METHODS IN MOVEMENT:
DECONSTRUCTING BIRD BEHAVIOUR WITH
WAVELETS

Maitreyi Sur

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ITC

FACULTY OF GEO-INFORMATION SCIENCE AND EARTH OBSERVATION

METHODS IN MOVEMENT:
DECONSTRUCTING BIRD BEHAVIOUR WITH
WAVELETS

DISSERTATION

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by

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born on March 24th 1985

in Allahabad, India

This thesis is approved by
Prof. dr. A. K. Skidmore, promoter
Dr. A. G. Toxopeus, co-promoter
Dr. T. Wang, co-promoter

"He was not bone and feather but a perfect idea of freedom and flight,
limited by nothing at all"

— Richard Bach, *Jonathan Livingston Seagull*

To my parents
Samir and Krishna Sur.

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1 Introduction

Part of this chapter is being revised to be submitted as a review paper: In preparation

1.1 Background

1.1.1 Movement ecology: beginning and scope

Most species of the protists and animal kingdom are mobile at some stage of their life cycle. Movement in the animal kingdom is one of the defining life processes and plays a key role in almost all ecological processes such as acquisition of food, defence against predators, reproduction, competition and migration. Despite its importance as a pivotal ecological process, movement ecology has a short history in ecological theories essentially due to lack of appropriate movement data. Some early theoretical models of animal movement such as random walks and correlated random walks can be traced over the years (Kareiva and Shigesada 1983; Okubo 1980 ; Patlak 1953a, b) but empirical evidence supporting these models have not been adequate (Bergman et al. 2000) nor have critical analyses been made about these theoretical models. There is emerging need to update or even correct the underlying algorithms and assumptions of these theoretical models (Nathan 2008). Movement ecology has recently become progressively more prominent, given the increased threat to wildlife from changes in land use pattern and fragmentation, the spread of diseases and problems of invasive species (Patterson et al. 2008). Therefore, to understand fundamental behavioural and ecological processes it is essential to understand the patterns of animal movement and the mechanisms responsible for them.

The earliest research on individual movement analysis can be traced to the theoretical papers by C. Patlak (Patalak 1953a, b) where he derived equations to study movement as an approximation to diffusion, with random walk (RW) being modelled, using a directional persistence towards an external stimuli. The models of these papers remained untested for a long time till Kareiva and Shigesada derived some of the same results from an independent but notable experimental work on cabbage white butterflies (*Pieris rapae*) (Kareiva and Shigesada 1983). They quantified movement using move lengths and probability distribution of turning angles. Movement was modelled as correlated random walks (CRW) and the experiment showed that net displacement of ovipositing cabbage white butterflies is aptly predicted as CRW but nectar-feeding butterflies violate CRW assumptions.

The Kareiva and Shigesada study entailed a tedious procedure of manually observing and following 200 butterflies. Since then enormous strides have been made in the technology that aid in collecting meticulous movement data. Nowadays entomological research on movement is being undertaken by tagging insects, such as honey bees and butterflies, with harmonic tags (6-20 mg in weight) and radar modifications (Riley et al. 2005). These technologies not only have high spatial and temporal resolution but also are progressively

becoming lighter in weight leading to an explosive possibility of tracking a wide range of species that are smaller and more cryptic. Whilst videotaping and locomotion compensators are preferred methods in laboratory studies, data from such sources are difficult to interpret given the artificial conditions (Turchin 1998). For field data however, data collection has now become a new area of expertise in its self. The simple mark- recapture method of tracking animals has now evolved from the widely used colour marking (Southwood and Henderson 2009) to radioactive markers, elemental markers and genetic markers (Akey 1991; Akey et al. 1991). The mark recapture methods falls under the category of tracking organisms or groups of organisms at a certain location, and more often than not deal with modelling patterns of space use by animals. Similarly other methods and devices that use data from disturbance caused by the presence of an animal in an area under study are radars, thermometers, cameras, thermal cameras, passive infrared sensors, microphones and geophones which collect data without direct interaction with the animals (Baratchi et al. 2013). The most staggering advancements however have been in the technology surrounding radio transmitters, GPS satellite tags and electronic tags. These devices are especially suited to collect data on individual animal movements with high accuracy furnishing ecologists and mathematicians with a minefield of data for quantifying, up-scaling and modelling statistical properties of moving animals (Giuggioli and Bartumeus 2010).

