University of Reading

Characterising Animal Foraging Behaviour and Implications for Resource Management

Thesis submitted for the degree of Doctor of Philosophy

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Declaration

I confirm that this is my own work and the use of all material from other sources has been properly and fully acknowledged

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Abstract

The spatial-dynamics of animal movement behaviour are still under-studied and remain less understood than desired. Exploration of this phenomenon leads to important economic, ecological and natural-resource management implications. Yet despite the recent advances in technology and scientific methods, questions remain in terms of understating the complexities of movement patterns and robust quantification. Key factors impeding the investigation have been the lack of accurate data and incisive mathematical and quantification models.

Animal movement in general, and foraging in particular, are vital characteristics of species which constantly adapt to changes in physical, biological, and social dynamics. Measuring animal movement patterns poses critical questions surrounding specification of appropriate representations of data generation. Accurate methods that identify underlying patterns from incomplete or imprecise raw data are therefore much desired in movement analysis. A better and deeper understanding of the actual heterogeneous patterns of movement can enable more effective management, conservation and development activities.

Since the initial identification of a specific pattern termed Lévy flights in foraging animals by Viswanathan et al. (1996, 1999), many later studies have explored this phenomenon. Lévy flight is a special type of random walk derived from the so-called power-law distribution. A vast and diverse variety of foraging animals have been found to exhibit this movement pattern. However, Edwards (2011) overturned previous conclusions surrounding the existence of Lévy flights within a diverse sample of ecological settings, including five species: reindeer in Sweden (Mårell et al. 2002); side-striped jackals in Zimbabwe (Atkinson et al. 2002); microzooplankton (Bartumeus et al. 2003); grey seals (Austin et al. 2004); and humans in the form of fishers (Bertrand et al. 2007; Marchal et al. 2007) and hunter gatherers (Brown et al. 2007). Re-analysing the above data sets using a modern likelihood approach, Edwards found that Lévy flights pattern is not as common a phenomenon as once thought.

The overarching aim of this thesis is to contribute to a better understanding of animal foraging movement patterns, and thus inform the improved management of the landscapes in which

foragers are found. Central to achieving this aim is the testing of the hypothesis that Lévy flight is not a common phenomenon in nature, through the adaptation and application of two robust Bayesian statistical approaches to a number of distinct data sets. The results obtained through Bayesian approaches are compared with previous findings.

Methodologically, this thesis employs the Standard Bayesian estimation approach (SBEA) (likelihood-based Bayesian method) and the Approximate Bayesian Computation (ABC) (likelihood-free Bayesian method), to re-analyse three of the original data sets re-analysed by Edwards (2011). These data sets include; (a) Dobe Ju/'hoansi human hunter-gatherers in Botswana and Namibia (Brown et al. 2007) (b) reindeer in Sweden (Mårell et al. 2002) and (c) Dutch beam-trawler fishing boats (Marchal et al. 2007). Standard Bayesian analysis is dependent on the specification of a likelihood function. For more complex models such as those for identifying movement patterns, specifying a likelihood function is computationally difficult. Therefore, the application of a simulation-based likelihood-free ABC method provides additional precision and robustness.

Results reveal that irrespective of the species or foraging objective, humans in the form of hunter gathers and fishers, as well as reindeer, exhibit a bounded Lévy flight foraging pattern. This finding disproves and simultaneously improves the previous findings by Edwards (2011) and other original authors. The thesis also finds that foraging patterns evolve with the availability of prey across time, which is in par with earlier studies. In terms of the methodology, comparing the two Bayesian techniques, the thesis concludes that the likelihood-free Bayesian framework is better able to capture the underlying patterns of animal movement compared to the conventional approaches. This is a crucial finding specifically in terms of animal movement exploration where there is a lack of precise and complete data.

Rather than simply assume that a Bayesian approach is "better", in this thesis the robustness and relevance of using Bayesian approaches is then further explored through a number of simulations and applications. First, movement patterns are simulated to ensure that the two Bayesian methods do indeed recover the true movement pattern. Second, one of the datasets used is progressively truncated to determine how sensitive these methods are to the number of data observations. Third, a number of applications of these methods of relevance to resource management are discussed in the thesis, for which improvement and further modifications to Bayesian simulation-based methods allow more efficient and accurate investigations: wildlife corridors developed to minimise the negative impacts of fragmented landscapes; and optimal containment of invasive species. In each case, policy makers require improved understanding of how species move and the rate of spread of species, respectively, often when there is little available data.

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List of abbreviations

ABC	Approximate Bayesian Computation
ABM	Agent-based Models
BMA	Bayesian Model Averaging
CRW	Correlated Random Walk
IBM	Individual-based Models
LFFH	Lévy flight Foraging Hypothesis
M-H	Metropolis-Hastings
MCMC	Markov Chain Monte Carlo
RW	Random Walk
SBEA	Standard Bayesian Estimation Approach
SMC	Sequential Monte Carlo
SSM	State Space Models
VMS	Vessel Monitoring System

Chapter 1 Introduction

1.1 Introduction to the study of animal movement

Animal movement in general, and foraging in particular, is a vital characteristic of any living organism. Over the past three decades, technology to explore and understand spatial and temporal movement patterns in a wide range of species from marine to terrestrial ecosystems has shown considerable advancements (Teimouri et al. 2018). These improvements include advances in animal tracking devices as well as enhanced conceptual frameworks in animal movement research (Tremblay et al. 2009).

Despite these advancements, the spatial-dynamics of movement behaviour and the spread process of species are still under-studied and remain insufficiently. Recent technological advancements such as powerful tracking devices, have, to some extent, overcome the limitations of accurate data collection techniques and the difficulty of precise quantification of the time-space interaction of individuals and species. For example, Liao et al. (2018) integrate GPS-tracking and field observations to determine cattle movement patterns in Ethiopia. More generally, telemetry technologies are making it possible for animals to be tracked remotely (Hooten et al., 2017; Thums et al., 2018), and Hays et al. (2016) have suggested that we are in a “golden age for animal movement studies” because of recent technical advances.

A key reason behind characterising animal movement is that capturing the dynamic nature of the interaction of species and natural resource abundance is an onerous statistical and mathematical task (Hooten et al. 2017; Brooks-Pollock et al. 2015). Therefore, scientists are increasingly focusing their attention on developing rigorous analytical modelling techniques to better capture underlying behaviours (Jonsen et al. 2006; Patterson et al. 2008; Codling et al. 2008; Gautestad and Myterud 2013). This is attempted by designing statistical and mechanistic models to make the most efficient use of raw data collected with the aim of addressing the emerging questions on animal movement patterns.

As scientific modelling and exploration techniques expand and the understanding of the underlying behaviours of movement improves, a number of policy questions with respect to the natural environment and resources arise. Some of the key questions involve “how”, “why”, “when” and “where” animals move as a result of transformed surroundings or in search of food. These questions are intrinsically interesting, particularly for ecologists. However, addressing these questions is also of importance for policy makers interested in, for example, containing invasive species in a cost-effective way. A better understanding of foraging patterns can improve management and conservation decisions such as evaluating potential impacts of habitat fragmentation on biodiversity through the identification of identification of cost-effective placement of wildlife passes or habitat corridors (Goodwin 2003; Allen and Singh, 2016). Both fisher livelihoods and fish stocks can be enhanced through improved allocation of spatial fishing rights. Indeed, more recently, quantitative modelling has focussed on the effect of policies on resource user behaviour, and thus the effect and effectiveness of management policies on the future state of the biophysical resource (Heinz and Strand 2006; Sims et al. 2007; Edwards et al. 2008; Kroetz and Sanchirico 2015).

Other such implications include reintroduction of key species, pest and disease control (Green et al. 2006; Bigras-Poulin et al. 2007; Lentz et al. 2016) and evaluating climate change impacts on species migration (Walther et al. 2002; Alerstam et al. 2006) and extinction and future infrastructure development planning (Colman et al. 2001, Nellemann et al. 2003). For example, understanding the invasion, plague and disease spread patterns (Arim et al. 2006; Morales et al. 2010) can signal better agricultural cropping decisions and pest and disease control. Investigations on animal movement across space and time are thus likely to continue to play an important role in understanding the benefits and costs of potential solutions to address important issues of resource management where humans and other species share landscapes.

A considerable part of the broad effort to understand animal movement deals with the analysis of forager movement patterns. The first attempts to model the behaviour of animal foraging were based on optimal foraging theory (MacArthur and Piyanka 1966) which in turn is based on the notion that animals expect to optimise resource or energy per unit effort (Perry and Pianka 1996). It was later observed that distinct foraging strategies evolve as a response to the availability and distribution of a resource (Bartumeus et al. 2003; Bazazi et al. 2012). According to Viswanathan et al. (1996), Benhamou et al. (2007) and Reynolds et al. (2009) different foraging strategies exhibit distinctive spatial properties and optimise search strategies which are dependent on the resource availability (Benhamou et al. 2007; Humphries et al. 2010). These empirical studies on foraging identify optimal movement patterns by computing the frequency distribution of the distances travelled, or movement step lengths, between reorientation events (Shlesinger 1986 and Viswanathan et al. 2010).

These early studies established the existence of a foraging pattern termed ‘Lévy flight’, which was found to occur in a wide range of animals irrespective of the species. However, the influential empirical conclusions of the first two studies by Viswanathan et al. (1996, 1999) and several further studies on Lévy flight identification in ecology have since been overturned by Edwards et al. (2007, 2011). This suggests that the data may have initially been misinterpreted and that inappropriate methods may have been used. Methods similar to Viswanathan et al. (1996) such as simple log-transformation of histograms and log-binning methods were subsequently employed for later studies, but those methods too have since been shown to be inaccurate (Edwards et al. 2007, 2008 and 2011; Sims et al. 2007; and White et al. 2008). Edwards et al. (2007) employed a maximum likelihood approach to overturn the previous conclusions of Lévy flight existence after re-analysing many of the previously published data sets.

Many other authors have pointed out that Lévy flight may not be a suitable model, and therefore have proposed alternative models characterise foraging patterns (Benhamou 2007; Buchanan 2007; Bartumeus and Levin 2008, Humphries et al. 2010; Reynolds 2012; Plank et al. 2013). Benhamou (2007) showed that overlooking the habitat types of the foragers as well as the behaviour among them can lead to false identification of search behaviour as a Lévy flight. Auger-Méthé et al. (2015) showed that the methods used to model foraging patterns are not sufficiently robust or adequate to differentiate between Lévy flight and other very similar models such as composite correlated random walks. Auger-Méthé et al. (2015) further state that although methodological developments have been introduced to approximate models such as composite correlated random walks (Reynolds 2012; Gautestad 2013), these models do not sufficiently incorporate an essential factor in movement analysis which is the turning angles of foraging animals (Jansen et al.2012; Plank et al. 2013). According to the explanation by Auger-Méthé et al. (2015), changing the distribution of step length and the turning angle can affect the fit of the movement model. Thus, the incorporation of the turning angle as well as the distribution is important in characterising movement. Pyke (2015) also discusses why

Lévy flight may not be a suitable model to explain the search pattern of a foraging animal and also states that the term Lévy flight has been used inaccurately in place of Lévy walks in movement literature. Pyke (2015) further explains how certain assumptions in Lévy flight models are not valid in reality and thus it may be time to abandon Lévy flight as a model of foraging behaviour. Therefore, this contradiction of findings over a significant movement hypothesis over the years signals the need for a statistical approach that can capture the complexity in animal foraging patterns.

1.2 Motivation aims and objectives

This study is motivated by a lack of dominant statistical models to account for the uncertainty in modelling movement behaviours (Jonsen et al. 2005; Edwards et al. 2007; Sims et al. 2008; Hooten et al. 2017), which leaves policy makers with insufficient tools to manage landscapes optimally where humans and foraging animals coexist. Therefore, this thesis is focused on developing a practical analytical framework to obtain ecologically relevant behavioural information from movement data, overcoming the challenge of mathematical and statistical limitations in an effort to contribute a more robust methodology to the evolving literature.

The lack of accurate quantification methodologies is a major factor limiting the advances which need to be further focused in making inference in animal movement modelling in general and foraging movement in particular (Edwards 2011; Humphries et al. 2012; Plank et al. 2013; Pyke 2015). Due to the uncertain nature of animal (including human) foraging Bayesian model selection may offer a more flexible approach compared with earlier approaches, as it allows parameterization of complex mathematical models and simultaneously accounts for parameter and model uncertainty (Hoeting et al. 1999; Beaumont 2010; Hooten and Hobbs 2015). Therefore, the broader aim of the study is to contribute to the understanding of the complex and heterogeneous behaviour of organisms in ecology through characterization of forager movement paths. This thesis therefore focuses on establishing an improved statistical framework (or frameworks) for analysing and interpreting data obtained on the movements of foragers so as to improve the management of landscapes where humans and foraging species co-exist.

The aim of this thesis is achieved through addressing the research questions specified below:

- To what extent can the use of Bayesian methods deliver an improved understanding of foraging patterns?
- Do Bayesian methods used in this thesis confirm or over turn the conclusions in the literature concerning animal movement and particularly the widespread finding of Levy flight?

The specific objectives of the study, that enable the research questions to be answered, are:

- To develop appropriate Bayesian approaches to more accurately characterise the movement patterns of animal and human foraging;
- To use these methodological frameworks to test the hypothesis of Lévy flight existence, based on Edwards (2011);
- To compare and contrast the applicability and suitability of the statistical frameworks used previously for analysis;
- To explore the robustness of the Bayesian approaches used in this thesis, focusing particularly on the number of models tested and the size of the dataset;

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1.3 Thesis overview

Following on from this introductory Chapter 1, Chapter 2 reviews the literature on movement analysis and how it has evolved over time. Chapter 3 details the methodological approach taken in the thesis. The analyses in this thesis use as a starting point the linear displacements between successive locations visited by the specific foragers, also known as the ‘step-lengths’. This is a commonly used metric in the analysis of animal movement data. It is often used in conjunction with the angle between the locations, known as the ‘turning angle’. The movement (step-length) data, in this chapter, are analysed using Bayesian methods. The full breadth and depth of models analysed are compared to the proposed alternative of Lévy flight, which is a special type of random walk with a power-law distribution which, as mentioned earlier, gained a considerable foothold in the recent scientific debate. In order to suggest the appropriate technique, this chapter includes an extensive review of the literature and a comparison of the frequentist and Bayesian techniques used in movement analysis.

The chapter provides detail of the two Bayesian methodological approaches employed throughout the thesis for analysing three different foraging datasets to assess the validity of Lévy flight existence hypothesis in ecology based on the paper by Edwards (2011). The first is the standard Bayesian estimation approach (SBEA), which is a likelihood-based technique; the second is a likelihood-free approximate Bayesian computation (ABC) approach. Approximate Bayesian computation is a relatively new approach in Bayesian statistics. Compared to the standard Bayesian estimation approach (SBEA), ABC approaches bypass the evaluation of a likelihood function. The need for a likelihood function is overcome by simulating data from a proposal distribution and searching for parameter values that produce simulated data close to the observed data. Thus, this thesis highlights the theoretical differences between the likelihood-based (SBEA) and the likelihood-free (ABC) approach and the use of which in animal movement modelling.

Chapter 4 employs the two methodological approaches on the first foraging data set; human foraging in the form Ju/'hoansi (herein termed as !Kung) hunter-gatherers. Chapter 5 analyses the movement pattern of foraging of reindeer (*Rangifer tarandus tarandus* L.), again using the two methodological approaches, but this time for a non-human forager. Chapter 6 employs the two methods to analyse human foraging data in a different setting in the form of large-scale fishers, which are profit maximising enterprises. Each of the chapters 4, 5 and 6 contains an introduction to the foraging data used, a review of the literature, the method, results and an application and/or discussion of the implications

The final chapter, Chapter 7, concludes, focusing on the implications of the findings from the previous chapters. It discusses how each objective of the thesis is achieved based on the inferences obtained from each of the frameworks. The two techniques have their own strengths and weaknesses in their application to movement data. Hence, these are compared and their suitability for movement analyses is discussed. Movement analysis is an evolving field of science, and so this chapter closes by stating the challenges faced and identifying areas for future work.

1.4 Contribution

Two key statistical approaches, likelihood-based standard Bayesian estimation approach (SBEA) as well as a likelihood-free Approximate Bayesian computation (ABC) approach, are selected based on their strengths to be applied to movement data obtained from secondary published sources. These two methods are selected as they are flexible and powerful tools that can provide a reliable output which is simply to be interpreted in terms of the behaviour of the individual or population. Both these methods have been used in movement analysis (Jonsen et al. 2003,2005; Sirén et al. 2018) but to the author’s best knowledge, have not been employed to analyse foraging behaviour. Moreover, previously they have not been used to analyse the three data sets; !Kung hunter gatherers, reindeer and fishermen used in this thesis.

The desired statistical outcome of the thesis is to explore each method and identify which approach is the most effective, why it is preferred, and to identify the differences between the approaches. Because the choice of model can have an impact on the output and the subsequent inferences, these need to be understood in some detail at the outset of a movement study.

From an ecological perspective, it is essential to find statistical models which not only provide a theoretical fit to the data but also provide a sound and conveniently interpretable output which is realistic in terms of the ecology of the species. These inferences can then be integrated into bio-economic modelling, thus makeing use of the movement data to answer much wider ranging ecological questions. Animal movement data can be extremely difficult and expensive to collect and basic analyses typically do not do justice to the data.

A widely debated issue in the Lévy flight literature is the difference in foraging behaviour between humans and other animals. Yet human foraging has not been widely explored in the literature. Understanding human movement and foraging patterns could signal important implications in a variety of fields such as genetics, epidemiology and as archaeology. This indicates the need for a more powerful but flexible approach. A Bayesian model comparison technique provides this and can with relative ease account for many sources of variations especially in terms of human foraging as well as contributing to the building of pragmatic statistical models addressing the questions focused in this study. This thesis contributes to this area of research by applying rigorous Bayesian approaches to both human and animal foraging data sets, and thus explicates the similarities and differences in human and non-human foraging patterns.

The need for a better understanding of movement processes is addressed here, particularly in the light of global environmental issues such as climate change, disease outbreaks and biological invasions. It is essential that statistical modelling approaches be able to be adapted to cater for these developing areas of science. Three challenges in movement analysis are identified by Nathan et al. (2008). These are (a) splitting the movement path into strings of unique units which can be used to calculate the step-lengths and turning angles making up the movement path; (b) classifying these step-lengths and turning angles; (c) integrating the movement data and analysis within an environmental context using metrics and techniques. These three challenges require statistical analyses. This thesis focuses on techniques and ways of improving the analyses to achieve the outcomes of the third challenge. Chapters 4, 5, and 6 demonstrate the application of the findings in practical scenarios through simulations.

There is a considerable volume of studies in the field of movement behaviour modelling that have compared and contrasted the results from a variety of methods to understand the impact that the choice of analysis can have on the results of the study. This study can be considered an ensuing movement study as a vast number of movement analyses have already been published using a wide variety of techniques. This study adapts and customises both approaches in order to make it more suitable for this specific application to !Kung, reindeer, and fishermen movement data.

1.5 General notation used throughout the thesis

The observed step length or distance measured (l) consists the data used for the study which is denoted as $\mathbf{y} \equiv (y_1, y_2, .., y_N)'$.· I use $f(\cdot)$ to denote, generically, an appropriate probability density function; and $f(\mathbf{y}|\boldsymbol{\theta})$ to denote the conditional distribution or the likelihood function for the data given the parameter, which may be vector-valued, $\boldsymbol{\theta}$. $f(\boldsymbol{\theta})$ denotes the distribution of the parameters in the absence of data, which is henceforth referred to as the ‘prior probability density function (prior pdf) or ‘prior’. For each model, I have obtained the “posterior probability density function (posterior pdf)’ by multiplying the likelihood by the prior. This joint distribution is $f(\mathbf{\theta}|\mathbf{y})$.

My interest centres on model comparison or selection. For this reason, the “marginal density of the data” also termed “the evidence” or “marginal likelihood” makes the quantity $f(\mathbf{y})$. The value of $f(\mathbf{y})$ is of over-arching importance as I have calculated the ‘evidence’ for each model $f(y|M)$ under each analytical approach. This notation is used consistently throughout the thesis where I have laid out the analytical approaches beginning from the next chapter. Chapter 2 lays out an extensive review of the evolution of movement modelling and the basis for selecting the Bayesian paradigm.

Chapter 2 Modelling of Animal Movement Patterns in the Literature

This chapter discusses the evolution and the application of different models used in the literature to explore animal movement patterns in general and foraging in particular. Movement is a defining characteristic in any organism. Most ecological processes such as survival, migration, invasions and reproduction are directly related to movement. Understanding the underlying process and patterns of movement can have important economic implications mainly in terms of ecological, resource and environmental conservation and management.

Owing to the lack of appropriate data collection devices and mathematical models for analysis, the study of animal movement played a peripheral role up until the 1960s. More recently, with the advancement of data collection and analytical techniques, especially in the field of ecology, movement explorations are now at the forefront of ecological research and are gradually carving a niche in environmental and resource economics and management as well. Indeed, with the recent technological development, researchers have come up with a variety of modelling approaches, and conceptual and methodological frameworks to analyse and understand movement paths which may have movement behaviours. Some of the most widely used models from the inception of these studies include random walks (RW), including uncorrelated and correlated random walks, diffusion, Lévy flights, fractal analysis, first passage time (FPT) and multi-behavioural approaches. Among these models, random walks and their diffusion approximations were most popular during the early stages of movement research (Okubo 1980; Kareiva 1990; and Turchin 1998).

This chapter provides an overview of the evolution and the use of these different approaches to model animal movement, particularly in the ecology literature. It also outlines the basis for the selection and application of the Bayesian approach which is used for analysis in this thesis. A key focus of this thesis is modelling of forager movement patterns, and thus this chapter pays particular attention to this specific element of the literature.

2.1 The early animal movement literature

Methods and approaches to analyse animal movement initially started as organism-centric modelling such as fractal analysis and have moved to correlated movement models. The movement of an animal before an encounter such as with its prey can be considered a search process. Diffusion and dispersal are generally considered search processes. During a search, the organism is looking for the presence of an object of interest (e.g. food), thus it involves some degree of uncertainty as both spatial and temporal spread of targets are unknown to the searching animal. Animals are assumed to move in a random search pattern to optimise the chance of resource encounters by covering a certain region through a probabilistic event such as food or breeding habitats. Random search is a stochastic process which means that the pattern or the process is derived from probability laws.

Certain animals may have memory or sensory cues to locate targets, which implies that their searching behaviour may not be inherent but is also governed by other internal and external factors. However, it is not possible to completely ignore the fortuitous identification as uncertainty in nature is unavoidable and in uncertain environments, search success can be thought to increase through random search strategies. Börger et al. (2008) and Gautestad (2013) have discussed the challenges of incorporating memory in to theoretical frameworks of movement modelling. An animal’s search pattern for an object of interest can influence research on various fields such as population studies, anthropology and genetics as it may lead to many behavioural patterns.

2.2 Diffusion models and random walks in ecology

Many of the models described here were first used in chemistry, physics, biology and other related fields to analyse particle movement analysis. They have proven to be powerful models in movement analysis. The three most commonly used random walk models in movement analysis are uncorrelated random walks, correlated random walks, and Lévy flight (Okubo et al. 1980; Kareiva and Shigesada 1983; Okubo and Levin 2002). When a movement consists of a large number of random walks, it is called a diffusion model. Diffusion models are better able to estimate populations rather than individual variation in movement and are less powerful in relation to correlated random walks in animal movement analysis. Researchers identified that the diffusion models are not able to capture the behavioural dynamics of moving animals, such as where the animal is or behavioural switching. Both correlated random walk and diffusion models have been widely used in movement analysis. In summary, both these models bear close similarities. While correlated random walk models describe how an individual particle moves, diffusion models explain how a population of particles moving in a particular random walk spread.

Therefore, a more developed modelling approach was needed and later studied resolved to employ correlated random walk models to study animal foraging patterns. These models are discussed in the following sub-sections.

2.2.1 Correlated and uncorrelated random walks

Robert Brown (1828) first introduced a random walk model named Brownian motion using pollen particle motion. Random walk theory was subsequently developed following his publication. The interest for understanding how organisms move dates back to early 1900 (Fisher 1922 and Dobzhansky and Wright 1943). Some of the first models of Animal movement using diffusion models can be traced back to Fisher (1937) and Skellam (1951). Skellam’s (1951) seminal article can be considered the first to address animal movement patterns explicitly. This article was the first to formalise animal movement as a mathematical relationship to model dispersal analogous to molecular diffusion. Using North American muskrat (*Ondatra zibethicus*) expansion, Skellem (1951) elaborated several mathematical formulations for dispersal and migration based on a random walk and diffusion patterns for population growth.

The uncorrelated random walk can be considered as the simplest form of individual animal movement with random angles between independent step lengths. Hence the name as there is no correlation between successive step lengths in any direction, where turning angles follow a uniform distribution such as in Brownian motion (Benhamou et al. 2007).

The first rigorous analysis of individual movement patterns can be found in Patlak (1953). He explicitly considers step lengths and turning angles and time intervals to predict diffusion and displacement. Another notable study by Kareiva and Shigesada (1983), unaware of Patlak's (1953) work, used a similar method to analyse searching behaviour of cabbage white butterflies (*Pieris rapae*) and pipe-vine swallowtail (*Battus philenor*) and identified their movement in terms of turning angles and move lengths follow correlated random walk. Their paper introduced Correlated Random Walk (CRW) patterns for animal movement.

Correlated random walks consist of step lengths drawn from a probability distribution which may be Gaussian or exponentially decaying distribution where turning angles follow a non-uniform distribution such as an exponential distribution (Bartumeus et al. 2005). In correlated random walks, step lengths are correlated with directional persistence (the subsequent step is more likely to be in the same direction (Shlesinger and Klafter 1986) with the initial direction of movement gradually disappearing over time (Benhamou 2004). These types of walks are defined by a step length distribution with a finite variance.

Notable studies which explicitly used CRW include reindeer movement analysis by Mårell et al. (2002) Elk movement by Morales et al. (2004) and Fortin et al. (2005). These studies conclude that the organisms shift their habitats depending on predator movement. Correlated random walk models, although closely related to diffusion models, are distinct as they describe the behaviour of an individual organism whereas a diffusion model describes the behaviour or dispersal of a population. CRW models can therefore be considered as more developed diffusion models. Some of the other notable papers which focuses on CRW include Siniff and Jessen (1969); Jones (1977); Shigesada (1980); Kareiva and Shigesada (1983); Bovet and Benhamou (1988); Okubo and Levin (2002) and Hillen (2002).

Bovet and Benhamou (1988) also emphasized that movements of living organisms cannot be easily described by simple equations as applied in physics or chemistry to understand particle movement. Thereafter, as a more realistic solution, Turchin (1998) proposed random walk models to study animal trajectories, suggesting probabilistic formalism would account for latent behaviours of animals. In movement modelling, a random walk linked with a specified step length distribution yields the distance a particle occurs during a given time (Börger et al. 2008).

Switching random walk models are being used to detect the switching of states or modes while animals are foraging or moving in general. Benhamou (2007) states that the foraging or movement pattern of an animal can be a mixture of classical random walk models. These movements can be correlated or uncorrelated depending on internal and external factors such as the state or mode of movement. Benhamou (2007) shows that a forager looking for patchily distributed resource following a Brownian movement pattern can be erroneously identified as a Lévy walker. This paper also states that the random walks may alternate within patches as well. Moreover, in patchy and non-fractal environments, Lévy flight like patterns may also emerge due to the power-law distribution of resources. Benhamou (2004) and Zollner and Lima (1999) state that foraging could be better understood through composite or mixture of random walk patterns which can explain when a forager should enter and leave a patch of resources as well as the optimum allocation of foraging effort. Benhamou (2007) show that identification of an actual Lévy flight pattern depends on two conditions. First is that the observed step lengths obey a power-law distribution corresponding to a true Lévy flight pattern. Second, is that the pattern must be intrinsically generated as opposed to a by-product of interacting with environmental conditions. If the pattern is a seemingly Lévy flight (a Lévy flight-like) movement then there is a high possibility that it is a mixture of random walk processes (Bovet and Benhamou 1988, Codling and Hill 2005).

2.2.2 Lévy flight models

French mathematician Paul Lévy introduced the Lévy flight model in 1925 defining it as a random walk in which step lengths show a heavy tailed probability distribution moving in random directions that can range within a circle (Viswanathan et al. 1996; Pyke 2015). Each step is assumed to begin where the previous step ended. The change in direction of Lévy flight movement patterns is assumed to follow a uniform distribution with no correlation between successive steps (Dray et al. 2010). Lévy flights are a particular case of Pareto distribution. Lévy walks can be explained as a pattern of short step clusters connected with an occasional very large step (Figure 2.1). In a more general form, the probability density functions of these distributions can be written as a power-law distribution as below.

$$P(l)\ \alpha\ l^{-\mu} \qquad [2.1]$$

P(l) (Equation 2.1) is the probability of distance (length) moved. The parameter, μ which is the power-law exponent is related to different types of redistribution kernel. $1 < \mu \leq 3$ corresponds to a Lévy flight whereas $\mu = 2$ indicates an optimal foraging strategy under certain conditions. Parameter values; $\mu \geq 3$ corresponds to a Gaussian distribution or Brownian motion while $\mu < 1$ exhibits a probability distribution which cannot be normalised (Viswanathan et al. 1996, 1999). Lévy flight distribution is also referred to as a Pareto distribution (Edwards 2011; Plank et al. 2013). Gautestad (2011); Pyke (2015) and Lundy et al. (2013) state that Lévy flight distributions can also be generated by alternative distributions such as Poisson, Inverse-power-law and Negative exponential distributions. Lévy walkers can select steps from all possible directions where each step begins from the end from the preceding step. Therefore, Lévy flight distribution pattern follows a uniform distribution of direction. In a Lévy flight movement pattern, unlike the other random walks, the length of the step is chosen randomly from a Lévy flight distribution unless terminated by a food or target encounter (Viswanathan et al. 1999). In general, Lévy flight pattern has become important in studies relating to super diffusion as this pattern gives rise to faster diffusion compared to normal diffusion resulting from other patterns such as Brownian motion. From the 1980s, scientists studying diffusion (Shlesinger and Klafter 1986) have suggested that it is possible for foraging or moving animals to follow this pattern to locate food more efficiently (Shlesinger 2009).

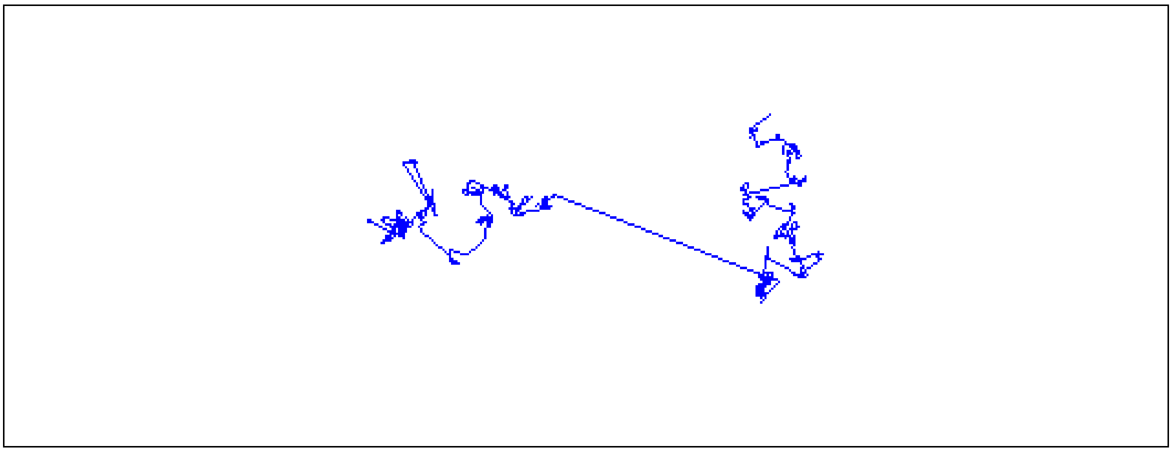

Figure 2.1: Lévy distribution

Lévy flights differ from other random walks as each step in this movement is chosen from a Lévy probability distribution unless the steps are terminated by a target or a resource encounter such prey or food.

Lévy flight theory was first applied in physical and chemical systems, specifically in the context of fractal patterns with no characteristic scale. Lévy flights, or walks,[1] are a special type of random walk that have recently been widely used for movement analysis. Lévy walks are also uncorrelated but with a heavy tailed power-law step length distribution with an infinite variance and has no characteristic scale. Literature identifies Lévy walks to be the most efficient search pattern for foraging (Viswanathan et al. 1996; Bartumeus et al. 2005) while later publications argue the validity and conclusions (Benhamou 2007; Edwards 2011).

Lévy flight pattern in foragers gave rise to the Lévy flight foraging hypothesis (LFFH). LFFH states that because Lévy flights/walks can optimise search efficiencies, natural selection should have led to adaptations for Lévy flight foraging (Viswanathan et al. 2008). Where foraging is of concern, the original attempts to model foraging behaviour was in the context of optimal foraging theory (MacArthur and Piyanka 1966) which assumes that animals strive to optimise energy or, in other words, obtain the highest quantity of resources per unit effort (Perry 1996). With the increase of foraging research, it was observed that foraging strategies are resource dependent and evolve in response to the distribution of resources (Viswanathan et al. 1996; Benhamou et al. 2007 and Reynolds et al. 2009).

Different foraging strategies exhibit distinctive spatial properties and optimised search strategies which are dependent on the resource availability (Humphries et al. 2010; Benhamou et al. 2007). These empirical studies on foraging identified optimal patterns of movement on the basis of the frequency distribution of distances travelled between reorientation events which are referred to as movement steps (Viswanathan et al. 2011; Shlesinger 1986).

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[1] In literature related to movement, the two terms Lévy flights and Lévy walks have been used interchangeably (James et al. 2011; Humphries and Sims 2014; Sims et al. 2014)

Applying Lévy flight theory in ecology for the first time, Viswanathan et al. (1996, 1999) presented evidence of Lévy flight movement patterns in wandering albatrosses, bumblebees, and deer. This application followed many similar conclusions of Lévy flight existence, in relation to the movement of a wide range of species such as reindeer in Sweden (Mårell et al., 2002), jackals in Zimbabwe (Atkinson et al., 2002), microzooplankton (dinoflagellates) in experiments (Bartumeus et al. 2003), grey seals in the North Atlantic Ocean (Austin et al. 2004). Some studies also explored human foraging behaviour. These included Dobe Ju/'hoansi human hunter-gatherers in Botswana and Namibia (Brown et al. 2007), Peruvian purse-seiner fishing boat movement (Bertrand et al. 2007), Dutch beam-trawler fishing boat movement (Marchal et al. 2007) and Hadza hunter-gatherers in Tanzania (Raichlen et al. 2014).

Lévy flights have been a popular mean of analysing animal foraging and movement data over the past decade. Yet Humphries et al. (2010) showed that animals do not follow Lévy flight movement pattern all the time, nor in all types of environments, and that other behaviour patterns intermingle. This study also emphasises the need to test the predictions of the Lévy flight foraging hypothesis to determine whether foragers undertake this theoretically optimal movement pattern depending on the environment and resource conditions. Humphries et al. (2016), using Bigeye tuna *(T. Obesus)* foraging data confirmed the hypothesis of Lévy flight movement pattern and showed that identification of this pattern can be a useful indicator of foraging activity for individuals whose foraging cannot be observed directly.

The identification of Lévy flights in movement patterns in general and foraging, in particular, carries implications for various theories in numerous fields such as ecology (e.g. optimal foraging theory), anthropology and archaeology. Interestingly, identification of Lévy flight can be extended to applications in the fields of marketing (e.g. agri-food markets), economics and information technology as well.

Motivated by Viswanathan et al.'s (1996) paper several other authors investigated the pattern beyond qualitative observations. Via a simulation study, Bartumeus et al. (2002, 2005) concluded that if the targets are sparsely distributed with large interaction distances, the encounter rates can be significantly higher for a Lévy search than for a Brownian search. By adopting Lévy flight movement patterns, foragers are able to search a greater area while minimising the probability of visiting already visited sites. Complementing the findings by Bartumeus et al. (2002, 2005), simulating the behaviour of monkeys, Boyer et al. (2006) found that Lévy walks are not an inert strategy but rather a consequence of resource distribution. These results also conform to the results found by Ramos-Fernandez et al., (2004, 2013) using spider monkey foraging data.

Since the first application of Lévy flight to study animal movement by Viswanathan et al. (1996), Lévy flight has evolved as a controversial approach. Many of the criticisms have been based on the validity of the assumptions and methodological shortcomings. Pyke (2015) particularly emphasises on the reasons behind abandoning Lévy flight as a foraging hypothesis altogether. An important issue leading to this abandonment emphasised in Pyke (2015) is that many of the papers neglect the cognitive abilities of all organisms in concern. Levy flight foraging theory assumes a featureless environment and that organisms are completely unaware of their surrounding indicating they have no sensory cues of the prey or food target (Pyke 2015). Heineman et al. (2008) and Hillesland et al. (2009) found that even the simplest organisms such as bacteria use sensory cues and responds to chemical and physical factors such as temperature in the surrounding. Hillesland et al. (2009) also found that bacteria evolved with higher foraging proficiency that were caused as result of limitations of prey distribution. Given the fact even these simplest organisms use sensory cues, other more advanced organisms and animals are undoubtedly expected to use more sophisticated sensory and cognitive abilities while foraging to increase their efficiency (Gautestad 2011). Reynolds (2010) and Ferreira et al. (2012) show that all organisms naturally do not exist in featureless environments. They further state that even the unavailability of a food resource, temporary or seasonal availability also act as a cue for the foragers. Therefore, it is clear that the assumption of organisms being completely unaware of the surrounding with no sensory cues is an assumption that does not hold while foraging.

Based on their study on *Manta alfredi* foraging in lagoons, Papastamatiou et al. (2012) suggest that foragers constantly turn in a biased direction to maintain a home range. This is due to the fact that they possess a reference memory which tells them where the high-quality patches are in a given area and a working memory to avoid already visited patches (Van Moorter et al. 2009). Apart from memory, cognition and sensory cues, another important factor that has been omitted by scientists is the communication among animals. Not only do foragers remember, they may also share information through communication. Brown et al. (1991) shows how cliff swallows effectively shares information while foraging. The general spatial scale at which organisms sense and respond to is generally about one body length (Pyke 2015). Pyke and Carter (2012) based on the bumblebee foraging study show that if the information is shared or communication is considered, bees respond to a special scale which is larger than one body length. Therefore, the special scale could also be a factor that needs attention in Lévy flight modelling. However, monitoring of actual spatial scaled may pose challenges through natural or technological limitations.

Another important factor omitted or assumed constant in Lévy flight analysis is the speed of the foragers (Papastamatious et al. 2012 and Miramontes et al. 2012). Pyke (2015) states that although foragers move with a variation in speed and distance, this factor is not considered at all or is assumed constant (James et al. 2011). Body orientation of an individual is another factor that has not been considered in Lévy flight modelling (Pyke 2015). All animals including the simplest organisms have a front, a rear or at least and axis of body orientation. All moving animals constantly changes their direction, speed as well as body orientation (Reynolds and Rhodes 2009; Bazazi et al. 2012). Pyke and Carter (1992) based on their study on pollinating bumblebees concluded that the directionality of foraging bumblebees is due to their cognition or memory of direction. The bumblebees were shown to keep track of their arrival direction and depart in the same direction even when the flower patches were turned to another direction. Therefore, this also shows evidence of memory as well as the importance of considering direction in movement modelling.

The Lévy flight hypothesis assumes none or zero directionality as well as no correlation between movement directions in foraging (Dray et al. 2010; Chapperon and Seuront 2013). Visser (2007) shows that organisms move in a zigzag manner alternating between left and right directions. Also, Benhamou and Bovet (1989), Mueller et al. (2011) and Bazazi et al. (2012) show that foragers respond to the availability of food and may turn more with sharp turning angles and decreasing speed leading to an area-restricted search pattern.

Lévy flight analysis also omits the decision-making process of animals. As discussed above, the decision-making process involves, senses, memory, knowledge communication as well as the responses to these factors reflected by a change in speed, direction and body orientation. It would also be imperative to consider the evolution and adaptive abilities of animals in nature as foraging efficiency is undoubtedly affected by these factors (McFarland 1977; Pyke et al. 1977).

A majority of studies that conclude Lévy flight foraging patterns have only considered one dimension (Brown et al. 2007; Sims et al. 2008; Humphries et al. 2010). However, animals such as birds and fish can be seen to utilize another dimension such as depth while otherwise moving in a horizontal linear path. These vertical moment changes can also result in a fat tail of distribution (Sims et al. 2012).

From a modelling point of view, Lévy flight allows the variation of the exponent parameter μ only and most studies compare Lévy flight to Brownian distribution and overlooks other movement models (Raposo et al. 2009 and James et al. 2011). Also, Pyke (2015) states that most studies are biased in trying to confirm the movement distribution as a Lévy flight distribution by specifying an arbitrary minimum and maximum value and restricting the Lévy flight portion of the distribution (Lopez-Lopez et al. 2013) concluding an inevitable Lévy flight distribution.

Pyke (2015) further states that most studies concluding Lévy flight analysis assumed that the reason an animal stops while searching is due to a food encounter. It is therefore important to record all stops made due to food encounters and other reasons during data collection and select the stops due to food encounters for analysis. Very few studies have successfully attempted this method (De Jager et al. 2014).

Another factor which is largely overlooked in movement studies is the energy expenditure of foragers which has a significant impact on their path (Shepard et al. 2009). Most studies assume turn cost or cost of movement to be constant (Bartumeus et al. 2005). According to Newton’s first law, the forager will have a constant movement velocity until acted upon by an external force. Thus, a forager will require extra energy to turn while moving. Cooke (2008) shows how turn costs can be important in explaining the change in movement paths by demonstrating how small prey such as Gazelle chased by large predators such as Cheetahs take sharp turns while on the run or why large prey try to outrun small predators for survival (Handcock et al. 2009). Using a modelling-based approach, Wilson et al. (2013) showed that conventional foraging models such as Lévy flight are invalid as they do not take in to consideration the cost of turning (Visawanathan et al.1996) and ignore the fact that energy expenditure of the movement path is mainly due to turning and not due the distribution of steps. Using mammal foraging data, Wilson et al. (2013) further shows that foragers continue to move in s straight line unless the benefits of turning offsets the costs.

