp}\left\{-\frac{d^2}{2\nu}\right\} + \int_0^d nr^{n-1}\text{exp}\left\{-\frac{r^2}{2\nu}\right\} dr\right). \end{aligned} \tag{5.27}$$

Substituting (5.27) into (5.20) gives the reduction formula for $n > 1$ as

$$E(T_d^n) = -d^n\text{exp}\left\{-\frac{d^2}{2\nu}\right\} + \int_0^d nr^{n-1}\text{exp}\left\{-\frac{r^2}{2\nu}\right\} dr. \tag{5.28}$$

Since the standard normal distribution function is expressed as

$$\phi(x) = \frac{1}{\sqrt{2\pi}} \int_{-\infty}^x \text{exp}\left(-\frac{u^2}{2}\right) du, \tag{5.29}$$

then the integral in (5.28) can be expressed in terms of ϕ using (5.29), that is; when $n = 1$, the integral in (5.28) becomes:

$$\begin{aligned} \int_0^d nr^{n-1}\text{exp}\left(-\frac{r^2}{2\nu}\right) dr &= \int_0^d \text{exp}\left(-\frac{r^2}{2\nu}\right) dr \\ &= \int_{-\infty}^d \text{exp}\left(-\frac{r^2}{2\nu}\right) dr - \int_{-\infty}^0 \text{exp}\left(-\frac{r^2}{2\nu}\right) dr \\ &= \int_{-\infty}^\infty \text{exp}\left(-\frac{r^2}{2\nu}\right) dr - \int_d^\infty \text{exp}\left(-\frac{r^2}{2\nu}\right) dr - \int_{-\infty}^0 \text{exp}\left(-\frac{r^2}{2\nu}\right) dr \\ &= \int_{-\infty}^\infty \text{exp}\left(-\frac{r^2}{2\nu}\right) dr - \int_{-\infty}^{-d} \text{exp}\left(-\frac{r^2}{2\nu}\right) dr - \int_{-\infty}^0 \text{exp}\left(-\frac{r^2}{2\nu}\right) dr \\ &= \int_0^\infty \text{exp}\left(-\frac{r^2}{2\nu}\right) dr - \int_{-\infty}^{-d} \text{exp}\left(-\frac{r^2}{2\nu}\right) dr. \end{aligned} \tag{5.30}$$

Changing variables and limits, we get:

$$\left.\begin{aligned} u = \frac{r}{\sqrt{\nu}}, \quad \text{implying that} \quad dr = \sqrt{\nu}du \\ r(\infty, 0, -d, -\infty) \to u\left(\infty, 0, \frac{-d}{\sqrt{\nu}}, -\infty\right) \end{aligned}\right\} \tag{5.31}$$

Substituting (5.31) into (5.30) gives;

$$\begin{aligned}\int_0^d nr^{n-1}\text{exp}\left(-\frac{r^2}{2\nu}\right)dr &= \sqrt{\nu}\int_0^\infty \text{exp}\left(-\frac{u^2}{2}\right)du - \sqrt{\nu}\int_{-\infty}^{\frac{-d}{\sqrt{\nu}}}\text{exp}\left(-\frac{u^2}{2}\right)du \\ &= \sqrt{\nu}\left\{\frac{1}{2}\sqrt{2}\sqrt{\pi} - \sqrt{2\pi}\cdot\frac{1}{\sqrt{2\pi}}\int_{-\infty}^{\frac{-d}{\sqrt{\nu}}}\text{exp}\left(-\frac{u^2}{2}\right)du\right\}. \quad (5.32)\end{aligned}$$

Applying (5.29) on (5.32) gives;

$$\begin{aligned}\int_0^d nr^{n-1}\text{exp}\left(-\frac{r^2}{2\nu}\right)dr &= \sqrt{\nu}\left\{\frac{1}{2}\sqrt{2}\sqrt{\pi} - \sqrt{2\pi}\phi\left(\frac{-d}{\sqrt{\nu}}\right)\right\} \\ &= \sqrt{\frac{\nu\pi}{2}}\left\{1 - 2\phi\left(\frac{-d}{\sqrt{\nu}}\right)\right\}. \quad (5.33)\end{aligned}$$

Therefore, when $n = 1$, the moments of R are expressed as;

$$E(T_d^1) = \sqrt{\frac{\nu\pi}{2}}\left\{1 - 2\phi\left(\frac{-d}{\sqrt{\nu}}\right)\right\} - d\text{exp}\left(-\frac{d^2}{2\nu}\right). \quad (5.34)$$

For the recurrence relation of $n > 1$ to be obtained, we re-write (5.28) as;

$$E(T_d^n) = -d^n\text{exp}\left(-\frac{d^2}{2\nu}\right) + n\nu\left\{\frac{1}{\nu}\int_0^d r^{n-2}\text{exp}\left(-\frac{r^2}{2\nu}\right)rdr\right\}. \quad (5.35)$$

But the term in the braces of (5.35) is $E(T_d^{n-2})$, and substituting it yields;

$$E(T_d^n) = -d^n\text{exp}\left(-\frac{d^2}{2\nu}\right) + n\nu E(T_d^{n-2}). \quad (5.36)$$

Substituting $n = 2$ in equation (5.36) gives;

$$E(T_d^2) = -d^2\text{exp}\left(-\frac{d^2}{2\nu}\right) + 2\nu E(T_d^0). \quad (5.37)$$

Combining (5.21) and (5.37) we get;

$$E(T_d^2) = -d^2\text{exp}\left(-\frac{d^2}{2\nu}\right) + 2\nu\left\{1 - \text{exp}\left(-\frac{d^2}{2\nu}\right)\right\}. \quad (5.38)$$