For the last 25 years, there has been a constant increase in the number of species that have been tracked using telemetry devices. The spectrum of species tracked range from the smallest larvae, plankton and fish in laboratory settings (Bearon et al. 2004; Parrish et al. 2002; Seuront et al. 2004; Uttieri et al. 2005) to salmon, sturgeon, pinniped, shark and blue fin tuna in the wild (Block et al. 1998; Costa et al. 2010; Gutenkunst et al. 2007; Heupel and Hueter 2001; Lepage et al. 2005; Newman 1998; Ransom et al. 2007; Raum-Suryan et al. 2004). Telemetry data is now available for long-distance migrating birds such stork, hawk, goose and albatross (Aarvak and Oeien 2003; Fritz et al. 2003; Haines et al. 2003; Shimazaki et al. 2004; Weimerskirch et al. 2002) to terrestrial animals such as elk, reindeer, bear, deer, elephant and tree dwelling monkey, marten, dugong (Ager et al. 2003; Mårell et al. 2002; Messier et al. 1992; Nams and Bourgeois 2004; Ramos-Fernandez et al. 2004; Sheppard et al. 2006; Wittemyer et al. 2008).

The technological advancement in collection of empirical data has initiated a new wave of scientific research with movement as the central theme. The major themes addressed in animal ecology and conservation using this new technology includes resource selection and corridor mapping (Frair et al. 2010; Sawyer et al. 2006; Thirgood et al. 2004; Whittington et al. 2005), behaviour (Jonsen et al. 2007), migration (Bunnefeld et al. 2011; Liminana

et al. 2007; Meyburg et al. 2003) and home range studies (Moorcroft et al. 2006), demographic studies (Haydon et al. 2008; Heupel and Simpfendorfer 2002), movement ecology (Sims et al. 2008), human wildlife conflict studies (Whittington et al. 2005) and climate change vulnerability studies (Durner et al. 2009). The volume of papers on quantifying movement of organisms arguably acknowledges that it is an important aspect of understanding ecological dynamics. With this there is also an increased awareness that the field of movement ecology requires generalized and unifying analytical methods that can pervade a range of species for an array of ecological issues (Nathan 2008).

1.1.2 Evolution of animal movement studies

Due to advancement in telemetry technology and variety of spatio-temporal data of moving animals, quantification and analysis of movement is undergoing gradual changes. This evolution in movement ecology is a result of two important factors. First is the cross-disciplinary approach in dealing with basic ecological problems that are bringing mathematicians and ecologists together. Second is the adaptation of concepts from physics and statistics to extract information from large data sets. The changes in a modelling movement can be understood by the following differences in concepts and approaches.

1.1.3 Eulerian versus Lagrangian approach

Movement models are steadily trending towards analyzing individual movement of organisms from spatial distribution of populations (Nathan 2008). This dichotomy in modelling is the basic difference between Lagrangian and Eulerian approaches (Turchin 1998). The Lagrangian approach is based on tracking individual animals of a population by appending telemetry devices to them. The modelling is accomplished by characterizing the trajectory by means of variables such as step length, turning angles, velocity and acceleration to probe behavioural response and mechanics of movement. Advances in the Lagrangian field of analysis have been due to collection of spatio temporal data with higher resolution over larger distances (Nathan 2008). The Eulerian approach on the other hand is centered around a space, from where densities and fluxes of moving organisms are measured (Turchin 1998) to understand spatial distribution and habitat usage by animals. The diffusion model of studying animal movement is the simplest example of the Eulerian approach (Turchin 1998). For an all-inclusive study of a population and its movement ecology, however it is essential to consider both approaches in tandem.

1.1.4 Descriptive versus quantitative approach

Ecological studies have a long history of descriptive studies wherein observations and patterns are recorded in relation to variables such as a species, place or time. Telemetry data from tracked animals often encompass massive data sets that are not easy to analyze and interpret. Inferences are often made by descriptive and visual approaches to describe areas visited by animals and time spent in specific locations. Such studies often lack a clear reproducible hypothesis and can highlight patterns but do not establish causality. For example, movement trajectories can be easily viewed in a spatial frame or a temporal frame by simply using Google Earth in order to observe most visited locations. Such an approach is tedious and often represents the movement of discrete variables of a population resulting in ambiguity from conflicting data sets. However for fast moving, animals with an assortment of movement patterns, such as pelagic seabirds, sometimes visual analytics combined with detailed descriptive analysis may reveal unexpected ecological incites. However, in order to garner ecological information from huge repositories of data, robust statistical and mathematical analyses are required together with improved methods of data management and processing. Quantitative approaches are necessary to test fundamental biological hypothesis and comparative studies across species and taxas (Giuggioli and Bartumeus 2012). In addition, raw data require a stage of data processing to account for errors, missing data and noise. Popular techniques in quantitative analysis of movement involve detecting outliers (Sur et al. 2014), clustering (Lee et al. 2007), regression and pattern recognition (Dodge et al. 2008b).