Auger-Methe et al. (2015) discusses the importance of choosing the most accurate method for characterising underlying movement paths, particularly Lévy flights, as other movement patterns such as correlated random walks are often misidentified as Lévy flights. This is mainly due to the fact that most methods cannot distinguish the actual pattern accurately.

Benhamou (2007), Plank and Codling (2009), Auger-Methe et al. (2011) and Codling and Plank (2011) also state that Lévy flights could be confounded with the composite correlated random walk model as they show similar movement patterns. Auger-Methe et al. (2015) successfully applied a hidden Markov model to differentiate Lévy flights from a composite random walk model. Initially Auger-Methe et al. (2015) carried out a simulation exercise incorporating behavioural persistence and turning angles. Maximum likelihood estimation was applied with a likelihood function specified for a hidden Markov model. Akaike weights were then used to compare the models in concern. This method was then applied to polar bear (*Ursus maritimus*) foraging patterns to test the applicability of the statistical measure. Their results show that this method could be successfully used to differentiate Lévy flights from composite correlated random walk models. They further discuss the importance of the statistical measure in accurately identifying the foraging pattern.

2.3 Non-Random walk approaches to modelling movement

2.3.1 Fractal analysis

Fractal analysis was first introduced by Beniot Mandelbrot (1977) in his book to describe the organisation of galaxies. Fractal analysis is different from other methods in as much as it is not based on a random walk process. Rather, fractals are geometric patterns of dispersal or distribution found in many natural phenomena. Since their introduction in 1977, fractals were widely employed by ecologists to study movement dynamics. Some early note-worthy paper includes Dicke and Burrough (1988), Milne (1990), Johnson et al. (1992), and Wiens et al. (1995). These papers used fractal analysis on the assumption of scale invariance which was proved wrong by Turchin (1996) due to inaccurate computations. Dicke and Burrough (1988) was the first to introduce fractals as a method to explore animal movement patterns. In a much later study, Benhamou (2004) used fractal analysis with several variations and extensions to include complex switching behaviours.

2.3.2 First passage time analysis

First passage time analysis was first used by Johnson et al. (1992) followed by several other papers including Fauchald and Tveraa (2003). This method is used to make predictions from time series Markov processes of movement data. That is, it predicts the state of an animal in a future time. First passage time analysis has been used in ecology to predict several important phenomena such as extinction of species (Dennis et al. 1991); particle decay in physics and chemical kinetics and cellular transport; and economic problems such a stock prices and future market variations (Siegert 1951; Szabo et al. 1980). Since Fauchald and Tveraa (2003), other notable papers that use first passage time analysis for animal movement analysis are Frair et al. (2005), Weimerskirch et al. (2005), Bailey and Thompson (2006) and Pinaud and Weimerskirch (2007). However, first passage time analysis suffers from drawbacks, mainly as it is non-statistical and is not able to characterise movement scales.

Grurarie et al. (2015) applied a first passage time method by fitting a Gaussian mixture model to quantify wolf movement patterns. This paper concludes that compared to other methods such as Bayesian partitioning of Markov models and behavioural change point analysis, the first passage time method is the only approach which quantifies the intensity of space use and also picks up the behavioural changes. Freitas et al. (2018) applied the first passage time method on loggerhead sea turtles to quantify search effort. They conclude that these pelagic species adjust their search foraging strategies according to environmental conditions. Le Corre et al. (2014) applied first passage time method to characterise the migration path of female Caribous to detect the migration pattern and seasonal range use. Barraquand and Benhamou (2008) applied first passage time approach on simulated foraging data to identify how search effort is allocated according to habitat features and underlying latent behaviours of animals.

2.3.3 Continuous time movement models

Continuous time movement models are widely used to analyse animal movement patterns as these models can relate movement data with the changing environment. Hanks et al. (2015) and Buderman et al. (2018) applied continuous time Markov chain on mountain lion and northern fur seal movements data. Johnson et al. (2018) developed a continuous time semi Markov model by incorporating both temporally dynamic animal movement as well as changing habitat conditions. They concluded that this method is a more feasible approach to incorporate dynamic conditions and movement behaviour than the method developed by Hanks et al. (2015). Pohle et al. (2017) applied a model selection procedure using hidden Markov models to study muskox movement. Hooten et al. (2017) explains how hidden Markov models can successfully be applied to telemetry data to characterise animal movement incorporating space use as well as resource availability.

Michelot et al. (2018) introduced a Langevine diffusion as a continuous time model to characterise animal movement. The importance of this method is that it can be applied to irregular telemetry data and also provides a robust biostatistical framework to estimate and identify long-term habitat selection behaviours from correlated movement data. Michelot and Blackwell (2018) further applied a Bayesian continuous time random walk model using a Markov chain Monte Carlo algorithm. This method made use of a state-space formulation to accommodate irregular sampling frequency and measurement error of telemetry data to identify latent behavioural states of grey seals (*Halichoerus grypus).* Fleming et al. (2017) introduced the use of Kalman filters to continuous time movement models to be able to model a large array of movement behaviours such as mode switching, migration and range shifting. Hanks et al. (2012) use a continuous time Bayesian discrete-space model. This method incorporates both location as well as changing directional behaviours using a varying-coefficient framework.

2.3.4 State-Space models

State-space models (SSM) are an extension of correlated random walk models. Several recent studies have used SSM to analyse animal movement data. Some of the notable literature includes Vincent (2002), Jonsen et al. (2003, 2006), Morales et al. (2004), Ovaskainen et al. (2008), Patterson et al. (2008), McClintock et al. (2012) and Grurarie et al. (2016). State-space models use scholastic time series which is made up of an observation model and a process model. Process models can be analysed as a random walk model with parameters that respond to other external factors.

State space models probabilistically predict the future state of a system from its previous state. The advantage of using state space models is that one can couple a statistical model of the observation with the model of movement dynamics which could include behavioural as well as environmental effects. However, the limitation of state space models is that they are very much dependent on the behavioural hypotheses and underlying movement model associated with them.

In a more recent paper, using polar bear movement data, Auger-Methe et al. (2016) shows how state-space models can be accurately used in the presence of a large number of parameters. Jonsen (2016) showed that the joint estimation state – space approach is the best framework to model error- prone location data. Polansky et al. (2015) used a state-space model and a behavioural change point analysis to study how cognition structured the movement patterns of animals in different ecological settings. They further showed that environmental as well as social factors can drive goal-based movement in several species. Gardner et al. (2018) showed that spatial capture-recapture state- space models can be efficient and flexible approaches for long term monitoring of moment behaviours such as population migrations. Dorazio and Price (2018) applied a state-space model using hidden Markov models to detect the behavioural switching of fish movement.

Hidden Markov models are also widely used to estimate animal movement. These models assume that each data point from a time series observation arise from a number of N possible states. Leos-Barajas et al. (2017) in a recent paper proposed one of the first approaches to modelling animal movement behaviour at multiple time scales using a hierarchically structured hidden Markov model. McClintock (2017), using a hidden Markov approach on foraging reindeer Langrock et al. (2013) showed the feasibility of the hidden Markov based approach in a simulation data before fitting the actual observed data. They further show the importance of these models for a broader understanding of internal and external factors influencing a moving or foraging animal.

2.3.4 Agent or Individual-Based simulation models

Agent-based models (ABM) or Individual-based models (IBM) are widely used for animal movement analysis as they are able to capture individual movements as well as interactions between individuals and the environment. ABM is a simulation approach used to analyse movement across space and time (Siniff and Jessen 1969; Gardner et al. 1989; Gross et al. 1995; Malanson and Armstrong 1996; Turchin 1998; Malanson 1999;

Turner et al. 2001 and Grimm et al. 2017). Some of the challenges of using ABM for animal movement analysis is that spatial adaptation and the representation of environmental factors and computation can also be difficult.

The drawback and limitations in the above methods call for a more powerful but flexible approach. Bayesian techniques are deemed appropriate in this regard. Therefore, with the advancement of computer power lately, Bayesian methods are increasingly being used for movement analysis. Most methods are coupled with Markov chain Monte Carlo methods. Some of the popular Bayesian methods used in movement modelling includes Hierarchical Bayes methods (Gelfand and Smith 1990; Wikle 2003 and Clark, 2005). Hidden Markov methods and State-Space approaches (Jonsen et al. 2003, 2005; Morales et al. 2004 and Whoriskey et al. 2017)

Hidden Markov methods and State-Space approaches enable the partitioning of movement paths into different phases and identify behaviours. For example, a switching between behaviours could signal different types of interactions and conditions such as a particular habitat type or a process such as migration or foraging. Therefore, these methods have become increasingly popular in recent years.

2.4 Quantifying movement patterns

Appropriate quantification has always been a challenge in analysing movement. Accurate quantification is key to identifying actual movement patterns of organisms in nature as it facilitates the comparison of movement trajectories across space, through time, and between individuals. Movement patterns can be quantified in terms of individual steps or in terms of how steps relate to one another (Kareiva and Shigesada 1983). Thus, steps are the basic unit of movement analysis (Calenge et al. 2009). Trajectories can be defined in terms of steps, the straight-line distance between successive relocation (Root and Kareiva 1984). Individual steps are quantified in terms of step length, movement direction, turning angles and displacement. This thesis uses step lengths and turning angles as the basis metric of quantification.

Animal movement paths may involve a mixture of movement patterns as these organisms tend to switch behaviour while moving. Therefore, the classification of these patterns poses a challenge. Moreover, it is evident that animal movement patterns are also influenced by several external factors such as the environment, species interaction etc. Thus, it is essential that these factors are also taken into account where possible (Reynolds 2010). In terms of human foraging modelling, it becomes even more complex due to humans' cognitive abilities (Gautestad 2013)

Movement quantifications were originally carried out using classical or frequentist statistical methods. However, Bayesian approaches are now increasingly being used owing to the greater flexibility of the methods and the computational advancements. My thesis employs a Bayesian analytical framework for analysis which is detailed in the sections below and in the following chapters.

2.5 Frequentist vs Bayesian theory

The difference between frequentists and Bayesians involves the definition of probability. Some of the key differences between the two paradigms are that frequentists believe data to be repeatable in random samples while Bayesians believe that data are observed from the realised sample. In frequentists view, the underlying parameters remain constant during this repeatable process, while in Bayesian theory, parameters are unknown and describe a probability distribution. Thus, in frequenticism, parameters are fixed while for Bayesians parameters are random variables while data are fixed. Bayesian methods thought to be computationally difficult. Lately however, owing in part to computational advances, Bayesian methods are becoming widely popular in various fields.

2.6 Concluding thoughts

This chapter began by reviewing the evolution of modelling approaches to analyse movement with a special emphasis on foraging analysis with selection emphasis on foraging. It then briefly introduces the suitability of the Bayesian framework which I shall explain and employ in the following chapters. Chapter 3 shall outline the methodological framework based on the Bayesian model selection approach employed in the thesis which I have highlighted above to analyse foraging data of different species. In conclusion, this chapter has demonstrated how academic thinking on movement patterns have evolved over time from simple to sophisticated and from probabilistic to simulation-based models underlying actual movement behaviour.

Understanding animal movement patterns can suggest important management and policy implications. Appendix 1 summarises conclusions and implications made from animal movement studies. These are extracted from the original papers to show how movement research have been and can be applied and policy suggestions can be made. These implications and applications motivated the applications made in the following chapters.

Chapter 3 Bayesian Approaches to Understanding Animal Movement

This chapter develops Bayesian methods appropriate to improve the understanding of forager movement patterns using a Bayesian estimation framework. First, building on Chapter 2, I provide a detailed presentation of the two Bayesian approaches employed: the standard Bayesian estimation approach (SBEA) in 3.1; and the approximate Bayesian Computation (ABC) approach in 3.2. Finally, in Section 3.3, I demonstrate the application of the model selection approach.

3.1 The standard Bayesian estimation approach

The basis for Bayesian inference is derived from Bayes' theorem originally introduced by Rev. Thomas Bayes (1701-1706). It is a theorem of probability that helps understanding with regards to how a probability of an outcome is affected and updated with a new piece of evidence. Bayes' theorem shows the conditional probability, or 'posterior probability', of an event A after B is observed in terms of the 'prior probability' of A, the prior probability of B, and the conditional probability of B given A. In Bayesian inference, 'A' may represent the hypothesis, parameter ($\boldsymbol{\theta}$), or the model to be tested, while 'B' represents the data (y). Therefore, Bayes rule updates the belief about the parameter θ in light of the new evidence B. Thus, Bayesian inference can be considered to update the prior belief into posterior beliefs conditional on data.

Bayesian inference constitutes of three main components: 1) the prior $f(\boldsymbol{\theta})$, which is the set of prior distributions for parameter set $\boldsymbol{\theta}$ which uses the probability to quantifying uncertainty about $\boldsymbol{\theta}$ before data is observed; 2) $f(y|\boldsymbol{\theta})$ is the likelihood or likelihood function, in which all variables are related in a full probability model; 3) the posterior $f(\boldsymbol{\theta}|y)$ is the joint posterior distribution that expresses uncertainty about parameter set θ after taking both the prior and the data into account.

3.1.1 The prior distribution

The prior probability distribution, $f(\boldsymbol{\theta})$, often called simply the prior of an uncertain parameter θ, is a probability distribution that expresses uncertainty about θ before the data is observed. The prior distribution is expected to represent the current state of knowledge, or the current state of uncertainty, about the model parameters prior to data being observed. There are two key approaches to choosing a prior. The first approach involves choosing an informative prior distribution. With this strategy, the statistician uses her knowledge about the substantive problem to construct a prior distribution, that may be based on other data and expert opinion if possible, that properly reflects her beliefs about the unknown parameters.

3.1.2 The likelihood function and the posterior distribution

Once the data are observed, the likelihood function (likelihood), $f(\mathrm{y}|\boldsymbol{\theta})$ is constructed. The likelihood is the joint probability function of the data, but viewed as a function of the parameters, treating the observed data as fixed quantities. Therefore, it is the data generating function and the information about θ coming directly from the data contained in the likelihood. Values of the parameters that correspond to the largest values of the likelihood are the parameters that are most supported by the data.

In the Bayesian framework, all of the information about the parameter coming directly from the data is contained in the likelihood. Values of the parameters that correspond to the largest values of the likelihood are the parameters that are most supported by the data.

Bayes' theorem is then applied to obtain the posterior distribution $f(\boldsymbol{\theta}|\mathbf{y})$ which is the probability distribution of the parameters once the data have been observed. The information from the prior $f(\boldsymbol{\theta})$ is combined with the information about the parameter in the likelihood function $f\,(\mathbf{y}\,|\boldsymbol{\theta})$ to create the posterior distribution $f(\boldsymbol{\theta}|\mathbf{y})$ of the parameter. All inferences then arise from the posterior distribution. Once the posterior distribution has been determined, inferential conclusions can be summarised with an appropriate analysis. Point estimates of parameters are commonly computed as the mean or the mode such as the highest point of the posterior distribution.

It is now possible to compute the marginal likelihood $f(\mathbf{y})$, which is the probability of observing the data y averaged across the entire parameter space. If the Bayesian model choice is required, then the quantity $f(\mathbf{y})$ as below is central to solving the problem. When the model choice is of interest, it is typically referred to as the marginal likelihood or the evidence (Equation 3.1).

$$f(\mathbf{y}) = \frac{f(\mathbf{y}|\boldsymbol{\theta})f(\boldsymbol{\theta})}{f(\boldsymbol{\theta}|\mathbf{y})} \qquad [3.1]$$

The Bayesian computation undoubtedly requires greater computing power than most frequentist methods. This is mainly due to the intractability of the equations in computing the posterior distributions.

3.1.3 Markov chain Monte Carlo

Bayesian models are usually fitted using Monte Carlo Markov Chains (MCMC) (Morales et al. 2004). Markov chain is a random process with a finite state-space and the Markov property, meaning that the next state depends only on the current state and not on the past states. Monte Carlo method is an algorithm used for simulation which relies on repeated pseudo-random sampling for computation. The union of Markov chains and Monte Carlo methods are called MCMC. MCMC is a class of algorithms used to sample from the posterior distribution by implicit integration to obtain sample estimates of the quantities of interest. Bayesian inference primarily deals with integrals in computing posterior joint distributions. This procedure often requires computing intractable integrals. Bayesians use sampling techniques based on MCMC to sample from the posterior.

The Markov chain simulates drawing sequentially the posterior distribution, running a large number of times in a way that the unknown parameter depends on the previously sampled value (Gelman et al. 2004). The most common MCMC algorithms are the Metropolis-Hastings algorithm and Gibbs sampling.

3.1.4 Metropolis-Hastings algorithm

Metropolis et al. (1953) proposed an alternative to sampling directly from the prior $f(\theta)$ which was later generalised by Hastings (1970) and now called the Metropolis-Hastings (M-H) algorithm. Metropolis-Hastings is a generalised version of the basic Metropolis

Algorithm introduced by Hastings (1970)**.** Metropolis Hastings was specially developed to deal with full conditional computations that are difficult to deal with and is an efficient and powerful technique (Chib and Greenberg, 1995). It is based on an acceptance-rejection sample technique where at each iteration, a new parameter θ value is proposed and accepted based on an evidence ration for the proposed versus the current value of θ. Metropolis Hastings algorithm proceeds by initially proposing a new value θ* for each unknown parameter θ sampled from a proposal distribution $f(\theta^* | \theta)$. To assess the possibility of θ* with respect to the target distribution, an evidence ratio is computed. The proposal distribution could be to draw from independent proposals (Hastings, 1970) or could be a random walk proposal where θ* is drawn from a distribution parameterized in terms of the current value θ.

3.1.5 The Gibbs sampler

The Gibbs sampler is a special case of the Metropolis-Hastings algorithm and is considered one of the simplest MCMC algorithms (Chib and Greenberg 1995; Press 2003). It is an MCMC technique mainly used for posterior computation when the posterior distribution for each parameter is known. Therefore, Gibbs sampler is particularly used for inference made using conjugate priors. Casella and George (1992) defined the Gibbs sampler as a technique for generating random variables from a (marginal) distribution indirectly, without having to calculate the density. While the Gibbs sampler is most often used in the Bayesian context, it can also be applied in classical likelihood calculations (Casella and George 1992). In the Bayesian approach, the Gibbs sampler is used to generate posterior distributions. It allows complex joint densities to be estimated using a sequence of easier-to-compute conditional densities (Albert and Chib 1993).

Once the observations have been generated to approximate the joint density; the mean, variance or any other characteristic of the joint density can be calculated (Casella and George 1992). Gibbs sampling works by decomposing a posterior distribution into simpler, easy-to-sample-from distributions for each unknown parameter with the assumption that it is multivariate.

3.1.6 Standard Bayesian estimation approach

Bayesian Model selection has become one of the most important tools in many fields. For instance, researchers often test competing hypotheses, theories, or models in ecology as well as in social sciences using the Bayesian model selection approach. The main question that researchers try to decide using model selection methods is which model is more plausible or better supported by the observed data. These methods allow researchers to compare models or theories and compute which model fits best.

Based on Bayes' theorem, Bayesian model selection blends prior knowledge of the system with observational data. The prior distribution and the likelihood function contain the prior and information contained in observational data. The prior probability distributions are used to describe the uncertainty surrounding all unknowns. The posterior distribution provides a logical post data summary of the remaining uncertainty which is relevant for model selection after observations.

The inference on model parameters is made using the posterior distribution obtained from the combination of the likelihood function and the prior. The model selection problem defines a numerical measure of the marginal likelihood or model evidence in favour of one model among other models. The model with the highest evidence is the preferred model. Model choice within any framework is usually a trade-off between how complex the model is and how well the model fits the data. The evidence is important for discriminating between models.

Bayesian inference for model selection and parameter estimation can be defined as the process of fitting a probability model to data. The results are in the form of a probability distribution of the model parameters and its predictions (Gelman et al. 2008). The parameters for each proposed model are estimated in the form of a posterior distribution. The evidence or the marginal likelihood of each model is calculated from this posterior parameter probability distribution. Finally, the probability of each model is computed using the evidence to compare and select the best fit model (Koop 2003; Bisaillon 2013). Where M is the number of models proposed, Bayes' theorem as rewritten in equation 3.1 can be used to compute the probability of each model given the available data where $f(M|y)$ is the marginal likelihood (evidence) of model M given by the data y.

3.1.7 Bayesian conjugate and non-conjugate models

In Bayesian theory, conjugate distributions are considered as distributions where both the prior probability distribution and posterior probability distribution belong to the same family or in other words have the same functional form. For example, a Gaussian likelihood function and a Gaussian conjugate prior results in a Gaussian posterior distribution which is conjugate. Similarly, a conjugate prior distribution for an exponential likelihood is a Gamma distribution which results in Gamma posterior distribution which is conjugate.

One problem in the implementation of Bayesian approaches is analytical tractability. For a likelihood function $f(\boldsymbol{\theta}|\mathbf{y})$ and prior distribution $f(\boldsymbol{\theta})$, to calculate the posterior distribution it is necessary to evaluate the integral to make an inference. Conjugacy is always preferred because the prior and the posterior can be treated in the same way because they are in the same family which makes computation relatively easy and tractable in terms of integration. However, sometimes a non-conjugate prior is also needed for more complex analysis. For example, where a normal distribution is considered, the conjugate prior is an inverse gamma distribution. But it may be required to use a different prior such as a log-normal distribution when it is another model among several competing models. In such an instance, the integral becomes intractable as well.

Non-conjugate prior distributions can make interpretations of posterior inferences less transparent and computation more difficult, though this alternative does not pose any conceptual problems. However, in practice, for complicated models, conjugate prior distributions may not be possible (Gelman et al. 2004).

Bayesian data analysis was initially seen to be out of reach for special cases other than for conjugate models. With the introduction of advanced computation algorithms such as Markov chain Monte Carlo techniques discussed above and greater machine power, Bayesian inference gained wide popularity in numerous fields including ecology.

3.1.8 Model averaging

Bayesian model averaging is the Bayesian solution for incorporating model uncertainty (Hoeting et al. 1999). The principle behind model averaging is that when several plausible models exist for a question in hand, the inference should be averaged over all models instead of basing it on one single model (Koop 2004). Quantities of interest can often be expressed as a weighted average of model specific quantities, where the weights depend on how much the data support each. The weights are usually posterior model probabilities. If the posterior probability is concentrated on a single model, then model uncertainty is not an issue and both model selection and model averaging will lead to similar results. In many cases, model uncertainty dominates other forms of uncertainty, such as parameter uncertainty and sampling variation (Hoeting et al. 1999). Bayesian model averaging and model selection may seem straightforward to implement although it can be computationally difficult. The two major challenges confronting the practical implementation of Bayesian model averaging are choosing prior distributions and calculating posterior distributions. Since model averaging deals with several models, specifying an informative prior can be difficult in all cases and can resolve to use alternate prior specifications.

3.2 Approximate Bayesian Computation (ABC)

In the following Section 3.2.1, I introduce approximate Bayesian computation, a particular approach that has been developed for likelihood-free analysis. In Section 3.2.2, I explain the historical developments, rationale behind approximate Bayesian computation and its widespread application through a review of the relevant literature. Section 3.2.3 explains the generic methodology.

3.2.1 Introduction to Approximate Bayesian Computation

Bayesian analysis is heavily dependent on the likelihood function as it is of central importance for implementing Bayesian analysis. The likelihood function shows the probability of the observed data for a particular statistical model and leads through an integration procedure which enumerates the support that the data gives in choosing among several models. For simple models, the analysis of the likelihood function can typically be derived. However, for more complex models, the formula used to analyse the likelihood might be indefinable or computationally difficult to evaluate.

There are many models particularly in the social sciences, ecology and medical sciences for which, due to computational or simulation-based complexity, specifying a likelihood can be difficult or mathematically impossible. Thus, the application of standard methods of Bayesian estimation, as well as frequentist maximum likelihood estimation, has been impossible (Myung 2003).

A common limitation of most existing analytical methodology, irrespective of school of thought, is that they work only for models with a particular property. Namely, if the observed data '**y**', are given, the models must calculate the likelihood $f(\mathbf{y}|\boldsymbol{\theta})$ which is the probability of obtaining the observed data for each possible model. Model selection in this thesis is performed on the basis of this probability.

Stochasticity is an inherent character in ecological models. For simple stochastic processes, assumptions are made in order to directly calculate the likelihood $f(\mathrm{y}|\boldsymbol{\theta})$. Hence, the likelihood is tractable. Statisticians, especially Bayesians, have made a great effort to make likelihoods tractable by introducing a latent variable through methods such as state space models (Patterson et al. 2008) or hierarchical Bayesian models (Clark and Gelfand,2006). Despite these efforts, likelihood calculations for complex stochastic models are mathematically constrained. As an alternative, scientists have used stochastic simulation (Grimm and Railsback 2005; Wilkinson 2009; Hartig et al. 2011).

These stochastic simulation models help analysts to sample from stochastic processes without having to be dependent on conditional probabilities in order to keep $f(\mathbf{y}|\boldsymbol{\theta})$ tractable. Therefore, these simulation-based models are appropriate for stochastic processes such as animal movement analysis. Given the fact that humans are complex animals with several latent underlying states, these models can be considered ideal for this analysis. Whilst, for a standard statistical model, $f(\mathbf{y}|\boldsymbol{\theta})$ can be directly calculated or in other words is "tractable", for simulation based techniques, likelihood is estimated by creating random draws from a simulation process.

In the recent past, a number of such simulation-based techniques have been tried and tested in order to model stochastic processes for likelihood-free inference. These methods approximate $f(\mathbf{y}|\boldsymbol{\theta})$. Approximate Bayesian computation (ABC) is one such widely used, popular method. Other alternative but similar methods include indirect inference (Gourieroux et al. 1993) and pattern-oriented modelling (Grimm et al. 2005). Each of these methods is based on the essential principles of reducing data dimensionality and approximating likelihood by drawing data from models until a sufficient probability of mirroring or simulating '**y**' is attained.

In summary, ABC bypasses the computation of likelihood by repeated sampling or simulating data from an approximating model. Therefore, ABC methods are becoming increasingly important as they allow inference from previously problematic models mainly due to computational complexities.

It is widely regarded that ABC methodology originated, not in the formal theoretical statistics literature, but rather, in the population genetics literature just over a decade ago (Tavare et al. 1997 and Beaumont et al. 2002). Since these original papers appeared, the advancement in both the understanding of ABC methodology, ABC models, and the numerical simulation algorithms, has resulted in the spread of ABC investigations in a range of diverse disciplines.

The first approximate-Bayesian-computation related ideas date back to the 1980s. Rubin's (1984) article on likelihood-free methodology is one of the first articles to highlight the importance of computational methods to estimate the desired posterior distribution without reference to an explicit likelihood function. It introduced a hypothetical sampling mechanism which is very similar to the ABC rejection sampling scheme to infer from the posterior distribution.

Diggle and Gratton (1984) first introduced a simulation method in order to carry out statistical inference when the likelihood is intractable. This paper employs a non-Bayesian approach to address the intractability. They approximated the likelihood by running several simulations for each grid point on a parameter space followed by a smoothing technique. Thereafter, several more non-Bayesian approaches were used in order to address the inference problem when the likelihoods are unknown (Gourieroux et al. 1993 and Newton et al. 1994). Diggle and Gratton's (1984) approximation targeted the likelihood instead of the posterior distribution and was not identical to the ABC approach introduced later. The basic concept of likelihood-free methodology in relation to ABC in the Bayesian literature arose initially in the paper by Tavare et al. (1997). This seminal article is the first rudimentary specification of a frequentist ABC methodology. The authors of this paper developed two basic rejection sampling ABC algorithms.

These algorithms were used to tackle a problem in statistical genetics, which is related to inference about coalescence times, based on DNA sequence data. Following this paper, several papers (Fu and Li 1997; Weiss and von Haeseler 1998; Pritchard et al. 1999; Tishkoff et al. 2001 and Estoup et al. 2002) discussed advances to the rejection sampling framework. Among these papers, Pritchard et al.'s (1999) paper introduced approximate "matching" of the observed data and the simulated data sets.

There have been several subsequent additions. Extending the ideas of earlier authors, the paper by Beaumont et al. (2002) introduced a novel development to the likelihood-free literature which established the term "ABC" or approximate Bayesian computation. Beaumont et al. (2002) makes approximations to the ABC posterior density estimation, which is achieved by fitting a local-linear regression of simulated parameter values upon simulated summary statistics. The inference combines many of the advantages of Bayesian statistical inference with plurality of general assumptions that do not limit attentions to only one likelihood.

The next important methodological development came from Marjoram et al. (2003) and Plagnol and Tavare (2004). In order to overcome the computational restrictions associated with the rejection algorithm when the rejection probability is directly related to the tolerance level, they developed a Markov chain Monte Carlo (MCMC) as an alternative. This method was more efficient as the rejection probability criteria is replaced by direct comparison between the simulated data and the actual data.

The second aspect, they introduced, was the concept of using an approximation, by introducing the tolerance level. In this case, the samples only come from the true target posterior, once the stationary regime is reached by the MCMC sampler. These developments resulted in the MCMC-ABC approach which became a popular alternative. Following the use of the initial MCMC-ABC technique, there have been several extensions exploring the MCMC-ABC sampler (Peters and Sisson 2006; Bortot et al. 2007).

Several subsequent papers discussed alternative extensions. Reeves and Pettitt (2005) presented an initial theoretical framework for approximate Bayesian computation models. This paper explicitly described the exact nature of the ABC approximation as it linked the concepts of indirect inference with the related ideas found in likelihood-free methodology. A more recent paper by Blum (2009), looked at ABC methodology from a non-parametric perspective using non-parametric statistics for the summary statistics. Leuenberger et al. (2009) employed a regression-based approach to improve the posterior approximation in ABC.

The ABC - sequential Monte Caro sampling (SMC) methodology is a widely used subsequent notable development. Sisson et al. (2007) made extensions to partial rejection control involving the aspects presented in Liu (2001) introducing the population-based sequential Monte Carlo sampling algorithm. Based on the sequential Monte Caro samplers (SMC) used by Peters (2005) and Peters (2008) introduced ABC-SMC algorithm to sample from the targeted ABC posterior distribution. Further variations and extensions to likelihood-free ABC methodology can be found in the work by Joyce et al. (2008) Ratman et al. (2009) and Toni et al. (2009).

Approximate Bayesian computation has become an increasing popular technique for analysing complex models due to its many beneficial features. One of the key reasons for this popularity is that ABC can be used to analyse any complex model given that a set of data can be simulated from the model thus allowing the estimation of parameters that closely reflect complex biological and ecological processes (Beaumont et al. 2002). Another appealing feature of ABC is that in comparison to most other approaches, this approach is simpler and can be applied to both stochastic and deterministic models without any change (Toni et al. 2009).

Approximate Bayesian computation is also a flexible and simpler approach as it can be used to estimate models that are too complex to be handled by likelihood-based models (Hamilton et al. 2005). Toni et al. (2009) explains that ABC algorithms such as ABC –

Sequential Monte Carlo algorithm can also be used without any further computational costs to gain information about the model sensitivity to parameters.

In this thesis I have employed Approximate Bayesian Computation mainly due to the strong support it provides in model selection. The model averaging procedure used for the standard Bayesian approach assumes that the model set is complete and error-free. Although the Approximate Bayesian Computation performs by approximating the likelihood function by summarizing the generated data, it can still account for the model errors (Wilkinson 2013). Further, Beaumont et al. (2002), Majoram et al. (2003) and Wilkinson (2013) show that the approximate Bayesian computation give exact results under the assumption of model error which guides the choice of tolerances level and summary statistics used. Therefore, in this thesis, the ABC framework is used on the justification that, ABC accounts for the model errors in the model set, in a way that model averaging under the standard Bayesian approach does not.

3.2.2 The Widespread application of ABC

Owing to its weaker maintained hypothesis, the approximate Bayesian computation provides greater flexibility in analysing complex models used in various fields of science. Thus, ABC is now widespread throughout a range of diverse disciplines. The ABC method is more prominent in the field of biology in general and genetics in particular. In terms of biologically inspired applications, ABC found its roots in statistical genetics where much of the original methodology and popularity for ABC methods arose.

As pointed out in Sisson (2006), the adoption of ABC methodology in biological modelling can be attributed to the fact that in many biological applications, the models typically consist of a large number of parameters for which specifying likelihoods are difficult or impossible. The presence of a large number of parameters, in combination with complex models, can result in likelihoods that are computationally prohibitive or impossible to estimate. In this case, ABC has been extensively used in the field of genetics in order to analyse a range of complex settings (Beaumont et al. 2002; Marjoram et al. 2003; Estoup et al. 2004 and Hamilton et al. 2005).

The papers by Estoup et al. (2004) and Hamilton et al. (2005) use ABC to analyse models which aim to make inference with regard to the spatial expansion dynamics of an invading species. The paper by Tanaka et al. (2006) used ABC to analyse transmission rate of Tuberculosis. Some other notable papers which have utilised ABC methodology in biological applications include Butler et al. (2006) to categorise mixtures of nutritional components in food products and Luciani et al. (2009) to model drug-resistance in mycobacterium tuberculosis, Ratmann et al. (2009) to investigate protein networks and structure evolution, Koerich et al. (2008) to explore chromosomal evolution, Toni and Stumpf (2009) to test biochemical signalling pathways. In addition to these biological applications, in the physical sciences, a significant paper by Grelaud et al. (2009) considers model choice using ABC in the setting of Gibbs random fields.

ABC is becoming a popular method in the field of ecology, in general, and population genetics and conservation, in particular. As its efficiency and robustness were recognized, its popularity increased, and the method began being used in a wide variety of sub-fields in ecology (Lopes and Beaumont 2009). The widespread use of ABC in conservation and in population genetics has meant that its tools have become an integral part of conservation and population genetics studies (Chan et al. 2006; Evans et al. 2008; Aspi et al. 2009), epidemiologic studies (Shriner et al. 2006; Tanaka et al. 2006; Toni et al. 2009), and studies in ecology (Jabot and Chaves 2009). In ecology, ABC is commonly used as a tool to quantify endangered populations, to measure effective population sizes, analyse gene flow or genetic heterogeneity (DeSalle and Amato 2004).

The ABC methods have shown themselves particularly useful for the estimation of complexity due to their flexibility and robustness. Furthermore, ABC methods seem suitable to study complex population and animal movement patterns of particular importance in conservation genetics. For example, in order to employ spatial dispersal models for conservation studies which are too complex for traditional statistical approaches.

One of the first applications of ABC in conservation was to infer the spatial expansion dynamics of the invasive species *Bufo marinus* (Estoup et al. 2001). Another example of a study on invasion scenarios using ABC was performed by Miller et al. (2005) who studied the introduction routes of the western corn rootworm (*Diabrotica virgifera*

virgifera) into Europe. Chan et al. (2006) applied an ABC method to estimate the timing and severity of a bottleneck in an endemic subterranean rodent (*Ctenomys sociabilis*). Johnson et al. (2009) used ABC to study a critically endangered Madagascar population of fish-eagle (*Haliaeetus vociferoides*).

Habitat fragmentation investigations are now in the forefront of conservation studies. The ABC approach is being used to explore these complex scenarios in order to arrive at better policy decisions. Evans et al. (2008) applied an ABC algorithm to provide evidence for habitat fragmentation in populations of Celebs toads (*Bufo celebensis*) living in the Indonesian island of Sulawesi. Witzenberger and Hochkirch (2008) studied the loss of genetic diversity of a single endangered population of field crickets (*Gryllus campestris*) in northern Germany by translocating groups of individuals to form isolated populations. They used ABC to calculate the effective population size of these populations at different time points.

Work by Aspi et al. (2009) used ABC to calculate the occurrence of migration between populations of the Russian wolf (*Canis lupus*) and effective population sizes in order to obtain migration values. The ABC technique was also used as a tool on a typical isolation-migration model to estimate several demographic parameters (e.g. effective population size, migration rates and divergence times) of two populations of the endangered yellow-eyed penguin (*Megadyptes antipodes*) (Lopes and Boessenkool 2010).

The ABC was widely associated with individual based modelling (IBM) technique in ecological science. Some of the key work in this area by Topping et al. (2012), Thiele et al. (2014) and Van der Vaart (2015) draws attention to the benefits of ABC in ecological modelling particularly within IBM. A more recent article by Hartig et al. (2015) investigate the feasibility of using ABC to calibrate and evaluate complex IBM structures and showed that ABC has the potential to represent uncertainty in model structure, parameters and predictions, and to embed the often complex process of optimising an IBM' structures and parameters within an established statistical framework. In this context, ABC is thereby making the process more transparent and more objective.

As discussed above, ABC can consider a wide variety of models with considerable degree of complexity. . To the best of my knowledge, ABC has not yet been applied or used to understand conventional agricultural economic or environmental economic problems, which deal with complex modelling structures like ecological structures. Also, to my best knowledge, ABC has not been used to understand the foraging patterns of animals in nature.

3.2.3 Approximate Bayesian computation in principle

The development of ABC methodology requires several components which include:

- an intractable or unavailable target posterior distribution that the ABC posterior will approximate;
- a technique to simulate data from the unavailable model, given a set of parameters
- summary statistics for the actual data and the simulated data;
- a distance metric to quantify the difference between the two sets of summary statistics;
- a tolerance level to specify an accuracy level for distance metric quantifications; and
- a numerical sampling algorithm such as rejection sampling, Markov chain Monte Carlo (MCMC) sampling or Sequential Monte Carlo (SMC) sampling.

The generic procedure for ABC draws a candidate parameter, θ, from a proposal distribution (Turner and Van Zandt 2012). The most common distribution for this is the prior distribution $f(\boldsymbol{\theta})$ corresponding to the likelihood approximated distribution. This parameter is then used in order to simulate an artificial data set $\mathbf{z}$ $(\mathbf{z_1, z_2, z_3 \ldots z_n})^T$ from the desired model with the same number of observation as the observed data $\mathbf{y}$ $(\mathbf{y_1, y_2, y_3 \ldots y_n})^T$. This is done in order for both data sets to have the same distributional properties. The goal is to approximate the posterior distribution $f(\boldsymbol{\theta}|\mathbf{z}) \propto f(\mathbf{z}|\boldsymbol{\theta})\, f(\boldsymbol{\theta})$, where $f(\mathbf{z}|\boldsymbol{\theta})$ is the likelihood of the artificial dataset $\mathbf{z}$. The simulated data set z is then compared to the observed data set y. This is done by computing a distance function $\rho(z, y)$ and a tolerance level ε. If $\delta(\mathbf{z, y})$ is less than or equal to a specified value of ε, the parameter θ or otherwise it is discarded.

For ease of computation, the distance $\delta(\mathbf{z, y})$ is often defined as the distance between the summary statistics (e.g. mean or median) of the data sets $\mathbf{z}$ and $\mathbf{y}$. If the summary statistics are sufficient, then the resulting approximation of the posterior distribution will be good enough as long as ρ(**z, y**) is less than a specific tolerance value ε (Beaumont 2010).

The simplest ABC algorithm is the ABC rejection sampling algorithm (Beaumont et al. 2002). This algorithm discards the candidate parameter **θ** if it does not meet the criterion ρ(**z, y**) ≤ ε. Another popular ABC algorithm consists of embedding Markov chain Mont Carlo sampling in to ABC technology (ABC - MCMC). This procedure is based on the Metropolis – Hastings algorithm where θ is drawn from the proposal distribution conditioned on an initial value. Unlike the simple rejection sampling technic where the acceptance probability is computed from the likelihood, ABC-MCMC technique uses **θ** to produce the simulated data set **z** from the model. Thereafter, the distance ρ(**z, y**) between the observed and simulate data, **z** and **y** is computed and θ is accepted if ρ(**z, y**) ≤ ϵ and set $\boldsymbol{\theta}_{(s)} = \boldsymbol{\theta}$. If ρ(z, y) > ϵ, **θ** is rejected.

Sequential Monte Carlo sampling within the context of ABC what is commonly known as ABC - SMC is another widely used technique. This technique differs from the MCMC approach by its use of a particle filter (Turner and Van Zandt 2012). Unlike the MCMC sampler which draws a candidate **θ** one at a time from the proposal distribution or, from the prior distribution relating to the approximating likelihood distribution, the SMC works with a pool of candidates which is drawn from the proposal distribution. These candidates are called particles which are simultaneously obtained by using particle filter. In each iteration, the particle is perturbed and filtered, bringing the particles closer and closer to the high density posterior region. Three main SMC samplers are particle rejection control (PRC), population Monte Carlo (PMC), and sequential Monte Carlo (SMC).

3.3 Application of Bayesian methods in this thesis

3.3.1 Application of standard Bayesian estimation approach

The example below illustrates the procedure of the standard Bayesian estimation approach employed in this thesis. If the exponential model is the model of concern, this is a conjugate model. Thus, the likelihood function or the data generating function has a probability distribution as follows (Equation 3.2).

$$f(y|\lambda) = \begin{cases} 0, & \text{if } y < 0 \\ \lambda \exp(-\lambda y), & \text{if } y \geq 0 \end{cases} \qquad [3.2]$$

Where y is the step length and y_i is a single step length $(\mathbf{y_1, y_2, y_3 \ldots y_n})^T$. The parameter λ is a member of the open unit interval {0, +∞} and 1/ λ is the first central moment of the distribution. Bayesian analysis proceeds by employing the gamma distribution which is the conjugate prior distribution corresponding to the exponential likelihood. Parameter λ is defined as θ throughout the example.

The gamma prior distribution has the probability density function (Equation 3.3)

$$f(y, \lambda|\alpha, \beta) = \begin{cases} 0, & \text{if } y < 0 \\ \frac{\beta^{\alpha}}{\Gamma(\alpha)} y^{\alpha-1} \exp(-y\beta) & \text{if } y \geq 0 \end{cases} \qquad [3.3]$$

Where α >0 and β>0 are the shape and rate parameters, respectively.