5.1.2 Determination of conditional mean and variance

To obtain the non-truncated moments, we take limits as $d \to \infty$ in (5.34) and (5.38). This gives;

$$\begin{aligned}\lim_{d\to\infty} E(T_d^1) &= \lim_{d\to\infty}\left[\sqrt{\frac{\nu\pi}{2}}\left\{1 - 2\phi\left(\frac{-d}{\sqrt{\nu}}\right)\right\} - d\text{exp}\left(-\frac{d^2}{2\nu}\right)\right] \\ &= \sqrt{\frac{\nu\pi}{2}} = E(R^1). \quad (5.39)\end{aligned}$$

$$\begin{aligned}\lim_{d\to\infty} E(T_d^2) &= \lim_{d\to\infty}\left[-d^2\text{exp}\left(-\frac{d^2}{2\nu}\right) + 2\nu\left\{1 - \text{exp}\left(-\frac{d^2}{2\nu}\right)\right\}\right] \\ &= 2\nu = E(R^2). \quad (5.40)\end{aligned}$$

Therefore, using (5.39) and (5.40), we obtain the mean and variance of the distance R moved from the origin as;

$$\begin{aligned} E(R) &= \sqrt{\frac{\nu\pi}{2}}, \quad \text{and} \qquad (5.41) \\ Var(R) &= E(R^2) - \left[E(R^1)\right]^2 \\ &= 2\nu - \left(\sqrt{\frac{\nu\pi}{2}}\right)^2 \\ &= \frac{\nu}{2}(4-\pi) \quad \text{respectively.} \qquad (5.42) \end{aligned}$$

The conditional moments $E(R^n|R \leq d)$ can be determined from the truncated moments above, that is;

$$E(R^n|R \leq d) = \frac{E(T_d^n)}{E(T_d^0)}. \qquad (5.43)$$

When $n = 1$, we substitute (5.21) and (5.34) into (5.43) to obtain the conditional mean as;

$$\begin{aligned} E(R|R \leq d) &= \frac{E(T_d^1)}{E(T_d^0)} \qquad (5.44) \\ &= \frac{\sqrt{\frac{\nu\pi}{2}}\left\{1 - 2\phi\left(\frac{-d}{\sqrt{\nu}}\right)\right\} - d\exp\left(-\frac{d^2}{2\nu}\right)}{1 - \exp\left(-\frac{d^2}{2\nu}\right)}. \qquad (5.45) \end{aligned}$$

Using truncated moments, the conditional variance can also be obtained as;

$$\begin{aligned} \mathrm{Var}(R|R \leq d) &= E(R^2|R \leq d) - [E(R|R \leq d)]^2 \\ &= \frac{E(T_d^2)}{E(T_d^0)} - \frac{E(T_d^1)}{E(T_d^0)}. \qquad (5.46) \end{aligned}$$

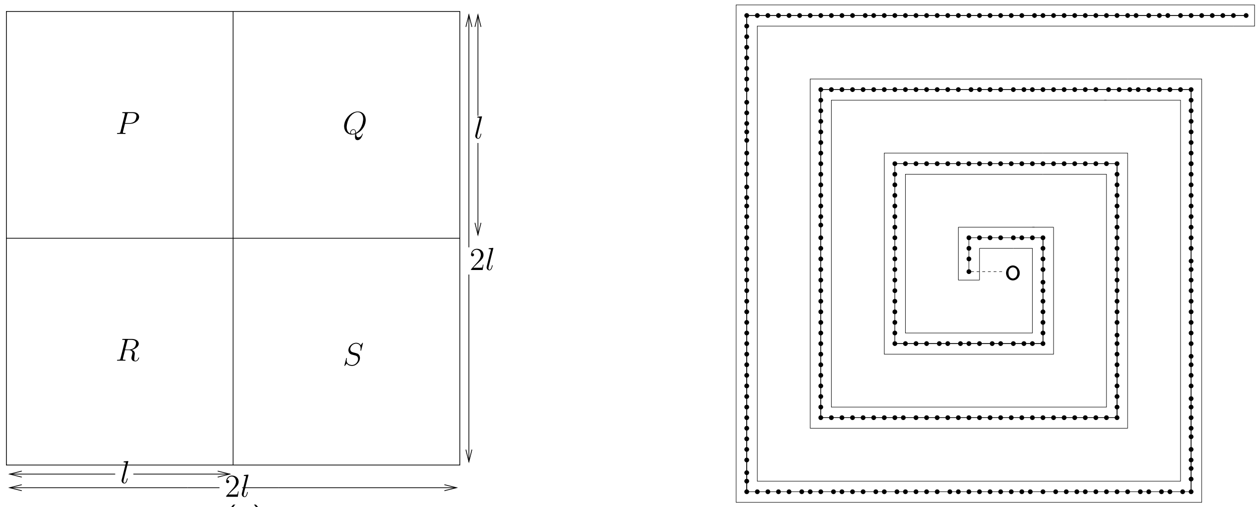
When $n = 2$, we substitute (5.21), (5.38) and (5.44) into (5.46), thus getting the conditional variance as;

$$\mathrm{Var}(R|R \leq d) = \frac{2\nu\left\{1 - \exp\left(-\frac{d^2}{2\nu}\right)\right\} - d^2\exp\left(-\frac{d^2}{2\nu}\right)}{1 - \exp\left(-\frac{d^2}{2\nu}\right)} - [E(R|R \leq d)]^2. \qquad (5.47)$$

Conditional moments play a significant role in cases where the insects are only sampled at short distances from the initial point, as compared to the capacity of insect dispersal being studied. In experiments where the area under consideration is relatively large, appropriate approximations are improvised to suit the reliability of the results [HL89]. For example, in Jackson's $(1941, 1946)$ experiment with tsetse flies, the area he considered was quite large. This makes (5.41) and (5.42) to be used as suitable approximations to (5.45) and (5.47) respectively.

5.1.3 Diffusion in a rectangle

In Jackson's (1941) experiment, tsetse flies were released in a 4×4 mile square (fig:5.1) were the relative probability of recapturing the flies in the quadrant of their release and in adjacent quadrants was observed. In this section, we discuss the probability of the insects released at time $t = 0$ at some random point in rectangle P, being present in rectangle Q at time t.