1.1.5 Organism centric modelling versus quantification of statistical properties of the movement path itself

The bulk of early, as well as current research on movement includes organism centric modelling. This is rooted in theoretical and empirical studies based on diffusion and random walk models. The random walk models have remained popular because they are considered as the natural spatial extension of the Lotka-Volterra model, which is one of the basic theoretical models for inter-specific interaction and dynamics of biological systems (Turchin 1998). The defining paper that streamlined the use of diffusion models in spatial spread of population was published in 1951 by Skellam (1951). The random walk model was applied as a starting point to derive spatial distribution of population densities. However, the issue of randomness of animal movement is a debatable subject and this kind of modelling has some misleading notions. The basic notion is that the resolution of the data effects whether a movement is a correlated random walk or random walk. At very low temporal resolution, movement is bound to be correlated, and at a very high resolution the movement may even appear random (Gurarie 2008).

For example, the frequent erratic movements of an insect might appear random but each individual reacts to a multitude of factors ranging from environmental cues to internal biophysical factors. Because of the complexity of the large number of variables required to model movement deterministically, a more parsimonious approach is now being used by applying stochastic models. Such approaches are called behaviour minimalism, where one can argue that although individual movements may reveal some form of randomness, spatial distribution of the population is certain to have regular features. Consequently, there is an increase in research focusing on statistical approaches that characterize the movement trajectories and movement patterns. This body of literature includes fractal analysis, Levy walk studies and the more recently, wavelet analysis. Since the overarching range of this thesis includes description and extension of these methods with special emphasis on wavelet analysis to derive practical information on ecological processes, they will be discussed in due course.

1.1.6 Single scale versus multiscale scale approach

The word "scale" refers to the resolution and extent at which patterns are measured, perceived or represented (Bissonette 1997). Since the 1980's the concept of variability of animal behaviour with spatial and temporal scales has received considerable importance (Schneider 2009) and as Levin (1992) put it "...the problem of pattern and scale is the central problem in ecology, unifying population biology and ecosystem science, and marrying basic and applied ecology". Studies related to biological aspects of animals such as foraging, dispersal patterns, and population dynamics (Lewis 1993) have been undertaken at specific extents. Wiens (1989) called the extent of scale for a particular biological phenomenon as "domains". Scale domains are defined as "regions of the scale spectrum over which the structure and the functional relationships between variables describing a particular object of interest (process, entity, phenomenon) do not change or change monotonically (in an easily predictable way) with change in scale" (Ratze et al. 2007). In other words Wiens (1989) coined the different hierarchical levels in the range of spatial scales to which animals respond to as "domains" and the boundaries between them as "transitions". For movement patterns, the concept of domains and transitions of scales is an important consideration. They help in objectively identifying scales at which animals respond to their environment (Fritz et al. 2003). In addition, a hierarchy of scales can be identified where dominant changes in movement patterns are observed.

The burgeoning amount of data in the field of animal movement has advanced the concept of scale to the fore. Patterns in movement have been known to emerge at particular spatial and temporal scales. To study scale

specific responses of animals, like movements, multi-scale hierarchical study designs are being used rather than single scale studies. Multiscale analysis can be defined as “analysis with respect to multiples of a unit of measurement” (Schneider 1994). However typically scales of study are chosen according to availability of habitat and climate data or defined arbitrarily or coincided with plant community composition (Johnson et al. 2002). The problems of single scale studies are that it limits ecological understanding and they do not reflect the hierarchical way in which the animals respond to their environment over several spatial and temporal scales (Bissonette 1997). Very little has been done to stratify movement strategy according to the scale at which the changes in behaviour occur.