For the observed data, $\mathbf{y} = (\mathbf{y_1, y_2, \ldots\ldots y_n})^T$, and a gamma prior with $\alpha = \alpha_0$ and $\beta = \beta_0$, the posterior distribution of λ is also a gamma distribution where (Equation 3.4),

$$f\ (\lambda|\alpha, \beta, y)\ (\alpha = \alpha_0 + n, \beta = \beta_0 + \sum_{i=1}^{n} Y_i) \qquad [3.4]$$

3.3.2 Application of Approximate Bayesian computation

In this thesis, I use a simple rejection algorithm performed as follows. First, a candidate parameter value **θ** is sampled from a proposal distribution. For the first candidate, the reasonable choice for this distribution is the prior $f(\boldsymbol{\theta})$, corresponding to the proposal generating distribution. Subsequently the candidate parameter is used to simulate a data set **z** from the model of interest that has the same number of observations as the observed data set y so that the distributional properties of the simulated data **z** and any summary statistics computed from **z** can match those of the observed data **y**.

The example below illustrates the procedure, using the exponential distribution. As explained in Section 3.3.1, the exponential data generating function has the following probability density function (Equation 3.2)

$$f(y|\lambda) = \begin{cases} 0, & \text{if } y < 0 \\ \lambda \exp(-\lambda y), & \text{if } y \geq 0 \end{cases} \qquad [3.2]$$

The gamma prior distribution has the probability density fucntion

$$f(\lambda|\alpha, \beta) = \begin{cases} 0, & \text{if } y < 0 \\ \dfrac{\beta^{\alpha}}{\Gamma(\alpha)} y^{\alpha-1} \exp(-y\beta) & \text{if } y \geq 0 \end{cases} \qquad [3.3]$$

For the observed data, $\mathbf{y} = (\mathbf{y_1}, \mathbf{y_2}, \ldots \mathbf{y_n})^T$, and a gamma prior with $\alpha = \alpha_0$ and $\beta = \beta_0$, the posterior distribution of λ is also a gamma distribution where,

$$f\ (\lambda|\alpha, \beta, y)\ (\alpha = \alpha_0 + n, \beta = \beta_0 + \textstyle\sum_{i=1}^{n} Y_i\ ) \qquad [3.4]$$

Unlike in the standard Bayesian approach, in this case I assume that the exponential likelihood is unavailable. Due to this unavailability, the exact computation of the posterior is also unavailable. Therefore, the ABC rejection algorithm is used to simulate an artificial data set **z** by drawing samples from the gamma prior in equation 3.3.

The simulated data, **z**, is compared to the observed data, y, by computing a distance between them given by a distance function $\delta(\mathbf{z}, \mathbf{y})$. If $\delta(\mathbf{z}, \mathbf{y})$ is small enough, less than some value, ϵ, then the simulated data **z** is close enough to the observed data y that the candidate parameter value, $\boldsymbol{\theta}$, has a non-zero probability of being in the approximate posterior distribution $f(\boldsymbol{\theta}|\ \delta(\mathbf{z}, \mathbf{y}) \leq \epsilon)$. Therefore, if $\delta(\mathbf{z}\ \mathbf{y})$ is less than or equal to ϵ_0, $\boldsymbol{\theta}$ is accepted as a sample from the approximate posterior, otherwise it is discarded (Turner and Sederberg 2012). The data sets are initially sorted using the sorting convention.

The simulated data set is sorted as $\mathbf{z}_1 \leq \mathbf{z}_2 \leq \ldots \mathbf{z}_{n-1} \leq \mathbf{z}_n$ based on the original data sortation in the same fashion as $\mathbf{y}_1 \leq \mathbf{y}_2 \leq \ldots \mathbf{y}_{n-1} \leq \mathbf{y}_n$. For computation ease, $\delta(\mathbf{z}, \mathbf{y})$ is defined as the mean squared error between $\mathbf{z}$ and $\mathbf{y}$ as below in (Equation 3.5).

$$\delta(z, y) \;=\; \sum_{i=1}^{N} \frac{(z_i - y_i)^2}{N} \qquad [3.5]$$

The ABC algorithm used for the analysis was carried out as shown in Table 3.1

Table 3.1: Rejection sampling algorithm

1 Data are sorted according to the sorting protocol
2 A candidate parameter $\boldsymbol{\theta}$ was drawn from a likelihood approximating prior/proposal distribution $f(\cdot)$
3 The candidate parameter is used to simulate a dataset $z \sim f\,(\mathbf{z}|\boldsymbol{\theta})$ with the same number of observations as observed data $\mathbf{y}$
4 The proposal data are sorted and the distance is then applied and then $\boldsymbol{\theta}$ is accepted if $\delta(\mathbf{z},\mathbf{y}) \leq \varepsilon$

A sample of 10000 iterations were drawn from the proposal distribution for each of the distribution in concern. The marginal likelihood or the evidence was computed from the accepted draws for each model.

This procedure was performed for all 22 (44 with log trandformations) models used in the thesis, adopting the previously applied likelihoods $f(\mathbf{z}|\boldsymbol{\theta})$ as proposal generating distribution $f(\mathbf{z}|\boldsymbol{\theta})$.

3.3.3 Model selection in approximate Bayesian computation

The model selection for ABC follows the same procedure as explained in 3.1.6 for standard Bayesian estimation approach (SBEA). As ABC bypasses the estimation of likelihood, the marginal likelihood is considered as evidence in this section. The evidence is computed through approximation using the rejection sampling algorithm. In this case, the average (marginal) acceptance rate is proportional to the marginal likelihood or evidence. As the exact same tolerance level ϵ is used for each model, the constant of proportionality is the same, and therefore the estimate of the ratio of marginal likelihoods is given by the ratio of acceptance rates. Given relative acceptance rates and priors on the models, posterior probabilities are obtained (Estoup et al. 2004).

In this thesis, I use MCMC – Metropolis-Hastings framework to perform model selection. Unlike in the standard Bayesian method, in the absence of the likelihood, the use of Monte Carlo simulations avoids the need to use an explicit likelihood function. The evidence or marginal likelihood in this case is also the prior predictive distribution. Prior predictive distributions obtained for each model were converted to probabilities for reporting convenience as shown in equation 3.6. Appendix 2 lays out how the computations were done in MATLAB©

$$\text{Implied probability } = \frac{f(\mathbf{y}|\mathbf{M_i})f(\mathbf{M_i})}{\sum_{i=1}^{M} f(\mathbf{y}|\mathbf{M_i})f(\mathbf{M_i})} \qquad [3.6]$$

3.4 Concluding thoughts

This chapter outlined the two Bayesian approaches employed within the thesis, namely the standard Bayesian estimation approach and the Approximate Bayesian Computation approach. Using an example under each method, it further demonstrated how each of the methods were used to select the model that supports data best from a competing set of models using an example.

Chapter 4 Revisiting Human Foraging Patterns

This chapter revisits one particular data set; Ju/’hoansi hunter-gatherer (!Kung) movement data that was originally analysed by Brown et al. (2007), and then reanalysed by Edwards (2011), in order to demonstrate how Bayesian methods can be used to better understand and characterise movement patterns of foraging animals. The chapter first provides the background to the dataset used, from the initial data collection by Yellen in 1977 to both Brown and Edwards’ reanalyses. The chapter then, in section 4.2, provides detail on how Edwards (2011) reanalysed the dataset. Section 4.3 applies the Bayesian model selection framework to test the hypothesis that Lévy flight movement patterns exist in foraging animals.

The reason behind selecting the human hunter-gatherers or !Kung data are two-fold. One, I considered it interesting to explore human foraging as it is relatively more complex compared to other animals mainly due to our enhanced cognition which encompasses greater uncertainty (Gautestad 2012, 2013). This uncertainty would be better captured by a Bayesian framework (Hooten and Hobbs 2015). Two; it was one of the complete data sets provided by the owners of the data used in Edward’s re-analysis.

Very few studies have explored human foraging. However, using similar analytical approaches as Brown et al. (2007) and Viswanathan et al.(1996), researchers have found some support for Lévy flights in humans (Bertrand et al. 2007; Marchal et al. 2007; Brockmann et al. 2007; Brown et al. 2007; González et al. 2011 and Raichlen et al. 2014).

4.1 Lévy flights in animal movement analyses

Exploration of animal foraging or search patterns for food has been at the forefront of movement research during the past few years. Lévy flight theory, borrowed from physical sciences, is widely used to characterise animal foraging which gave rise to the Lévy flight foraging hypothesis. Lévy flight differs from other random walks as each step length is assumed to be drawn from Lévy probability distribution unless and until terminated by a resource encounter (Pyke 2015). It is used to characterise the spatial distribution of foragers as well as to determine optimal search strategies of foragers searching for randomly distributed targets (Viswanathan et al. 1996).

Lévy flight theory was initially tested for animal foraging by Viswanathan et al. (1996) using foraging data on wandering albatross *Diomedea exulans*, which found a power law distribution of flight-time intervals. In his paper, Viswanathan formulated a generalised form of these step length distributions as probability density functions which is a power law probability distribution.

Lévy flight movement pattern shows a high probability of large step lengths with an infinite variance indicating that it is a scale invariant distribution with no fixed characteristic scale. According Viswanathan et al. (1996), a Lévy flight movement pattern with a power law exponent μ value equal to 2 suggests an optimal search behaviour. The publications by Viswanathan et al. (1996, 1999) which concluded the Lévy flight behaviour in wandering Albatrosses, bumble bees, and deer, became quite popular among ecologists studying animal movement. With this publication, interest in Lévy flight pattern in studying animal movement has increased in the last few years compared to the period 1980-2000 (
Figure 4.1).

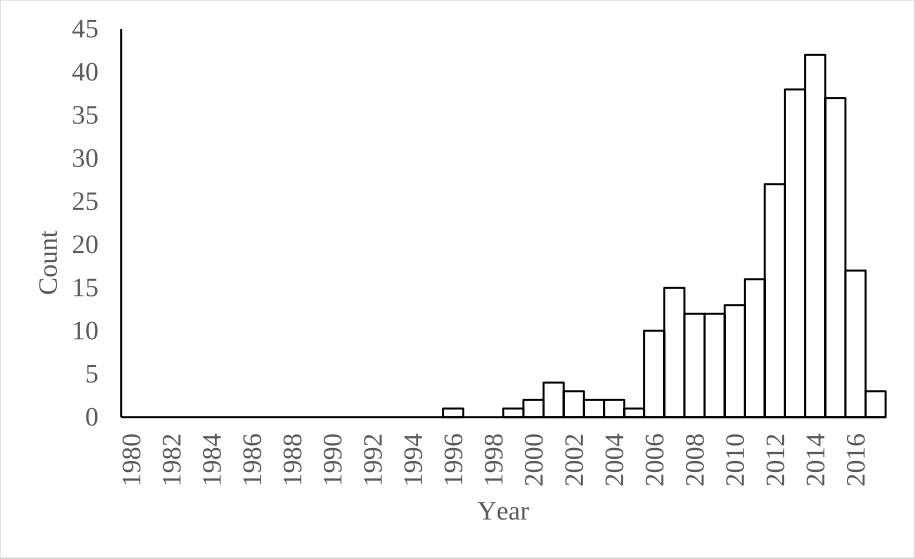


Figure 4.1: Numbers of published Lévy flight related articles per year (1980 - 2016)

Source: The Web of Knowledge site; from searching for published artcile on 'Lévy flight foraging', 'animal foraging and movement patterns'

In tandem with Viswanathan et al.'s (1996) evidence, many subsequent studies used a similar approach to conclude this pattern in a wide range of species from micro-plankton to humans (Atkinson et al. 2002; Mårell et al. 2002; Austin et al. 2004; Boyer et al. 2006; Bartumeus eta al. 2008; Humphries et al. 2010 and Jager et al. 2011). In parallel, several criticisms emerged. Edwards (2007, 2008, 2011), Sims et al. (2008), White et al. (2008) and Pyke's (2015) criticisms suggest erroneous methodological applications and explore alternate methods. These papers criticised the use of methods such as simple log transformation or regression based on a histogram employed to estimate the exponent μ (Sims et al. 2008; White et al. 2008). Edwards' (2011) papers are explored in detail below.

4.2 Edwards' re-analysis summary

Edwards (2011) was the first to overturn earlier findings of Lévy flight in nature. He suggested a more quantitative method using the likelihood and Akaike weights to estimate the power-law exponent μ. He reanalysed 17 data sets from previously published studies which had concluded Lévy flight behaviour. These data sets include the movement patterns of reindeer in Sweden (Mårell et al. 2002), jackals in Zimbabwe (Atkinson et al. 2002), microzooplankton (dinoflagellates) in experiments (Bartumeus et al. 2003), grey seals in the North Atlantic Ocean (Austin et al. 2004) to human movement such as Dobe Ju/'hoansi human hunter-gatherers in Botswana and Namibia (Brown et al. 2007), Peruvian purse-seiner fishing boats (Bertrand et al. 2007) and Dutch beam-trawler fishing boats (Marchal et al., 2007). Edwards (2007) indicated that the data were misinterpreted using inaccurate methods in the original studies.

Edwards' (2011) most prominent criticism was concerning Sims et al. (2007) estimation of the dimensionless parameter μ. Initially, Sims et al. (2007) showed that the simple log transformation of a histogram which was used in the earlier studies was inadequate and proposed a log binning method. Edwards (2007) and White (2008) then showed that the log-binning method is erroneous and proposed a simulation-based method to determine μ. Some other problems detected in the original papers as per Edwards were improper testing of the alternative hypotheses and test of goodness of fit. For example, a power-law distribution was initially assumed in the original papers and μ was estimated without considering alternative hypotheses.

Edwards (2011) re-analysed the original data using a frequentist model selection approach using likelihood and Akaike weights. In contrast to the unbounded power-law distributions concluded in the original studies, he found that Lévy flight is not a common phenomenon in ecology.

To test the second objective of this thesis, which addresses the hypothesis that Lévy flight movement pattern exists in foragers, I use a Bayesian model selection framework. In this chapter, I focus on the movement of human foraging using the !Kung Ju/hoansi movement patterns. This data set was initially collected by Yellen (1977). In an attempt to identify their foraging pattern, Brown et al. (2007) used a histogram-based method and concluded that their movement between camps can be modelled as a Lévy flight. They further explained the evidence that humans as foragers follow Lévy flights search patterns during their subsistence strategies and perform optimal searches. These data were later re-analysed by Edwards (2011) along with several other data sets on other forager movement. Edwards overturned the conclusion with the finding that the unbounded exponential is the best-supported model for !Kung foragers.

4.3 Methodology and data

Yellen (1977) describes the movements of the Ju/'hoansi/ !Kung hunter-gatherers during hunting and collecting trips made in 1968 for a period of 6 months. The !Kung are hunters and foragers who lived in and around the Kalahari Desert in Botswana and Namibia. They lived at the Dobe water-hole during the dry season, a permanent water source. During and after the rains the social group broke into smaller subgroups and moved out into the surrounding areas and built short-term camps near seasonal or temporary water sources (Yellen 1997; Brown et al. 2007). At each of these camps, the group exploited the nearby food sources and after consuming most of the desirable food, they moved to another temporary camp. After spending varying amounts of days, they returned to Dobe for a few days before leaving on another trip. The data analysed by Brown et al. (2007) consisted of the locations of these camps occupied by one small group from January 27 to July 11, 1968.

4.3.1 Bayesian estimation approach for re-analysis of !Kung data

I employ both Bayesian estimation approaches explained in Chapter 3. First the standard Bayesian estimation approach which is the likelihood-based technique. Then the likelihood-free approach termed approximate Bayesian computation (ABC).

A great amount of uncertainty exists in exploring laws, patterns or habits that govern ecological systems and biotic interactions such as the movement patterns of humans. These uncertainties include stochasticity as nature is seldom deterministic and cognitive abilities are high in humans compared to other species. In such complex situations with great uncertainties, the best method is to use a technique which helps choose among competing hypotheses that receives the best or the most support from the data (Johnson and Omland 2004). As explained in Chapter 3, choosing the best model that most supports the data from a competing set of models in statistics is called model selection or models comparison (White and Lubow 2002).

In the case of foraging, individuals and populations may move in a pattern where the step length can be modelled as different distributions which could be underlying the actual movement pattern. Literature has tested several models. In the case of !Kung movement these models included the normal, uniform distributions as well as the bounded and the unbounded variants of the exponential and the power-law models (Brown et al. 2007 and Edwards et al. 2011). For this analysis, I test several other plausible models in addition to these models.

A Bayesian model selection method to my best knowledge has not been used in reanalysing any of the datasets mentioned in Edwards (2011) including the !Kung data in Brown et al. (2007). Thus, considerable scope exists for exploration of the Lévy flight existence hypothesis against alternative competing model structures.

4.3.2 Data measurements

The step lengths of !Kung movements are drawn from Map 7 in Yellen (1977, p. 60) (Figure 4.2). The distance between the camps on Map 7 is measured in the order in which they were occupied to test whether the pattern conforms to a power law distribution of step lengths predicted by a Lévy flight.

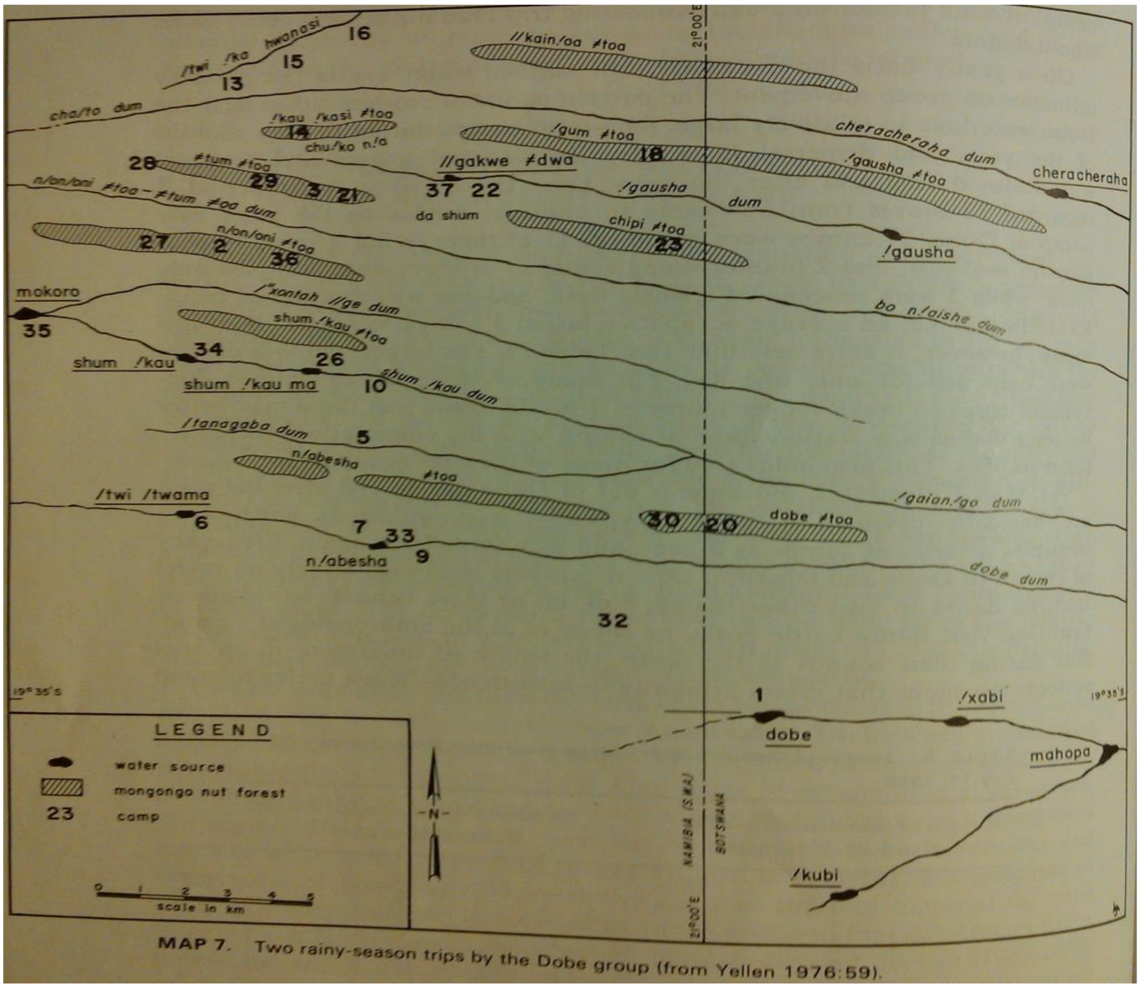


Figure 4.2: Map 7 in Yellen

Source: Yellen,1977, p. 60, Figure 5

The step length and the angles of movement can be represented as below (Figure 4.3)

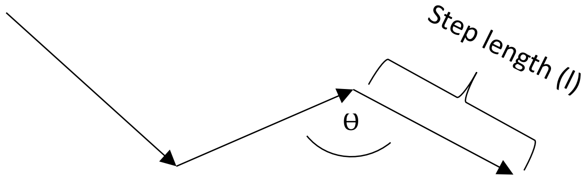


Figure 4.3: Movement pattern measurements

The distances were measured by the authors from the mid-point one numeral on the map to the mid-point of the other numeral. When a particular camp number did not appear on the map, the measurement was measured to the number of the first camp of the same name on the list (Table 4.1). For example, camp four is not available on the map, hence the distance was measure to camp 2. The camp numbers which do not appear in the map are given in the “Remarks” column of Table 4.1. In order to be consistent, following Brown et al. (2007), the millimetres on the printed map were converted to geographic distance using a scaling factor of 5/27.

Table 4.1: Distances between successive camps

From Camp	To Camp	Measured distance (mm)	Geographic distance (Km)	Remarks
1	2	94.3	17.463	
2	3	14.7	2.722	
3	4	14.7	2.722	Measured to No. 2
4	5	34.7	6.425	
5	6	24.2	4.481	
6	7	19.4	3.592	
7	8	53.7	9.944	Measured to No. 1
8	9	44.8	8.296	
9	10	26.7	4.944	
10	11	28.9	5.3518	Measured to No. 2
11	12	14.7	2.7222	Measured to No. 3
12	13	18.8	3.4814	
13	14	10.9	2.018	
14	15	10.9	2.018	
15	16	9.3	1.722	
16	17	16.8	3.111	Measured to No. 14
17	18	42.8	7.925	
18	19	82.7	15.314	Measured to No. 1
19	20	25.7	4.759	
20	21	67.1	12.425	
21	22	16.6	3.074	
22	23	22.8	4.222	
23	24	68	12.592	Measured to No. 1
24	25	44.8	8.296	Measured to No. 9
25	26	26.1	4.8333	
26	27	27.8	5.148	
27	28	12.1	2.240	
28	29	14.6	2.70	
29	30	70.9	13.12	
30	31	28.4	5.25	Measured to No. 1
31	32	20.2	3.740	
32	33	28.5	5.277	
33	34	37.1	6.870	
34	35	21.2	3.925	
35	36	32.3	5.981	
36	37	21.8	4.037	
37	38	85	15.740	Measured to No. 1

Source: scaled off Map 7 of Yellen’s (1977) monograph.

The distribution of !Kung movement steps-lengths is shown in figure 4.4. The histogram shows a power-law type distribution with a fat tail. This indicates that movement step lengths of the hunter-gatherers follow a right skewed distribution with a higher number of smaller steps lengths and fewer long step lengths. From a graphical point of view, this may indicate that the best fit distribution could be one drawn from an exponential, weibull family, gamma, log-normal or power law family.

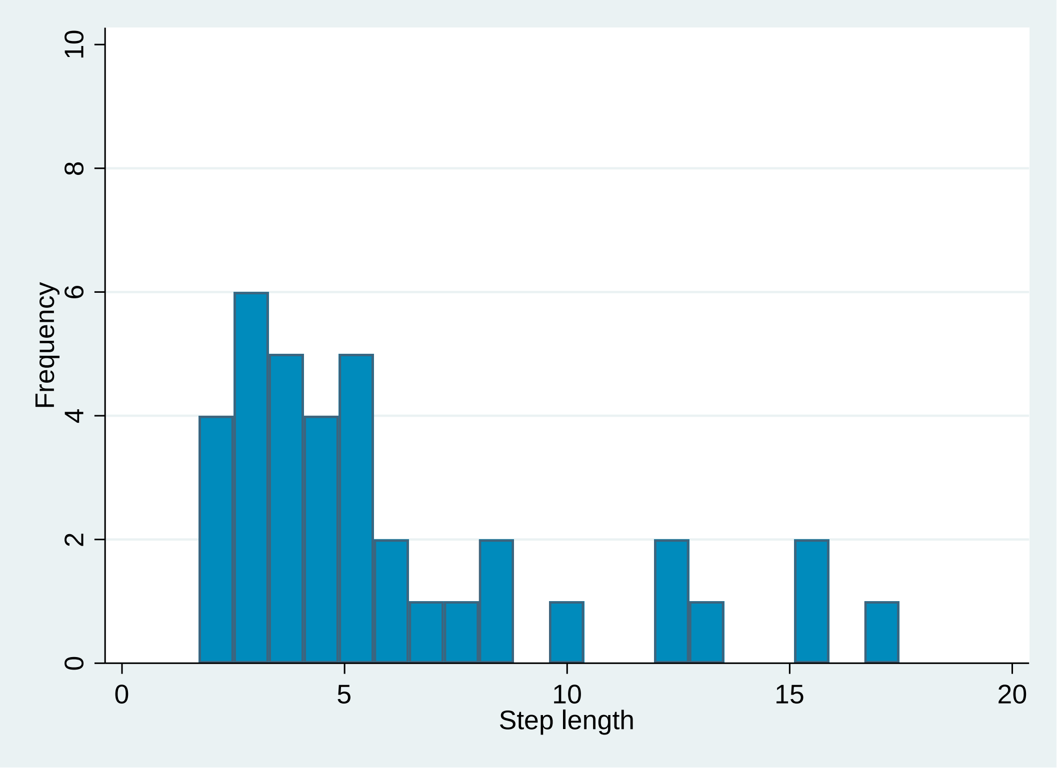


Figure 4.4: Step length distribution of the !Kung between camps

Source: Based on the data from Brown et al., (2006)

The fact that this distribution cannot be confirmed graphically calls for a more numerical and objective quantification beyond graphical representation. I investigate the underlying distribution that best supports the data characterising the movement pattern. This is done with reference where necessary to the previous frequentists approaches used to analyse the !Kung movement patterns initially by Brown et al. (2007) and then by Edwards (2011).

Once the step-lengths were measured, the next important parameter was to measure the turning angle in order to simulate the movement paths and include the random-walk model in the computation. Each turning angle was measured in degrees using a protractor and converted to radians. To include the turning angles in the computation, I have used the ‘circular functions’ theory from Chiang (2005).

For this purpose, the diagram in Figure 15.3 in Chiang, p. 519 was used in order to provide the information in the two-space.

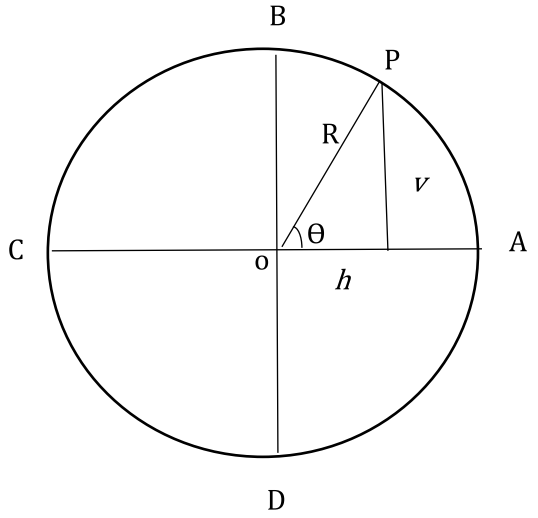


Figure 4.5: Circular functions theory

According to the circular functions theory, $v_{(t)}$ and $h_{(t)}$ denote movements in the vertical and horizontal directions at time 't' of an individual. Given the random-walk structure of this individual, it converts the observed step-lengths within each of the data sets into their corresponding vertical and horizontal coordinates. Figure 4.5 depicts a circle with radius 'R,' origin 'O,' and a radius vector of length 'OP' stemming from the origin and coinciding at the perimeter at point 'P.' The Vector OP generates horizontal and vertical movements of lengths 'h' and 'v' and generates an angle 'θ.'

The ratios v/R and h/R change when we alter the angle θ or in other words the direction changes. This gives rise to the trigonometric relations $\sin\theta \equiv v/R$ and $\cos\theta \equiv h/R$. Therefore, given an angle displacement θ and a radial measure, R, it is now possible to generate a random walk from the relations $h = R\cos\theta$ and $v = \sin\theta$.

Given an angle at time t, $\theta_{(t)}$, and a quantity, $R_{(t)}$, measured in radians using the protractor, it is now possible to compute differences in horizontal and vertical translation arising from the step lengths. The movement patterns were simulated using this procedure for the each of the different models considered in the thesis using this method.

4.4 Analysis

I have considered several plausible candidate models that could underlay the distribution pattern of the !Kung. These models are Normal, Uniform, Exponential, Pareto (power-law), Weibull, Extreme-Value, Gamma, Bounded Exponential and Bounded Power-law distributions. The models also included the exact models analysed by Edwards (2011) and variants of those models. Bounds were considered as the minimum and maximum data points (step lengths) of the data set which is 1.72 Km and 17.46 Km respectively for !Kung hunter-gatherers.

The Lévy flight hypothesis states that the exponent μ takes the value $1<\mu\leq3$. Most publications which conclude the existence of Lévy flight do not consider the bounds of the power-law distribution. Bounded versions only of exponential and power-law models are used for analysis in this thesis. All other models are used only in their unbounded forms. This is mainly due to the fact that apart from exponential and power-law distributions, other distributions decay very fast and as a result extremely high values are unlikely. Therefore, bounds or truncation is not needed to avoid extreme values. On the other hand, power-law and exponential distributions decay slowly enough to allow extremely high values. Therefore, bounds are essential and truncated forms are logical for analysis.

4.4.1 Analysis using likelihood-based standard Bayesian estimation (SBEA) approach

All plausible candidate models in their unbounded and bounded forms (22 models in total) were used to perform the model selection using MATLAB© software (Table 4.2). Under the assumption that observed step-lengths within the data are identically and independently distributed and are exchangeable, the data give rise to a marginal likelihood or evidence for the data $f(\mathbf{y})$ (computation described in Chapter 3).

Table 4.2: The 22 models considered for analysis

Model No	Model
1	Normal
2	Uniform
3	Exponential
4	Pareto
5	Weibull
6	Gamma
7	Edwards Exponential (Estimated λ|fixed a)
8	Edwards Exponential (Estimated λ|fixed b)
9	Edwards Exponential (Estimated λ| no parameters fixed)
10	Edwards Exponential (Estimated λ and a|fixed b)
11	Edwards Exponential (Estimated λ and b|fixed a)
12	Edwards Exponential (Estimated λ |fixed a & b)
13	Edwards Exponential (Estimated λ & a|no fixed parameters)
14	Edwards Exponential (Estimated λ & b|no fixed parameters)
15	Edwards Exponential (Estimated λ , a & b)
16	Edwards Power-law (Estimated μ|fixed a)
17	Edwards Power-law (Estimated μ |fixed b)
18	Edwards Power-law (Estimated μ , fixed a & b)
19	Edwards Power-law (Estimated μ | no parameters fixed)
20	Edwards Power-law Estimated μ and b|fixed a)
21	Edwards Power-law (Estimated μ and a|fixed b)
22	Edwards Power-(Estimated μ, a & b)

The marginal likelihood is computed for each model which is the basis used for model comparison. Then models were averaged by weighting the step lengths by assigning an equal weight to each of the models in order to evaluate the evidence in support of each alternative.

In the cases of normal, uniform and exponential model evaluations, the quantity, $f(\mathbf{y})$, is available by direct calculation. However, in the case of the power-law distribution, the quantity $f(\mathbf{y})$, is unavailable by direct calculation and was estimated instead. I followed the robust technique introduced for estimating ‘the evidence’ by Chib (1995) and Chib and Jeliazkov (2001) in which the Metropolis-Hastings sampling scheme was used. Variants were also included for the exponential and the power-law model in bounded form.

Conditional on a particular model, specifically, Normal, Uniform, Exponential, Pareto, Weibull, Extreme-Value, Gamma, Bounded Exponential or Bounded Power distribution, candidate observations or ‘predictions’ were derived through simulation under the alternative sampling schemes and the extent to which the observations resemble the observed data, $\mathbf{y}$. The model selection programme was run for 50000 iterations.

Where the appropriate posterior predictive distribution is unavailable in closed form, predictions were simulated by sampling from the posterior distribution for the parameters using either a Gibbs or Metropolis-Hastings sampling scheme and marginalising these quantities by applying the Monte Carlo formulae. The evidence was then converted into implied probabilities by dividing the marginal likelihood of an individual model by the sum of marginal likelihoods (Equation 4.1). Also, the predictions were tested for their fit using plots.

$$\text{Implied probability } = \frac{f(\mathbf{y}|, \mathbf{M_i})f(\mathbf{M_i})}{\sum_{i=1}^{M} f(\mathbf{y}|\mathbf{M_i})f(\mathbf{M_i})} \qquad [4.1]$$

4.4.2 Analysis using likelihood-free approximate Bayesian computation (ABC) approach

I applied a simple rejection ABC algorithm as explained in Chapter 3. The model selection for ABC followed the same procedure as explained under in Chapter three for standard Bayesian estimation approach. As ABC bypasses the estimation of likelihood, the marginal likelihood is termed as evidence in the Chapter 3. The evidence was computed through approximation using the rejection sampling algorithm. I use MCMC – Metropolis-Hastings framework to perform model selection (Turner and Van Zandt 2012). The evidence or marginal likelihood in this case is also the prior predictive distribution. Prior predictive distributions obtained for each model were converted to probabilities for reporting.

The next step was to perform the model selection exercise to select the best model out of the 22 plausible models considered in the thesis. Table 4.2 shows the list of models analysed.

Models 1-6 consists of conjugate models. Models 7-15 consists of different variants of exponential models derived from the exponential models analysed by Edwards (2011). Models 16-22 consists of different variants of power-law models derived from the powerlaw models analysed by Edwards (2011). Models 3 and 12 are the unbounded exponential and bounded exponential models respectively used in Edwards (2011). Models 4 and 18 are the unbounded power-law (pareto) and bounded power-law models used in Edwards (2011). Appendix 3 shows how the models were specified using Edwards (2011). Appendix 4 lays out the distributions used.

4.5 Results from the model selection

Results from the two model selection approaches; SBEA and ABC, are depicted by Figures 4.6 and Figure 4.7. Figure 4.6, which presents output from the standard model selection approach, model 18, a bounded power-law model, shows the highest support for the data with a probability of 22%. However, this is closely followed by model 12, a bounded exponential model, with a probability of 21%. These data suggest that one particular model cannot be concluded as the best model. However, as a group, the power-law models show slightly higher afffinity in supporting the data compared to the exonential models.

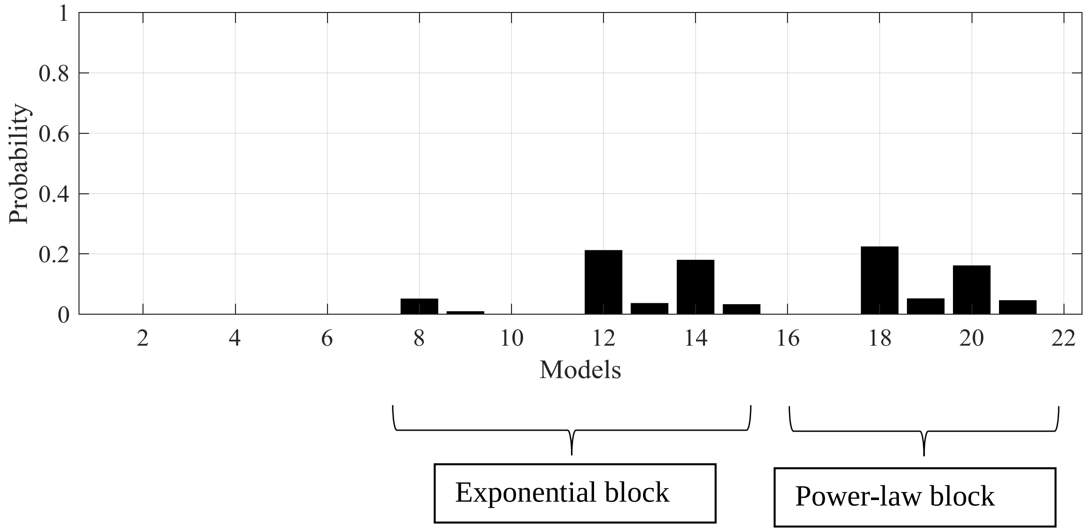


Figure 4.6: Implied probabilities across 22 models (SBEA)

Figure 4.7 depicts how the models perform under the approximate Bayesian computation (ABC). Model 18 which is the same bounded power-law model resulted from the SBEA approach best supports the data with a probability of 46%. The second-most supporting model is model 12 as resulted from the SBEA.

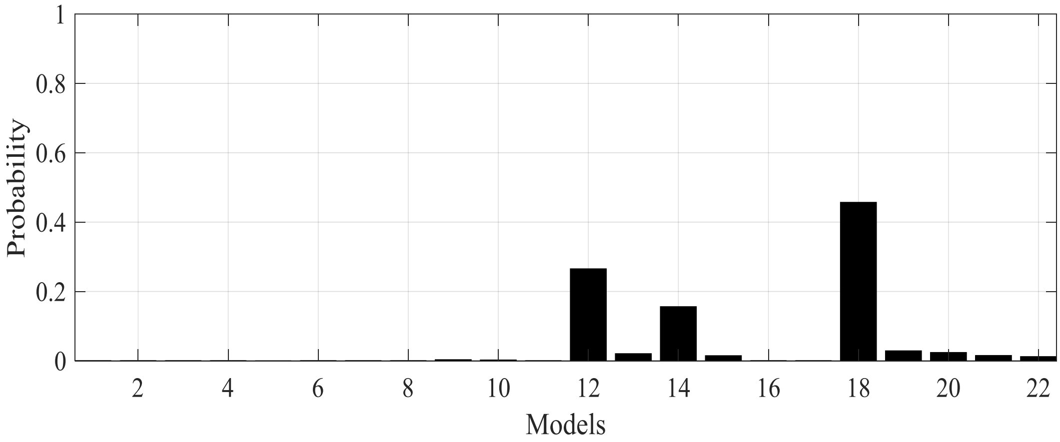


Figure 4.7: Implied probabilities across 22 models (ABC)

The fact that model 18 is seen as the most dominant model from both approaches with higher support from the ABC approach, suggests that the power-law model with fixed minimum and maximum bounds best supports Kung foraging data.

It was then of interested to see how the power-law exponent (μ) varies for the dominant power-law model under the two approaches. The dominant power-law models were run for 50000 iterations and the μ variations were recorded in the form of trace plots.

The parameter μ for model 18 can be seen to lie between 1 and 3 for the SBEA approach (Figure 4.8).

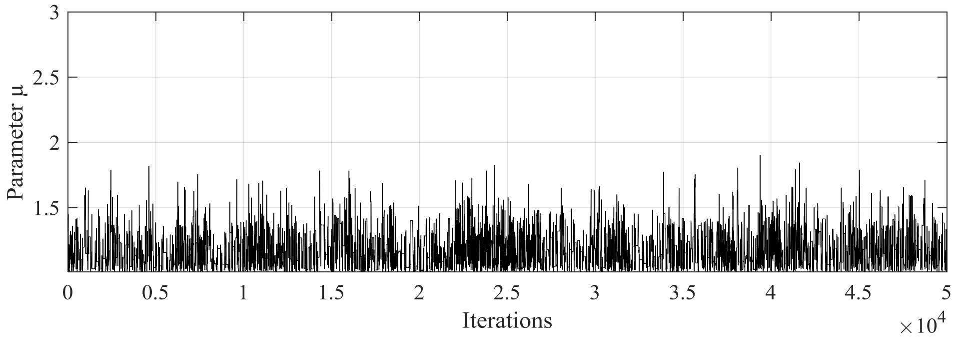


Figure 4.8: Trace plots of exponent (μ) distribution of the bounded power-law model (SBEA)

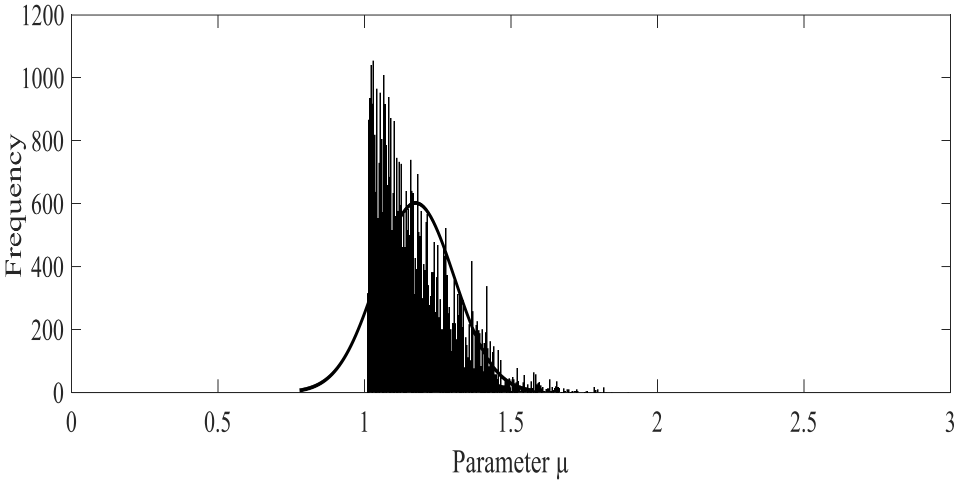


Figure 4.9: Distribution of the exponent parameter (μ)

Figure 4.9 and Table 4.3 shows the distribution and the exponent parameter μ obtained from model 18. It can be seen that μ is distributed with a mean of 1.17, a standard deviation on 0.13 and lies within a range between 1 and 3.

Table 4.3: Measures of central tendency and spread of the parameter μ

Mean	1.17
Median	1.14
Standard deviation	0.13
Q1	1.07
Q2	1.14
Q3	1.25
Inter quartile range (IQR)	0.18

Although this shows that it lies within the Lévy flight range of 1-3, it is does not represent an optimal foraging pattern (μ=2).