(a) (b)

Figure 5.1: Jackson's large square experiment (Fig: 5.1(a)). Tsetse were captured throughout the inner 4×4 mile square, marked with dots of artists' oil paint, according to date and quadrant of capture, and released. Subsequent marking parties noted the date and quadrant for each recaptured fly. The distribution of recaptures between the four quadrants was used to estimate emigration. Jackson's (1946) square spiral flyround (Fig: 5.1(b)). In this type of experiment, young tseyse (male G. morsitans) were released at point 0 and recaptured on the flyround marked here as the line with dots. The distance between two consecutive dots is equivalent to 100 yards. The dashed line between 0 and the nearest arm of the flyround indicates a portion of the flyround added for a later experiment. The distance between the initial point 0 and the outer arm of the flyround was ± 2100 yards.

The sides of P and Q are considered to be parallel to the axes, and this is basically for simplicity purposes. The two dimensional problem converts to a one dimensional problem because the X position does not depend on the Y position. Therefore, the resulting probabilities are multiplied to give the overall answer. For a one dimensional X motion of the particle, we consider the initial point to be chosen uniformly from the interval $[p, q]$. But since the probability density function of a continuous distribution is

$$u(z) = \begin{cases} \frac{1}{q-p} & \text{for} \quad p < z < q \\ 0 & \text{otherwise} \end{cases}, \tag{5.48}$$

then at some time t, the particle will be in the interval $[r, s]$ with probability determined using

(5.1) and (5.48) as;

$$\frac{1}{q-p}\int_p^q \frac{1}{\sqrt{2\pi\nu}}\int_r^s \text{exp}\left(-\frac{(x-z)^2}{2\nu}\right)dxdz = \frac{1}{q-p}\int_p^q \left\{\frac{1}{\sqrt{2\pi\nu}}\int_r^s \text{exp}\left(-\frac{(x-z)^2}{2\nu}\right)dx\right\}dz. \quad (5.49)$$

Considering the integral in the braces of (5.49), we get;

$$\int_r^s \text{exp}\left(-\frac{(x-z)^2}{2\nu}\right)dx = \int_{-\infty}^s \text{exp}\left(-\frac{(x-z)^2}{2\nu}\right)dx - \int_{-\infty}^r \text{exp}\left(-\frac{(x-z)^2}{2\nu}\right)dx. \quad (5.50)$$

Changing variables and limits, we get;

$$\left.\begin{aligned} u = \frac{x-z}{\sqrt{\nu}}, \quad \text{implying that} \quad dx = \sqrt{\nu}du \\ r(s, r, -\infty) \to u\left(\frac{s-z}{\sqrt{\nu}}, \frac{r-z}{\sqrt{\nu}}, -\infty\right) \end{aligned}\right\}. \quad (5.51)$$

Substituting (5.51) into (5.50) gives;

$$\begin{aligned} \int_r^s \text{exp}\left(-\frac{(x-z)^2}{2\nu}\right)dx &= \sqrt{\nu}\int_{-\infty}^{\frac{s-z}{\sqrt{\nu}}} \text{exp}\left(-\frac{u^2}{2\nu}\right)du - \sqrt{\nu}\int_{-\infty}^{\frac{r-z}{\sqrt{\nu}}} \text{exp}\left(-\frac{u^2}{2\nu}\right)du \\ &= \sqrt{2\pi\nu}\left[\frac{1}{\sqrt{2\pi}}\int_{-\infty}^{\frac{s-z}{\sqrt{\nu}}} \text{exp}\left(-\frac{u^2}{2\nu}\right)du - \frac{1}{\sqrt{2\pi}}\int_{-\infty}^{\frac{r-z}{\sqrt{\nu}}} \text{exp}\left(-\frac{u^2}{2\nu}\right)du\right]. \end{aligned} \quad (5.52)$$

Applying (5.29) on (5.52) we get;

$$\int_r^s \text{exp}\left(-\frac{(x-z)^2}{2\nu}\right)dx = \sqrt{2\pi\nu}\left[\phi\left(\frac{s-z}{\sqrt{\nu}}\right) - \phi\left(\frac{r-z}{\sqrt{\nu}}\right)\right]. \quad (5.53)$$

Substituting (5.53) into (5.49) gives

$$\frac{1}{q-p}\int_p^q \frac{1}{\sqrt{2\pi\nu}}\int_r^s \text{exp}\left(-\frac{(x-z)^2}{2\nu}\right)dxdz = \frac{1}{q-p}\int_p^q \left[\phi\left(\frac{s-z}{\sqrt{\nu}}\right) - \phi\left(\frac{r-z}{\sqrt{\nu}}\right)\right]dz \quad (5.54)$$

as the probability that at some time t, the particle will be in the interval $[r, s]$. From (5.54), consider the integration of $\int_p^q \phi\left(\frac{s-z}{\sqrt{\nu}}\right)dz$. Using integration by parts, we have:

$$\text{Let} \quad \frac{dv}{du} = 1 \quad \text{implying that} \quad v = z - s \quad (5.55)$$

$$\text{Also, if} \quad u = \phi\left(\frac{s-z}{\sqrt{\nu}}\right), \quad \text{then} \quad \frac{du}{dz} = -\frac{1}{\sqrt{\nu}}\phi'\left(\frac{s-z}{\sqrt{\nu}}\right) \quad (5.56)$$

Since the function in (5.29) is continuous, then its derivative with respect to x is;

$$\phi'(x) = \frac{1}{\sqrt{2\pi}}\text{exp}\left(-\frac{x^2}{2}\right). \quad (5.57)$$

Applying (5.57) on (5.56) we get;

$$\begin{aligned}\frac{du}{dz} &= -\frac{1}{\sqrt{\nu}}\cdot\frac{1}{\sqrt{2\pi}}\text{exp}\left\{-\frac{(s-z)^2}{2\nu}\right\}\\ &= -\frac{1}{\sqrt{2\pi\nu}}\text{exp}\left\{-\frac{(s-z)^2}{2\nu}\right\} \qquad (5.58)\end{aligned}$$