1.2 Research objectives

Jonsen et al. (2008) noted “our ability to analyze movement patterns ... has been far outstripped by our ability to collect individual movement data”. There is an emergent need for generic robust mathematical techniques that can obtain relevant biological and ecological information from various kinds of movement data. In the various chapters in this dissertation, we use the tracking data for Lesser Black-backed gulls (*Larus fuscus*) as a repository of information to test rigorous mathematical techniques to identify individual movement patterns and their underlying ecology; elaborating the usefulness of mathematical models and empirical data in generating hypothesis about fundamental biological processes. Four fundamental issues were identified from the literature presented above:

1.2.1 Problem statements

- i. Movement analysis for animals is challenging because they are explained by a complex interaction between the organism’s internal state and external influences.
- ii. Data from tracking animals are always multi-dimensional and non-independent.
- iii. Multi scale analysis of movement data is an under studied phenomenon due to lack of availability of data and has largely focused on biology than method.
- iv. Extensive availability of tracking data requires consensus in the use statistical and analytic approaches that can accommodate the dynamics of movement varying over time and space.

The movement patterns of animals, in particular migratory birds like the Lesser Black-backed gulls, is a result of complex confluence of behavioural processes interacting with landscape patterns and climatic conditions (Dalziel et al. 2008). But it has proved challenging to discern the interaction between behavioural processes and the bio-physical factors affecting movement

(Dalziel et al. 2008). One difficulty of analyzing migratory movements is because the underlying mechanisms act over different ranges of spatial and temporal scales and birds perceive and respond to different motivators at different scales (Nams 2005). For example most studies on registration of flight routes for analysis and navigation studies have been performed by various methods, each at a limited range of geographical scale (Table 1) (Alerstam 1996).

Table 1: Some methods used to collect data and analyze flight routes and orientation of birds at different geographical scales (Alerstam 1996)

Basis of analysis	Geographical scale				
	10^4	10^3	10^2	10	1
Distribution data	×	×			
Ringing recoveries	×	×	×		
Radio telemetry, Satellite based	×	×	×		
Aerial tracking		×	×		
Radio telemetry		×	×	×	
Extrapolation from radar/optical registration		×	×	×	
Tracking radar registration			×	×	
Optical Tracking					×

The result is that the spatial and temporal complexity of factors effecting movement patterns might be masked or misinterpreted if not analyzed at the right scale. Therefore, to efficiently identify behavioural processes and landscape patterns affecting movement of birds, it is imperative to identify spatial and temporal scales at which they affect the movement patterns.

One method to detect these characteristic patterns of movement pathways is to detect cyclical trends at different scales. Cyclicity or repetitive patterns of movement pathways can give key insight to behavioural signals. Regular temporal oscillations in natural factors (such as light, temperature, spatio temporal resources) and internal states (internal physiology, long-term memory) contribute to specific movement patterns at multiple scales. As the different factors change over time, these movement mechanisms operate on fairly regular, but different, frequencies reacting to these factors. Of the various statistical methods available, the wavelet analysis of complex trajectories is capable of detecting interesting cyclic patterns and other latent behavioural patterns. The non-parametric nature of the wavelet analysis makes them ideal tools to probe into the statistical properties of movement trajectories and their relationship to physiological, ecological and climatic factors.

The issue of detecting movement 'patterns' is central to the problem of movement analysis and the issues addressed in this thesis, it is important that the term 'pattern' itself is clearly defined. In general movement patterns "include any recognizable spatial and temporal regularity or any interesting relationship in a set of movement data, wherein the proper definition of "pattern interestingness" depends on the application domain" (Dodge et al. 2008a). The current increase in research on the analysis of movement using tracking data has seen the classification of 'movement patterns' based on a number of different parameters. With no agreement on the relevant pattern recognition techniques appropriate for movement data, it is important that the basis of pattern recognition should at least have certain basic characteristics like efficiency (usable on big data sets), effectiveness (capable of accurately detecting patterns, not artefacts), generality (can be potentially used on other datasets as well) (Dodge et al. 2008a), and simplicity (insights from apparently complex patterns of movement). In the present study the basis of pattern recognition will be the 'constancy' in the movement variable, which means that patterns will be recognized when the movement variables remain the same or change insignificantly for a particular duration (Andrienko et al. 2007).

Overall research objective:

This dissertation aims to address the current problems in methods in movement ecology using empirical data of Lesser Black-backed gulls using the robust mathematical tool of wavelets to address those problems.