Model 18, which was the ABC approach, also shows a μ between 1 and 3 which indicates a Lévy flight pattern. The μ seems to lie between 1 and 3 with a mean of 1.5 and a standard deviation of 0.36 showing less fluctuation (Figure 4.10, 4.11 and Table 4.4).

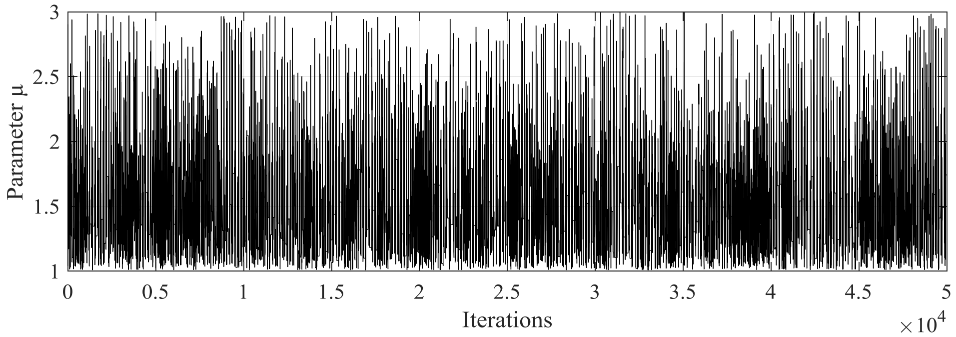


Figure 4.10: Trace plots of exponent (μ) distribution of the bounded power-law model (ABC)

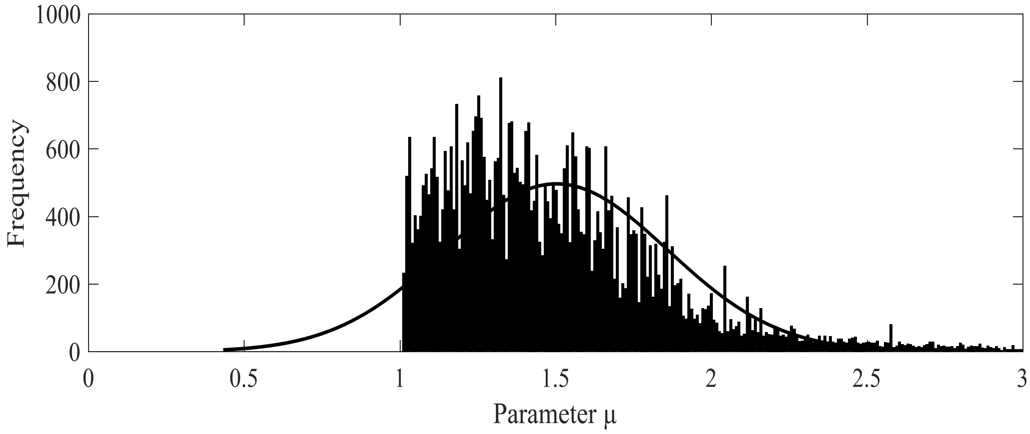


Figure 4.11: Distribution of the exponent parameter (μ)

Table 4.4: Table Measures of central tendency and spread of the parameter μ

Mean	1.50
Median	1.43
Standard deviation	0.36
Q1	1.24
Q2	1.43
Q3	1.68
Inter quartile range (IQR)	0.45

4.6 Discussion in the context of human foragers

The results suggest that the bounded power-law models seem to support the !Kung foraging data more than the other models. Brown et al. (2007) originally concluded that the !Kung hunter gatherers' foraging pattern follows a pure or unbounded power-law distribution. More specifically that paper concludes that the foraging pattern follows an optimal Lévy flight foraging pattern with a μ=2. Edwards (2011) from the re-analysis showed that the hunter- gatherers follow a bounded exponential model while the bounded power-law model cannot be ruled out as both models show very close evidence ratios from the maximum likelihood estimation approach.

This chapter shows that the foraging pattern of the !Kung hunter gatherers can be better represented by a bounded power-law model although the bounded exponential model cannot be ruled out. My findings are also in par with other studies that have explored the human foraging and travel. For example, Raichlen et al. (2013) found that the movement patterns of men in the Hadza hunter gatherer groups of Tanzania followed a truncated power-law distribution. They explain that the longer step lengths can be truncated after successful capture of animal prey or collection of honey.

In the case of !Kung hunter gatherers, two assumptions underlying the Lévy flight foraging hypothesis may not hold completely. The first assumption is that the food or resources are randomly distributed. The second assumption is that foragers move randomly when they cannot detect prey in the neighbourhood. Yellen (1977) and Brown et al. (2007) states that the !Kung are not fully aware of the resource distribution in the surrounding area. This suggests that they must actually search for locations of food sources. Therefore, !Kung were searching in an area where food sources were not in abundance specifically with regards to the animal prey. However, other food resources such as fruits and nuts may not have been so sparsely distributed. Compared to other foragers, due to the higher cognitive ability memory of humans, it cannot be said that the hunters have no knowledge about the resource distribution. !Kung hunter gatherer foraging does not therefore fully conform to the Lévy flight foraging assumptions (Viswanathan et al., 1996).

Because these groups camp at particular locations and search around the camp area, it can be said that the area of search is restricted. Thus, a bounded power-law distribution may well represent the foraging compared to an unbounded Lévy/power-law distribution. However, the resulting bounded power-law pattern cannot confirm that it is the optimum foraging pattern. A reasonable interpretation might be that !Kung hunter-gatherers achieved a near optimal search pattern while behaving rationally in adapting to a spatially complex and unpredictable environment.

In this chapter I examined possible candidate models as evaluating alternate hypotheses to identify the best model among competing explanations. The choice of model, however, was not simple as the number of possible models is potentially infinite. Therefore, I made sure that I included and evaluated all models used in literature amongst other possible models for testing the hypothesis. For example, if a uniform distribution is assumed, it can be expected that if resources are uniformly distributed across the landscape, the groups of hunter-gatherers might move relatively similar distances each time they shifted camp. In such a case, the step lengths might be driven by external forces, such as the locations of other social groups, rather than by the distribution of resources. Other scenarios could also be imagined that would lead to a relatively even pattern of movements.

According to Raposo et al. (2011), truncated or bounded power law models suggest that foraging strategies may reflect the complexity of the local habitats and diversity of search targets for human hunter–gatherers. and may represent a response to a diverse set of targets. The analysis suggests that an exponential pattern could also support the data or in other words, there is another underlying foraging pattern.

According to Bazazi et al. (2012), the power-law exponent that lies between 1 and 2 signals a response to a diverse set of targets varying from more homogeneous distribution to heterogeneous distribution. Realistically, the !Kung groups set camps at where they know food is likely to be in abundance. From there they set off on their search. Therefore, the environment does change from homogenous to heterogenous distribution with regards to food. This may well explain the range of μ values as well as the prominent exponential distribution. The !Kung foraging strategy therefore reflects a highly dynamic environment in the forest landscapes where they hunt. Therefore, there foraging patterns may switch when they forage for a wide variety of food types. They face different ecological environmental factors such as mobility of animal prey, preferred and seasonal fruits and nuts and diverse range of landscapes (i.e. tuber to trees with honey). Thus, the switching in their foraging behaviour is expected compared to other species. De Jager et al. (2014) also show that external cues, such a depletion of local search targets, may trigger changes between exponential distributions. My findings show that human hunter-gatherers perform a Lévy flight distribution in within a limited range. It also shows that their cognition and memory has not impacted the movement pattern very much as animals (non-humans) have also been found to follow truncated power-law patterns.

These findings can have implications for understanding human movement patterns in several fields. For example, investigating human spread is crucial in population and genealogy studies to know how we move both in the present and the past (i.e. migration). This supper-diffusive pattern in human movement may have led our ancestors to reach and discover optimal living conditions (Anton et al. 2003).

Brantingham et al. (2006) explain that patterns of raw material transport found in archaeological records often follow power law distributions. The findings in this chapter suggest that to some extent, humans use scale-invariant super-diffusive movement patterns that may switch depending on external factors. Studies by Brockman et al. (2006), Gonzales et al. (2008) and Rhee et al. (2011) also suggest that human movement patterns may switch due to external factors. Gonzales et al. (2008), analysing mobile phone calls received, report that humans tend to perform Lévy walks within heterogeneously bounded areas. Rhee et al. (2011) find that humans switch their movement pattern from supper-diffusive to sub-diffusive behaviour, indicating heavy-tailed patterns in a confined or limited area. Undoubtedly, these pattern identifications can be useful in understanding the spread of disease and planning urban landscapes and telecommunications (Rhee et al. 2011).

It could also be said that Lévy flight foraging in humans may have started and evolved since our pre-historic ancestors. Therefore, understanding how hunter-gatherers survive through foraging is important in designing landscapes and infrastructure in these areas and in evolution studies.

Another area where understanding human movement patterns can be important is epidemiology. Human travel can easily spread diseases across seas and continents. For example, knowing that human travel patterns decay as a power-law tail indicates that the disease spread may also follow a similar pattern. The fact that the energy of the disease vectors also decreases signals optimal control measures of a disease. Therefore, understanding human mobility can have important implications in different forms.

4.7 Implications and applications

In this section I consider the implications of restricting the number of candidate models when attempting to determine the model that best fits the data observations, and the implications of working with very small numbers of observations. I demonstrate these two elements of Bayesian estimation using the !Kung data set. First in Section 4.7.1 I reproduce the calculations above but using only the same candidate models that Edwards used. Second, in Section 4.7.1 I reproduce the calculations for various subsets of the already small !Kung data set.

4.7.1 Restricting the Bayesian analysis to Edwards (2011) four candidate models

This section is aimed at analysing the four models compared by Edwards (2011) to analyse the Kung foraging data. Out of the 22 models (Table 4.2) I have considered in the thesis, I have selected the four exact models considered by Edwards (2011) to compare the results from the maximum likelihood estimation and the standard Bayesian approach. The four models compared by Edwards (2011) are as follows:

- Model 1: Unbounded Exponential
- Model 2: Unbounded Power-law
- Model 3: Bounded Exponential
- Model 4: Bounded Power-law

The standard Bayesian estimation results, for only the four candidate models, show that model 4, which is the bounded power law model specified in Edwards (2011), supports the data, as opposed to his finding of model three, the bounded exponential model (Equation 4.13).

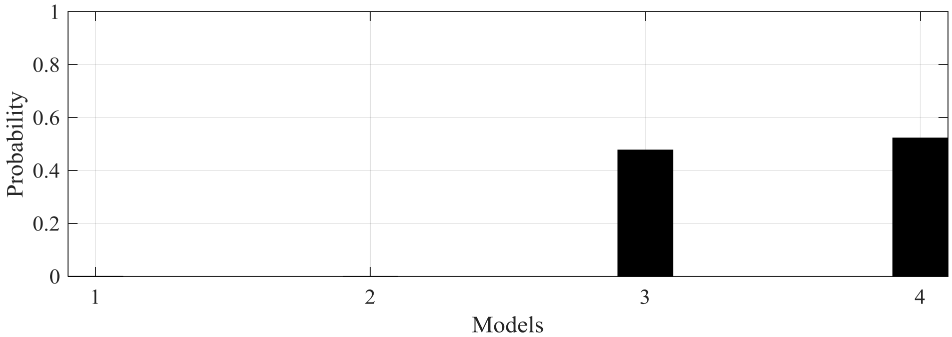


Figure 4.12: Model comparison of Edwards (2011) models using SBEA approach

Using ABC, comparing the same four candidate models used by Edwards (2011), gives similar results but with greater support (higher probability) for model 4 (Figure 4.13). Model 4 in my set of models is model 18, which is also the dominant model. This model showed a lower probability when analysed with the full set of candidate models, in comparison to the probability of 53% when only the four models are considered.

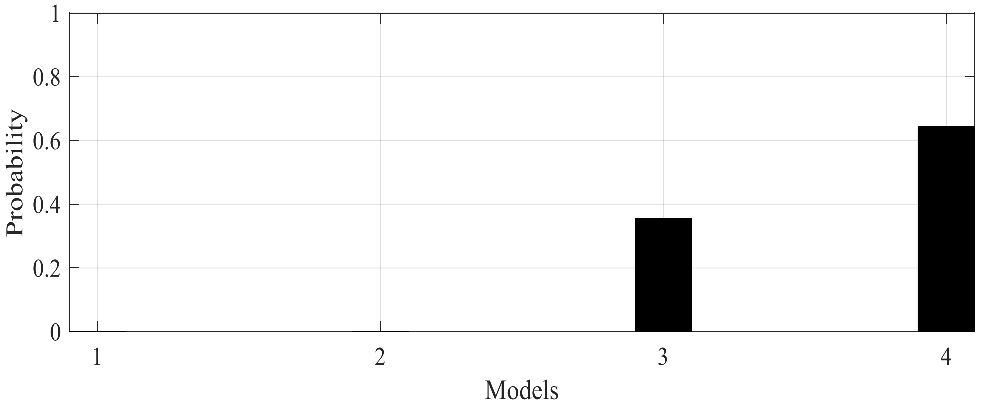


Figure 4.13: Model comparison of Edwards (2011) models using ABC approach

These results contrast the findings by Edwards (2011) in terms of the dominance. However, the findings agree with Edwards where he states that the bounded power law models cannot be ruled out. The dominant bounded exponential model found in his analysis (model 3 in Figure 4.13) is the second best closely following the power-law model for my analysis.

4.7.2 Implications for small datasets

The exponent (μ) is a crucial parameter in characterising the movement pattern of the animals as it defines whether the pattern is a Lévy flight or not. Data is a limitation in most movement studies. Particularly in the case of !Kung hunter gathers, only 37 step lengths were recorded for analysis. Therefore, it was of interest to explore the effect of the number of steps on the variation in μ.

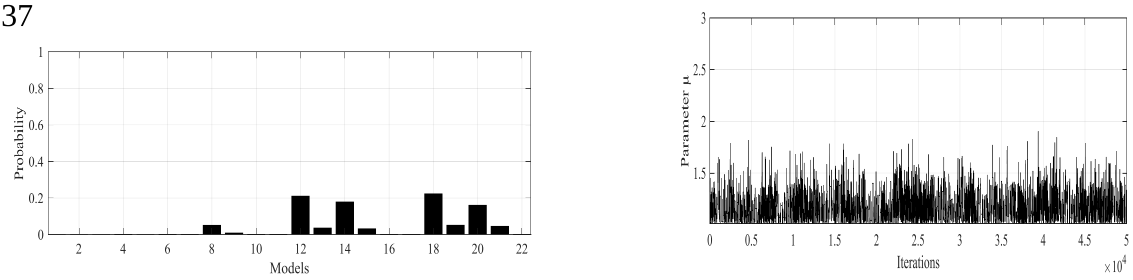
Sims et al., (2007) states that the number of steps used for analysing the underlying foraging distribution can influence the accuracy of the Lévy-flight exponent μ. Using a simulation study, they show that when the number of steps increased from 50 to 1000, the standard deviation of the Lévy flight exponent parameter μ decreased from 0.3 to 0.09. This finding motivated me to investigate whether the number of movement steps used for analysis has an impact of the μ and the resulting models. Therefore, the number of steps was reduced systematically from n=37 (total number of step lengths measured of !Kung hunter gatherer foraging) to n=30, n=20, n=10, and finally n= 5. The first 30, 20, 10 and 5 steps were selected gradually. The resulting models from the model selection exercise and the corresponding exponent values were recorded.

First, this analysis was carried out with the standard Bayesian estimation approach (SBEA). Figure 4.14 shows the dominant model 18 remains unchanged irrespective of the number of steps. However, when the number of steps is reduced from 37 to 5, although the dominant model 18 remains dominant, although the probability of support fluctuated within a narrow range. The parameter μ increased from an average of 1.17 to an average of 1.32.

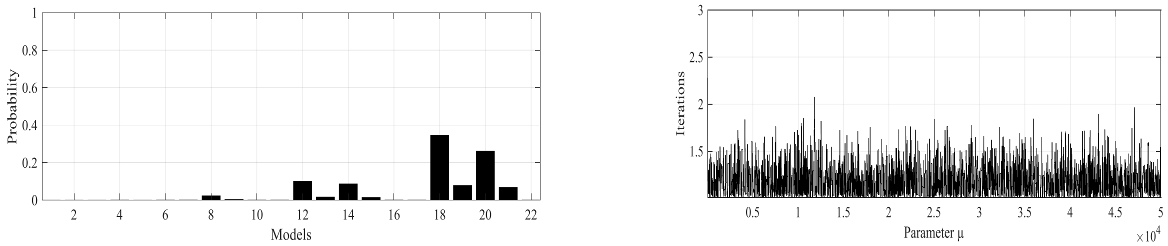
The same analysis was carried out using the Approximate Bayesian Computation. Figure 4.15 shows that model 18 remained dominant irrespective of the number of steps with a slight fluctuation of the supporting probability values. The corresponding parameter μ increased gradually from 1.6 for n=37 to 1.81 for n=5. The increments were much less than for the results from the SBEA.

This simulation exercise shows that the number steps does affect the model selection as well as the accuracy of the resulting Lévy flight exponent μ. It is therefore evident that the exponent parameter μ tends to increase as the number of steps reduced. This exercise suggests that the movement or foraging data sets should be appropriately large enough to accurately detect the underlying models, optimal Lévy flight parameter μ in particular and other behavioural changes in general.

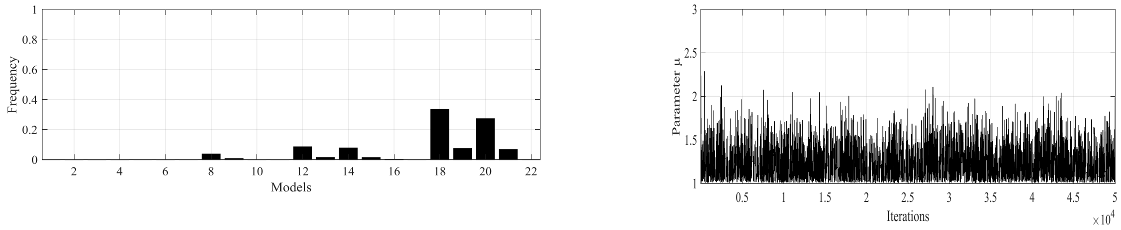
n=37



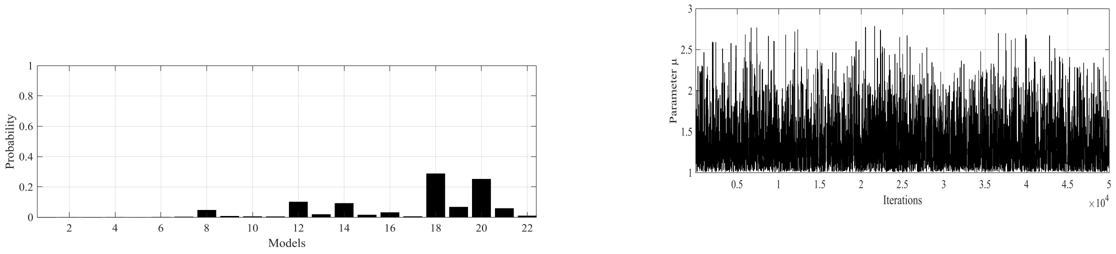
n=30



n=20



n=10



n=5

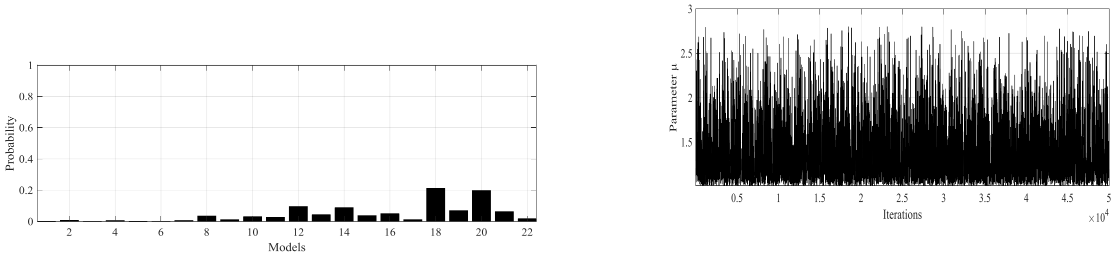
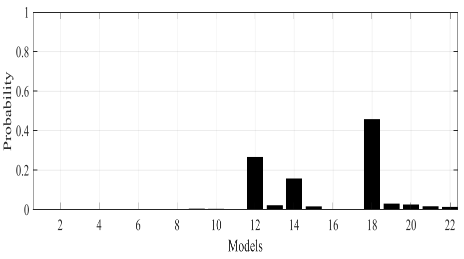
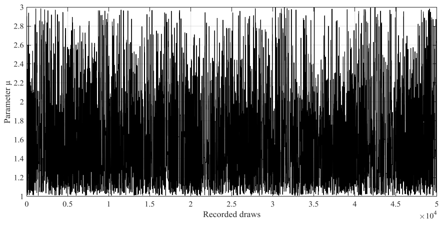


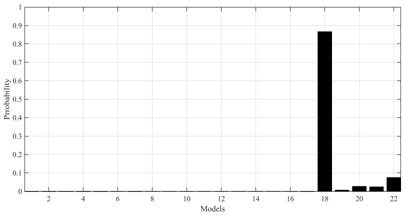
Figure 4.14: Impact of change in number of steps on model selection and parameter μ (SBEA approach)

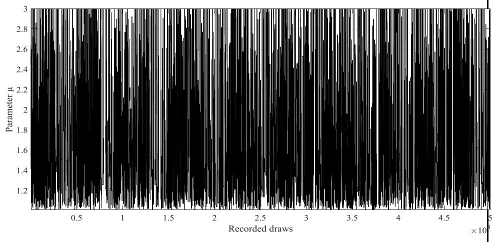
n=37	



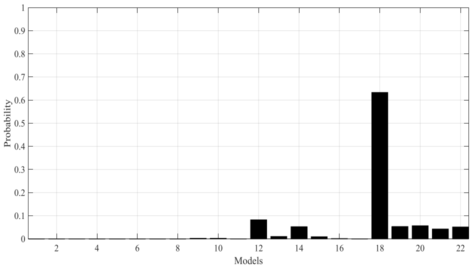


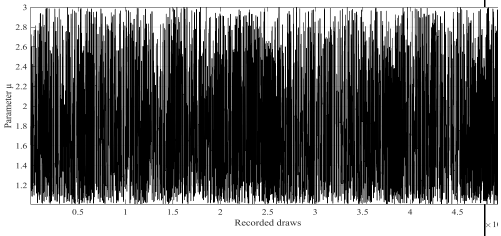
n=30



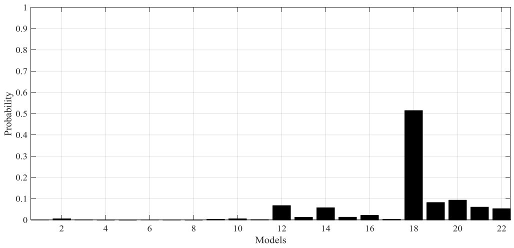


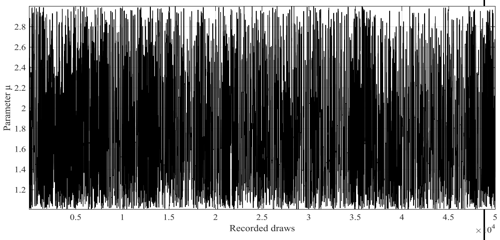
n=20



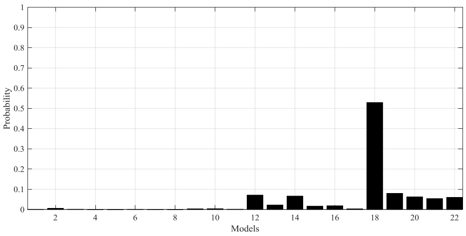


n=10





n=5



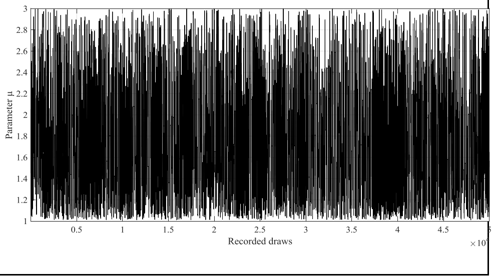


Figure 4.15: Impact of change in number of steps on model selection and parameter μ (ABC approach)

Chapter 5 Revisiting Reindeer Foraging Patterns

This chapter uses the common methodology developed and discussed in Chapter 3 to apply the two same Bayesian methods to a different set of foraging data; in this case that of semi-domesticated reindeer (*Rangifer tarandus tarandus* L.). Section 5.1 gives an introduction to the reindeer ecology and management. Section 5.2 outlines the previous analyses of the same dataset including the original study. Then section 5.3 explains the methodology and data used in this chapter. Section 5.4 discussed the findings of the chapter and compares the results with that of the two previous studies. Section 5.5 highlights the implications and applications arising from the findings.

Understanding the foraging pattern of reindeer can have important management and policy implications. For example, identifying the spatial heterogeneity of these large herbivorous animals can suggest optimum conservation measures such as the design of habitat corridors. Also, landscape modifications required for infrastructure development in these areas can be carried out in accordance with the herding activities to minimise disturbance to their natural habitats and behaviours.

In Chapter four, the foraging pattern of human hunter gatherers was re-investigated. The more rigorous investigation using the Bayesian approach suggested that a bounded Lévy flight distribution was more representative of the movement patterns observed than a pure unbounded Lévy flight. This finding overturns the previous inference and conclusions made on the same data set. Therefore, it is of interest to apply the which can be expected to follow a different foraging pattern.

5.1 Introduction to reindeer ecology and management

Reindeer (Rangifer tarandus L.) is one of the most important large herbivores which belongs to the native large-sized herbivore community in northern Fennoscandia (Skjenneberg and Slagsvold 1968; Bernes et al. 2013). More specifically, it belongs to the deer family (Cervidae) and is classified as a grazer/browser that is intermediate between bulk feeders and concentrate selectors (Hofmann 1989; Hanley 1997). Presently, reindeer are semi-domesticated in Sweden as well as most parts of Finland and Norway (Mårell and Edenius 2006; Sandström et al. 2003, 2007). Literature does not classify reindeer herding exclusively (Skarin and Ahman 2014) and the term ‘semi-domesticated’ is not defined in animal breeding literature (Clutton-Brock 2012). However, breeding literature explains that domestication or taming of reindeer as a process of training them to be more accustomed to humans (Baur 1992).

In most parts of Sweden, reindeer husbandry is the sole preserve of the Sami community (Bernes et al. 2013). In these areas, reindeer play ecologically, economically, and culturally important roles. Two main types of reindeer husbandry exist in Sweden. Sami communities bordering the Baltic sea and Finland keep their reindeer in the boreal forests all year round. Sami communities further to the west, bordering Norway, let their reindeer migrate between the winter ranges in lowland boreal forests and the summer ranges at high altitudes in the Scandinavian mountains (Mårell and Edenius 2006; Bernes et al. 2013). Reindeer are the only semi-domesticated animals allowed to free range all year round.

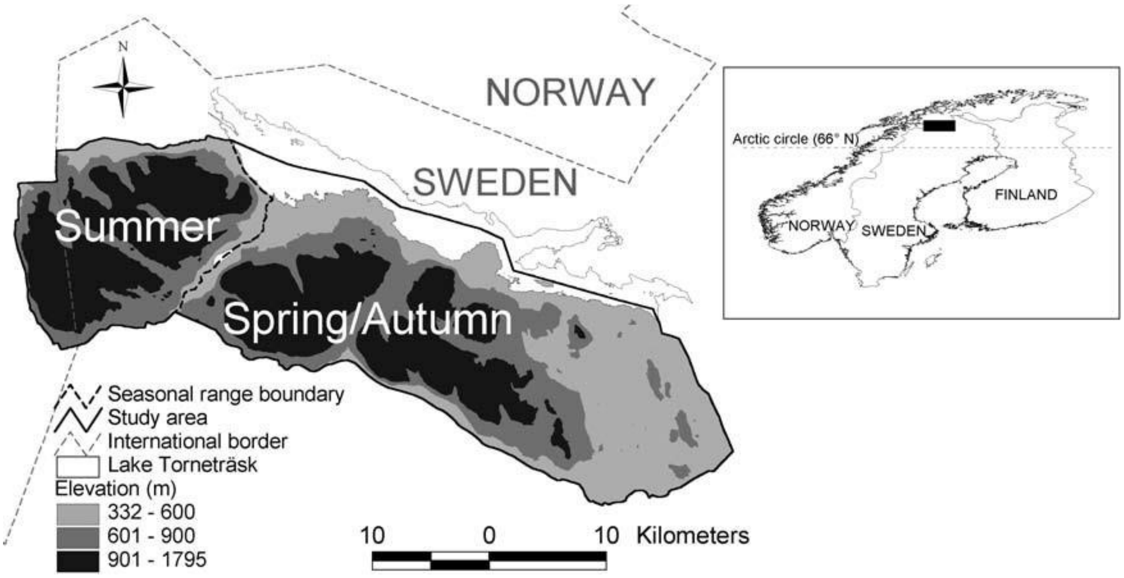
Reindeer herding by the Sami community in Sweden is generally extensive where these animals move freely in the landscape for most of the year with minimum influence and management by the herders except for occasional gatherings and shifting for supplementary feeding. Reindeer are semi-domesticated and herded mainly for milk, meat, hides, antlers and transportation.

According to Gates et al. (1986) and Post and Klein (1999), although winter feeding conditions are harsh, it is the summer feeding conditions that have been demonstrated to control reindeer population dynamics (Tveraa et al. 2003). This is mainly because summer feeding decides survival in the winter for both adult and young reindeer. Energy and nutritional demands of female reindeer are highest during summer. Young calves need to double their weight during the summer period in order to be ready for winter. Adult reindeer also need to build up sufficient energy reserves during the summer to face winter. Therefore, a better understanding of reindeer habitat and foraging needs, through a better understanding of their movement patterns during summer, is important for the improved management of reindeer populations.

The diet of these reindeer is highly mixed, and they adapt their diet to local conditions (White et al. 1981; Mårell and Edenius 2006). Their diet consists mainly of energy-rich lichens during winter which changes to a more protein-rich diet dominated diet and dominated by graminoids (grasses, sedges etc.), herbs and shrubs during summer (Beck and Peek 2005). The diet also overlaps with the annual physiological cycle of the female reindeer as they need a high-protein diet to support growth and lactation during late spring and summer (Klein 1990). Over the seasons, many reindeer herds migrate long distances between summer and winter pastures, and between pastures of different kinds within the seasonal ranges (Barnes et al. 2013).

5.2 The original analyses and Edward's re-analysis

Mårell et al. (2002) collected data on the foraging and searching behaviour of 17 female semi-domesticated reindeer (*Rangifer tarandus tarandus* L.) in Nothern Sweden. This study was carried out in a mountainous landscape of sub-arctic northern Sweden including Abisko National Park (68˚19'N, 18˚40'E). The total study area of 2100 km^2 used by the semi-domesticated reindeer herd belonging to Gabna Sami community was defined by the spring, summer and autumn ranges (Figure 5.1). This area is characterised by a long-term average annual mean temperature of -0.8˚ C, and mean temperature of the warmest month, July, is 11.0˚ C (Alexandersson et al. 1991). The elevation in the area ranges from 332 to 1803 m.



Source: Mårell and Edenius (2006)

Figure 5.1: Study area (2100 km^2 range)

A key objective of the study carried out by Mårell et al., (2002) was to analyse the extent to which movement patterns of reindeer relates to the availability of food resources using several models of searching behaviour such as fractal analysis, correlated random walks, and Lévy flights. They carried out a pre-survey in the summer of 1998 to characterize the behaviour of the reindeer. They tagged eight female reindeer with radio collars in July 1998 to determine the area in which to search systematically and observe reindeer habitat selection. During the pre-survey, they identified five time periods (A-E) during which the foraging behaviour of the reindeers was observed to be different. These five time periods were categorised according to their herding activities and environmental characteristics. The five time periods were: period A from the end of May to mid-June (just after the calving peak to the time of birch leafing out); period B from mid-June to the beginning of July (movement of the herd into the western most parts of the study area); period C from the beginning of July to the end of July (movement of the herd back to the east of the study area); period D from the end of July to mid-August (first hard frost and snowfall at high altitudes in the area); and period E from mid-August to mid-September (gathering and slaughtering of males).

In the following year (1999), the team followed the reindeer using laser-range binoculars from the last week of May until the mid September from a distance far enough not to disturb their natural behaviour. A hierarchical system was employed to select the animals for observation. First, the area to search for reindeer groups was determined using telemetry. Second, the first group of reindeer detected was selected for observation. Third, one female reindeer with a collar was randomly selected to be followed. Each animal was observed for a maximum of 30 minutes and positions were recorded every 30 seconds. These recordings were used to characterise the movement path.

Period A is referred to as “late spring”. Recording sequences B and C (“summer”) have been combined by Mårell et al. (2002), as they are close in time, observed in similar habitats, thus did not differ. The recording sequence from period D has been excluded by Mårell et al. (2002) from the original analysis due to incomplete recordings because of severe weather conditions. The recording sequences from period E (“late summer”) are from a single day in mid-August, but because of dramatic shifts in the use of feeding area and habitat, these observations have not been merged with those from other periods by Mårell et al. (2002).

Mårell et al. (2002) employed a log-log regression (log frequency of step lengths against log step lengths) to compute the Lévy flight parameter μ for the movement paths. They found that the frequency distributions of movement lengths during foraging resembled the distribution function of Lévy flights, $1 < \mu \leq 3$, during all three-time periods. Thus, their analysis suggested the reindeer movement could be represented by a Lévy foraging pattern irrespective of the season. Edwards (2011) reanalysed the same datasets using modern likelihood and Akaike weights approach to test the alternative models, namely, bounded and unbounded versions of exponential and power-law models (explained in Chapter 3). Edwards (2011) Found that the bounded power-law model supports the movement paths in periods A and B+C while an exponential model is consistent with period E data. Given the differences in results, between Edwards (2011) and Mårell et al. (2002), it was of interest to employ the Bayesian approach to characterise the movement pattern underlying their foraging to test the validity of the previous findings.

5.3 Methodology and data

This chapter used the exact same raw data sets analysed initially by Mårell et al. (2002) and then re-analysed by Edwards (2011). These raw data sets included the reindeer foraging positions (X, Y co-ordinates) during the 3 time periods (A, B+C, and E). Reindeer positions were reported every 30 seconds. These coordinates were used to derive the distance between two positions and the turning angles to characterise the movement paths. The distances between two foraging points, the turning angles and the foraging paths were computed and plotted using MATLAB©. Descriptive statistics were computed, histograms were produced and matched with the statistics reported in the original papers to verify the accuracy of the data. Mårell et al. (2002) and Edwards (2011) employed a classical approach to quantify the movement pattern. Applying the Bayesian approach allowed me to capture the latent behaviours and make more accurate inference. Therefore, I applied both the standard Bayesian estimation approach (SBEA) and the Approximate Bayesian computation (ABC) methods on all data sets as explained in Chapter 3. Data sets for all three time periods were analysed using the 22 models (44 with log transformations) as specified in Chapter 4 under both Bayesian approaches.

5.4 Results

Table 5.1 shows the characteristics of the foraging paths of the reindeer during three different time periods. First, the animals seem to have walked much farther during 30 seconds within the 30-minute period an animal was observed in period E (mean distance of 19.9m) compared to period A (mean = 3.63m) and period B+C (mean = 6.26m). This is not surprising because there is a lower availability and distribution of the preferred food species during late summer, so the animals have to put more effort into foraging in order to find food species. The recording sequence refers to one reindeer at a time. For example, number '1' is the first reindeer observed in time period 'A' on 1st June for 60 times.

Table 5.1: Descriptive statistics of the foraging paths of 17 female reindeer

				Distance[c](m)	
Recording sequence No	Time period[a]	Date	No. of times[b]	Mean	Standard deviation
1*	A	1 June	60	5.7	7.3
2	A	1 June	59	3.9	3.8
3	A	1 June	58	2.1	2.8
4*	A	7 June	54	4.1	5.0
5*	A	7 June	61	3.8	4.6
6	A	7 June	61	2.2	1.7
7*	B	29 June	61	2.7	2.3
8*	C	8 July	59	6.1	6.5
9*	C	8 July	61	7.7	9.4
10*	C	8 July	48	9.7	12.1
11	C	10 July	36	5.4	6.4
12	C	12 July	24	6.4	7.8
13	D	6 August	61	3.1	3.5
14*	E	18 August	38	19.1	7.5
15	E	18 August	30	13.7	8.5
16*	E	18 August	24	23.4	9.8
17*	E	18 August	28	24.8	20.2

Source: Mårell et al., (2002)

[a] Period A, end of May to mid-June; period B + C, mid-June to the end of July; period E, mid-August to mid-September.
[b] Number of times during the recording sequence that the position of the animal could be established precisely.
[c] Distance moved by the animal per 30s.
*10 out of 17 foraging paths that were used in the analyses of feeding-site selection and characteristics.

Figure 5.2 shows the site positions of the reindeer over the season. It depicts where the reindeer clustered during three period they were observed. The x and y axes are coordinates. Reindeer observations start from period A depicted in blue dots and the observations ended in period E where they have moved to the positions shown in red. Each point in the cluster is a reindeer with a radio collar.

Figure 5.2 indicates that the animals have moved further away from the feeding places where they grazed during late spring by late summer. As they are constantly in search of the preferred food species they seem to travel further away as the resources deplete. Thus, this behaviour can be accounted for by the distributional differences of food species as well as the density. It is also interesting to observe that the feeding is more concentrated in late spring and early summer compared to mid-summer period as the reindeer seems to cluster in a restricted area while feeding. Mårell et al. (2002) finds that they gather and concentrated where 'heath' plant communities dominate during late spring and late summer.

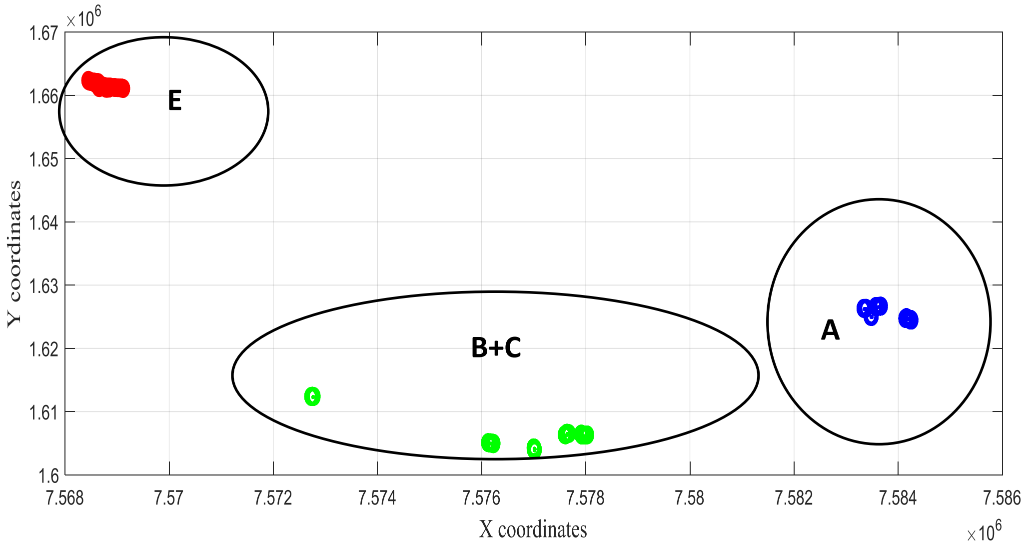


Figure 5.2: Site positions of the reindeer in each time period

I then analysed the movement path of one reindeer (reindeer 1) from period A to depict how step-lengths or distance can be observed in two-dimensional space. The path was drawn using the exact raw coordinates provided in the data. Reindeer '1' in period 'A' were observed at 60 positions which are labelled in the path. The step length was considered as the distance between two consecutive positions.

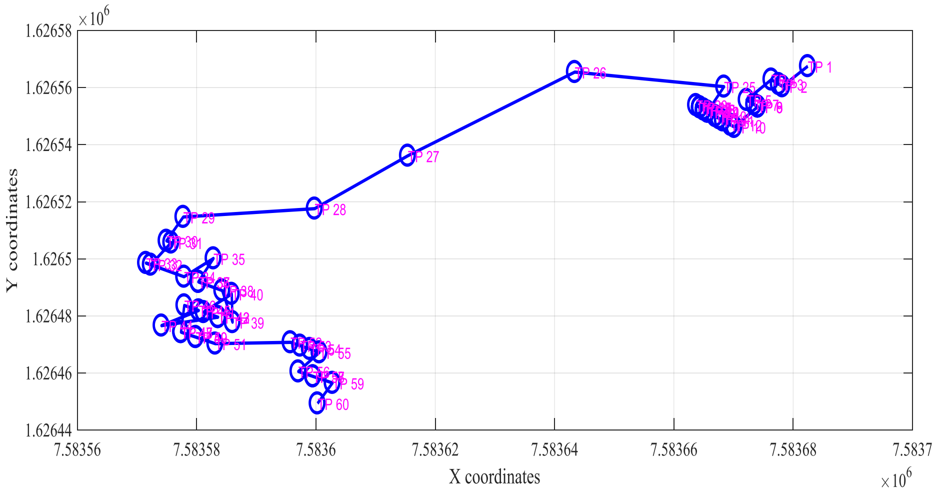


Figure 5.3: Movement path of reindeer 1 in time period A

Figure 5.3 demonstrates how the movement path of this particular reindeer comprises clusters of shorter step lengths connected by a small number of longer step lengths during the foraging period under investigation.

5.4.1 Results from the Bayesian model selection approaches

This section compares the results from the two Bayesian approaches to identify the model that best supports the data for each period. The 22 models specified in Table 4.2 have been analysed in this chapter as well. In the probability graphs below, the most dominant model, the “best” model, is defined as that with the highest probability compared to all other models analysed. A probability of 1 is expected for the dominant model suggesting that the data are completely supported or in other words, the underlying behaviour of the movement path is characterised by the dominant model. The minimum and maximum bounds fixed for the models were the minimum and maximum data points for each time period.