Substituting (5.55), (5.56) and (5.58) into (5.23), and applying the *fundamental theorem of calculus*[1] gives;

$$\int_p^q \phi\left(\frac{s-z}{\sqrt{\nu}}\right)dz = \phi\left(\frac{s-z}{\sqrt{\nu}}\right)(z-s)\Big|_p^q + \frac{1}{\sqrt{2\pi\nu}}\int_p^q (z-s)\text{exp}\left\{-\frac{(s-z)^2}{2\nu}\right\}dz. \qquad (5.59)$$

$$\begin{aligned}\text{But}\quad \frac{d}{dz}\left[\text{exp}\left\{-\frac{(s-z)^2}{2\nu}\right\}\right] &= -\frac{(z-s)}{\nu}\text{exp}\left\{-\frac{(s-z)^2}{2\nu}\right\},\\ \text{implying that}\quad \int_p^q (z-s)\text{exp}\left\{-\frac{(s-z)^2}{2\nu}\right\}dz &= -\nu\text{exp}\left\{-\frac{(s-z)^2}{2\nu}\right\}. \qquad (5.60)\end{aligned}$$

Substituting (5.60) into (5.59) gives;

$$\begin{aligned}\int_p^q \phi\left(\frac{s-z}{\sqrt{\nu}}\right)dz &= \phi\left(\frac{s-z}{\sqrt{\nu}}\right)(z-s)\Big|_p^q - \frac{\nu}{\sqrt{2\pi\nu}}\text{exp}\left\{-\frac{(s-z)^2}{2\nu}\right\}\Big|_p^q\\ &= \phi\left(\frac{s-z}{\sqrt{\nu}}\right)(z-s)\Big|_p^q - \sqrt{\frac{\nu}{2\pi}}\text{exp}\left\{-\frac{(s-z)^2}{2\nu}\right\}\Big|_p^q. \qquad (5.61)\end{aligned}$$

Similarly;

$$\int_p^q \phi\left(\frac{r-z}{\sqrt{\nu}}\right)dz = \phi\left(\frac{r-z}{\sqrt{\nu}}\right)(z-r)\Big|_p^q - \sqrt{\frac{\nu}{2\pi}}\text{exp}\left\{-\frac{(r-z)^2}{2\nu}\right\}\Big|_p^q. \qquad (5.62)$$

Substituting (5.61) and (5.62) into (5.54) gives;

$$\begin{aligned}\frac{1}{q-p}\int_p^q \frac{1}{\sqrt{2\pi\nu}}\int_r^s \text{exp}\left(-\frac{(x-z)^2}{2\nu}\right)dxdz = \frac{1}{q-p}\Bigg[\phi\left(\frac{s-z}{\sqrt{\nu}}\right)(z-s) - \phi\left(\frac{r-z}{\sqrt{\nu}}\right)(z-r)\\ + \sqrt{\frac{\nu}{2\pi}}\left(\text{exp}\left\{-\frac{(r-z)^2}{2\nu}\right\} - \text{exp}\left\{-\frac{(s-z)^2}{2\nu}\right\}\right)\Bigg]_{z=p}^{z=q} \qquad (5.63)\end{aligned}$$

Using (5.63) provides results which are of interest in Jackson's data analysis. Considering a square L of side $2l = q-p$ in (fig:5.1) where the release point of the insects is randomly chosen, the probability $\mathscr{P}_L(t)$ that the insects are still in the large square L after time t can be computed as follows: Since the movement pattern is two dimensional, let $\mathscr{P}_{pq}(t)$ and $\mathscr{P}_{pr}(t)$ denote the

[1] The fundamental theorem of calculus states that, if f is continuous on the closed interval $[p,q]$, and F is the anti-derivative of f, then; $\int_p^q f(x)dx = F(q) - F(p)$.

probabilities along X and Y directions respectively. Also note that for the insects to be still in square L, $p = r$ and $q = s$. This means that;

$$q - p = q - r = s - p = 2l \quad \text{and} \quad r - p = s - q = 0. \tag{5.64}$$

Applying (5.64) onto (5.63) gives;

$$\begin{aligned}
\mathscr{P}_{pq}(t) &= \frac{1}{2l}\left\{\left[-\phi\left(\frac{-2l}{\sqrt{\nu}}\right)(2l) + \sqrt{\frac{\nu}{2\pi}}\left(\exp\left(-\frac{2l^2}{\nu}\right) - 1\right)\right]\right. \\
&\quad \left. - \left[-\phi\left(\frac{2l}{\sqrt{\nu}}\right)(-2l) + \sqrt{\frac{\nu}{2\pi}}\left(1 - \exp\left(-\frac{2l^2}{\nu}\right)\right)\right]\right\} \\
&= \phi\left(\frac{2l}{\sqrt{\nu}}\right) - \phi\left(\frac{-2l}{\sqrt{\nu}}\right) - \frac{1}{2l}\cdot 2\sqrt{\frac{\nu}{2\pi}}\left(1 - \exp\left(-\frac{2l^2}{\nu}\right)\right) \\
&= \phi\left(\frac{2l}{\sqrt{\nu}}\right) - \phi\left(\frac{-2l}{\sqrt{\nu}}\right) - \sqrt{\frac{\nu}{2\pi l^2}}\left(1 - \exp\left(-\frac{2l^2}{\nu}\right)\right).
\end{aligned}$$

Since we are considering a square, then by symmetry; $\mathscr{P}_{pq}(t) = \mathscr{P}_{pr}(t)$. Therefore,

$$\begin{aligned}
\mathscr{P}_L(t) &= \mathscr{P}_{pq}(t)\cdot\mathscr{P}_{pr}(t) \\
&= \left[\phi\left(\frac{2l}{\sqrt{\nu}}\right) - \phi\left(\frac{-2l}{\sqrt{\nu}}\right) - \sqrt{\frac{\nu}{2\pi l^2}}\left(1 - \exp\left(-\frac{2l^2}{\nu}\right)\right)\right]^2.
\end{aligned} \tag{5.65}$$