1.2.2 Wavelet analysis in movement ecology

Ecological data of any type, has an inherent complexity due to variables varying in non-linear manner (Cho and Chon 2006). For instance, far ranging animals such as migratory birds are faced with changing ecological constraints such as resource distribution, climatic factors and human disturbance along their migratory route (Fritz et al. 2003). These result in specific movement responses that are dependent on the constraints and are scale oriented. Therefore reversing the logic characterizing the movement path of animals can provide us with insight into the environmental and internal factors effecting movement at different scales. The requisite for characterizing movement pathways are statistical methods falling under the category of time series analysis. One of the fundamental time series analysis tools used in ecology and population distribution studies are spectral analysis. Spectral analysis based on the Fourier method have been used in ecology for more than 50 years to partition variance of a series into different oscillating components with different frequencies (Cazelles et al. 2008b; Platt and Denman 1975). However, spectral analysis that assumes stationarity of data is not suitable for movement data because of their non-stationarity features.

For this purpose an extension of the Fourier analysis, the wavelet analysis, is appropriate to analyze and visualize complex movement data. Wavelets are capable of:

- Handling irregular data sets which are aperiodic, noisy and intermittent
- Represent complex structures without the knowledge of underlying mechanism
- Finding scale dependent regularities
- Behavioural monitoring using movement statistics.

The wavelet estimates the frequency content of a signal as a function of time as well as scale. In other words, patterns such as periodic components of a signal can be traced through time. The extensions of wavelet analysis namely cross wavelet and wavelet coherency further allows analysis of dependencies between two time series. The first significant paper that utilized wavelets to analyze movement is the paper by Wittemyer et al (2008). They noted that frequency domain method of the wavelet analysis provides compact summaries of temporal autocorrelation, which in turn show seasonal and diurnal based periodicities. The details and application of wavelet analysis in movement data will be discussed in the subsequent chapters.

1.2.3 Research Questions

This work is essentially methodological, and can be summarized by two fundamental questions that have been investigated in this thesis:

- i. Can wavelets be used as a mathematical tool to analyze temporally localized statistical properties of movement trajectories to derive ecological answers
- ii. Can animal movement be explained as a transitions between different modes of movement with multiscale properties

1.3 Empirical data used

The tracking data of Lesser Black-backed gulls (*Larus fuscus*) was provided by Sovon, the Dutch Centre for Field Ornithology, Beek-Ubbergen, the Netherlands, and used as the empirical data for each of the chapters. The Lesser Black-backed gulls were tracked using GPS PTT's (Platform Transmitting Terminal) as part of The European Space Agency (ESA) FlySafe Project (Ens et al. 2008). The aim of the project is to "Integrate different existing space and non-space systems across national borders to improve military flight safety by reducing the risk of bird aircraft collisions" (Ens B.J. 2008).

In May-June 2007, 14 Lesser Black-backed gulls were caught from their nest in Vlieland using the self-operating fall trap. Each of these was equipped with

solar powered Argos/GPS PTT manufactured by Microwave Telemetry Inc. The GPS PTT had a 3-year operating time and a GPS accuracy of ± 18 m. Two kinds of GPS PTT's were used; 22 g recorded only the location, and the 30 g PTT that also recorded the altitude above sea level (accuracy ± 22 m), heading (accuracy $\pm 1^\circ$) and ground speed (accuracy ± 1 km/h). The duty cycles for the transmitters were as follows:

22 g transmitters:

- A. fixes every second hour from 8:00 – 18:00 (6 fixes per day)
- B. like A, plus fixes at 1:00, 3:00, and 23:00 (9 fixes per day)

30 g transmitters:

- C. fixes from 0:00 – 24:00, 2 hour steps (12 fixes per day)
- D. fixes from 5:00 – 22:00, 1 hour steps (18 fixes per day)
- E. fixes from 0:00-24:00, 4 hour steps (6 fixes per day)

The data was transmitted according to the SiV™ Technology meaning that the transmitters attempted to communicate with a satellite only when there was a satellite in View (SiV). The transmitters were programmed to make contact with the Argos satellites every three days with a repetition period of 60 seconds to send the data. The data are packed into messages containing five or three positions, depending on whether the transmitter is programmed to take 2D or 3D GPS fixes. The data from the GPS-PTT was collected by the Argos /CLS system, Toulouse, France. The data was initially received via email every four days and later downloaded directly from the ARGOS server SARA. The data is now stored in the ESA SARA database.