For Period A, the Standard Bayesian estimation approach (SBEA) indicates that model 20 dominates while for ABC approach, model 22 is dominant (Figure 5.4 and 5.5). Model 20 is a bounded power-law model with a minimum value bound. The minimum value the minimum is 1m. Model 22 is also a bounded power-law model with the minimum and maximum bounds estimated by the model.

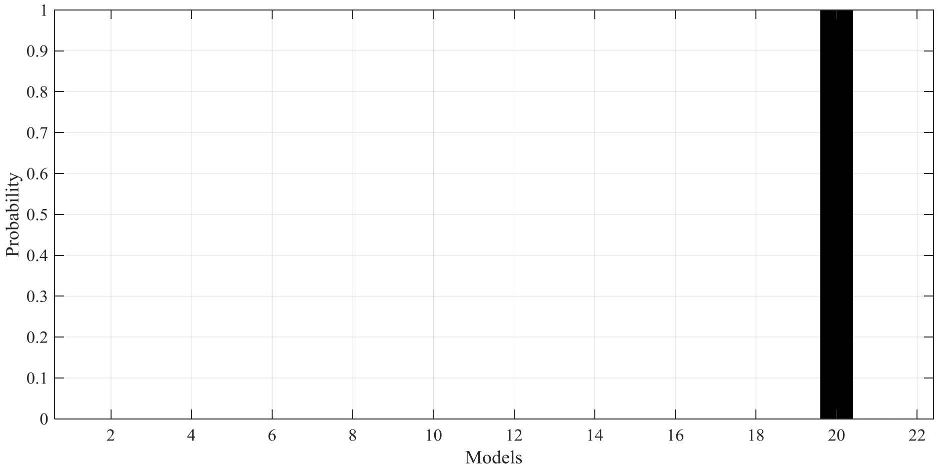


Figure 5.4: Implied probabilities across models for Period A (SBEA)

The ABC approach shows that model 22 supports data with a probability of 64% followed by model 21. Both are bounded variants of the power-law model seem to show a probability of 1 indicating that it fully supports data compare to all the other models.

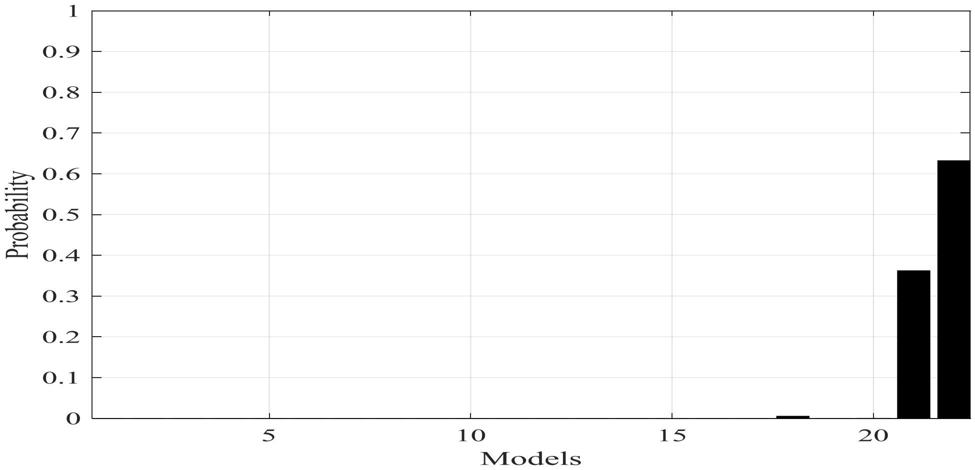


Figure 5.5: Implied probabilities across models for Period A (ABC*)*

The outcome shows that two different models seems dominant from the two methodological approaches (SBEA and ABC). The two models are bounded version of the power-law model. Therefore, although one model cannot be said to dominate the movement behaviour in period A, it could be seen that in period A, the movement step lengths follow a power-law distribution pattern. The fact that both approaches results in bounded power-law model is another indication that the movement cannot produce extremely long step lengths but instead are truncated within a range. Appendix 5 shows the results from the model selection exercise carried out for the individual reindeer in period A.

Figure 5.6 shows the results from the two model selection exercises for Period B+C. SBEA results suggest that there is only one model that supports data which is model 20 the same as period A with a probability of 1 (Figure 5.4). ABC results also show that the similar to period A model 22 is the dominant model but with a higher probability of 95% (Figure 5.7b).

Both dominant models are bounded power-law models similar to period A. For period B+C, the minimum bound is 1m whereas the maximum is 40.59m. Model 22 is the power-law model with μ, minimum and maximum bounds estimated. The fact that a bounded power-law model dominates in both approaches suggests that a bounded power-law is the underlying behaviour of the step lengths of the reindeer in period B+C.

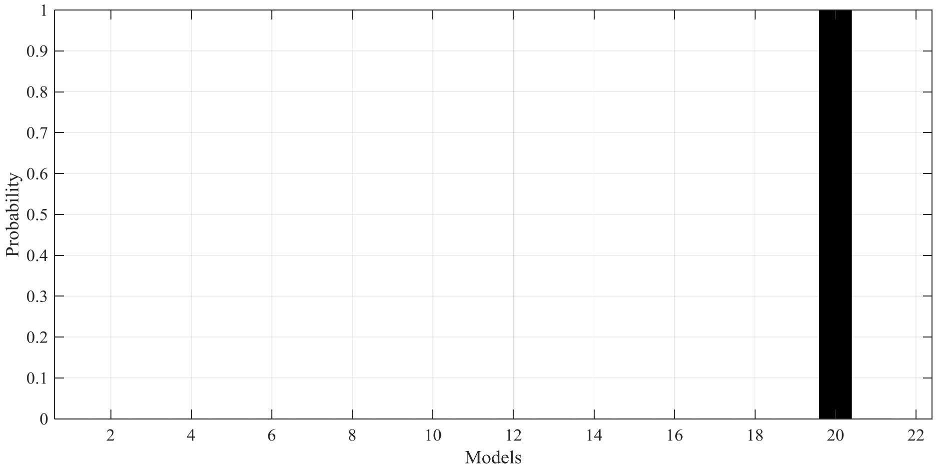


Figure 5.6: Implied probabilities across models for Period B+C (SBEA)

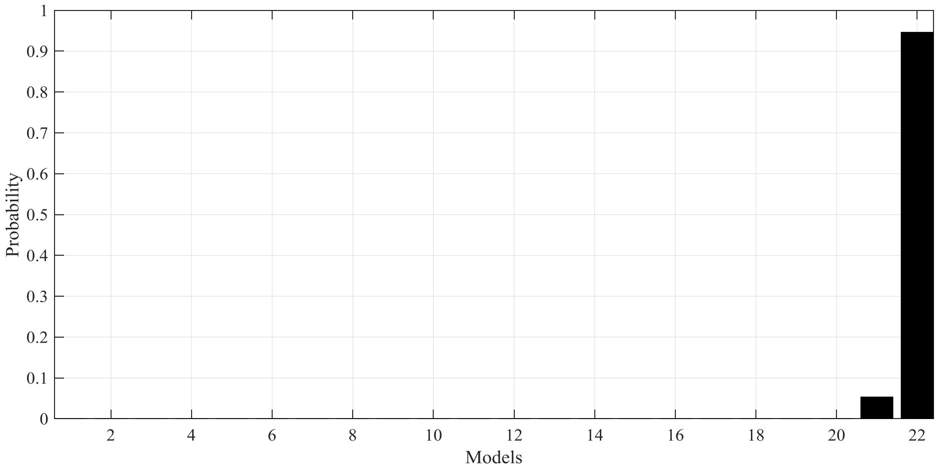


Figure 5.7: Implied probabilities across models for Period B+C (ABC)

Figure 5.8 shows the results for period E. SBEA approach selects model 14 as the dominant model with a probability of 1. Model 14 is a bounded exponential model with no fixed parameters (Figure 5.8). The minimum and maximum bounds of model 14 were not fixed. The ABC approach shows that the most dominant model is model 11 which is a bounded exponential model (Figure 5.9).

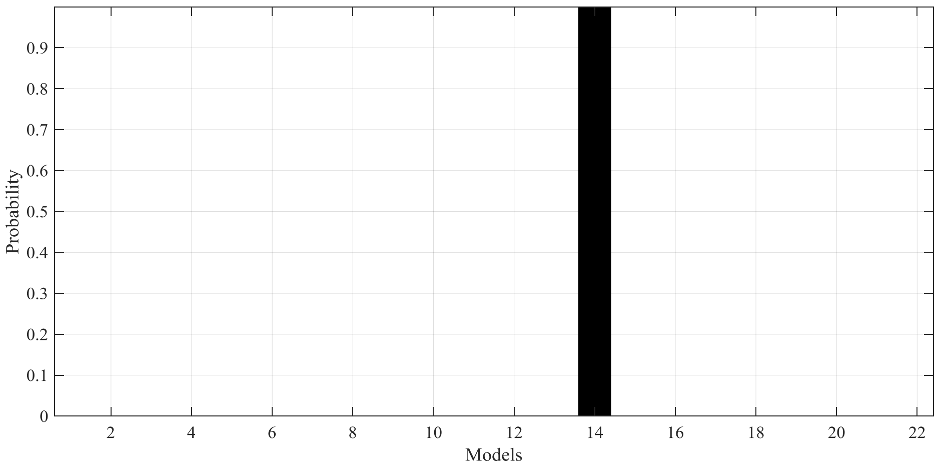


Figure 5.8: Implied probabilities across models for Period E (SBEA)

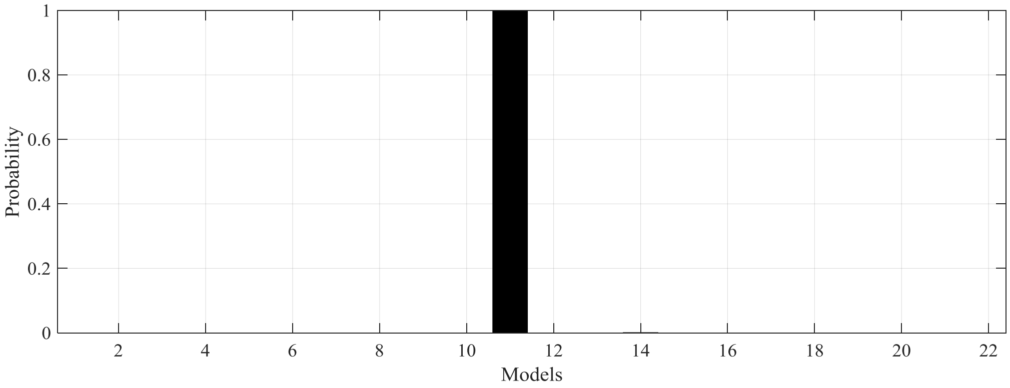


Figure 5.9: Implied probabilities across models for Period E (ABC)

Both approaches select variants of bounded exponential model to be the dominant one. Based on the analysis, the movement steps in Period A and B+C are well supported by a bounded power-law model whereas the movement in period E supported by a bounded exponential.

5.4.3 Comparing the results with the two previous studies

Table 5.2 shows that the results for all three time periods overturn the conclusions of the original study (Mårell et al., 2002) for an unbounded power-law distribution for the foraging reindeer. However, the results do not completely rule out the existence of a power-law distribution but instead indicate that a bounded power-law most supports data.

Table 5.2: Conclusions from each study

	Original conclusion From Mårell et al., (2002)	Edwards' Conclusion From Edwards (2011)	Conclusion from the Bayesian analysis
Period A	Lévy flight μ = 2 Unbounded power-law	Bounded Power-law	Bounded Power-law
Period B+C	Lévy flight μ= 1.8 Unbounded power-law	Bounded Power-law	Bounded Power-law
Period E	Lévy flight μ= 1.8 Unbounded power-law	Unbounded Exponential	Bounded Exponential

Comparing results with Edwards' findings, the results are very much on par and comparable with those of Edwards, particularly for the first two time periods. For periods

A and B+C, my finding that the data are consistent with a bounded power-law model confirms Edwards' findings. However, for period E, Edwards concluded an unbounded exponential model whereas my results conclude a bonded exponential model. As both likelihood and likelihood-free approaches suggest the bounded version of the exponential distribution, it can be concluded that for period E, it is the most supported model. Further to Edwards' conclusion, because I have used various forms of a bounded version of models, which included unfixed bounds. Thus, this also suggests that fixing the maximum bound does not increase the likelihood of such a model. Instead, the bounds could vary within a range.

As the period A and B+C movements are best supported by the bounded power-law distribution, it was of interest to check how that exponent parameter μ behaves for the two periods. Figures 5.10 and 5.12 show the behaviour of the exponent parameter resulting from each statistical approach (SBEA and ABC respectively) for period A. Figures 5.10, 5.11 and Table 5.3 shows the behaviour of the exponent parameter μ for model 20 for period A. The parameter fluctuates with a mean of 1.70 and a standard deviation of 0.1for the 50000 iterations. This suggests that although the movement patter can be characterised as a bounded power-law or in other words a bounded Lévy flight, the foraging is not optimal. Figures 5.12, 5.13 and Table 5.4 shows the trace plot and central tendency of μ for model 22. The parameter μ fluctuates with a mean of 2.13 and a standard deviation of 1.23. Thus, the pattern can be characterised as a bounded Lévy flight movement pattern which does not show optimal foraging.

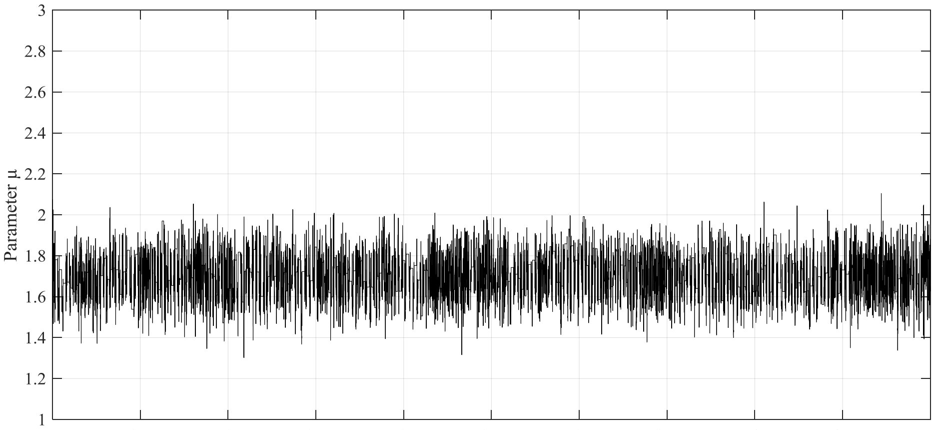


Figure 5.10: Trace plots of exponent (μ) distribution of the bounded power-law model for Period A (SBEA)

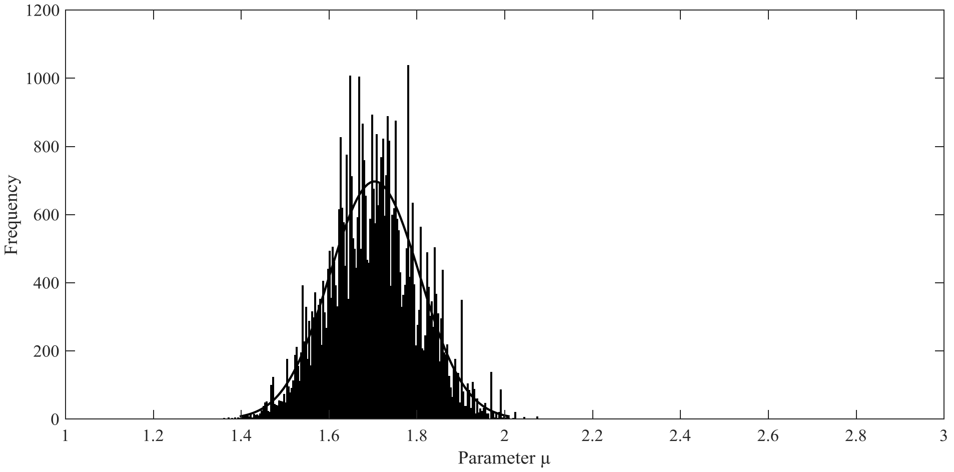


Figure 5.11: Distribution of the exponent parameter (μ)

Table 5.3: Measures of central tendency and spread of the parameter μ

Mean	1.70
Median	1.70
Standard deviation	0.10
Q1	1.63
Q2	1.70
Q3	1.77
Interquartile range (IQR)	0.14

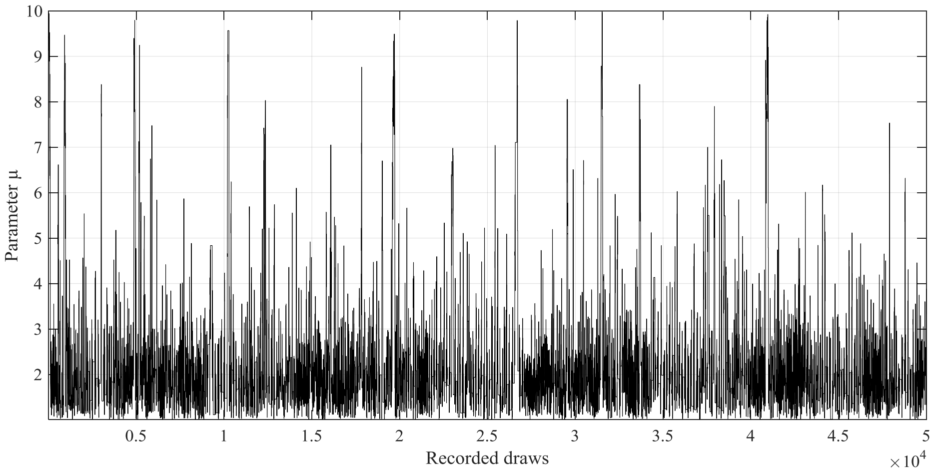


Figure 5.12: Trace plots of exponent (µ) distribution of the bounded power-law model for Period A (ABC)

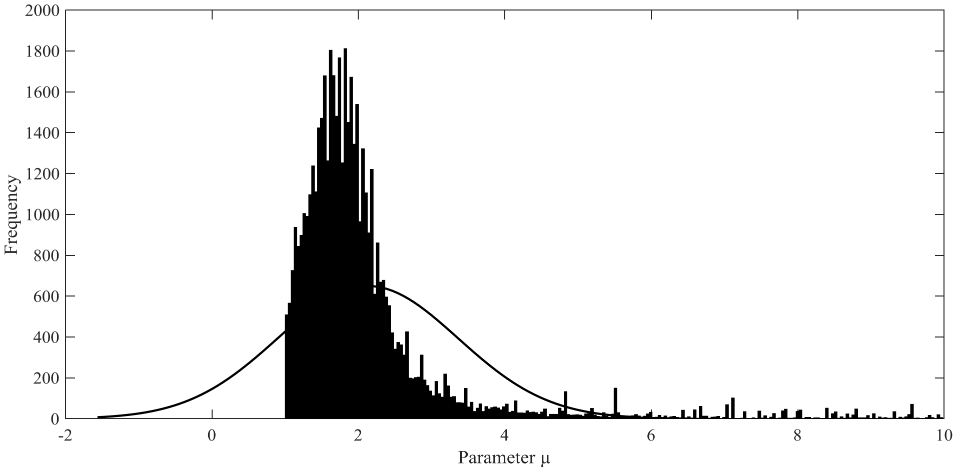


Figure 5.13: Distribution of the exponent parameter (µ)

Table 5.4: Measures of central tendency and spread of the parameter µ

Mean	2.13
Median	1.83
Standard deviation	1.23
Q1	1.51
Q2	1.83
Q3	2.23
Interquartile range (IQR)	0.72

Both trace plots for period A shows that µ fluctuates between the range1-3. This implies that for period A the movement path can be represented by a bounded Lévy flight.

Trace plots were then drawn for period B+C as shown in figures 5.14, 5.15and Table 5.5 shows that the exponent parameter fluctuates with a mean of 1.68 for model 20 for the SBEA approach. The trace plots for model 22 from the ABC approach for period B+C in figures 5.16, 5.17 and Table 5.6 shows that the exponent parameter fluctuates with a mean of 1.80 and a standard deviation of 1.05.

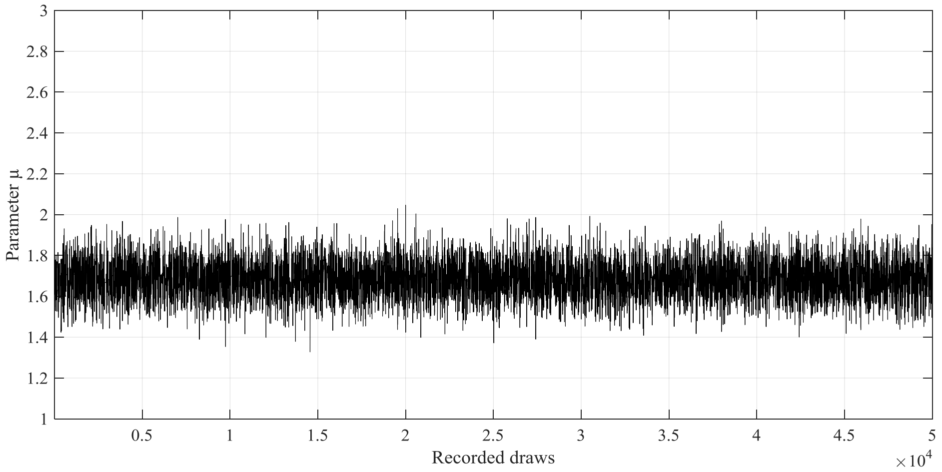


Figure 5.14:Trace plots of exponent (μ) distribution of the bounded power-law model for Period B+C

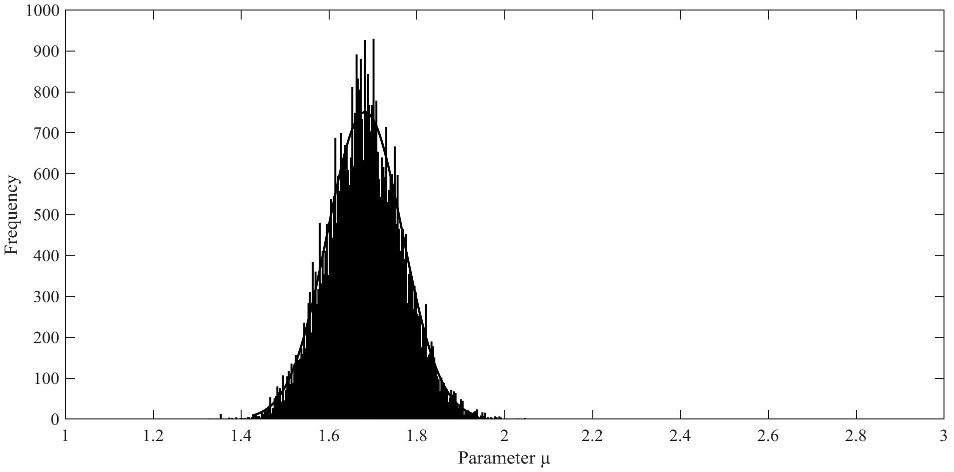


Figure 5.15: Distribution of parameter (μ)

Table 5.5: Measures of central tendency and spread of the parameter μ

Mean	1.68
Median	1.68
Standard deviation	0.09
Q1	1.62
Q2	1.68
Q3	0.74
Interquartile range (IQR)	0.11

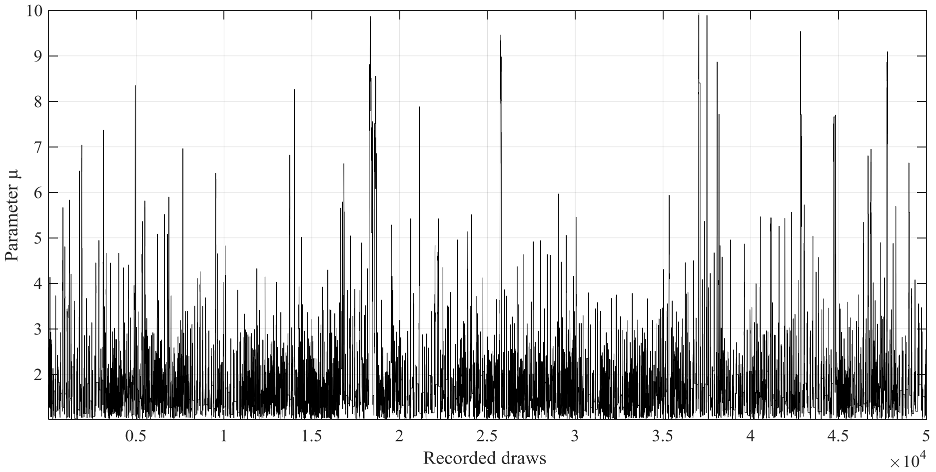


Figure 5.16: Trace plots of exponent (µ) distribution of the bounded power-law model for Period B+C

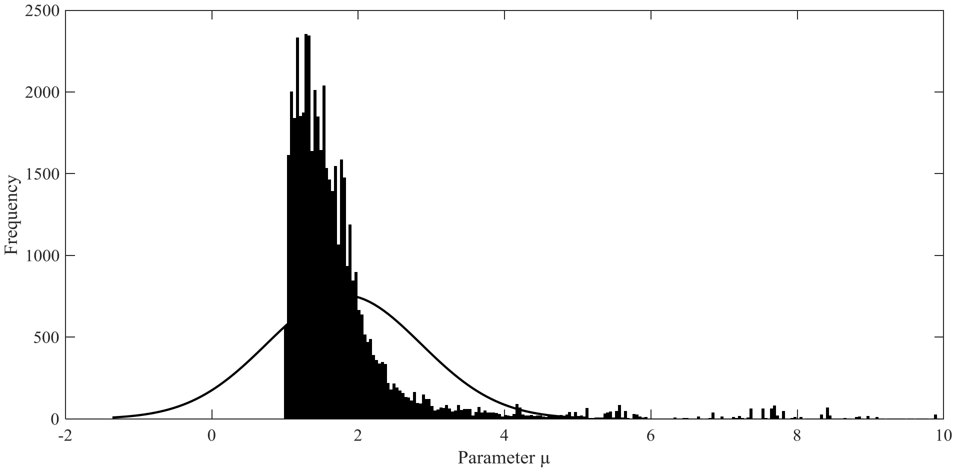


Figure 5.17: Distribution of parameter (µ)

Table 5.6: Measures of central tendency and spread of the parameter µ

Mean	1.80
Median	1.53
Standard deviation	1.05
Q1	1.27
Q2	1.53
Q3	1.89
Interquartile range (IQR)	1.61

As a whole the parameter µ for period B+C lies between 1-3 similar to period A. However, the difference is quite high between the two approaches; SBEA and ABC. Thus, it is difficult to conclude about the optimality of the foraging behaviours but could be said that it is less than optimal. As the parameter lies within the Lévy range, it could be said that for period B+C, the movement pattern can be represented by a bounded Lévy flight distribution is the most probable model for the foraging reindeer. For period E, a bounded exponential is most suitable to characterise the movement paths.

5.4.1 Movement Characterisation of the Reindeer Paths

Histograms shown in **Error! Reference source not found.** below represent the step length distribution of all the reindeer in each time period. These were drawn using the raw data. The histograms of the raw movement data for each time period shows the distribution of the step lengths. Histograms (**Error! Reference source not found.** a,b,c) were recreated to match the histograms in Edwards (2011). These figures show that each time period consisted of recordings with no movement. These would have been modes of a reindeer laying down or standing or non-recorded movement within 30s interval. Both Mårell et al. (2002) and Edwards (2011) did not consider the zeros in the time periods. I analysed the models with and without zero values. However, the inclusion of zero values posed a problem for some models in the model selection exercise, which is discussed in Chapter 3). The zeros were therefore excluded to overcome programming limitations and also in order to be consistent with the two previous analyses (Mårell et al. (2002) and Edwards (2011)) allowing the comparison of inference.

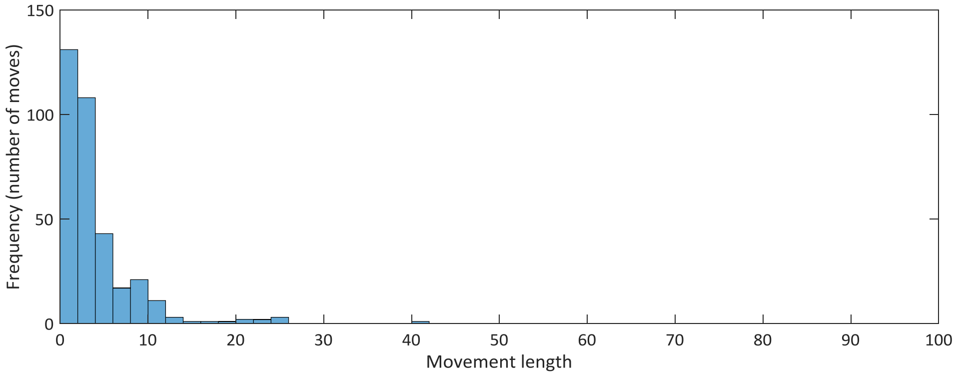


Figure 5.18a: Time period A

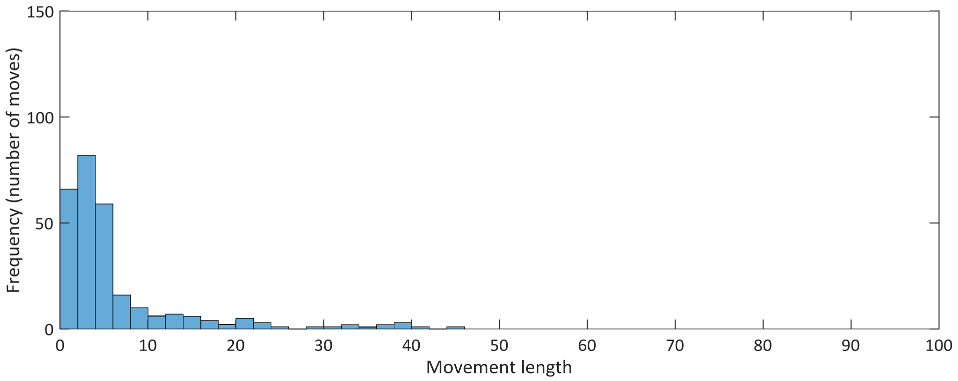


Figure 5.18b: Time period B+C

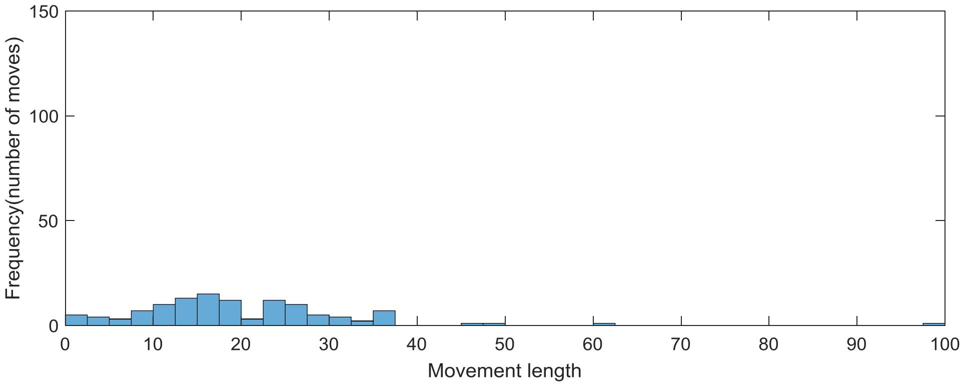


Figure 5.18c: Time period E

Figure 5.18: Step length distribution

The minimum and maximum values (step length range) for each period are: Period A 1-40.53m, Period B+C – 1-45.59m, Period E –1-98.09m. For each of the data sets, the power-law tails were assumed to start at the minimum value of 1. Edwards (2008) states that a simulated data set that follows a power-law distribution is expected to have 1% of the data that is 100 times the minimum value. The histograms in **Error! Reference source not found.** do not show the range of data that satisfies this criterion. Except for figure 4.18c (period E), the other two histograms (periods A and B+C) do not show movement lengths between 90-100m long. Thus these data cannot be expected to produce the heavy tails required for a pure power-law distribution as originally found in Mårell et al. (2002).

The turning angles of the animal paths are also of importance to test the correlation of movement step lengths (Zar1984). **Error! Reference source not found.** shows how the turning angles are distributed in each of the three time periods. The distribution of the turning angles gives an idea of the correlation of the random walk.

Error! Reference source not found. shows that the frequency distribution of turning angles is concentrated around a mean of zero (m = 0) for all three time periods. Zero movement lengths were not excluded in this analysis. A turning angle of zero corresponds to resting behaviour (Teimouri et al. 2018). A mean of zero indicates that the small turns are much more likely than large ones for the foraging animals. Also, it demonstrates positive autocorrelation in consecutive step movements or in other words directional persistence (Fortin et al. 2005). Small turning angles produce larger ratios and thus these movement paths result in larger displacement or faster spread of species (Hui and Richardson 2017).

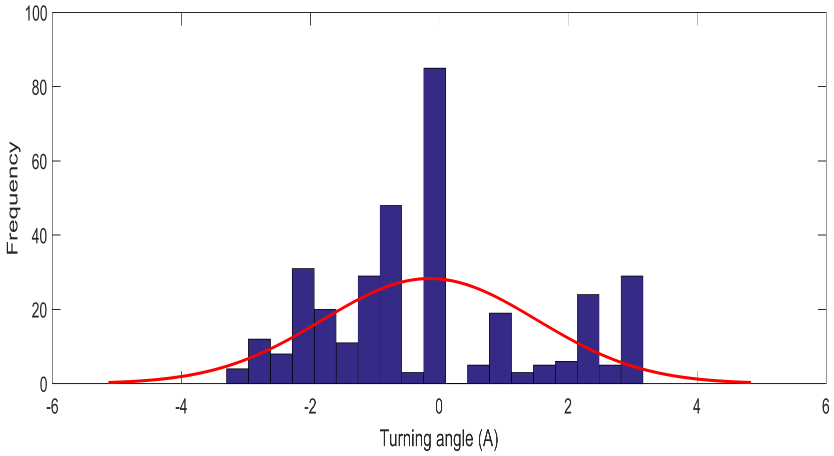


Figure 5.19a: Time Period A

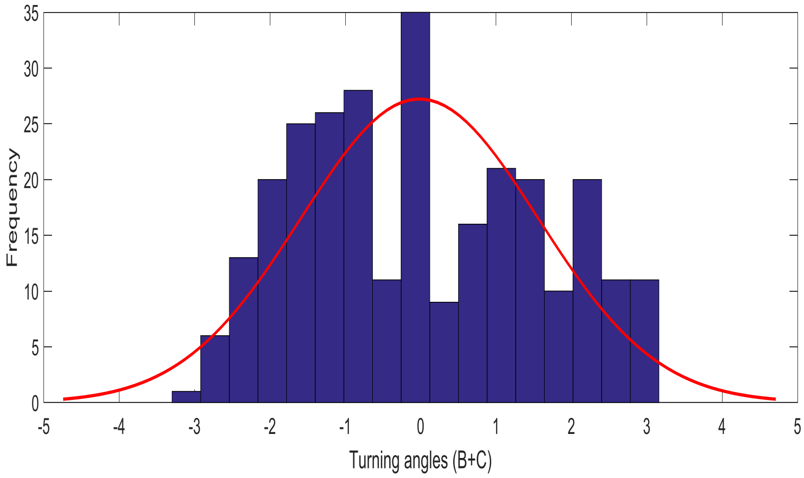


Figure 5.19b: Time Period B+C

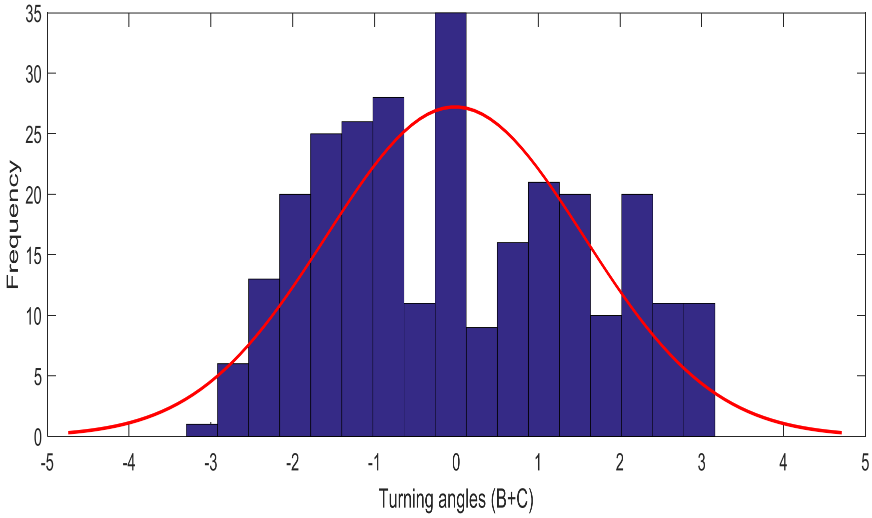


Figure 5.19c: Time Period E

Figure 5.19: Turning angles distribution

Source: angles computed using raw data received from Mårell et al. (2002)

From a graphical point of view, the movement paths illustrate a path with fewer large step lengths and large number of smaller step lengths suggesting a possible power-law distribution. Therefore, it was then of interest to apply the Bayesian model selection techniques to test the underlying models of movement in order to characterise the actual foraging paths. Thus, the next section discusses the results from the application of the standard Bayesian estimation technique and the approximate Bayesian technique.

5.5 Discussion in the context of seasonality

According to Mårell et al. (2002), the density of the preferred plant species is an important decisive factor in feeding-site selection as reindeer do not feed at a site unless there is a minimum quantity of the preferred plant species. This is also supported by the findings by Bergerud (1972) and Gaare and Skogland (1975) which mention that the food of reindeer differs between late spring and late summer. One major difference is a preference for mushrooms in late summer. Therefore, the observed change in searching behaviour during the study period may have been a result of the fact that mushrooms are spaced differently over time.

The exponent parameter μ of the bounded power-law models for the time period A and B+C Shows that the reindeer movement are not optimal as it is less than 2 (Viswanathan et al.1996) except for the μ value 2.13 For period A from the ABC approach. This can be expected as foragers do not visit the previously visited sites and keep moving to other foraging sites over the seasons. Thus, although the plant species may be regenerative, due to the time-lag, the reindeer do may move in search of patches that have their preferred food species. This argument is also strengthened by the fact that during period B+C which is the summer period, when the food is in more abundance, the μ is closer the 2. The fact that μ also supports the findings by Bazazi et al., (2012) that μ lies between when resources are relatively homogeneous in the summer.

The results find two different distribution patterns during the two time periods (A and E) that the food is relatively less abundant than in the summer. The fact that reindeer follow a foraging pattern represented by a truncated Lévy flight pattern in period A when the food is in abundance is an important finding as the original study identified no difference in the foraging pattern across the seasons. A key importance of identifying changing foraging behaviours across seasons is that heterogeneous behaviour suggests heterogeneous conservation and management measures for reindeer herding.

5.5 Implications and applications

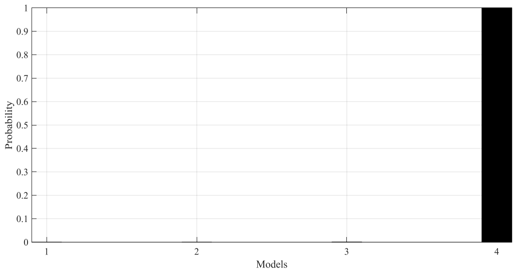
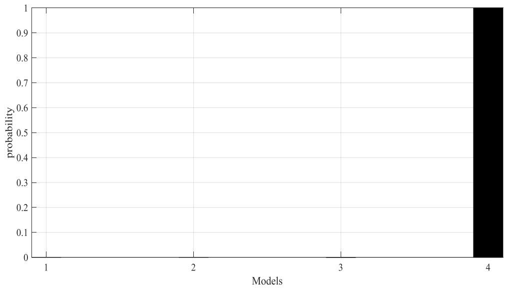
In this section I first undertake a similar analysis to that in Chapter 4, replicating the above analysis, but limiting the candidate models to those used by Edwards (2011). I then consider in Sections 5.5.2 and 5.5.3 how Bayesian approaches could contribute to improved policy concerning the management of landscapes occupied by both animal foragers and humans.

5.5.1 Implications of restricting the number of candidate models

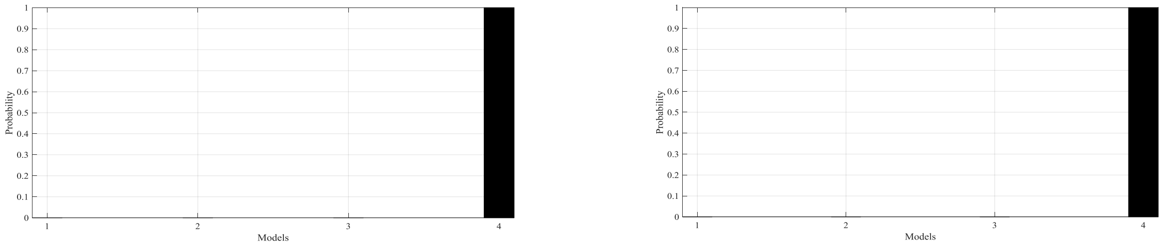
To compare Edwards’ (2011) approach more directly using Bayesian methods, similar to Chapter 4, I again selected the four candidate models as used by Edwards (2011):

- Model 1: Unbounded Exponential
- Model 2: Unbounded Power-law
- Model 3: Bounded Exponential
- Model 4: Bounded Power-law

Figure 5.20: Model comparison of Edwards (2011) model using SBEA and ABC approach shows that for periods A and B+C out of the four models, the bounded power-law models dominate followed by bounded exponential model. This is the same result found by Edwards (2011). For period E, the bounded exponential model dominates. When the same four models are considered, it can therefore be seen that the results from the Bayesian approach agree with those of Edwards (2011) for periods A and B+C. For period E, Edwards (2011) concluded an unbounded exponential model as opposed to a bounded.