Note 5.1. *Considering l to be relatively too large compared to $\sqrt{\nu}$, makes the expression to tend to an expression as follows; $\frac{2l}{\sqrt{\nu}} \to +\infty$, $\frac{-2l}{\sqrt{\nu}} \to -\infty$ and $\frac{-2l^2}{\nu} \to -\infty$. This implies that;*

$$\mathscr{P}_L(t) \approx \left[\phi(+\infty) - \phi(-\infty) - \sqrt{\frac{\nu}{2\pi l^2}}\left(1 - \exp(-\infty)\right)\right]^2. \tag{5.66}$$

Using (5.29) we get;

$$\phi(+\infty) = \frac{1}{\sqrt{2\pi}}\int_{-\infty}^{+\infty}\exp\left(-\frac{u^2}{2}\right)du = \frac{1}{\sqrt{2\pi}}\cdot\sqrt{2\pi} = 1 \quad \text{and} \quad \phi(-\infty) = \frac{1}{\sqrt{2\pi}}\int_{-\infty}^{-\infty}\exp\left(-\frac{u^2}{2}\right)du = 0. \tag{5.67}$$

Substituting (5.67) into (5.66) gives;

$$\begin{aligned}
\mathscr{P}_L(t) &\approx \left[1 - \sqrt{\frac{\nu}{2\pi l^2}}\right]^2 \\
&\approx 1 - 2\sqrt{\frac{\nu}{2\pi l^2}} + \frac{\nu}{2\pi l^2} \\
&\approx 1 - \sqrt{\frac{2\nu}{\pi l^2}}, \quad \text{because } \frac{\nu}{2\pi l^2} \text{ tends to zero, due to (Note: 5.1).}
\end{aligned} \tag{5.68}$$

Now, when the random initial points are restricted to the small square P of side l, then the probabilities $\mathscr{P}_P(t)$, $\mathscr{P}_Q(t)$ and $\mathscr{P}_S(t)$, that the insects will be in P, Q (or equivalently R) or

S can be determined using (5.63) as follows:
To determine $\mathscr{P}_P(t)$, let $\mathscr{P}_x(t)$ and $\mathscr{P}_y(t)$ be the probabilities along the X and Y directions respectively. Since it is a small square of side l, then $p = r$ and $q = s$. This implies that;

$$q - p = q - r = s - p = l \quad \text{and} \quad r - p = s - q = 0. \tag{5.69}$$

Applying (5.69) into (5.63) gives;

$$\begin{aligned}
\mathscr{P}_x(t) &= \frac{1}{l}\left\{\left[-\phi\left(\frac{-l}{\sqrt{\nu}}\right)(l) + \sqrt{\frac{\nu}{2\pi}}\left(\exp\left(-\frac{l^2}{2\nu}\right) - 1\right)\right]\right. \\
&\quad \left. - \left[-\phi\left(\frac{l}{\sqrt{\nu}}\right)(-l) + \sqrt{\frac{\nu}{2\pi}}\left(1 - \exp\left(-\frac{l^2}{2\nu}\right)\right)\right]\right\} \\
&= \phi\left(\frac{l}{\sqrt{\nu}}\right) - \phi\left(\frac{-l}{\sqrt{\nu}}\right) - \frac{1}{l}\cdot 2\sqrt{\frac{\nu}{2\pi}}\left(1 - \exp\left(-\frac{l^2}{2\nu}\right)\right) \\
&= \phi\left(\frac{l}{\sqrt{\nu}}\right) - \phi\left(\frac{-l}{\sqrt{\nu}}\right) - \sqrt{\frac{2\nu}{\pi l^2}}\left(1 - \exp\left(-\frac{l^2}{2\nu}\right)\right).
\end{aligned} \tag{5.70}$$

But because of symmetry, $\mathscr{P}_y(t) = \mathscr{P}_x(t)$, as it is a square under consideration. Therefore;

$$\begin{aligned}
\mathscr{P}_P(t) &= \mathscr{P}_x(t)\cdot\mathscr{P}_y(t) \\
&= \left[\phi\left(\frac{l}{\sqrt{\nu}}\right) - \phi\left(\frac{-l}{\sqrt{\nu}}\right) - \sqrt{\frac{2\nu}{\pi l^2}}\left(1 - \exp\left(-\frac{l^2}{2\nu}\right)\right)\right]^2 \qquad (5.71) \\
\mathscr{P}_x(t) &\approx \left[\phi(+\infty) - \phi(-\infty) - \sqrt{\frac{2\nu}{\pi l^2}}\left(1 - \exp(-\infty)\right)\right]^2. \qquad (5.72)
\end{aligned}$$

(5.72) is due to the application of (Note: 5.1). Now, substituting (5.67) into (5.72) gives;

$$\begin{aligned}
\mathscr{P}_P(t) &\approx \left[1 - \sqrt{\frac{2\nu}{\pi l^2}}\right]^2 \\
&\approx 1 - 2\sqrt{\frac{2\nu}{\pi l^2}} + \frac{2\nu}{\pi l^2} \\
&\approx 1 - 2\sqrt{\frac{2\nu}{\pi l^2}}, \quad \text{since } \frac{2\nu}{\pi l^2} \text{ tends to zero.}
\end{aligned}$$

For $\mathscr{P}_Q(t)$ to be computed, the dimensions of the square will take the form;

$$r - q = 0, \quad q - p = r - p = s - q = l, \quad \text{and} \quad s - p = 2l. \tag{5.73}$$

Taking $\mathscr{P}_x(t)$ and $\mathscr{P}_y(t)$ to be the X and Y directional probabilities, and applying (5.73) on