SBEA	**ABC**
a) Period A	
	

b) Period B+C



c) Period E

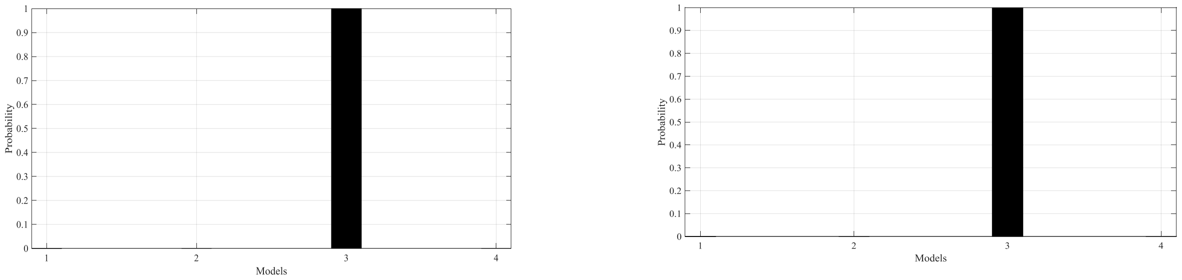


Figure 5.20: Model comparison of Edwards (2011) model using SBEA and ABC approach

This analysis, as for Chapter 4, raises issues concerning how the number of candidate models selected can influence the analyst’s conclusions over what model best represents animal movement patterns. Not surprisingly, when there are fewer candidate models, the dominant model has a higher probability associated with it. What becomes of particular concern is if increasing the number of candidate models changes the dominant model.

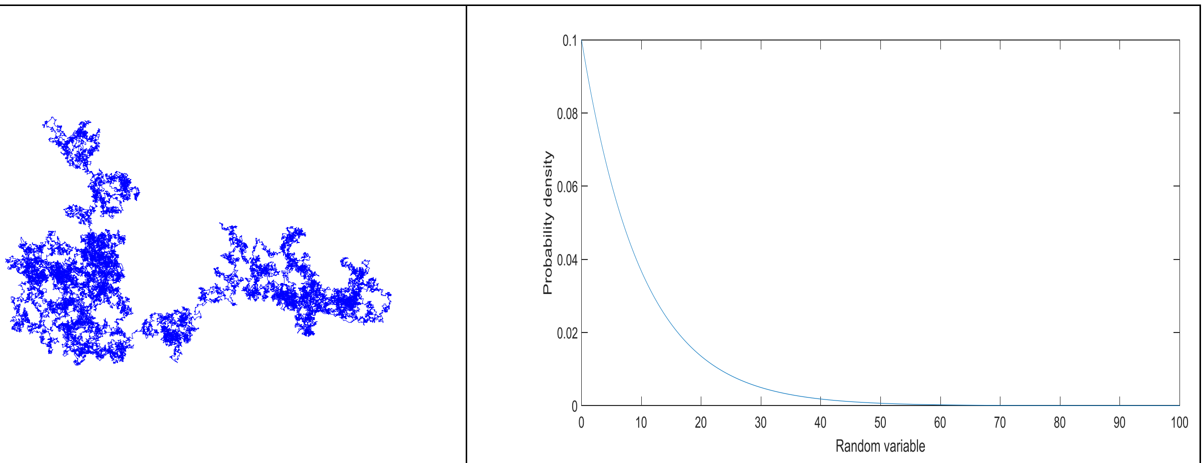
5.5.2 Application for invasive species containment

Understanding underlying distributions of movement patterns has important policy implications. One addressed here is invasive species and optimal control. Invasive species have long been studied in the ecology literature and are increasingly being investigated by environmental economists (Simberloff et al. 1992; Conrad et al. 2012).

When a species starts to invade a new area, policy makers and resource managers must determine the best way to contain that species. Setting up control measures such as a wall or mesh takes time. Thus, a decision might be made as to whether to try to contain the species within a small area, but risk it is escaping that area before the control measure is completed; or containing within a larger area and so accept a greater spread. To aid that decision, the analyst must determine the best fit representation of movement patterns so as to determine the likely speed of spread. This decision may need to be made when there are only a few movement observations. Bayesian approaches, such as those used in this thesis, are particularly useful in such a situation when there are only a small number of data points to work with.

In this section, to illustrate this idea, three movement distributions are compared visually, focusing particularly on fat tails and the implications for the speed and predictability of the spread of a species (

a)



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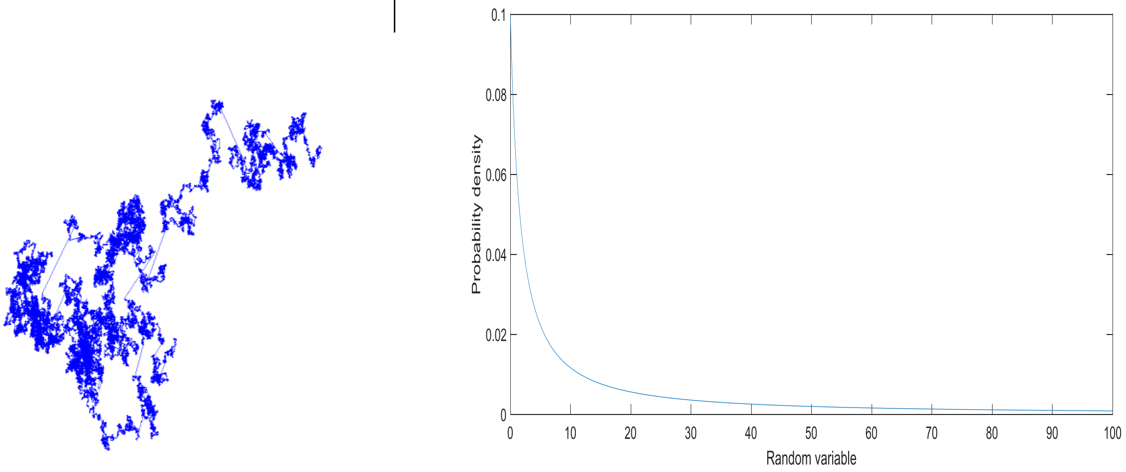


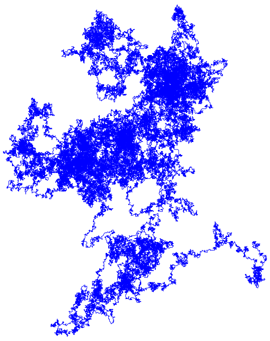
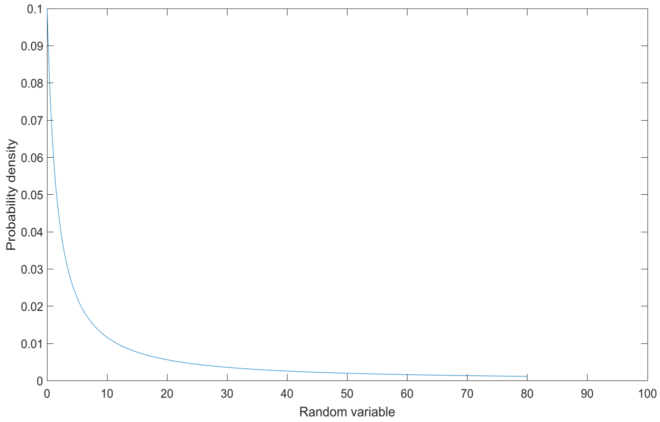
c) 	

Figure 5.21). These three distributions are chosen because they are the three distributions that seem to best support the reindeer movement data used in this thesis. Also, the original papers that analysed this dataset found these three to be the most supporting distributions.

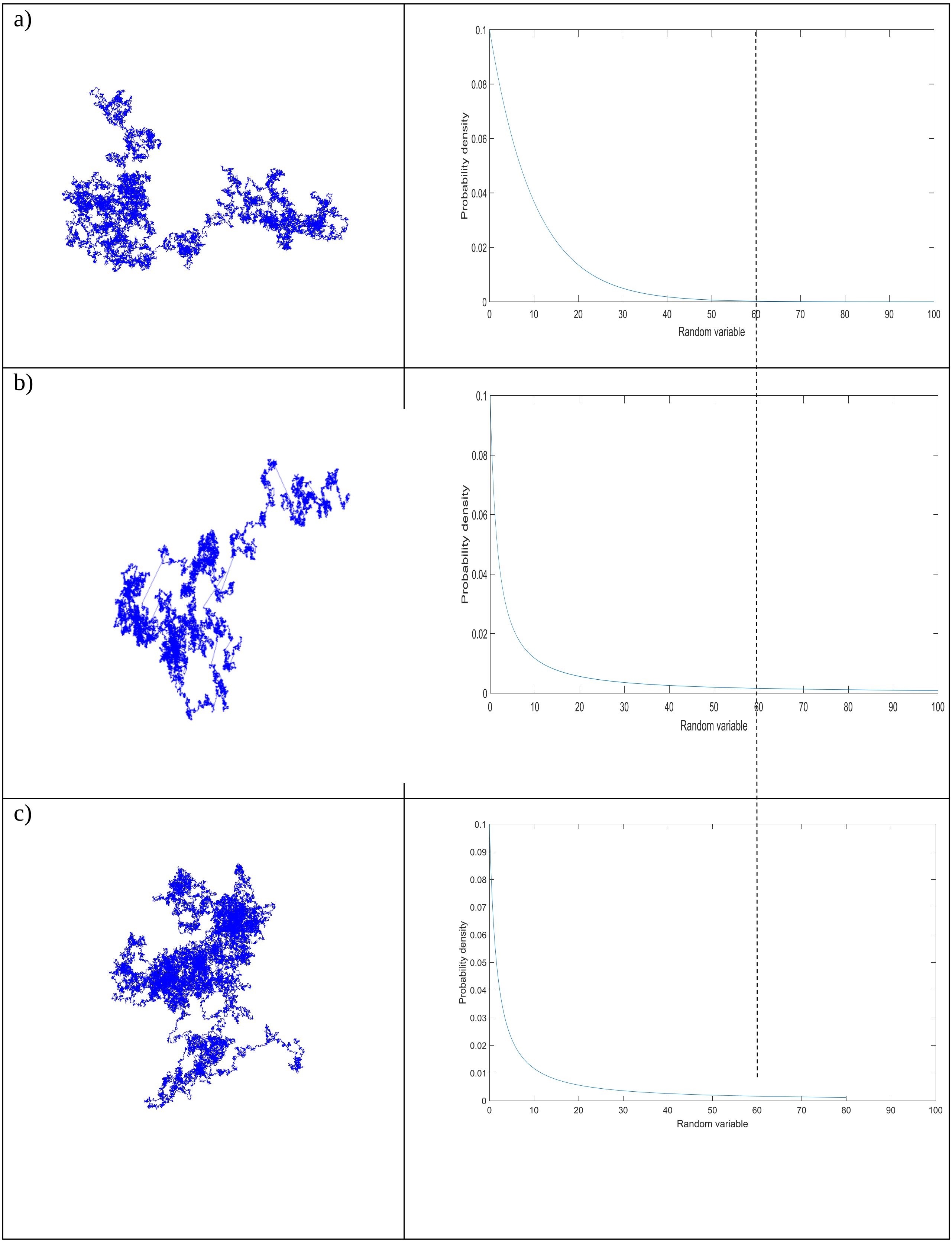


Figure 5.21: Simulated movement paths for different underlying distributions

(a) Exponential distribution (b) Power-law distribution (c) Bounded power-law distribution

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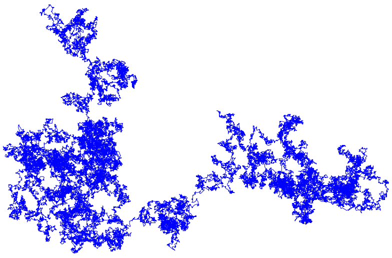
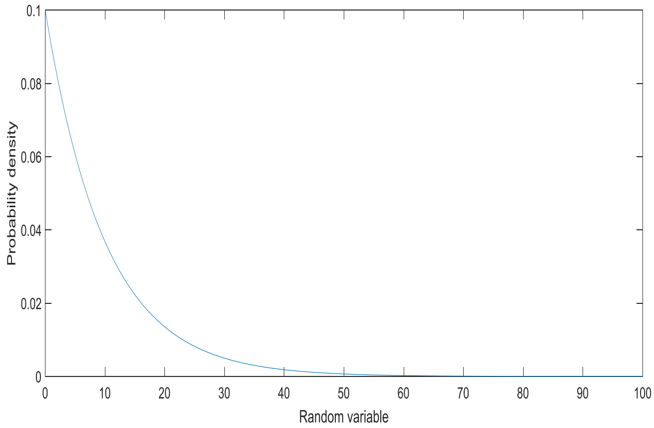
</td><td> </td></tr>
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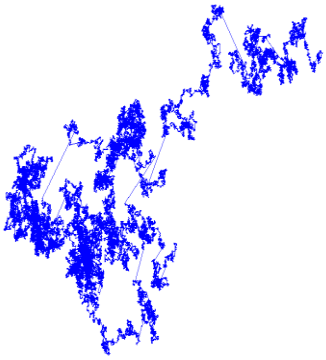
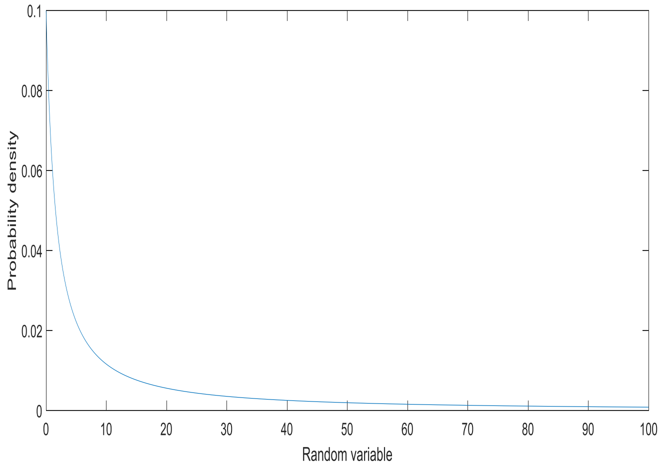
</td><td> </td></tr>
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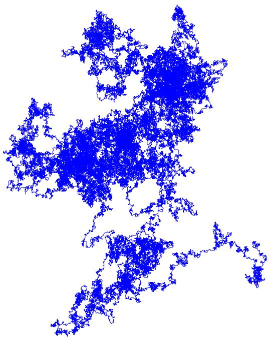
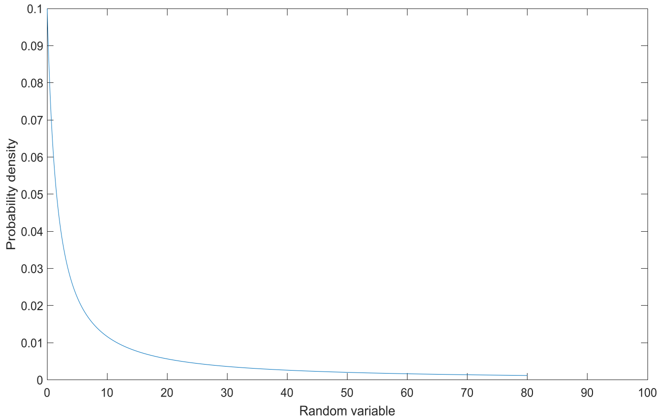
</td><td> </td></tr>
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Figure 5.21 show movement paths simulated from the corresponding adjacent distributions: exponential; power law; and bounded power law. Each movement path comprises for the same number of (n=10000) step lengths.

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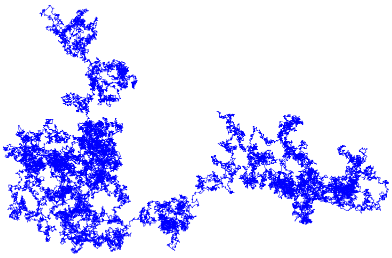
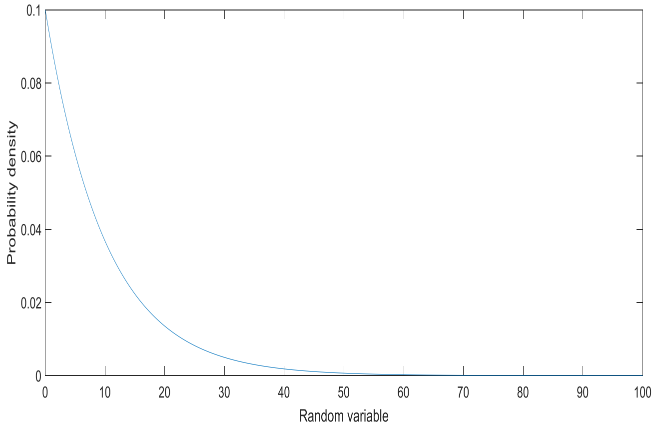
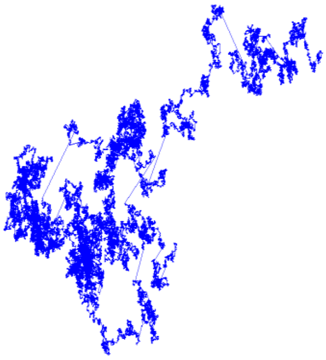
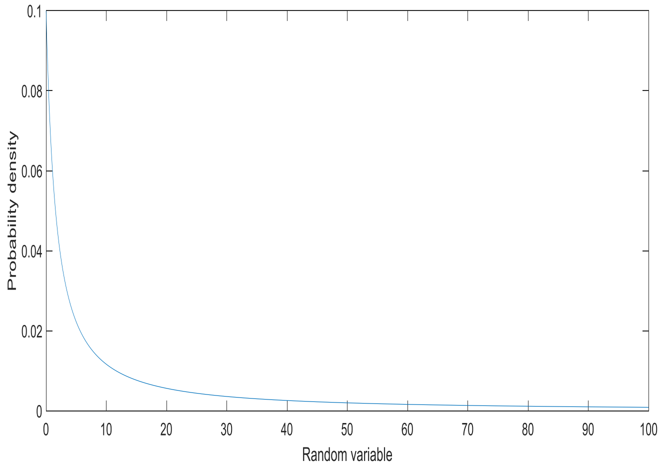
a) 	
b) 	

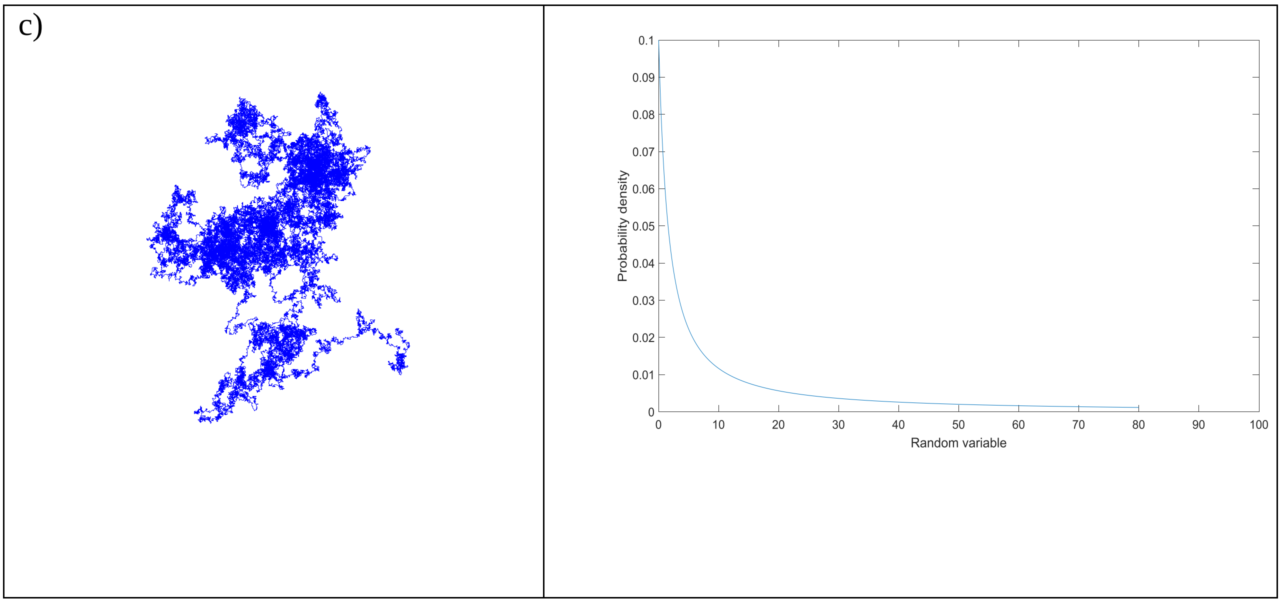


Figure 5.21 shows clearly the fatter/heavier tails of the unbounded or pure power-law and the bounded power-law distributions, as compared with the exponential distribution. Specifically, the vertical line drawn at random variable 60 (x=60) shows explicitly that distributions with heavy tails have more extreme step lengths (values in general) than other distributions. Thus, one would expect that, for movement data, we would observe a higher percentage of longer step lengths. And this is indeed the case in Figure 5.21b.

Error! Reference source not found. shows conceptually how containment measures can be designed and placed more efficiently and effectively through a better understanding the movement pattern of a pest or a disease. For example, if an invasive species is identified through the Bayesian methods developed and explored in this thesis to follow a Lévy flight distribution as in Figure 5.22. It indicates that this movement will produce intermittent long jumps. Therefore, simulations can be carried out to know how long a species or a group may take to reach a certain distance. This will indicate the distance at which the control measures such as a wall or mesh should be placed and equally importantly when building the containment should commence so as to be completed before the pest reaches a particular distance. Given that ungulates, such as deer, may transport vectors that carry pests and diseases (Weinhold, 2010), an improved understanding of the spatial foraging patterns of deer can help our understanding of what approaches might be needed to contain the spread of pests and diseases.

Further, unlike abiotic particles, pests and diseases may lose energy while travelling long distances. Thus, if we identify an unbounded power-law distribution, this also indicates that the disease vector or pest could fade or die out after a certain distance.

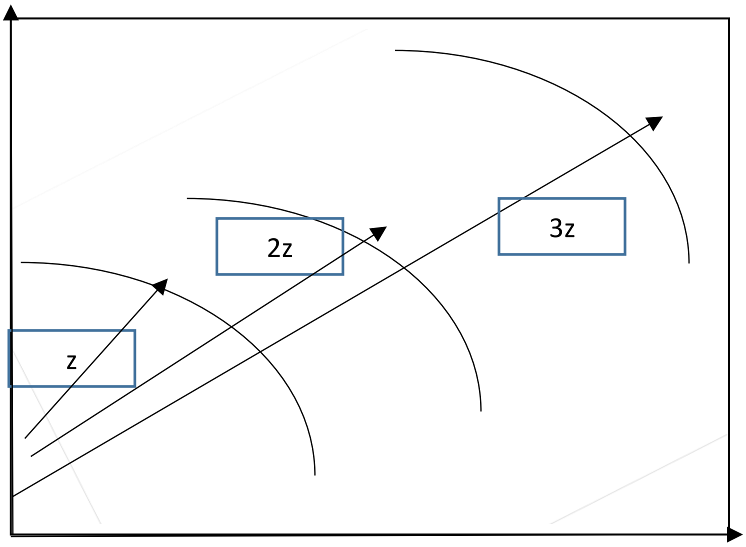


Figure 5.22: optimal containment to prevent spread, assuming a power law distribution

5.5.3 Concluding thoughts

The objectives of this chapter were four-fold. One was to improve the current understanding of the underlying foraging pattern of reindeer by using a more sophisticated method to analyse a previously analysed data set. This data set was particularly chosen also due to the fact that data has been collected in three different time periods with differing food availability. This allows for the identification of the impact of resource availability and seasonal changes on the foraging behaviour of a species. The second more broadly was to use a different foraging data set to determine whether these findings validate earlier findings that the Lévy flight foraging pattern is commonly found in nature. The third was to understand the impact of seasonality and resource availability of foraging patterns. The fourthwas to highlight how a better understanding of animal movement patterns has the potential to lead to better policies for the spatial management of species within a two-dimensional landscape.

Chapter 6 Fishing Boat Movement Patterns / Fisher Foraging

This chapter revisits another human foraging dataset in the form of fishermen foragers. A secondary data set of fisher movements, collected by Marchal et al. (2007) over a two-month period from Dutch fishing vessels, is investigated to determine whether previous findings using the data set are validated or contradicted when Bayesian methods are used. In contrast to !Kung hunter gathers discussed in Chapter 4, the “foragers” in this chapter are concerned with a profit making enterprise, However, both the fishers and !Kung hunter gathers are foraging for food items, albeit the former for income generation and the latter for consumption.

Similar to Chapter 4, the data set used in this chapter was originally analysed by Marchal et al., (2007), and then reanalysed by Edwards (2011). This chapter first discusses the literature on fisher foraging in Section 6.1. Then it provides the background to the dataset used, from the initial data collection by Marchal et al. (2007) to both Marchal et al.’s analysis and Edwards’ reanalyses in Section 6.2. The chapter then, in Section 6.3, provides detail on how the methodological framework employed in this thesis is used to analyse fisher foraging data. Sections 6.4 lays out the findings of the chapter while Section 6.5 discusses the findings. Finally, Section 6.6 discusses some of the implications of the results for policy and management.

Like every natural forager, fishers face the choice problem of choosing and retaining valuable prey. Therefore, in this respect, fishers can be considered as foragers. Specifically, in the case of commercial fishing, fishers as foragers typically optimise their profit by specializing in their preferred prey while ignoring or discarding the less valuable (MacArthur and Pianka 1961).

Fisheries science is mainly driven by management objectives that take into account marine ecosystem services and their conservation, and fishing catch, recognising the spatial allocation of fish, how and where fish move, and fishing effort (Begossi 1992; Dorn 2001; Bertrand et al. 2005; Joo et al. 2013). Exploring and understanding the spatial behaviour of fishermen is crucial in understanding how policy, management and conservation impacts fisheries through, for example, changing fishers' behaviour. Yet the reality is that, certainly in the economics literature, while fish movements have incorporated into spatial models, fisher movements have rarely. Early exceptions include Smith and Wilen (2003) and Bertrand et al. (2005).

More recently, Albers et al. (2018) has modelled fisher movement explicitly, with an optimisation model that recognises both that distance to fishing patches is costly for fishers and fish move freely among these patches. This paper demonstrates that if fishers know where fish stocks are, and the density of those stocks, they allocate their effort spatially trading off longer distances and greater stock densities. Smith and Wilen (2003) explains how the importance of understanding the spatial distribution of fishermen as a more widely distributed fishing industry or "patchy" behaviour of the fishermen would result in an almost uniform distribution of harvesting effort.

Begossi et al. (2005) studied the application of optimal foraging models to fishing communities in Brazil. They applied central place foraging models, taking into account the travel time to the fishing spot (distance cost) and the quantity of fish caught (benefit). Their findings show that movement of fishermen to distant places is related to the fish-market value of target fish. They further explain how decision-making processes underlying fishermen's movements are important to be taken into account for fishery management.

Poos and Rijnsdrop (2007) explored the spatial distribution dynamics of the Dutch fleet due to area closure. Rijnisdorp et al. (2013) investigated the impact of introducing a fishing quota system on fishing behaviour. They computed a fishing ground exploitation threshold called a 'giving up catch rate' and found that the observed giving up rate is less than the predicted rate. This difference was accounted for by the bias in fishermen behaviour driven by the individual quota system introduced. Poos et al. (2009) examined the potential segregation among competing trawlers using optimal foraging theory. They employed an ideal free distribution-like model to analyse Dutch trawlers with different competitive abilities. Their findings show that spatial segregation in fleet with unequal abilities due to external factors such as spatial segregation in prey species and market price difference. They further explain that differences in catch efficiency between vessels for a target species in combination with differences in the spatial distribution of the target species result in spatial segregation among vessel groups

Because traditional monitoring methods are costly, complicated, and difficult to control, lack of precise data in the field of fisheries has curbed the detailed investigation of fisher movement patterns and their implications for fish stocks and fisher livelihoods. However, today, recent technologies such as Vessel Monitoring Systems (VMS) have made it possible to monitor fishing boat locations in almost real-time with high accuracy and resolution. Fine-scale spatio-temporal details on fishing movement allows in depth exploration of fisher behaviour, effort and harvest or catch. As a result, scientists are developing mathematical and spatial models using fins-scale data to investigate the actual underlying behaviours of these human foragers.

6.1 Fisher movement characterisation in the ecology literature

Most of the studies that address fisher/fishing movement in ecology literature are centred around predator-prey relationships and spatial allocation of fishing effort. Studies that characterise predator movement patterns using random walk models to investigate fishermen foraging or movement in general are very limited. Even fewer studies investigate Lévy flight behaviour of fishing vessels. Bertrand et al. (2005) can be considered as the first to use trajectory data from a vessel monitoring system (VMS) to characterise fishing vessel movement. They explored Peruvian fishing boat trajectories using vessel trip data from November 1999 to March 2003. Histograms were computed for move-length frequency distribution of the fishing trips for each vessel and month using Scott (1979) rule. Then, following Viswanathan et al. (1999), least-squares linear regression was fitted through the tail as of the log-log plot of the move-length frequency distribution. The slope of the regression line was considered as the inverse power-law exponent (μ). Their paper concluded that fishermen perform a Lévy flight movement pattern with a μ=2.01 representing an optimal foraging pattern.

Bertrand et al. (2007) employed Peruvian fleet data from December 1999 to March 2003 in a different study but used the same method as Bertrand et al. (2005) to obtain $\mu=2$. As such, their findings suggest that human foraging is not fundamentally different from that of animal predators, which, unlike humans is not affect by human skill nor technology. They show that fishermen follow an optimum search strategy with a Lévy flight parameter of $\mu=2$ and suggest that fishers' spatial behaviour reflects to some extent the spatial movement of fish. Visawanathan et al. (1996) states that an optimal strategy for non-destructive foraging (where foragers can revisit previously visited sites) is to choose $\mu_{opt} = 2$. It is an optimum strategy as it allows the foragers to visit more new sites compared to other patterns such as Brownian. Shlesinger and Klafter (1986) also argues that foragers may perform Lévy flights because the number of new visited sites is much larger for agents that follow Lévy flight movement rather than Brownian.

Bertrand et al. (2008) found less diffusive Brownian-like movement in Peruvian vessels fishing where the fish stock is more aggregated signalling low effort in finding fish as they are abundant. Their data set consists of VMS data from Peruvian fishing vessels from January 1983 to September 2006. This paper did not focus on the Lévy flight existence in fishermen but on the impact of fish distribution on fisher behaviour. They explain that external forces such as large current waves cause aggregation of fish clusters. As a result, fishermen make less effort in finding fish due to the spatial contraction leading to less diffusive trips. Studies carried out later were very much focused on identifying behavioural modes/states from raw data as this information help compute fishing effort.

Bertrand et al., (2015) fitted a generalised and a bounded generalised pareto distribution to seabird and fishing vessel data to explore the foraging patterns using a maximum likelihood criterion. The first data set included four foraging trips by two seabird species, boobies (*Sula variegata*) and guanay cormorants (*Phalacrocorax bougainvilli*) from Isla Pescadores. The second dataset consisted of movements deployed by three industrial anchovy purse seiners, monitored by the Peruvian vessel monitoring system. Their results revealed that all four bird tracks and two of the three fishing vessels exhibits Lévy flight behaviour. They found that all their data sets can be described with a Lévy flight distribution. They further explain that overall, that the bounded generalised pareto distribution is applicable to any move length distribution, regardless of the forager trajectory under consideration. They further discussed the importance of this behaviour in finding new fishing sites and optimal exploitation of fishing grounds.

Marchal et al. (2005) similarly investigated the movement behaviour of fishermen and the key processes underlying their behaviours. They employed a log-log regression and found similar results to Bertrand et al. (2007), that Dutch boats exhibit a Lévy flight movement pattern. Both Bertrand et al. (2007) and Marchal et al. (2007) used distance between two "hauls" to analyse the movement path. A haul is a quantity of fish caught at draft of the net. Therefore, the length is interpreted as the distance covered by a fishing vessel between two fishing operations.

Several other studies explored the spatial distribution of fishermen but did not shed light on their foraging pattern. In fact, no other study apart from Bertrand et al. (2005, 2007, and 2013) and Marchal et al. (2007) investigates the existence of Lévy flight in fisher foraging. The main focus of the other studies that investigate fisher movement revolve around fisher spatial allocation on economic gains or identifying fisher states or modes. For example, Bertrand et al. (2008) and Joo et al. (2011) used other analytical methods which utilised speed, time and turning angles to identify fisher positions. Although they used distance and turning angle data to identify behavioural modes, their focus was on minimising estimation errors using neural networks rather than path characterisation. Employing Artificial Neural Networks, Betrand et al. (2008) discuss the importance of exploring the spatial distribution as it improves our understanding of fishers' behaviour and our ability to forecast the spatial allocation of effort.

They further state that understanding the spatial allocation directly impacts the effectiveness and sustainability of fishery management measures (Babcock et al. 2005). Joo et al. (2011) and Joo et al. (2013) employed two different approaches, artificial neural networks and hidden Markov models respectively, on Peruvian fishermen targeting anchovy to explore their spatial distribution. Joo et al. (2003) suggest that accurate identification of spatial behaviour of fishermen helps identify the effort deployed which is crucial to ensure fishers comply with control management measures such as inshore restrictions and protected areas.

Mendez et al (2009) modelled the individual decision by fishermen to return to the fishing ground of the previous trip for vessels engaged in the Portuguese coastal trawl fishery, using econometric discrete choice models. They found that fleet spatial distribution is heavily dependent on the fishermen’s expectations about catches (and therefore on profits) for the main target species. Although this paper investigated visiting previous sites which could have been represented by a Lévy flight pattern, this was not explored in the paper.

There exist a considerable number of studies in fisheries ecology that employ data from vessel monitoring systems to compute measures needed to explore fisher movement. These studies do not investigate the actual movement patterns. Nonetheless, they shed light on the importance and the use of raw data in analysing movement patterns. Russo et al. (2011) used vessel monitoring data i.e. distance to coast, turning angle and speed of the trawlers to classify movement paths to identify métiers based on fishing trip characteristics. They identified groups of vessels that have the same exploitation pattern métier such as gear used, fishing ground, target species, over time using position data. They state the importance of increasing sampling frequency to avoid the technical problems of low-frequency data in fisheries for an improved analysis of movement paths. A distinct part of the literature addresses behavioural states, as opposed to characterising a movement path from fishing data using classical and Bayesian statistical approaches. For example, the first application of Bayesian methods for fisher spatial distribution can be seen by Vermard et al. (2010).

This study also focused on detecting the behavioural modes of fishers instead of movement path characterisation. Vermard et al. (2010) applied Bayesian hidden Markov process to analyse boat trajectories in the Bay of Biscay using VMS data. Hidden Markov processes is a Markov process modelled assuming hidden or unobserved states. They identified behavioural states such as fishing, steaming and stopping. They inferred the most likely behavioural mode for each movement step from a set of priori defined behavioral modes. Walker and Bez (2010) and Peel and Good (2011) also employed Bayesian Hidden Markov models on fisher positions recorded from French trawlers and Australian trawlers respectively to detect behavioural modes such as stillness, tracking, and cruising from fishing observation data. Although these papers identified behavioural modes, they did not investigate movement paths. However, these papers shed light on the potential analytical techniques that can be used in movement characterisation. Walker and Bez (2010) introduced the Bayesian state-space model for analysing movement from tracking data.

Gloaguen et al. (2014) used a hidden Markov model with two behavioural states, steaming and fishing, to infer the sequence of non- observed fishing vessel behaviour along the vessel trajectory. They find that analysing the trajectories of individual vessels offers promising perspectives to describe the activity during fishing trips. Millischer and Gascuel (2005) employed an individual-based simulator with different random search models to investigate information transfer and vessel behaviour.

The majority of these studies mentioned above focus on detecting behavioural states as opposed to characterising a movement path from fishing data. Using raw data recorded, they discriminate between behavioural modes or states such as fishing, steaming or stopping. The discrimination allows the investigation of fishing impact on fishing on stocks and fisher performance measurements. However, none of these studies shed light on incorporating states identification in to foraging path modelling or identification of fishing path at large. Therefore, there is an evident lack of studies that investigate the movement path of fishers in fisheries literature.

6.2 The original analysis and Edward's re-analysis

Marchal et al. (2007) analysed Dutch fleet data with the objective of (i) characterizing the foraging efficiency of fishing vessels, belonging to different fleets, based on the Lévy flight theory; and (ii) to get better insights into the factors associated with fishers' foraging. They collected haul-by-haul catch and effort data for one Dutch and one French fleet. The analysis was carried out on the assumption that the trajectory of fishing vessels between two consecutive hauls is a straight line. The two fleets and data sets are described below.

The Dutch fleet investigated included large beam-trawlers (>300 HP) which targeted plaice and sole throughout the North Sea. These trawlers usually fish from Sunday night until Friday morning. They fish throughout day and night and need about 15 minutes for emptying the nets and setting the nets back into the water. During the weekend most of the vessels are in the harbour, although a small group of vessels sometimes go out to sea for a 2-weeks trip. Haul-by-haul data containing landing, vessel position and times were extracted from logbooks. Fishing grounds of the Dutch fleet under investigation are situated throughout the North Sea, but outside of the 12-miles zone, where these vessels are not allowed to fish (Figure 6.1). Most of the effort registered in the haul-by-haul data is located in the southern part of the North Sea.

The French fleet included large otter-trawlers (>40 m) registered in Northern France. This fleet was sub-divided into two groups of vessels. The first group of vessels operates mostly in the Northern North Sea and targets saithe, which is a commercially valuable fish. The second group operates off Western Scotland (sub-area VI) and in the Celtic Sea (sub-area VII), and targets deep-water species. Only the haul-by-haul catch and effort data provided by the first group of vessels were collected. These data were collected for most of the fishing trips operated by these vessels (Figure 6.1: Map of the area explored).

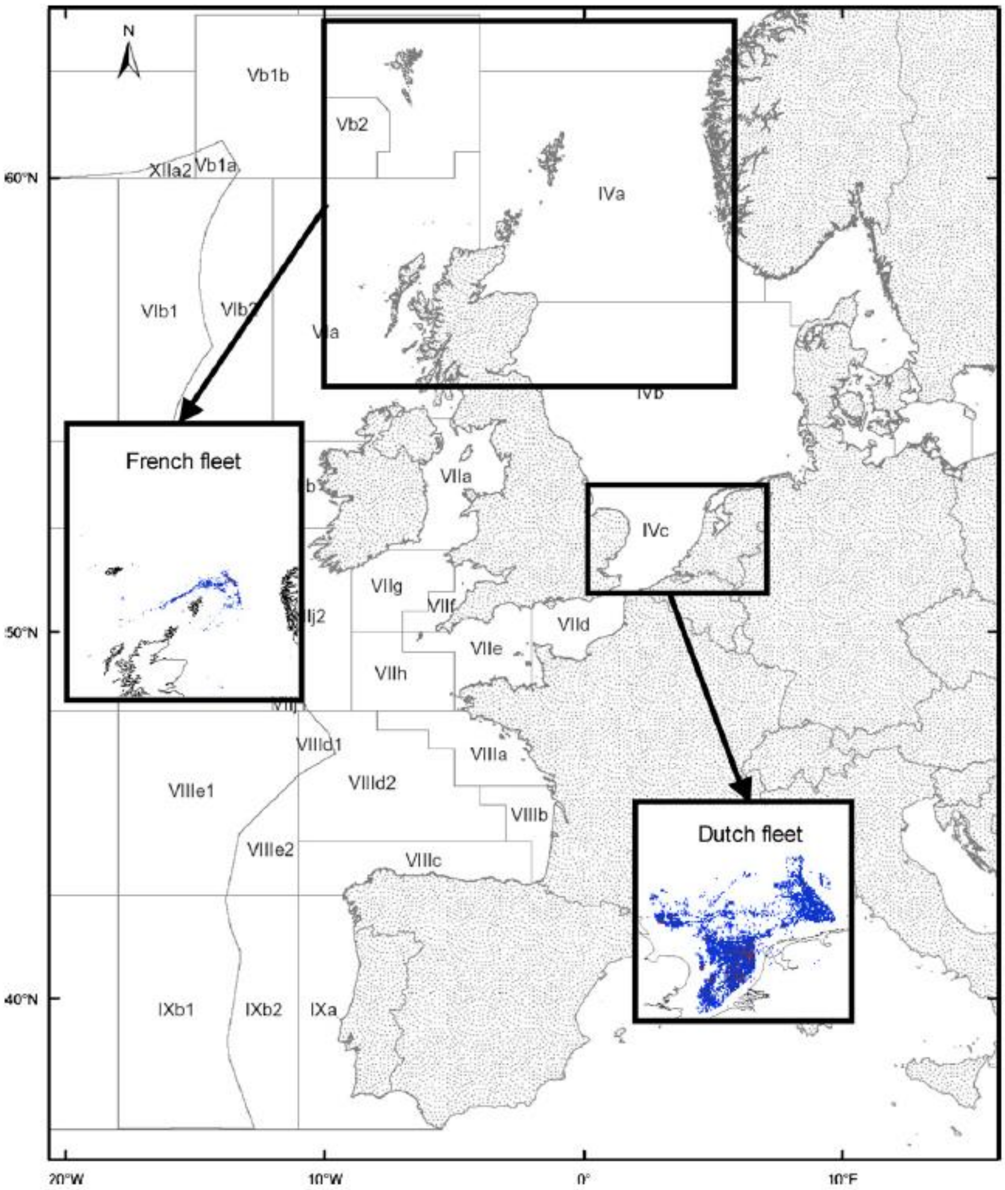


Figure 6.1: Map of the area explored

Source: Marchal et al. (2007)

Table 6.1 gives a description of the data on the Dutch and French beam trawlers originally analysed by Marchal et al. (2007). This thesis reanalyses the Dutch beam-trawler movement patterns.

Table 6.1: Fleet information of Dutch beam trawlers

Fleet	Period Investigated	No. of vessels per month	No. trips per month	No. of hauls per month

Dutch beam-trawlers	January 1995–December 2003	2 (0–4)	6 (0–16)	6 (0–16)
French Otter-trawlers	April 2003-September 2004	3(1-4)	6(3-13)	68(10-185)

Source: Marchal et al. (2007)

A haul can be considered as a quantity of fish, taken by a fishing net at a time. The distance or step length in the analysis was interpreted as the distance covered between two hauls. Marchal et al. (2007) calculated the frequency distribution of these distances between hauls for each fleet and each month. They use a method described by Scott (1979) to group step lengths into discrete classes. Then log-frequency was plotted against log (step length), using the arithmetic mean of the bins. A regression was then fitted through the data points. The parameter μ (Viswanathan 1996) was estimated as minus the slope of the regression (-μ). In this study, μ was found to be in the range 1.0-2.0 for both the French and the Dutch fleets. Marchal et al's. (2007) analysis of foraging efficiency therefore suggested that, for both the Dutch and the French fleets, the foraging strategy may reasonably be represented by a Lévy flight process. Their study therefore confirmed that the foraging behaviour of human beings is comparable to that of other animals.

Edwards (2011) re-analysed Marchal's data. Only two months of data were available from the Dutch fleet while French fleet data was not available at all. The two months available from the Dutch fleet were May 2001 and July 2003. Edwards applied the modern likelihood and Akaike weights approach to test the alternative models, namely, the bounded and unbounded versions of exponential and power-law models (explained in Chapter 3). Edwards (2011) found that the exponential model best supports foraging data for both months. These finding overturned Marchal et al. (2007)'s conclusion of Lévy flight or pure/unbounded power-law existence. Given the differences in results found in the two original papers, it was of interest to employ the Bayesian approach to characterise the movement behaviour to test the previous findings.

6.3 Methodology

This chapter employs the data sets originally used by Marchal et al., (2007) and re-analysed Edwards (2011), similarly using the data from May 2001 and July 2003. This has the advantage of making the findings comparable with both Marchal et al. (2007) and Edwards (2011).

The distance between two hauls is the step length. This is interpreted in Marchal et al. (2007) as the distance between two fishing operations. Turning angles were not provided in the raw data, and so random angles are specified, using MATLAB$^{©}$, to simulate the movement patterns for each month. The sample sizes are n=370 for May 2001 and n=342 for July 2003. In this thesis, to ensure that the data match Edwards, first I computed descriptive statistics, produced histograms and matched with those reported in the original papers.

Marchal et al. (2007) and Edwards (2011) both employed a classical approach to quantify the movement pattern. Applying the Bayesian approach here allows latent behaviours to be captured and as such any inferences are likely to be more accurate. Here I apply both the standard Bayesian estimation approach and the approximate Bayesian computation (ABC) methods on all data sets as explained in Chapter 3. Data sets for both months were analysed using the 22 models specified under both Bayesian approaches (Table 4.2).

6.4 Results

Figure 6.2 a and b recreate the histograms in Edwards (2011), showing standard histograms for Dutch fleet for (a) May 2001 and (b) July 2003. The step lengths for each data set appear to vary within a similar range.

These figures show a large number of zeros, which represent vessel stops. Marchal et al. (2007) does not discuss the inclusion of these zeros in their analysis but Edwards (2011) states that zeros are excluded from his and Marchal’s calculations. Zeros are therefore also excluded from my analysis, which both allows me to overcome programming limitations and to be consistent with the two previous analyses.

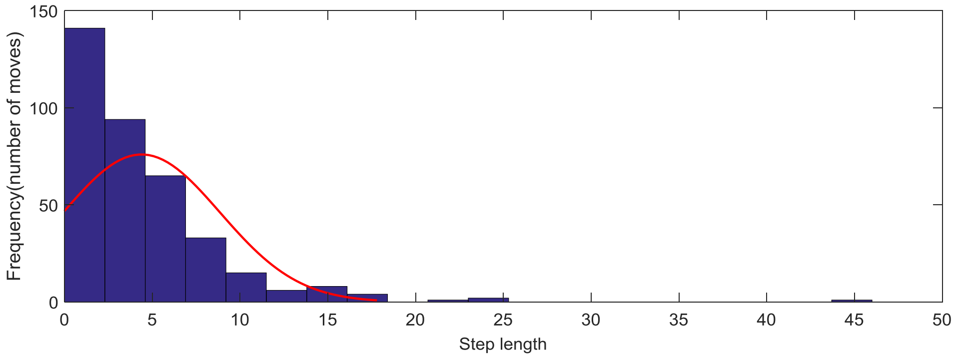


Figure 6.2: Histogram May 2001

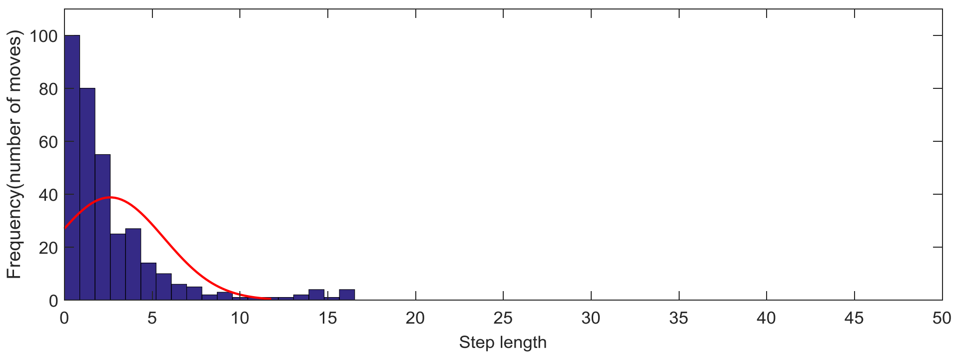


Figure 6.3: Histogram July 2003

Excluding zeros, the minimum and maximum values (step length range) therefore for each period are: May 2001- 0.25-44.46, July 2003 – 0.25-14.44. For each of the data sets, the power-law tails are assumed to start at the minimum value of 0.25. The two histograms in Figures 6.2 and 6.3 do not depict the range of data that satisfies the criteria for a pure power-law distribution (Edwards, 2008). For example, none of the histograms show movement lengths greater than 100m long (power-law distribution is expected to have 1% of the data that is 100 times the minimum value). Thus, these data cannot be expected to produce the heavy tails required for a pure/unbounded power-law distribution.

6.4.1 Results from the Bayesian model selection approaches

This section compares the results from the two Bayesian approaches and identifies the model that best supports the data for each period. In the probability graphs below, the most dominant model, the "best" model is defined as that with the highest probability compared to all other models analysed. The probabilities are computed using the marginal likelihood value as explained in Chapter 4.

For May 2001, the SBEA approach indicates that model 14 supports the data best (60% probability) (Figure 6.4). The dominant model 14 is a bounded exponential model. However, other bounded exponential models around model 14 also show likelihood of supporting the data to some extent.

The results from the ABC approach confirms the findings from the SBEA approach as it shows a clear dominance by model 14 with a probability of 72% (Figure 6.5). Model 14 is a bounded exponential model with unfixed bounds.

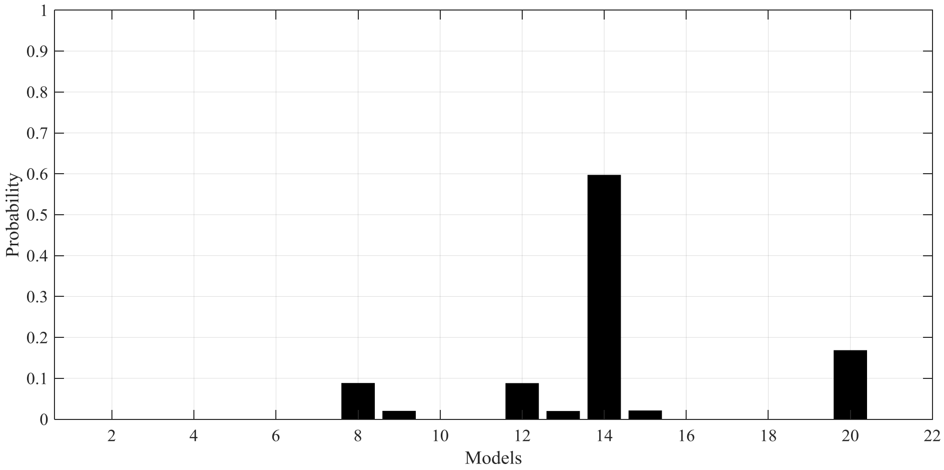


Figure 6.4: Implied probabilities across models for May 2001 (SBEA)

The SBEA approach shows that the bounded exponential block showed a relatively greater affinity of supporting the data compare to the power-law block. The dominant model and the second dominant model that supported data from the ABC approach also belonged to the exponential block.

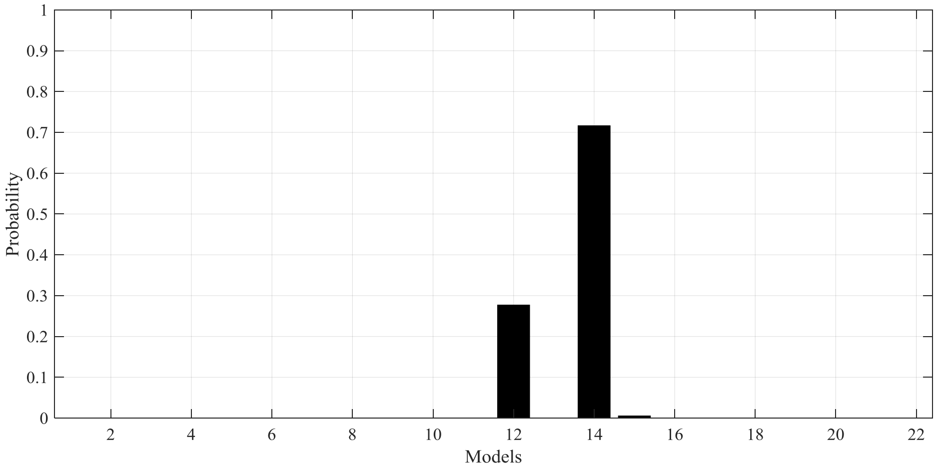


Figure 6.5: Implied probabilities across models for May 2001 (ABC)

Analysis of July 2003 data using the SBEA approach identifies several models that could support the data. Model 18 has the highest probability of 52%. This is a bounded power-law model (Figure 6.6). However, results show that though not dominant the exponential block also shows an affinity to support the dataset. Therefore, it is not possible to conclude that one model best supports the data as there are other model that show support to some extent. However, it could be said that the bounded power-law models show the highest affinity of being the best underlying models, using the SBEA approach. The minimum bound of this model was 0.25 while the maximum bound was 16.64.

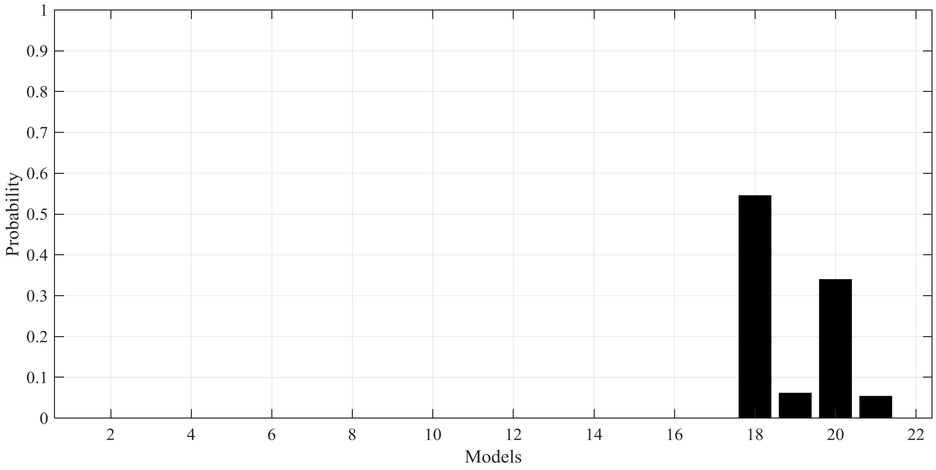


Figure 6.6: Implied probabilities across models for July 2003 (SBEA)

The ABC approach results one model, model 18 which is a bounded power-law model as the dominant model with a probability of 1 (Figure 6.6). Therefore, it could be said that bounded power-law model supports the foraging movement data of the vessels in July 2003.

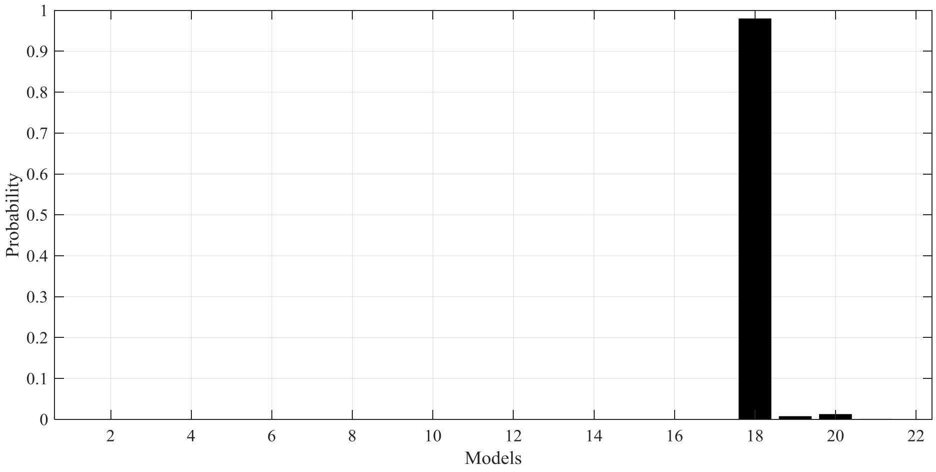


Figure 6.7: Implied probabilities across models for July 2003 (ABC)

It was then of interest to see how the power-law exponent parameter μ for those models that supported the data best. As per Viswanathan (1996), a power-law exponent (μ) between 1 and 3 reflects a Lévy flight foraging strategy. Figures 6.8, 6.9 and Table 6.2 show the behaviour of the power-law parameter μ which fluctuates with a mean of 1.62 and a standard deviation of 0.09.

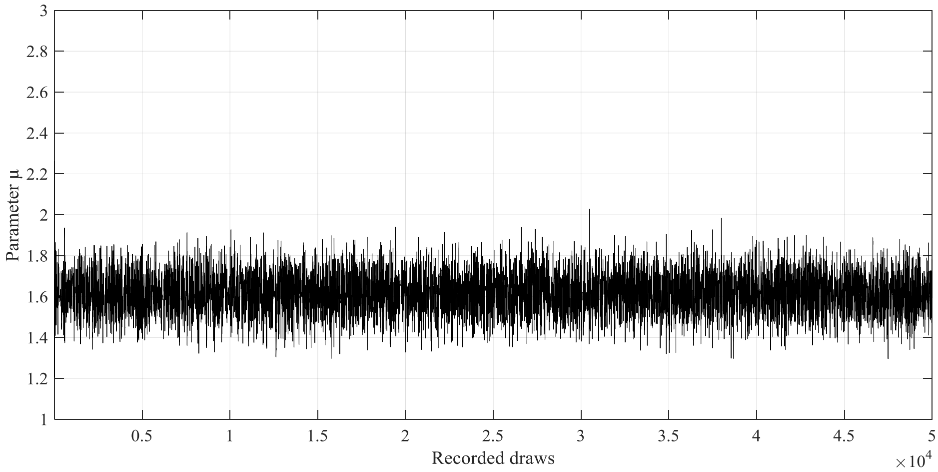


Figure 6.8: Trace plots of exponent (μ) distribution of the bounded power-law model for July2003(SBEA)

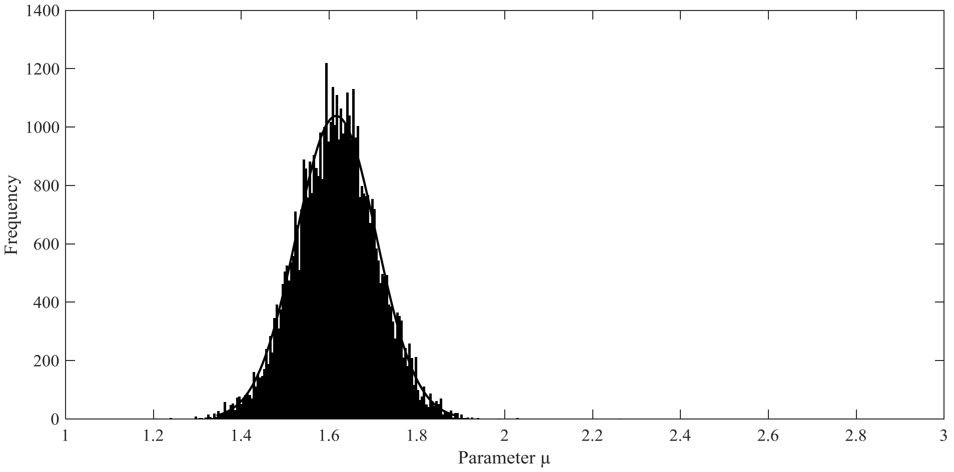


Figure 6.9: Distribution of the exponent parameter (μ)

Table 6.2: Measures of central tendency and spread of the parameter μ

Mean	1.62
Median	1.62
SD	0.09
Interquartile range	
Q1	1.55
Q2	1.62
Q3	1.68
Q4	
IQR	0.12

The dominant model for ABC approach is a power-law model with both minimum and maximum bounds estimated. The parameter (μ) fluctuates with a mean of 1.5 and a standard deviation of 0.39 (Figures 6.10, 6.11 and Table 6.3).

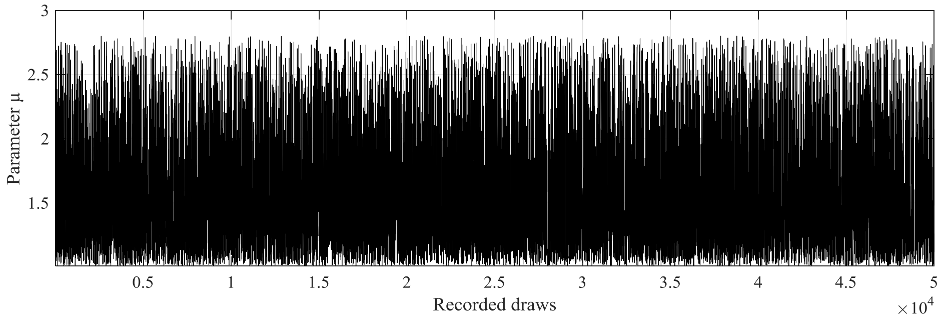


Figure 6.10:Trace plots of exponent (μ) distribution of the bounded power-law model for July2003 (ABC)

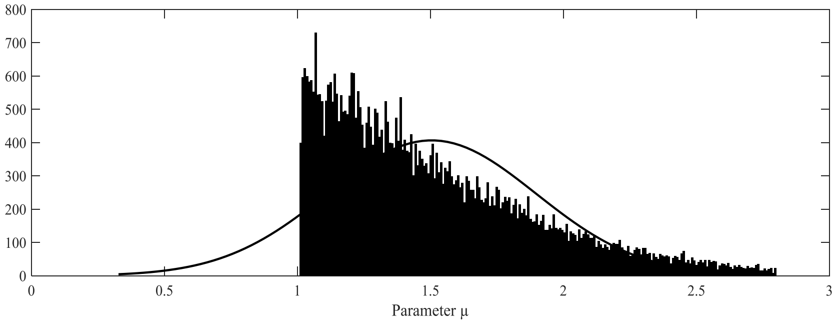


Figure 6.11: Distribution of the exponent parameter (μ)

Table 6.3: Measures of central tendency and spread of the parameter μ

Mean	1.50
Median	1.41
SD	0.39
Interquartile range	
Q1	1.19
Q2	1.41
Q3	1.74
Q4	
IQR	0.54

The fact that the parameter μ varies with a mean of 1.5 shows that the exponent lies well within the bounds of a Lévy flight although it cannot be considered optimum.

6.5 Discussion of re-analysis findings in the context of fishing behaviour

Histograms in Figure 6.2 suggest that from mere observation, a pure or unbounded power-law distribution would be unlikely, which contradicts the findings by Marchal et al. (2007). The two Bayesian methods similarly suggest that none of the data sets exhibits an unbounded power-law distribution, but rather the data follow a bounded power-law distribution.

Table 6.4 below compares the results from my analysis with that of the previous studies. For May 2001, Marchal et al. (2007) found an unbounded power-law to be dominant while Edwards (2011) found an unbounded exponential model to be dominant. The two Bayesian approaches employed in this chapter suggested that two very different models dominate the characterisation of the movement patterns, and both are in bounded form. The emphasis on ‘bound’ could also signal an area restricted search pattern by the fishers. However, as model 22 from the ABC approach shows a very high likelihood of supporting the movement data for period May 2001, it could be said that these vessels follow a bounded Lévy flight pattern during this period.

Table 6.4: Conclusions from each study

	Original conclusion From Marchal et al., (2007)	Edwards' Conclusion From Edwards (2011)	Conclusion from the Bayesian analysis
May2001	Lévy flight μ = 1.6 Unbounded power-law	Exponential	SBEA- Bounded Exponential ABC -Bounded Power-law
July2003	Lévy flight μ= 1.65 Unbounded power-law	Exponential	Bounded Power-law

For July 2003 data, again the findings in this thesis do not conform to previous findings. Marchal et al. (2007) found an unbounded power-law to be dominant while Edwards (2011) found an unbounded exponential model to be dominant.

The exponent parameter μ of the bounded power-law models for both time periods May 2001 and July 2003 show values between a 1and 3 confirming a bounded Lévy flight movement pattern. For May 2001, this value is exactly 1.9 which is very close to 2. Viswanathan et al.(1996) states that a μ=2 represents an optimum and efficient Lévy search pattern. For July 2003, both approaches show μ values between 1 and 3.

According to Viswanathan et al. (1996), μ=2 represents an efficient foraging strategy if food/prey is sparsely distributed. Marchal et al. (2007) states that the fish stocks in the North sea where the Dutch boats were fishing are over exploited beyond biological-safe limits. Therefore, these fish stocks do not show quick recovery time. As a result, this signals a 'destructive' foraging behaviour by fishers where they do not visit the previously visited sites (Viswanathan et al. 1996). This statement strengthens the argument that fishers indeed try to adopt the optimum foraging strategy where prey is not predictable.

6.6 Implications and Applications

In this section first I discuss the implications of a better understanding of movement patterns for fisheries management, drawing on the existing literature. Then, as per the earlier chapters, I reanalyse the data restricting myself only to the models used by Edwards.

6.6.1 Implications for fisheries management

Commercial fishery is mainly driven on revenue maximisation. Also, conservation is of core importance in fisheries. Therefore, exploring and identifying the actual behaviour can be beneficial to fishers and policy makers equally. For example, conventional policy making is known to rely on homogenous implementation whereas the most efficient way forward would be customised or heterogeneous implementations. Foraging behaviour of fishers as well as fish and other related species may vary with different seasons and in different conditions. Thus, it is important to understand how these variations occur in order to suggest the ideal policy and management implications.

Vessel movement can have serious direct and indirect impacts on the marine ecosystem. For example, vessels scrape and disturb substrates and benthos affecting fish mortality in the long run, in part by changing the spatial availability of food. Many studies have used the spatial and temporal behaviour of fishers in order to investigate their impact on the marine ecosystem. Understanding actual fisher movement patterns allows policy makers to predict where and when fishers will move next and how much of an area vessels cover. This information can allow policy makers and marine scientists to know what types of measure should be out in place for conservation. For example, the movement patterns identified can be incorporated to bio-economic models that can predict how much recovery time should be allowed for sediments and other species before fishing is allowed in those areas. The data can also be used to determine the implications of spatial zoning.

A considerable amount of work on spatial behaviour and movement of fishers has been focused on fishing effort and economic implications. Most of these studies do not identify the pattern of movement of the fishers. If the pattern is known, a simulation of the movement path can give information on the time a trawler passes a specific area, the intensity of fishing, areas not fished/untapped etc. This information can inform economists to design heterogeneous policies for specific fishing areas that will have a positive impact on fisher livelihoods and fish populations. For example, controlling the areas and intensity of fishing can allow adequate time for regeneration of fish. This in turn will be benefit the ecosystem as well as fishermen in the long run leading to sustainable fishing. Use of simulation-based techniques allow design of management and policy frameworks with less data requirement which is important in fisheries research as data are mostly hard to come by.

Marchal et al. (2007) used movement patterns in a bio-economic model to estimate fishing effort. Therefore, identifying the movement pattern can be used to measure the fishing efficiency and provide reliable indices to assess fisher performance in the sea. Dinmore et al. (2003) and Hiddink et al. (2006) construct models to predict the impact of area closure on species rich in benthic communities. They do not explicitly consider the underlying movement pattern of the vessels although spatial distribution is considered. These models could be extended to include the movement path to obtain improved results on prediction.

Another popular conservation method is the allocation of marine protected areas (MPAs). Information on the spatial distribution of fishermen can help to improve design and allocation of the protected areas. For example, simulation-based techniques on movement or foraging behaviour can identify the fishing effort and area covered within a particular time. This information can improve spatial planning to design optimal MPAs. Finally, properly designed policies allow appropriate management practices and regulation put in place to regulate catch and effort through specification of vessel quotas, fishery managed areas, total allowable catch and protected areas.

6.6.2 Restricting analysis of Edwards (2011) to his four models

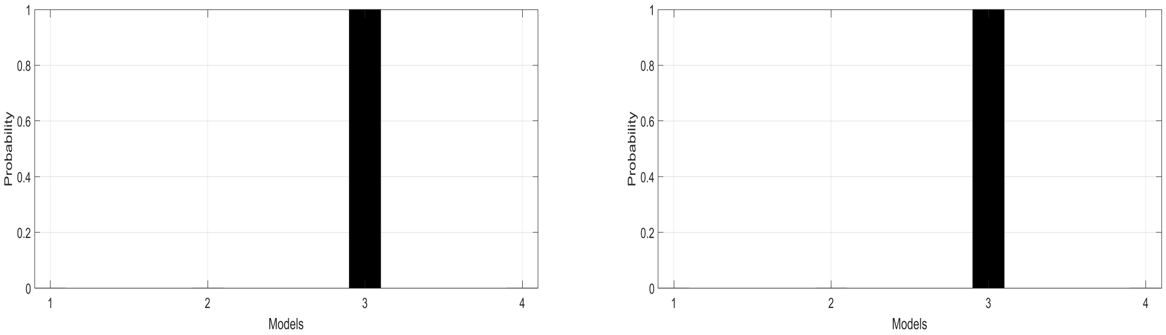
In order to compare the four models analysed by Edwards (2011) using the Bayesian approach as shown in Figure 6.12, I have selected two unbounded and bounded versions of the exponential and power-law models to represent Edwards (2011) models as follows;

- Model 1: Unbounded Exponential

- Model 2: Unbounded Power-law
- Model 3: Bounded Exponential
- Model 4: Bounded Power-law

SBEA ABC

May 2001



July 2003

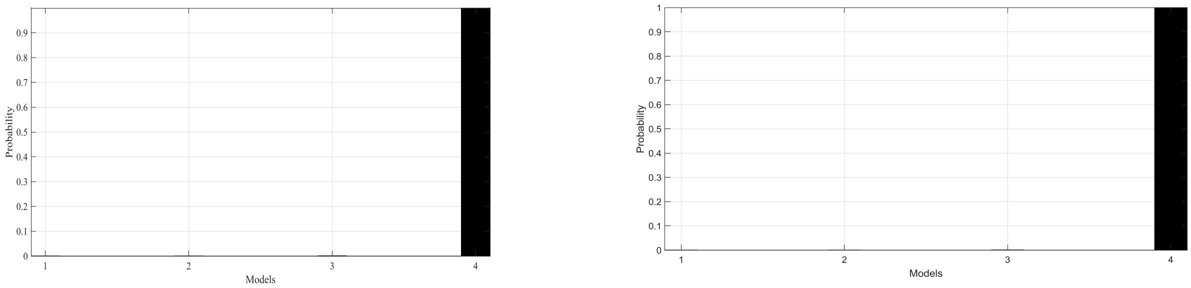


Figure 6.12: Model comparison of Edwards (2011) models using SBEA and ABC approaches

Edwards concluded an unbounded exponential distribution for both time periods for the Dutch fishing boats. The results (Figure 6.12) show that when the four models were analysed using the two Bayesian approaches, results vary to some extent. Data from May 2001 fishing boats results are consistent with Edwards' findings from both Bayesian approaches as the unbounded exponential distribution seem to support the data best.

Results for July 2003 fishing boat data contrast Edwards' findings. The SBEA approach suggests that the bounded exponential models best supports data while the ABC approach suggest that the bounded power-law model best supports data. Somewhat similar results were obtained when all 22 models were analysed. For May 2001 data, variants of the bounded exponential model dominated. This shows that having different bounds can detect the most likely underlying distribution pattern. For July 2003 data the same bounded power-law model was dominant when all 22 models were analysed.

Also the fact that the ABC approach results in a completely different bounded variant may be due to the strength that ABC methodology provides. The bounded models specified, under the ABC methods compared to the standard method bypasses the specification of the complex likelihood function thus providing greater precision and strength.

6.6.2 Concluding thought

This chapter demonstrated how the Bayesian framework can be used to analyse the fishermen foraging data. The results can be used to design more sustainable and cost-effective policy and management applications in fisheries. Appendix 6 shows a simulation of movement paths from distributions and possible implications for fisheries management.

Chapter 7 Conclusions

The overall aim of this thesis is to explore the application of two Bayesian techniques, the standard Bayesian estimation approach and approximate Bayesian computation using model selection to movement data, to suggest a better analytical framework. The study concludes that a modified version of approximate Bayesian computation is likely to provide stronger support to movement data analysis than the frequentist approaches that are more commonly used.

To my best knowledge, Bayesian model selection has not been applied to any of the data sets employed in this thesis. There is often a lack of accurate data to develop informed hypotheses in biological and ecological studies such as movement modelling due to the high uncertainty of latent behaviours. Therefore, researchers must rely on certain assumptions in analysing these data to choose the best supported hypothesis.

At the outset, to achieve its aim, this thesis aimed to undertake five broad objectives. The first objective was to develop appropriate Bayesian approaches to more accurately characterise the movement patterns of animal and human foraging. The second objective was to use these methodological advances to test the hypothesis of Lévy flight existence based on Edwards (2011). The third objective was to compare and contrast the conclusions obtained through the Bayesian methodological framework with that of previous studies. Objective four was to explore the robustness of the Bayesian approaches used in this thesis, focusing particularly on the number of models tested and the size of the dataset. The fifth objective was to provide examples of how Bayesian methods can be applied to important policy suggestions.

Through achieving these objectives, three specific research questions were answered. The first is to what extent the use of Bayesian methods can deliver improved understanding of foraging patterns, over the more commonly used frequentist methods. The second research question concerns whether the Bayesian methods used in this thesis confirm or overturn conclusions in the literature concerning animal movement and in particular Lévy flight, and the implications. The third research question addresses how the findings be effectively applied to practical aspects of natural resource management, whether the defragmentation of habitats through the application of corridors, or the cost-effective containment of invasive species.

In this concluding chapter, I consider how addressing these research questions has progressed understanding of animal and human forager movement patterns, and thus the management of habitats, whether those are the habitats of foragers, predators, or prey. I also highlight the additional questions that have come to light through my development and application of Bayesian methods, and the extent to which Bayesian methods might, or might not, be considered “better” than more commonly used frequentist methods. I do this by exploring the key contributions of the thesis in the following section. I then touch briefly on the limitations of the study, and possible next steps for research into animal and forager movement patterns, based on my findings.

7.1 Principal contributions of the thesis

7.1.1 Methodological advances

The major contribution of this study is the provision of a more robust analytical technique for analysing the movement of foragers, whether human or animal. The approximate Bayesian computation in particular overcomes many of the challenges in animate movement modelling to date. I used a modified and improved version of the original ABC rejection algorithm as explained in Chapter 3. I computed the posterior predictive distributions accordingly to compare with the standard Bayesian approach as the ABC does not allow the computation of the marginal likelihood in the absence of likelihood function. Also, the candidate set of models were selected to include plausible distributions that could underlay the movement pattern of foragers. The ABC method was tailored to increase the accuracy by using the sorting convention to sort the generated data. The modified ABC algorithm using the sorting convention provides a better computation compared to the conventional ABC techniques making it applicable to other movement data sets. When the generated data are sorted it matches the observed data better giving rise to more accurate predictions.

In addition to developing a rigorous Bayesian analysis technique for modelling forager movement, this thesis further contributes to a more general discussion of whether

Bayesian approaches have additional advantages over non-Bayesian approaches. One important element that was explored, for example, was the advantages Bayesian approaches might have when datasets are particularly small.

The thesis first set out to determine whether Bayesian methods could indeed improve understanding of foraging patterns. To do this, and thus achieve the first and second objectives, required the adaptation and application of a Bayesian model selection framework. More specifically two approaches, the standard Bayesian estimation approach and the Approximate Bayesian computation framework, were applied to three different foraging data sets that had been analysed previously by at least two different sets of authors, using frequentist methods. The model selection framework was used to select the most likely construct or the best model that supports data from a range of plausible candidate models. Unlike previous studies which analysed the same data sets used in this thesis using four plausible models, in this thesis a total of 22 models was selected for the analysis. The models selected in this thesis were variants of the most probable models. For example, the power-law model was specified with bounds or truncations with only a minimum, only a maximum, both minimum and maximum bounds and with a bound range. Thus the analysis in this thesis could also address whether the truncation of the model has any impact on the data and if so to what extent.

Another advantage of the two advanced Bayesian techniques adapted and applied in this thesis is that they assign probabilities to each of the tested models, which allows the analyst to understand to what extent a specific model supports the data. Animal movement in general, and foraging in particular, naturally encompass a certain level of uncertainty. For example, no two animals or individuals may move or forage the same way. Thus, characterising a movement pattern for an individual or a species requires a method that captures this variability and uncertainty. The model averaging techniques applied in the two Bayesian approaches allows this uncertainty to be captured. The set of models are weighted on their marginal likelihoods computed using the prior distributions and likelihood functions. This weighting reflects the degree or the extent to which a specific model is trusted to be the best model. The predictions from each model are then derived as the weighted averages of the predictions form each model from the set of models.

Bayesian methods are equipped with advanced techniques to capture uncertainty. One such technique is the Markov chain Monte Carlo (MCMC) method, as applied in this thesis, which can be used to iteratively derive a large number of samples from the posterior that uses a range of prior information through prior distributions. Thus, in contrast to methods used previously by researchers to analyse the same data sets, these procedures such as MCMC are well developed to incorporate the natural uncertainty in inference and making predictions.

In this thesis I employ both conjugate and non-conjugate models with informed priors to obtain the posterior distributions that were used to make the inference and predictions. The approximate Bayesian techniques employed in the thesis bypass the specification of the likelihood function which provides the benefit of calculating intractable likelihood functions. These methods therefore can increase the level of accuracy of the framework. Some of the models in the set of models are complex and the likelihood function cannot be easily specified. Therefore, by re-analysing the data sets using the ABC methods, it provides more precision to the analysis resulting in more accurate inference compared to the standard Bayesian estimation approach. In the thesis I further demonstrate that specifying bounds to both exponential and power-law models improves the rigour of the findings.

7.1.2 Insights into the robustness of Bayesian approaches

In this thesis I explored to what extent Bayesian methods stand up to dealing with small datasets and variations in the number of models tested. A common feature of each of the datasets that I analysed is that each has relatively few observations. This is common in many of the empirical papers addressing movement data, where data are hard and costly to come by. Van de Schoot (2015) showed how Bayesian techniques with informed priors outperforms maximum likelihood approach in the presence of small samples. That paper motivated me to see how Bayesian methods might work if the already small !Kung data set were truncated yet further (Chapter 4). To do this I repeated the Bayesian model selection cutting out increasing numbers of points in the already small data set. In total I tested subsets of the full !Kung data set comprising 30, 20, 10, and 5 points. The outcomes were somewhat surprising, with the same models being identified as most likely to represent the data even for just five data points. At this stage, further investigation would be needed to determine whether this is a consequence of the data, the method, or the limited ability of the methodologies to deal with very small datasets.

Many researchers have relied on classical or frequentist model selection methods to select from a set of candidate models mainly due to their comparative simplicity and computational ease. However, in the case of human and animal movement, it may not be adequate as frequentist or classical model averaging is not yet developed enough to be applied to overcome the stochasticity in ecological problems (Ellison, 2004). In contrast, Bayesian model selection is an established method to choose from a competing set of models. By taking a Bayesian model selection approach in this thesis, I can overcome statistical limitations by incorporating the existing data, even where datasets are relatively small, and irrespective of the prior knowledge available in order to arrive at the best supported hypothesis. Thus the standard Bayesian estimation approach and the approximate Bayesian computation used in this thesis overcome the limitations in other approaches and analyses using both a likelihood based and a likelihood-free approach.

Motivated again by Sims et al (2007) and Van de Schoot (2015), I also tested how the exponent parameter μ varies with the sample size. My findings corroborated these earlier findings, showing that the model probabilities and the μ's are affected by the sample size. Specifically the parameter μ was observed to drop with the decrease in the sample size. Overall it is difficult to come to any strong conclusion on the changing model probabilities or model support based on this additional analysis undertaken on various subsets of the !Kung data set. However, my research certainly raises questions as to the robustness of findings with respect to the size of the dataset.

Just as the number of observations in a dataset may matter, so too may the choice of how many models to test. In the original analyses of the datasets, the authors used a regression-based method. Edwards (2011) used maximum likelihood estimation to compare four models. When the Bayesian analysis in this thesis was restricted to choosing between just the four models analysed by Edwards, the results for certain data sets were consistent with those from the MLE method. For example, when only the original four models were analysed for the three time periods of the reindeer foraging data, using Bayesian approaches, the results showed the same models to be dominant. In other words, the same models were selected as most likely to represent the foraging data as those from the MLE method used by Edwards. When the same data set was analysed in this thesis using the 22 models with various different bounds or truncations, the same dominant distributions were identified, but with different bounds. This finding suggests that the Bayesian methods adapted in this thesis can improve the analysis of forager movement patterns by incorporating different variants of the models within a model comparison exercise.

7.1.2 Better insights into the existence of Lévy flight in ecology

One of the objectives of this thesis was to test the Lévy flight existence in ecology based on Edwards (2011) and validate the previous conclusions made on animal foraging patterns. The Lévy flight hypothesis is tested by employing both the standard Bayesian estimation approach and the Approximate Bayesian Computation to analyse three different foraging data sets; !Kung hunter-gathers, reindeer (*Rangifer tarandus tarandus* L.) and fishermen (Dutch-beam trawler).

The two previous studies that analysed !Kung foraging data by Brown et al., (2006) and Edwards (2011) concluded an unbounded or a pure Lévy flight foraging pattern and a bounded exponential foraging pattern respectively. Edwards (2011) also states that the bounded power-law model cannot be ruled out. My findings suggest that a bounded power-law model best supports data while the bounded exponential model cannot be ruled out. Thus, it could be said that the human hunter gatherers follow a bounded Lévy flight pattern. These human hunter gatherers search and hunt in a restricted area and return to the origin after a specified time period. Due to the memory cues and experience one of the key assumptions of Lévy flight foraging does not as they are not completely clueless of the environment. Therefore, the foraging pattern can be better represented by a bounded power-law pattern within a restricted area. These findings are also comparable with findings by Raichlen et al., (2013) who found a truncated power-law distribution pattern among hunting men in Hazda hunter gathers.

Lévy search patterns are considered optimal in previous publications which modelled animate foraging patterns (Viswanathan et al., 1996, 1999) as they are the best search patterns when the resources are not completely exploited and re-visit able. In the case of !Kung, according to Yellen (1977), the hunter gatherers do revisit their camps during the season at least for very short periods on the way to another camp. Therefore, this could also be a reason resulting in a bounded Lévy distribution.

The second data set employed was of reindeer foraging resulted in conclusions that conformed to the results found by Edwards (2011). It could be concluded that the reindeer followed a bounded power-law pattern during late spring and summer and switched to an exponential pattern during late summer. This data set allowed the exploration of the impact of food availability on the foraging pattern of animals as the data belonged to three different seasons. Another important finding was the change in the Lévy flight parameter μ with the availability of the food or resource over time. The μ was seen to increase close to $\mu=2$ when the food availability was greater in the summer season. It also suggest that the foraging behaviour switches from a supper diffusive behaviour to a diffusive behaviour over time with the availability of the target distribution. Mårell et al. (2002) states that the during late summer, the foraging was concentrated to patches and spent walking. This may be a reason for not observing longer jumps giving rise to power-law models during late summer as they also require to save energy for the forthcoming winter period.

The third set of data analysed was from Dutch fishing boat (fishermen). This dataset was important as it allowed the comparison of two human foraging patterns with different optimisation objectives. In contrast to the !Kung hunter-gatherers, the fishermen are revenue driven and efficient foraging is key for profit maximisation. However, Lévy flight foraging assumptions could be violated to greater extent than the hunter gatherer in this context as fishermen may be equipped with the knowledge and experience of fish locations. The first assumption in Lévy flight analysis is that the prey is randomly distributed. In this case, it is difficult to assume that the fish stocks are randomly distributed as schools of fish are clustered in the sea. The second assumption is that foragers may move randomly move from one target site to another when they cannot detect prey in their neighbourhood. This assumption is also violated because the experience and memory of fishermen allows them to travel directly towards known fishing grounds. Hence, the foraging pattern of the fisher may be better represented by a bounded or truncated Lévy flight distribution as fisher foraging is restricted to a particular area in the sea. Edwards (2011) found and exponential foraging pattern for the Dutch fishing boat movement where as my results suggest that their foraging can be better represented by a bounded exponential pattern for the data from the month of May and a bounded power-law distribution for the data for the month of July. The original studies do not mention any changes or differences in fish stock or other environmental factors that may cause this difference. However my findings are also supported by Bertrand et al., (2015) who states that vessel movement can be better represented by bounded Lévy flight pattern.

In the case of reindeer movement, the Lévy flight assumptions hold as the foragers can be assumed to have no information of the targets compared to the human foragers. Thus, comparing different datasets also allowed to test the scale invariant nature of the Lévy flight distribution pattern.