(5.63) gives:

$$\begin{aligned}
\mathscr{P}_x(t) &= \frac{1}{l}\left\{\left[\phi\left(\frac{l}{\sqrt{\nu}}\right)(-l) + \sqrt{\frac{\nu}{2\pi}}\left(1 - \exp\left(-\frac{l^2}{2\nu}\right)\right)\right]\right. \\
&\quad \left. - \left[\phi\left(\frac{2l}{\sqrt{\nu}}\right)(-2l) - \phi\left(\frac{l}{\sqrt{\nu}}\right)(-l) + \sqrt{\frac{\nu}{2\pi}}\left(\exp\left(-\frac{l^2}{2\nu}\right) - \exp\left(-\frac{2l^2}{\nu}\right)\right)\right]\right\} \\
&= \frac{1}{l}\left\{-2l\phi\left(\frac{l}{\sqrt{\nu}}\right) + 2l\phi\left(\frac{2l}{\sqrt{\nu}}\right) + \sqrt{\frac{\nu}{2\pi}} - 2\sqrt{\frac{\nu}{2\pi}}\exp\left(-\frac{l^2}{2\nu}\right) + \sqrt{\frac{\nu}{2\pi}}\exp\left(-\frac{2l^2}{\nu}\right)\right\} \\
\mathscr{P}_x(t) &\approx \left\{-2\phi(+\infty) + 2\phi(+\infty) + \sqrt{\frac{\nu}{2\pi l^2}} - 2\sqrt{\frac{\nu}{2\pi l^2}}\exp(-\infty) + \sqrt{\frac{\nu}{2\pi l^2}}\exp(-\infty)\right\} \\
&\approx \sqrt{\frac{\nu}{2\pi l^2}}. \qquad (5.74)
\end{aligned}$$

From (5.70), we get the expression of $\mathscr{P}_y(t)$ as; $\mathscr{P}_y(t) = 1 - \sqrt{\frac{2\nu}{\pi l^2}}$. (5.75)

$$\begin{aligned}
\text{Therefore,} \quad \mathscr{P}_Q(t) &= \mathscr{P}_x(t)\cdot\mathscr{P}_y(t) \approx \sqrt{\frac{\nu}{2\pi l^2}}\left(1 - \sqrt{\frac{2\nu}{\pi l^2}}\right). \\
\text{Similarly,} \quad \mathscr{P}_S(t) &= \left(\sqrt{\frac{\nu}{2\pi l^2}}\right)^2 \approx \frac{g}{2\pi l^2}.
\end{aligned}$$

Now, considering a scenario where the insects start dispersing from some fixed point inside a rectangle, with l_1, l_2, l_3 and l_4 as the distances of the sides of the rectangle from the initial point of the process, then the probability $\mathscr{P}_{rectangle}(t)$ that the insects will be within the rectangle at a time t later can be determined as follows:
Let $\mathscr{P}_x(t)$ and $\mathscr{P}_y(t)$ be the X and Y directional probabilities since the movement pattern is two dimensional. Therefore,

$$\mathscr{P}_x(t) = \frac{1}{2\pi\nu}\int_r^s \exp\left\{-\frac{(x-z)^2}{2\nu}\right\} dz. \qquad (5.76)$$

Substituting (5.53) into (5.76) gives;

$$\mathscr{P}_x(t) = \phi\left(\frac{s-x}{\sqrt{\nu}}\right) - \phi\left(\frac{r-x}{\sqrt{\nu}}\right). \qquad (5.77)$$

$$\text{But} \quad r - x = -l_1 \quad \text{and} \quad s - x = l_2. \qquad (5.78)$$

Substituting (5.78) into (5.77) gives;

$$\mathscr{P}_x(t) = \phi\left(\frac{l_2}{\sqrt{\nu}}\right) - \phi\left(\frac{-l_1}{\sqrt{\nu}}\right). \qquad (5.79)$$

Similarly, taking $r' - x = -l_3$ and $s' - x = l_4$, we get;

$$\mathscr{P}_y(t) = \phi\left(\frac{s'-x}{\sqrt{\nu}}\right) - \phi\left(\frac{r'-x}{\sqrt{\nu}}\right) = \phi\left(\frac{l_4}{\sqrt{\nu}}\right) - \phi\left(\frac{-l_3}{\sqrt{\nu}}\right). \qquad (5.80)$$

Using (5.79) and (5.80) we get;

$$\mathscr{P}_{rectangle}(t) = \mathscr{P}_x(t) \cdot \mathscr{P}_y(t) = \left[\phi\left(\frac{l_2}{\sqrt{\nu}}\right) - \phi\left(\frac{-l_1}{\sqrt{\nu}}\right)\right]\left[\phi\left(\frac{l_4}{\sqrt{\nu}}\right) - \phi\left(\frac{-l_3}{\sqrt{\nu}}\right)\right]. \quad (5.81)$$

Note 5.2. *The result (5.81) gives is obtained in many mark release experiments where animals are released from a single point [HL89].*

If the determined result in (5.81) was for a square of side $2l$, then $l_1 = l_2 = l_3 = l_4 = l$, implying that;

$$\mathscr{P}_{square}(t) = \left[\phi\left(\frac{l}{\sqrt{\nu}}\right) - \phi\left(\frac{-l}{\sqrt{\nu}}\right)\right]\left[\phi\left(\frac{l}{\sqrt{\nu}}\right) - \phi\left(\frac{-l}{\sqrt{\nu}}\right)\right] = \left[\phi\left(\frac{l}{\sqrt{\nu}}\right) - \phi\left(\frac{-l}{\sqrt{\nu}}\right)\right]^2. \quad (5.82)$$

5.2 Discussion of results

Tsetse dispersal studies carried out in the past [Jac41, Har81] used data that was produced in the 1930's and 1940's by Jackson. According to [HL89], there existed no other data that could be compared with the scope in the literature. Two basic types of experiments were performed by Jackson on the dispersal rate of the male G. morsitan tsetse flies.

In the first experiment, known as the *"square spiral"* experiment,Jackson released about 1750 young male G. morsitans at the centre of a square spiral path (Fig: 5.1(b)), and they were recaptured using hand nets by men who walked the entire spiral each day. He realised that the largest number of catches were made $3-4$ weeks after the release. This was contrary to his expectation of the peak occurring in the 1^{st} week due to flies' deaths immediately after release. The explanation to this contradiction was based on the low *"activity"* of tsetse during the first two weeks of adult life. However, [Har81] suggests that this contradiction is presumably because the probability of capture changed with the age of the fly. Jackson later used *"activity"* to mean the disposition of the tsetse to fly, and the word *"availability"* for the proportion of a population which a flyround actually catches [Har81].
Hargrove (1981) states that Rogers (1977) pointed out that (due to dispersal) the population was being sampled by a continually lengthening flyround, and the probability of capture was thereby increased. In compensation for this scenario, he calculated the area which would be covered after each day by a constant proportion of the population, and divided Jackson's (1946) recaptures by the length of the flyround in this area to produce a concentration rather than an absolute catch. He noticed a good correspondence between the figures. Despite the fact that the released flies will cover an increasing area of the spiral as the experiment progresses, this is altered by the fact that early in the experiment, the short length of the fly round effectively sampling the population would be drawing from a relatively more concentrated pool. So long as there is less tsetse, to the extent of not interfering with each other's capture, the total number of caught tsetse should be largely independent of the distribution of the population within the limits of the recapture area.

In the second experiment (referred to as the *"large square"* experiment), Jackson (1941) released tsetse in a 4×4 mile square area and observed the decline with time in the recaptures of the marked flies within the square. Marking the flies differently enabled Jackson to know the day (time) and the quadrant (sub-square) of their release. This made it possible for him to distinguish between declines due to death and emigration respectively. This also works for the distinction between the impacts due to birth and immigration.

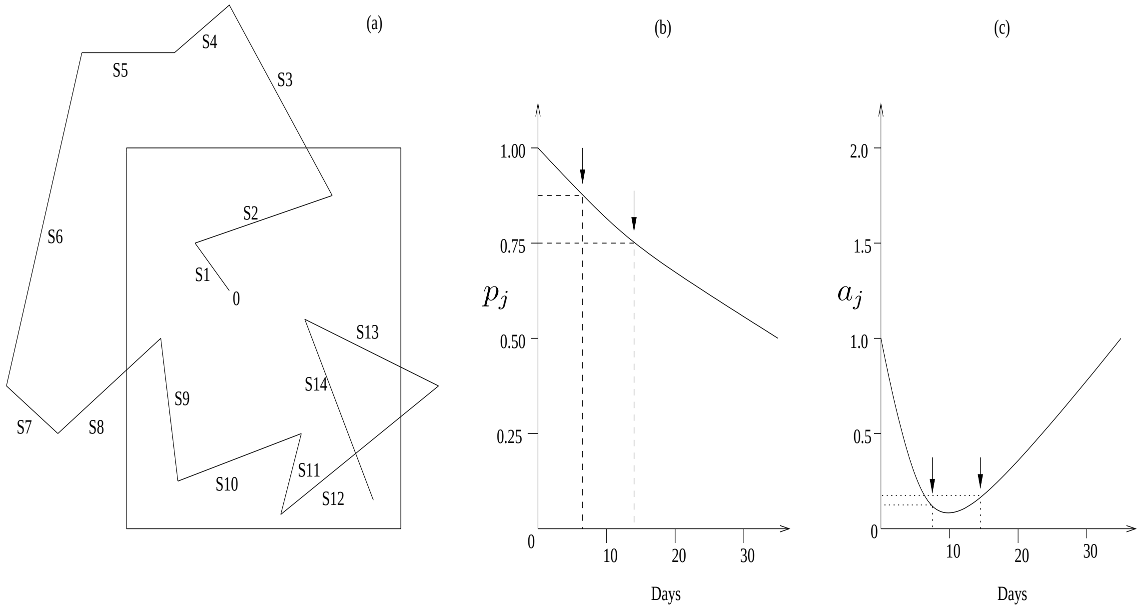
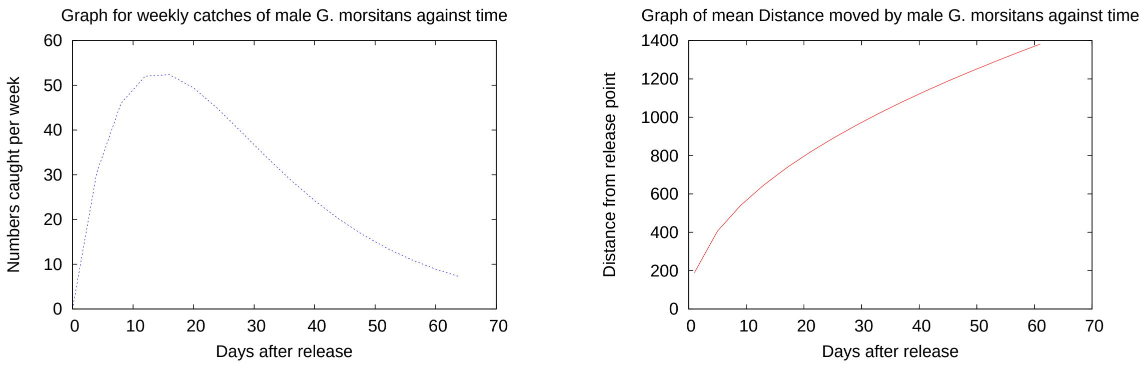


Figure 5.2: Jackson's (1941) large square experiment. Flies were released from randomly chosen points within a 4×4 unit square and allowed to make several moves, of variable length S_j, each move being in a random direction. The probability of the fly being captured on day j within the large square depends on its presence or absence within the sampling area (Fig: 5.2(a)), its probability of survival (Fig: 5.2(b)) and its availability (Fig: 5.2(c)) to the sampling system, as evaluated on day j. Therefore, on the 7^{th} day, the probability of capture was 0 because the fly was outside the large square. On the 14^{th} day, the probability of survival was 0.75, the availability was 0.15 and the fly was within the large square. Hence the probability of capture was $0.75 \times 0.15 = 0.1125$.