It was also of interest to establish any differences between the foraging behaviour of human foragers and other species. Results suggest that considering the three data sets, human foraging in the form of hunter gathers and fishermen and reindeer foraging, irrespective of other controlling factors such as memory use or target/food distribution, forages follow a truncated Lévy flight or truncated power-law pattern in most occasions unless limited by external factors.

My findings are comparable to the findings of other animal foraging pattern investigations by Humphries et al. (2010). They analysed the foraging patterns of fourteen species of open-ocean predatory fish such as sharks and big-eye tuna and concluded that animal foraging can be better represented by bounded Lévy distributions as opposed to an unbounded Lévy pattern.

7.1.3 Novel insights into improved habitat landscape management

Understanding patterns of species movement and dispersal has important implications for improved management of a broad spectrum of resources. Though this thesis very much focuses on methodological advances, I gained a number of insights into the management of managed landscapes and how Bayesian approaches may help provide greater cost-effectiveness. Two specific situations that I addressed were the de-fragmentation of habitats through the use of corridors, and trade-offs when attempting to contain an invasive species.

In highly fragmented landscapes, resource managers often must make difficult and costly decisions over where to locate habitat corridors, and how wide to make those corridors. Corridors are costly typically because people have to be moved off the land designated for a habitat corridor. Their houses or their crops may have to be relocated. Thus the narrower the corridor the lower the cost, but potentially the less effective it is in allowing populations to cross from one fragment of habitat to another. Any approach that can better model movement patterns, particularly where data are scarce, can contribute to better sizing and siting decisions for habitat corridors.

With regards to invasive species, I was motivated by a number of papers that address invasive species using diffusions models (for example Yamamura et al., 2007). Often these papers pick just one model, which is then parameterised using the available data. Yet, particularly where there may be few data observations to work with, efficient management requires the best estimate of underlying movement patterns, again pointing to the strengths of Bayesian methods such as those I develop in this thesis. Weinhold (2010) considers various vectors that spread disease, for example, bacteria are transmitted by the lone star tick which feeds on white tailed deer. A detailed understanding of deer movement patterns would provide insights into how rapidly this bacteria might spread and where to concentrate containment or elimination efforts. More generally, simulations of the best fitting or best supported models, integrated with covariates can result in more holistic outcomes leading to improved policy implications.

7.2 Principal Limitations of the thesis

Movement data are normally rich in information, allowing scientists to carry out robust inference of behavioural processes. However, these data are usually not collected as independent behavioural observations. The lack of such observations can make it difficult to properly interpret movement patterns. As a result, it prevents capturing the broader behavioural context of an animal such as switching between different patterns in relation to changes in their environment, resource distribution and availability.

The use of memory is an assumption disregarded in modelling Lévy flight optimality. Most animals, especially humans are known to use cognition or follow memory cues in order to refine search and movement strategies. However, because this thesis employs secondary data sets, it was not possible to integrate this aspect in to my analysis.

Another limiting factor was the absence of other covariates in the data set. These datasets used in this thesis primarily consisted only of the step lengths and turning angles. Had it consisted of other influential factors such as food distribution or environmental conditions, this could have been integrated into the study to investigate the relationships of which on foraging. For example, simulation could have been carried out to observe if it gives rise to different modes, to what extent the probabilities change and if it there is an impact of the Lévy flight exponent μ. Also. The data sets were of different sample sizes which or steps making it not directly comparable.

7.3 Moving Forwards for Animate Movements Research

My work has shed further light on the foraging patterns of human gatherers and fishers and animal foragers. This thesis demonstrates a number of advantages of using Bayesian approaches, as detailed above. Yet it also raises further questions as to whether Bayesian approaches are "better", and if so under what circumstances. Moreover, the Bayesian approaches detailed in this thesis do not attempt to understand or explain the underlying drivers of human and animal foraging. Rather, the approaches employed here, and the frequentist methodologies detailed throughout the thesis, attempt to represent the resultant movement patterns sufficiently well to be useful for researchers and policy makers.

With respect to the Bayesian approaches that are used in this thesis, a number of further improvements could be made. In particular, the thesis employed a modified version of the rejection algorithm of the ABC technique. It could be improved further using more efficient sampling techniques such as particle filtering and sequential Monte Carlo techniques (Turner et al., 2012). That is, rather than drawing candidate parameters θ^* one at a time, these algorithms work with large pools of candidates, called particles, simultaneously. The particles are stopped and filtered at each stage of the algorithm, bringing the pool closer and closer to a sample drawn from the desired posterior. However, these methods are computationally time-consuming.

Another approach that could be used to analyse the forager data sets is the mixture model. However, such a model requires independent behavioural observations so to be able to determine whether discriminate step-lengths are produced from a mixture of behaviours or a mixtures of individuals with different behavioural repertoires. For example, measured steps could be drawn from mixtures of exponential distributions. Therefore, a mixture model can be used to confirm that the step-length distribution follows only one observed model and not a mixture.

The analytical frameworks employed in this thesis, particularly the ABC methodology, could be tested on the other data sets re-analysed in Edwards' (2011) paper to explore further Lévy flight existence in nature. Another aspect of research which could be looked in to is incorporating three-dimensional data. The space used by foraging animals can be characterised not only by the (x, y) spatial dimensions but also by a third dimension z which could represent altitude, elevation or depth for airborne, terrestrial and aquatic individuals respectively. Most of the foraging studies tend to neglect the z dimension (Leis and Carson-Ewart 1999).

As data collection capabilities increase both tracking data and supplementary environmental data, the challenges and opportunities for statistical modelling work will increase as well. This study contributes to a baseline understanding of how one approach performs relative to another. It has highlighted how methodological modifications can make the most of the available data. The paradigm of 'movement ecology' can therefore be extended and be redefined as more research is done in this rapidly advancing area of ecological analysis.

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Appendix 1: Excerpts from key publications addressing animal movement and policy applications

	Title and authors	Journal	Date	Excerpts from the publications
1	Scale-Free Dynamics in the Movement Patterns of Jackals Atkinson, R. P. D., Rhodes, C. J., MacDonald, D. W. & Anderson, R. M	Oikos	2002	*Presented evidence for scale-free patterns in the foraging trajectories of side-striped jackals, a widely distributed African canid. Analysing the results of detailed radio-tracking studies conducted in Zimbabwe, they show that the night-time movement patterns adopted by the jackals exhibit long range correlations with no characteristic time scale. Also presents evidence for scale-free patterns in the foraging trajectories of side-striped jackals, a widely distributed African canid. They found that Lévy flights is well suited for locating food resources in a complex and unpredictable environment, and scale-invariant search paths may well be a response to fractally distributed resources in the landscape. Where individuals compete for resources, there may be selection pressure in favour of Lévy flights and against normal random (Brownian) movements, because Lévy flights are quicker to find new areas to exploit. Their study also raises the possibility that realistic patterns of animal movement can be incorporated into spatial models of disease spread (Macdonald 1980, Ball 1985, Smith and Harris 1991, Rhodes et al. 1998). The sprinkling of outbreaks of jackal (and fox) rabies ahead of main fronts, which is so characteristic of the disease, could conceivably be due to the virus 'freeing' the infected animal to make longer tracks across country. Even if infected, due to the power law nature of the step lengths, extremely long steps are still less likely than shorter ones, and this may explain why the majority of rabid dogs, for example, do not make such journeys (Haig 1977). Furthermore, the consequences of Lévy ranging behaviour extend to animal management and conservation. If Lévy foraging is a response to temporally and spatially unpredictable resources, then human activities which increase the proportion of such landscapes with an animal's territory could have dramatic effects on its movements.*
2	Intraspecific variation in movement patterns: modelling individual behaviour in a large marine predator.	Oikos	2004	*Found Lévy flight pattern in Grey seals. They explain how intraspecific variation in movement behaviour is an important characteristic in grey seal foraging ecology, underscoring the need to account for such variability in developing models of habitat use and predation. The ability to predict the population distribution and spread through the environment has important consequences for modelling resource and habitat use (Bergman et al. 2000). Understanding individual variability in movement patterns of grey seals will improve existing models of predation (Mohn and Bowen 1996) by permitting more spatially explicit estimates of predation mortality on prey populations.*

	Austin, D., Bowen, W. D. & McMillan, J. I.			
3	Animal search strategies: a quantitative random-walk analysis. Bartumeus, F., da Luz, M. G. E., Viswanathan, G. M. & Catalan, J,	Ecology	2005	*Lévy walks have fundamental properties (i.e., super-diffusivity and scale invariance) that allow a higher efficiency in random search scenarios. Specific biological mechanisms related to how animals punctuate their movement with sudden reorientations in a random search would be sufficient to sustain Lévy walk properties. Lévy walk properties are robust to any behavioural mechanism providing short-range correlations in the walk. They propose that some animals may have evolved the ability of performing Lévy walks as adaptive strategies in order to face search uncertainties.*
4	Helical Lévy walks: Adjusting searching statistics to resource availability in microzooplankton Bartumeus, F., Peters, F., Pueyo, S., Marrase, C. & Catalan, J.	PNAS	2003	*Suggest that, in a three-dimensional environment, a stronger helical component combined with a Lévy walk searching strategy enhances predator's encounter rates. Also shows that the chance of finding food in 3D environments depends not only on the* path lengths *(i.e., linear distances travelled) but also on the* whole shape *of the walk. The paper demonstrates the usefulness of random search theory for providing a more realistic view of ecological interactions*
5	How to reliably estimate the tortuosity of an animal's path: straightness, sinuosity, or fractal dimension? Benhamou, S	Journal of Theoretical Biology	2004	*Provides some help for distinguishing between oriented and random search paths, and depicts a general, comprehensive framework for analysing individual animals' paths in a two*-dimensional *space.*
6	How many animals really do the lévy walk? Benhamou, S.	Ecology	2007	*This paper concludes that the pattern observed in foraging animals could have been generated by a mixture of classical movement processes. Otherwise, it would be necessary to check whether the environment structure does not present Lévy walk pattern is not necessarily produced by a Lévy walk process but may emerge from the way the animal interacted with the environment structure through more classical movement processes. In any case, emergent movement patterns should not be confused with the processes that gave rise to them.*

				The fact that a heavy tailed, heterogeneous population of Brownian walkers (or an individual switching between different Brownian strategies) can produce heavy-tailed observations is quite different from saying that animals have evolved to spontaneously perform Lévy walk as an optimal search strategy.
7	How Many Animals Really Do the Lévy Walk? Comment Andy Reynolds	Ecology	2008	*Concluded that Lévy flights are known to constitute an optimal scale-free search strategy for the location of randomly and sparsely distributed targets that are not depleted once visited, but instead remain targets for future searches (Viswanathan et al. 1999). Benhamou (2007) suggested that such "non-destructive" foraging is a quite unrealistic situation. Return feeding on the same prey item is in fact not uncommon and has, for instance, been observed in predatory mites whose digestive pauses, which may last several hours, alternate with prey captures.*
8	Scale-invariant movements of fishermen: the same foraging strategy as natural predators. Bertrand, S., Bertrand, A., Guevara-Carrasco, R. & Gerlotto, F.	Ecological Application	2007	*human skills (technology, communication, or others) do not result in the fishermen's spatial behaviour being fundamentally different from that of animal predators.* *With respect to probability of prey encounter, their results suggest that fishermen, on average, evolved an optimal movement pattern (μ=2.00) among the family of Lévy walk random walks.* *This Lagrangian approach opens several perspectives in terms of operational management of the pelagic fish stock.* *Human skills (technology, communication, or others) do not result in the fishermen's spatial behaviour being fundamentally different from that of animal predators. With respect to probability of prey encounter, their results suggest that fishermen, on average, evolved an optimal movement pattern (μ=2.00) among the family of Lévy random walks. This Lagrangian approach opens several perspectives in terms of operational management of the pelagic fish stock.* *Paper suggests that owing to the high patchiness and temporal dynamics of the spatial distribution of small pelagic fish (Bertrand et al. 2004), anchovy aggregations may be qualified as sparse in the fisherman's point of view (they are out of the fishermen's detection range most of the time, imposing a searching effort) and the probability of finding fish in an already visited site is far from null. Hence, they argue that, even if stochastic in a way, the spatial strategy developed by fishermen is highly efficient and adapted to the features of the ecosystem they are exploiting.*

				The Lagrangian analysis of their spatial strategy used in the paper also provides concrete operational tools for fisheries monitoring and management. They showed in other respects (Bertrand et al. 2005) that fishermen's spatial behaviour (as described by µ) is a good indicator of fish distribution (as described by its fractal dimension). Therefore, the real-time monitoring of fishermen spatial behaviour as described by µ can be considered as an indicator of fish vulnerability and may serve as a warning signal for fisheries management.
9	Lévy trajectories of Peruvian purse-seiners as an indicator of the spatial distribution of anchovy (Engraulis ringens) Bertrand, S., Burgos, J. M., Gerlotto, F. & Atiquipa, J.	*ICES Journal of Marine Science*	2005	*µ statistic of fishing vessel trajectories constitutes a good candidate as an ecosystem indicator because: (i) Lévy flights are intuitively and statistically appropriate for describing the spatial behaviour of fishers; (ii) they can easily be related to fractal geometry, and are appropriate for describing multi-scale processes; (iii) µ is easy to compute and its interpretation is straightforward; (iv) the method can be applied in any ecosystem where VMS data are being collected; (v) owing to the ongoing development of VMS, its application should be cost-effective. µ may be a promising indicator of the degree of clustering of fish aggregations that could contribute to real-time monitoring of ecosystems.*
10	Using likelihood to test for Lévy flight search patterns and for general power-law distributions in nature Edwards, A. M.	Journal of Animal Ecology	2008	*The paper finds that calculating the maximum likelihood estimate of µ gives the most accurate results (having also tested the rank/frequency method).* *Likelihood has the further advantages of being the easiest method to implement, and of yielding accurate confidence intervals. Results are applicable to power-law distributions in general, and so are not restricted to inference of Lévy flights. suggest that Lévy flights might not be as common as previously thought*
11	Revisiting Lévy flight search patterns of wandering albatrosses, bumblebees and deer. Edwards, A. M., Phillips, R. A., Watkins, N. W., Freeman, M. P.,	Nature	2007	*The study of animal foraging behaviour is of practical ecological importance and exemplifies the wider scientific problem of optimizing search strategies*

	Murphy, E. J., Afanasyev, V., Buldyrev, S. V., da Luz, M. G. E., Raposo, E. P., Stanley, H. E. & Viswanathan, G. M.			
12	Lévy Flights in Dobe Ju/'hoansi Foraging Patterns Clifford T. Brown & Larry S. Liebovitch & Rachel Glendon	Human Ecology	2007	*Found that pattern of camp movement comprises a Lévy flight. The only reasonable interpretation is that the Ju/'hoansi achieved an optimal search pattern while behaving rationally in adapting to a spatially complex and unpredictable environment. Indeed, the Ju/'hoansi know where the waterholes, mongongo groves, and salt licks are in their territory, and they place their camps accordingly. Thus, the Ju/'hoansi Lévy flight exponent may well reflect the spatial distribution of resources as well as their decision-making processes.* *Since the model is designed to apply to animal or insect searching, it assumes little or no learning or memory, assumptions which are clearly not true in the case of human foragers. Since the Ju/'hoansi do know their environment well, their movement patterns are unlikely to be analogous to a random search. This leads to consideration of the other possible cause of their Lévy flights: a fractal distribution of resources.*
13	Environmental context explains Lévy and Brownian movement patterns of marine predators. Humphries, N. E., Queiroz, N., Dyer, J. R. M., Pade, N. G., Musyl, M. K., Schaefer, K. M., Fuller, D. W., Brunnschweiler, J. M., Doyle, T. K., Houghton, J. D. R.,	Nature	2010	*Strong support was found for Lévy search patterns across 14 species of open-ocean predatory fish (sharks, tuna, billfish and ocean sunfish), with some individuals switching between Lévy and Brownian movement as they traversed different habitat types. They tested the spatial occurrence of these two principal patterns and found Lévy behaviour to be associated with less productive waters (sparser prey) and Brownian movements to be associated with productive shelf or convergence-front habitats (abundant prey). The results are consistent with the Lévy-flight foraging hypothesis found in previous literature that organism search strategies naturally evolved in such a way that they exploit optimal Lévy patterns.*

	Hays, G. C., Jones, C. S., Noble, L. R., Wearmouth, V. J., Southall, E. J. & Sims, D. W.			
14	Linkage between fishers' foraging, market and fish stocks density: Examples from some North Sea fisheries. Marchal, P., Poos, J.-J. & Quirijns, F. (2007).	Fisheries Research	2007	*Foraging behaviour could reasonably be represented by a Lévy flight process, characterized by an exponentiation factor μ, for both fleets.* *Optimal foraging was found with μ = 1.5, suggesting a slow recovery dynamic of the stocks being harvested. High value per unit effort was achieved when foraging was close to optimal, as expected.*
15	Foraging and movement paths of female reindeer: insights from fractal analysis, correlated random walks, and Lévy flights. Mårell, A., Ball, J. P. & Hofgaard, A.	Can. J. Zool	2002	*They found that reindeer selected feeding sites with higher green biomass of Betula spp. and Salix spp. However, there was no sharp threshold for foraging as suggested by some models. The changed search pattern in late summer and the discrepancy between reindeer foraging paths and a correlated random walk model suggests that reindeer were responding to their environment by changing their searching behaviour. Other studies on reindeer have examined larger scale (habitat selection) or smaller scale selection (food-plant selection), but this study is one of few to examine the intermediate scale of selection (within a habitat), and it uses several models of searching behaviour (specifically, fractal analysis to evaluate the tortuosity of foraging paths, correlated random walks to evaluate the directionality of movement, and Lévy flights to examine the search for resources beyond sensory-detection range). The paper suggests that considering intermediate scales of the selection hierarchy could be a step towards improving our understanding of how herbivores relate to their habitats and food resources. Additionally, they suggest that such studies simultaneously evaluate several models of animal movements to gain better insights into how these foragers deal with uneven food distributions from both the temporal and the spatial perspective.*
16	Understanding movements of organisms: it's time to abandon the Lévy foraging hypothesis.	Methods in Ecology and Evolution	2015	*States that it is time now to abandon the Lévy hypothesis as a paradigm of movements of organisms. It would, for example, be interesting and worthwhile to know the extent to which Lévy patterns would be expected to occur as 'emergent properties' of largescale movement scenarios.*

	Methods in Ecology and Evolution Pyke, G. H.			
17	Evidence of Lévy walk foraging patterns in human hunter–gatherers., Raichlen, D. A., Wood, B. M., Gordon, A. D., Mabulla, A. Z. P., Marlowe, F. W. & Pontzer, H.	Proceedings of the National Academy of Sciences	2014	*They show that Hadza of northern Tanzania, perform Lévy walks in nearly one-half of all foraging bouts. Lévy walks occur when searching for a wide variety of foods from animal prey to underground tubers, suggesting that, even in the most cognitively complex forager on earth, such patterns are essential to understanding elementary foraging mechanisms.* *Because studies have not identified these types of search strategies in nonhuman primates using sophisticated statistical techniques, Lévy walks may have arisen with the evolution of a hunting and gathering lifestyle in human ancestors. The widespread use of this movement pattern among species with great cognitive variation suggests an important link between foraging patterns across different organisms, including humans. Future reconstructions of group movements and the evolution of human mobility patterns must take into account the likely scale invariance of human move steps.*
18	Incorrect Likelihood Methods Were Used to Infer Scaling Laws of Marine Predator Search Behaviour Andrew M. Edwards1, Mervyn P. Freeman, Greg A. Breed, Ian D. Jonsen	PLOS one	2012	*They demonstrate methodological issues in two recent studies that reached similar conclusions concerning movements of marine animals (Nature 451:1098; Science 332:1551). The first study analysed vertical movement data to conclude that diverse marine predators (Atlantic cod, basking sharks, bigeye tuna, leatherback turtles and Magellanic penguins) exhibited ''Lévy-walk-like behaviour'', close to a hypothesised optimal foraging strategy. By reproducing the original results for the bigeye tuna data, they show that the likelihood of tested models was calculated from residuals of regression fits (an incorrect method), rather than from the likelihood equations of the actual probability distributions being tested. This resulted in erroneous Akaike Information Criteria, and the testing of models that do not correspond to valid probability distributions. They demonstrate how this led to overwhelming support for a model that has no biological justification and that is statistically spurious because its probability density function goes negative. Re-analysis of the bigeye tuna data, using standard likelihood methods, overturns the original result and conclusion for that data set. The second study observed Lévy walk movement patterns by mussels. Edwards et al., demonstrate several issues concerning the likelihood calculations (including the aforementioned residuals issue). Re-analysis of the data rejects the original Lévy walk conclusion. Conclusions: Edwards et al., consequently question the claimed existence of scaling laws of the search behaviour of marine predators and mussels, since such conclusions were reached using incorrect methods. Further, they discourage the suggested potential use of ''Lévy-like walks'' when*

				modelling consequences of fishing and climate change, and caution that any resulting advice to managers of marine ecosystems would be problematic.
18	Overturning conclusions of Lévy flight movement patterns by fishing boats and foraging animals Andrew M. Edwards	Ecology,	2011	*Previous conclusions have been made using methods that have since been shown to be problematic: inaccurate techniques were used to estimate μ, and the power-law distribution was usually assumed to hold without testing any alternative hypotheses. Therefore, this paper address the open question of whether the previous data still support the Lévy* *flight hypothesis, and thus determine whether Lévy flights really are so ubiquitous in ecology. The paper finds that Lévy flight movement patterns are not the common phenomena that was once thought, and are not suitable for use as ecosystem indicators for fisheries management, as has been proposed.*
19	Lévy walk patterns in the foraging movements of spider monkeys (Ateles geoffroyi). Ramos-Fernandez, G.	Behav. Ecol. Sociobiol	2004	*Because spider monkeys are important seed dispersers for several tree species, in reality there could exist a bidirectional relationship between their foraging patterns and the distribution of trees. By foraging and dispersing seeds in such a pattern, spider monkeys might favour, in the long run, a self-similar distribution of the very same trees on which they feed.* *Another consequence of foraging in a Lévy walk pattern is that previously visited food sources may be revisited only after long periods of time, favouring the ripening of more fruit before the next visit. They found that the Lévy walks of females and males are different. Males have a larger proportion of long trajectories than females.* *They also have found a different value of the power law exponent for the length distribution of steps given by lone monkeys to that for steps given by monkeys when part of a subgroup. In particular, monkeys on their own seem to travel a higher proportion of long steps compared to short ones. One of the cited benefits of group foraging has been an improvement in the likelihood that the group would find food patches which an individual on its own would not find (Krebs and Davies 1993; Janson 1998). If spider monkeys do not have knowledge of the location of food sources, they could still find more fruiting trees when traveling in a subgroup than when alone. The same argument applies if spider monkeys know the location of fruiting trees: if they can share information on the known location of resources (as in baboons: Byrne 2000) it would seem logical that a subgroup would find more fruiting trees than a single individual, therefore decreasing the proportion of long steps. While there seems to be convincing evidence for fashioning to be favoured by a decrease in feeding competition, Lévy walks could also be favoured for the same reason. In a group of n Lévy walkers, the probability that individuals will remain near the origin (or cross each other's path if*

				they all start together at the same spot) is considerably less than for a group of Brownian walkers (Larralde et al. 1992). Long, infrequent trajectories in Lévy walks could be the cause of more group splitting, which in turn could decrease the constraints imposed on individuals in small subgroups to travel with the rest of the group, thus favouring variation in step length. An intriguing possibility is that, in a hypothetical ancestor with stable grouping patterns, group fissioning and Lévy walk foraging patterns could have reinforced each other for the decrease in feeding competition they provided. Then, social behaviours that maintained group membership even in the absence of visual contact would have been favored, leading to the fission fusion grouping pattern that we see today.
20	The Le´vy flight paradigm: random search patterns and mechanisms A. M. Reynolds, And C. J. Rhodes	Ecology	2009	*The results of the models described here suggest that Le´vy-flight search is a particularly useful strategy that can accommodate a wide variety of different search scenarios, and this has stimulated comparison with ecological data. Knowing how animals move around their environment is essential to understanding many ecological and population processes. This advance in the understanding of innate searching in homogeneous environments leaves open the impact that landscape heterogeneity and physical barriers can have on movement patterns*
21	Sims, D. W., Righton, D. & Pitchford, J. W. (2007). Minimizing errors in identifying Lévy flight behaviour of organisms.	Journal of Animal Ecology	2007	*Empirical reanalysis of data in published studies indicates that simple log transformation results in significant errors in estimating μ, which in turn affects reliability of the biological interpretation. The potential for detecting Lévy flight motion when it is not present is minimized by the approach described. They also show that using a large number of steps in movement analysis such as this will also increase the accuracy with which optimal Lévy flight behaviour can be detected.* *Their simulations also illustrate how a low number of step lengths measured for tracked animals can influence significantly the accuracy with which μ can be estimated. In their simulations, the standard deviation of the estimated Lévy exponent dropped from 0·3 to 0·09 when the number of steps used to recover the exponent was increased from 50 to 1000. This indicates that animal movement data sets need to be appropriately large to detect accurately a behavioural signal such as an optimal Lévy flight.* *The number of ecological studies citing Lévy flight behaviour is increasing as more authors become aware of their existence, and the need for accurate and unambiguous methods is clear. They advocate not only the use of accurate plotting methods shown here to identify the presence of Lévy flights, but these other techniques also*
22	Lévy flight search patterns of wandering albatrosses., Viswanathan, G. M.	Nature	1996	*Lévy flights help foragers visit new sites that other types of movement will not. This is the first attempt at studying LF search patterns in in animal behaviour*

23	Optimizing the success of random searches. Viswanathan, G. M	Nature	1999	*Search efficiency depends on the probability distribution of flight lengths taken by a forager that can detect target sites only in its limited vicinity. The paper shows that, when the target sites are sparse and can be visited any number of times, an inverse square power-law distribution of flight lengths, corresponding to Lévy flight motion, is an optimal strategy. He testes the theory by analysing experimental foraging data on selected insect, mammal and bird species, and find that they are consistent with the predicted inverse square power-law distributions.* $\mu=2$ *is optimum for a search in any dimension. Lévy flights, characterized by an inverse square distribution of step lengths, optimize random searches under specific conditions, when targets (such as prey) are scarce. Lévy flights are expected in places where prey is scarce (such as the open ocean), whereas a Brownian strategy is more likely to occur where prey is abundant (as in marine regions where the mixing of water bodies produces high densities of phytoplankton, zooplankton and organisms higher in the food chain). The observed pattern of switching between search modes is not entirely consistent with these expectations. But it is nonetheless plausible, as seen for instance in the data on a blue shark that moved from the prey-rich waters of the western English Channel to the oceanic environment of the Bay of Biscay.*
24	Ecology: Fish in Lévy-flight foraging. Viswanathan, G. M. (2010).	Nature	2010	*The fact that some organisms perform Lévy flights has deep implications that transcend those for marine ecosystems, and it raises many questions. Did humans disperse from Africa superdiffusively rather than diffusively? Does pollen from genetically modified crops spread superdiffusively? What are the consequences if influenza epidemics spread superdiffusively? In a reaction-diffusion context, superdiffusion leads to significantly increased overall reaction rates, because the reacting species — which may be chemical or biological — meet each other more often. What more can be learned about such interactions? These questions and many more await investigation. Why would animals adopt a Lévy-flight foraging strategy? In a Brownian random walk, the walker frequently returns to the same place. By contrast, Lévy walkers can outperform Brownian walkers by revisiting sites far less often*
25	Foraging success of biological Lévy flights recorded in situ Nicolas E. Humphriesa,b, Henri Weimerskirchc , Nuno Queiroza,d, Emily J.	PNAS	2012	*It is an open question how animals find food in dynamic natural environments where they possess little or no knowledge of where resources are located. Foraging theory predicts that in environments with sparsely distributed target resources, where forager knowledge about resources' locations is incomplete, Lévy flight movements optimize the success of random searches. However, the putative success of Lévy foraging has been demonstrated only in model simulations. They find that total prey masses captured by wandering albatrosses during Lévy movements exceed daily energy requirements by nearly fourfold, and approached yields by Brownian movements in other habitats. These results, together with the reanalysis of previously published albatross data, overturn*

	Southalla , and David W. Simsa,e,f			*the notion that albatrosses do not exhibit Lévy patterns during foraging, and demonstrate that Lévy flights of predators in dynamic natural environments present a beneficial alternative strategy to simple, spatially intensive behaviors. Their findings add support to the possibility that biological Lévy flight may have naturally evolved as a search strategy in response to sparse resources and scant information.*
26	Lévy flight search patterns of marine predators not questioned: a reply to Edwards et al. David W. Sims, Nicolas E. Humphries,	arXiv:1210.2288 [q-bio.PE]	2012	*Edwards et al. (2012) question aspects of the methods used in two of our papers published in Nature (2008; 2010) that report results showing Lévy-walk-like and Lévy-flight movement patterns of marine predators. The criticisms are focused on the applicability of some statistical methodologies used to detect power-law distributions. They reply to the principal criticisms levelled at each of these papers in turn, including their own re-analysis of specific datasets, and find that neither of the paper's conclusions are overturned in any part by the issues raised. Indeed, in addition to the findings of our research reported in these papers there is strong evidence accumulating from studies worldwide that organisms show movements and behaviour consistent with scale-invariant patterns such as Lévy flights.*
27	Le´vy flight and Brownian search patterns of a free-ranging predator reflect different prey field characteristics David W. Sims, Nicolas E. Humphries, Russell W. Bradford and Barry D. Bruce	Journal of Animal Ecology	2012	*Shark movements were best approximated by Brownian motion when hunting near abundant, predictable sources of prey (e.g. seal colonies, fish aggregations), whereas movements approximating truncated Lévy flights were present when searching for sparsely distributed or potentially difficult-to-detect prey in oceanic or shelf environments, respectively. Suggests that behaviours linked to decisions to make longer movement steps away from depleted food patches are heritable traits and not solely owing to simple interactions with food patches.*
28	Generalized Pareto for Pattern-Oriented Random Walk Modelling of Organisms' Movements	PLOS One	2015	*How organisms move and disperse is crucial to understand how population dynamics relates to the spatial heterogeneity of the environment*

29	Assessing Lévy walks as models of animal foraging.	Journal of the Royal Society Interface	2011	*There is really little or no reason why organisms should be expected to possess internal 'processes' that produce Lévy 'patterns', and good reason why they should adopt very different processes. If the restriction on the forager's memory is removed, allowing even a modest level of cognitive ability, a wide range of strategies becomes available. For instance, the forager can modify its behaviour depending on the amount of time since the last food item was detected or maintain some directional persistence from one step to the next, a strategy that may help the forager to move into the centre of a patch or to avoid excessive backtracking.* *Such strategies have more of a mechanistic basis in the behavioural biology of the forager than a pure LW. It is becoming increasingly apparent that a wide range of movement strategies not based on an LW can lead to the observation of heavy-tailed patterns. These include an apparent power-law distribution of observed move lengths, super diffusive movement, long-term correlations in the reorientation data and fractal movement paths. These scale-free characteristics can be generated via the interaction of the forager's behaviour with the distribution of food in the environment*

Appendix 2: Computing marginal likelihood and probabilities from the two approaches

(i) Standard model selection approach

- N =Sample size
- M = Number of models
- T = Number of transformations
- → S = M*T= 44
- I = Number of iterations

Code

- Nested do loops
- For m=1……M (=22)

```
For m=1……M (=22)
        t=1…….T (=2)
        i=1…….I (=10,000)
            Get (y|M,S,I) (M*T*I= 440,000)
             End
        End
    End
```

- Storage: array of 22*2*10,000
- $f(y|s) \equiv f(y|m,t)$

  $= \frac{1}{I}\sum_{i}^{I} f(y|m,t,i)$

  $= \frac{1}{I}\sum_{i}^{I} f(y|m,t)$

  $= f(y|m,t)$ calculated for 6 specifications
- $\hat{f}(y|s) \equiv \hat{f}((y|m,t)$

  $= \frac{1}{I}\sum_{i}^{I} \hat{f}(y|m,t,i)$

  $\neq \frac{1}{I}\sum_{i}^{I} \hat{f}(y|m,t)$ (Estimated for 16 specifications)

  $= \hat{f}(y|m,t,i) \equiv \sum_{J=1}^{J} \frac{1}{J}\hat{f}(y|\theta,m,t)$

  $= \Theta_{1,} \Theta_2, \Theta_3 \ldots\ldots\ldots \Theta_J \approx f(\Theta)$

- Probability (m,t) = $\frac{f(y|m,t)}{\sum_{m=1}^{M}\sum_{t=1}^{T} f(y|m,t)}$

(ii) Approximate Bayesian computation

- Data (y) are sorted according to the sorting protocol
- A candidate parameter θ drawn from a likelihood approximating prior/proposal distribution $f(\theta)$
- The candidate parameter is used to simulate a dataset $z \sim f(z|\theta)$ with the same number of observations as observed data y
- Compare sorted (y) and sorted (z)
- $\delta = \sum_{i}^{n} \text{sorted } z_i - \text{sorted yi}$
- $\delta \leq \delta(\text{target})$; accept θ
- Collect accepted θs
- Process $\theta_1\ \theta_2 \ldots\ldots\ldots\ldots \theta_n$
- $\hat{f}(y\,|\,m,t,i) = \frac{1}{S} \sum_{s=1}^{S} \hat{f}(y\,|\,\theta, m, t, i)$

  $= \Theta_1, \Theta_2, \Theta_3 \ldots\ldots\ldots \Theta_J$ drawn from $f(\Theta|m)$

  Subject to $\delta(z,y) \leq \delta(\text{target})$

  $Z \approx f(z|\theta)$

  $\theta \approx f(\theta|m)$

- Probability (m,t) = $\frac{f(y\,|\,\theta_S, m,t,i)}{\sum_{m=1}^{M} \sum_{t=1}^{T} f(y\,|\,\theta_S, m,t,i)}$

Appendix 3: Edwards Exponential Models

Unbounded Exponential
$f(x) = \lambda e^{-\lambda(x-a)}$ $x \geq a$

Bounded Exponential
$f(x) = Ae^{-\lambda(x-a)}$ $x \in \{a,b\}$

Edwards Power-law

Unbounded Power-law
$f(x) = CX^{-\mu}$ $x \geq a$

Bounded Power-law
$f(x) = CX^{-\mu}$ $x \in \{a,b\}$

Where the normalization constant $C = (\mu-1)/(a^{1-\mu}-b^{1-\mu})$ for $\mu \neq 1$ and $C = 1/(\log b-\log a)$. Parameter a is the minimum data value while the b is the maximum data value of the data set.
The levy flight hypothesis states that the exponent takes the value $1 \leq \mu \geq 3$.

Appendix 4: Probability Density Functions for the Models

Normal

$$f(x;\mu,\sigma) = \frac{1}{\sqrt{2\pi\sigma^2}} \exp\left\{-\frac{(x-\mu)^2}{2\sigma^2}\right\} \qquad -\infty < x < \infty \quad -\infty < \mu < \infty \quad \sigma > 0$$

Uniform

$$f(x) = \frac{1}{b-a} \qquad -\infty < a \le x \le b < \infty$$

Exponential

$$f(x) = \lambda e^{-\lambda x} \qquad x \ge 0$$

Pareto

$$p(x) = \alpha k^{\alpha} x^{-\alpha-1}, \;\; \alpha, k > 0, \;\; x \ge k$$

Weibull

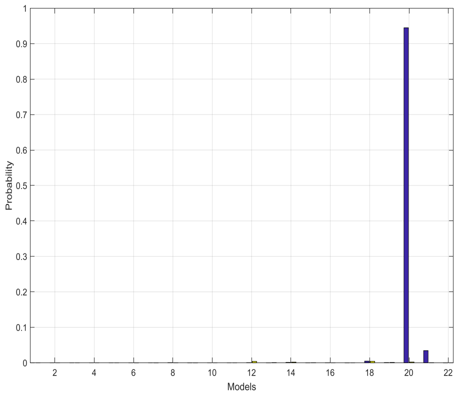
$$f(x;\alpha,\beta) = \frac{\alpha}{\beta^{\alpha}} x^{\alpha-1} e^{-(x/\beta)^{\alpha}} \qquad x \ge 0 \quad \alpha, \beta > 0$$

Gamma

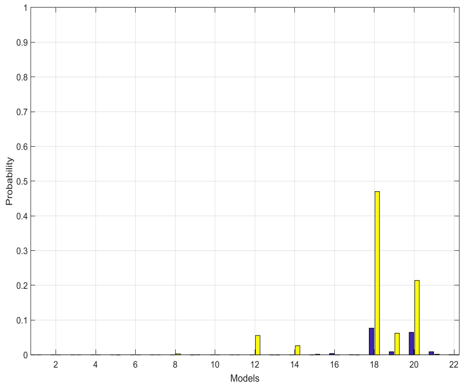
$$f(x) = \int_{x=0}^{x} \frac{1}{\Gamma(\alpha)\beta^{\alpha}} x^{\alpha-1} e^{-x/\beta} \qquad x \ge 0$$

Appendix 5: Model selection results for individual reindeer movement – Period A

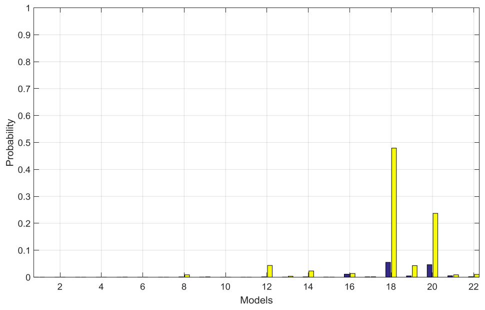
Reindeer 1



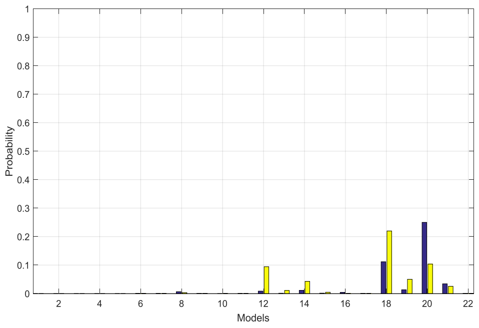
Reindeer 2



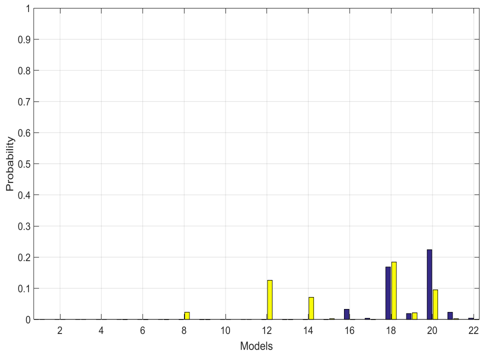
Reindeer 3



Reindeer 4



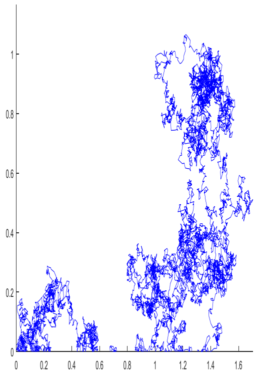
Reindeer 5



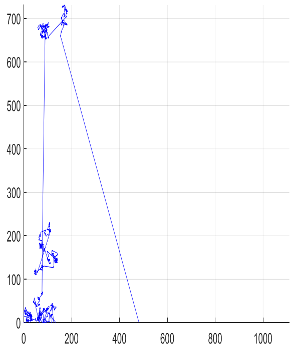
Appendix 6: Implications in fisheries

This section discusses how the understanding of foraging patterns can assist in designing management and policy implications. I have simulated four movement patterns (i) generated from an exponential distribution (ii) generated from a Lévy flight distribution with a μ=1.5 (iii) generated from a Lévy flight distribution with a μ=2 (iv) generated from a Lévy flight distribution with a μ=3. Each path was simulated for an equal number of steps (n=10000). Each was set to start at (0,0). The figures show that depending on the distribution pattern they move at different speeds and thus cover varying distances during a given time. A fishery managed area of a certain area could be assumed where the four patterns represent four different species set to start their foraging movement at the same time from the origin (0,0). The four species were assumed to be fishing vessels, competitors in the form of seabirds (i.e. albatrosses) and fish. The four movement paths were simulated to commence moving at the same time and end together with the same number of steps.

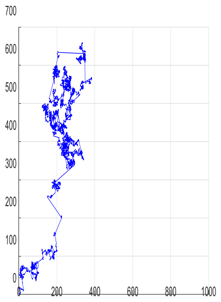
(i) Exponential distribution



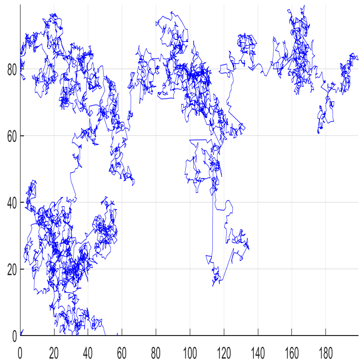
(ii) Power-law with μ=1.5



(iii) Power-law with μ=2



(iv) Power-law with μ=3



It can be observed that at the end of the fixed time period, individuals following a power-law distribution travel faster than the exponential movement pattern. Thus, two species following these two patterns will reach a boundary at different times. Even if two boats or two different species followed the power-law distribution, depending on the exponent parameter μ they will travel at different speeds and reach the boundary at different times. If those two species/objects are two fishing vessels and the rest are fish, we could see that, after a certain distance the vessels will not be able to obtain the target catch. Therefore, this will be a cost to the vessels. If the two objects, vessels and fish, follow the same movement pattern, then the vessels are likely to gain throughout the trip until they reach the boundary. This behaviour also helps decide management scenarios such as fishing quotas and total allowable limits to fish taking in to consideration the movement pattern of their targeted species.

further, if, for example, vessels and competitive birds are able to forage without conflict, then this is an indication that the birds will also get an opportunity to obtain quality food without having to change their direction or fly further which is a cost to the seabirds. From an ecological point of view, if fish are able to swim beyond the managed area where fishing is allowed, faster than the vessels, it is an indication of regeneration time for the fish. As the movement paths are different, distributions with different means and variances (for example the power-law distribution has infinite variance compare to the exponential distribution), but with the same number of steps, it also gives an understanding of which foraging pattern reaches the boundary with a shortest number of steps.