When the likelihood of the results being attributed to a random movement was examined, it was found that they could be compared with the decrease in the mean probability of capture of flies in the model system (Fig: 5.2(c)), where the flies take a number of steps each in a random direction. The mean probability comprises of atleast three components, that is: the probability (p_j) that the fly is alive on day j, the probability (a_j) that it will be caught if it is in some neighbourhood of the recapturing system, and the probability (q_j) that it is in that neighbourhood on day j. This probability depends on the length $(S_i, i = 1, j)$ of each daily displacement in the life of the fly, the number of steps (j) the fly has taken since its release, and the initial position from which the fly was released. In Jackson's 1941 model, the sampling is assumed to be even; the fly's probability of capture does not depend on its position within the sampling area, and flies outside this area have a zero probability of being captured. Changes due to daily death rate d_j and availability a_j were not considered in the previous models, though [Har81] states that Jackson's (1946) clearly appreciated that there were age-dependent changes in availability (his activity)

5.2.1 Distance travelled from a point source; square spiral data

Since the distance between the initial point of release and the point of recapture of each fly was noted by Jackson, then considering the recapture area to be approximately a circle of radius $d = 2100$ yards, the given data could be fitted to equation (5.45). The model only catered for 79% of the variance (Fig: 5.3(b)) when the diffusion coefficient was considered to be a constant (k) such that $\nu = kt$.
The value of k obtained by regression when substituted into equation (5.41) gives $E(R) = 175$ yards when the time $t = 1$ day [HL89]. This means that on average, a male G. morsitan will have moved a distance of 175 yards from the initial point of release after one day's dispersal. But the model [Har81] used predicted a distance of about 162 yards via the discrete "random walk"[2] approach, which is comparable with the 175 yards. When the same value of k is substituted into equation (5.21), it yields the expected probability of the surviving fly being within the limits of the spiral, for any time t after the start of the experiment. As the time after release increases, this probability and that of the fly surviving up to time t will both decrease monotonically. Therefore, the product of these two probabilities will also follow the same trend. This implies that if the spiral is sampled in a fairly uniform format as in [Har81], then the number of insects recaptured would also decrease monotonically with time after release. Since it is very difficult to find a



(a) (b)

Figure 5.3: Male G. morsitans caught weekly from a rectangular spiral flyround (Fig: 5.3(a)). This simulation is obtained from equation $R = k_1 t \exp(-k_2 t)$, where $k_1 = 10.08 \pm 1.37$ and $k_2 = 7.03 \times 10^{-2} \pm 5.68 \times 10^{-3}$. The units used are days^{-1}. Fig: 5.3(b), shows the apparent mean distance moved by the male G. morsitans against time after their release from the central point. This simulation is due to (5.45) with $\nu(t) = kt$, and $k = 0.0195(\text{yards} \times 10^3)^2$ days^{-1}. 2.8×10^{-3} is substituted as the asymptotic standard error for k.

function that describes the age-related change in capture probability [HL89], the product of the

[2] A random walk is the motion along a lineexecutedd by a particle which at each unit time, can move one unit to the left, move one unit to the right, or stand still, the probabilities of these transitions depending in general on the position of the particle, but being independent of time. We can therefore identify the possible positions or states of the particle with a finite or infinite set of integers. As before, we denote by $\mathscr{P}_{ij}^{(n)}$ the probability that the particle initially at position i will be at position j after n units (steps) of time.

two probabilities discussed in the paragraph above should be proportional to the recapture rate divided by the probability $\{E(T_d^0)\}$, that the fly is still within the spiral area being sampled. According to [HL89], when Jackson's 1946 data were treated in this way (Fig: 5.3(a)), they were well fitted by a function of the form

$$N = k_1 t \; \text{exp}(-k_2 t), \tag{5.83}$$

where N was the total catch of male G. morsitan flies on day t. Therefore, the recapture changes could be assessed as a product of a linear increment with age in the flies' probability of catches on a man flyround, with an exponentially decreasing probability of survival (i.e a constant death rate). Hargrove (1989) says that when Jackson's 1946 data was sampled in terms of a large square of side 3750 yards, the estimated value of k when substituted into equation (5.82) yielded a value of $\mathscr{P}_{square}(t)$ that was extremely close to the value $E(T_d^0)$ calculated above.

5.2.2 Diffusion out of a square; large square data

According to the results so far discussed, we can deduce that the diffusion coefficient for the male G. morsitans does not depend on the age of the fly. Taking the diffusion coefficient to be a constant with $\nu = kt$, then from Jackson's 1941 large square experiment, the probability of a fly being in a large square at time t after release can be determined using approximation (5.68).Attemptss to fit (5.68) to Jackson's 1941 data produces an inappropriate shape [HL89]. This reflects discontinuity in the observed function at the end of the 1^{st} week after release, and this is hard to explain using the model selected here. The explanation of this discontinuity is that perhaps the logic behind the results is faulty, but this is implausible.

The complex interaction of a strong sampling bias with an increase in the rate of fly dispersal with age contributed to observed losses from the square [Har81]. Analysis of Jackson's 1946 square spiral data in subsection (5.2.1) produced no evidence in support of the idea of a diffusion rate which increased with age. However, analysis due to the large square data favoured the idea that the rate of diffusion slowed down with time after release. The rapid dispersal immediately after release could be a result of an escape reaction, thus justifying the observed losses in the square [HL89]. But [Jac41] argues that this is not necessarily true because he was able to produce data which revealed the dispersal rate remaining abnormally high for several days after release. Alternatively, since the flies were randomly caught in a square and released at their point of capture, the population density remained the same at all release points, and this could have been responsible for the deviation of the dispersal rates after release. Due to the various unknown ages of the flies and the complex changes in probability of capture with age, one needs to interpret the results with care.

6. Conclusion

Since the simple diffusion equation selected here may be indeed too much of a simplification, then it suffices to put more complex models into consideration. According to [HL89], Taylor (1980) claims that data for the dispersal of "*G. palpalis*" and "*G.tachinoides*" conforms better to the generalised gamma distribution than the normal that has been discussed in this essay. Consideration of such models is beyond the scope of this essay. It is worth noting that if more complex models are to be considered, it would call for an increased number of parameters. However, [HL89] doubts if the data Jackson used could provide an acceptable basis for a test of the suitability of such models.

Further more, Jackson's classical mark-recapture experiment on male G.morsitans exposed many errors of interpretation thus leading to the distortion of the exact phenomena of tsetse dispersal. The incorporation of age dependent changes and changes due to death rates into a model of random movement would improve the fitting of Jackson's classical mark-recapture data thus producing a satisfactorily good basis for the ideas on tsetse dispersal and population dynamics in general.

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