An important aspect of the data to be considered is that the number of fixes received was found to be almost always less than that expected in each duty cycle. The reason for the variation in the number of fixes, especially during the winters (for birds wintering in the north) was because the GPS PTT's used were solar powered, and did not receive sufficient light levels during these months. The gaps in the data were accounted for by using smoothing techniques as discussed in the chapters.

1.3.1 Movement and behaviour of Lesser Black-backed gulls

Understanding how animals perceive and use their environment requires fine-grained movement data in their natural environment. Such data is now available from satellite tracking and GPS tracking data (Weimerskirch et al. 2002). The rationale behind using the tracking data of long distance migrating birds like the Lesser Black-backed gulls lies in the fact that they have a large spatial spread, show a wide range of movement behaviour and their ecology is well documented to test mathematical models to biological

hypothesis.

Fourteen (10 males/4 females) adult Lesser Black-backed gulls were tracked using Argos-GPS solar-powered Platform Terminal Transmitters (PTTs) (Microwave Telemetry Inc., Columbia, MD, USA) from their breeding colony in Vlieland, The Netherlands to their wintering sites in France, Portugal, Spain, and Morocco, and sometimes in England (Ens B.J. 2008). Most populations of this species are fully migratory and travel in stages, using many stopovers en-route. The autumn migration starts with the departure of non-breeding birds in late-June, the breeding birds following from late-July to September. The return migration takes place between February and late-June, with the species arriving at breeding colonies from March onwards, and breeding from late-April or May to mid-June. They breed in a colony, often with other gull species (especially Herring Gull (*Larus argentatus*), with the colonies ranging in size from a few pairs to several thousands (Camphuysen 2011; Davis and Dunn 1976). Outside of the breeding season, the species remains gregarious, normally migrating individually or in small groups of less than 10, and often feeding in flocks of hundreds of individuals on rubbish dumps or over shoals of fish at sea. It may feed singly or in small groups. Outside of the breeding season, the species chiefly inhabits inshore and offshore seas lagoons, estuaries, large lakes, rivers, canals, river weirs, flood-lands and sewage treatment areas. The species is an omnivorous, opportunistic feeder that forages extensively at sea. Its diet consists of small fish (especially Baltic herring (*Clupea harengus*), aquatic and terrestrial invertebrates (e.g. beetles, flies and larvae, ants, moths, grasshoppers, crustaceans, molluscs, segmented worms and starfish), bird eggs and nestlings, carrion, offal, rodents, berries and grain. It often follows fishing fleets, feeding on material discarded from the catch. In both seasons, it is often seen foraging on arable land, pastureland, and on refuse dumps. The population breeding in the Vlieland region has been studied extensively. The tracking data now gives an opportunity to analyse their movement away from the breeding grounds and provide a better understanding about the movement behaviour of the birds.

Figure 1-1: Photos show 1) the 22g and 30 g solar powered GPS Platform PTT 2) Lesser Black-backed gull with a mounted PTT 3) Breeding site on the island Vlieland, The Netherlands. (courtesy for photo 1 and 2: Report FlySafe project (Ens B.J. 2008))

Figure 1-2: Plot of GPS fixes of 14 Lesser Black-backed gulls from June 2007 to June 2010 attached with GPS PTT's showing a general picture of the breeding site, the migratory route and the wintering sites.

1.4 Overview of chapters

The various chapters of this thesis advance the use of wavelets as a robust practical method to address the major problems in movement analysis as well as predict ecological processes, viz.:

- i. **Chapter 2:** In this chapter, distinct strengths of fractals and wavelets analysis paradigm are used for better understanding animal movement behaviour and factors influencing movement at different spatio temporal scales.
- ii. **Chapter 3:** In this chapter, we demonstrate the usefulness of cross wavelet analysis (as a signal for correlation between two signals) for the segmentation of movement trajectories into extensive and intensive search strategies.
- iii. **Chapter 4:** This chapter proposes an approach to detect behavioural change points in animal movements at migratory scales using discrete wavelet transforms. We compare two methods by applying the already accepted Lavielle method (Lavielle, 1999, 2005) with discrete wavelet analysis.
- iv. **Chapter 5:** In this chapter, we mine periodic behaviour of moving animals in relation to periodic environmental cues by using cross wavelet analysis and show relevant correlations.
- v. **Chapter 6:** This chapter is based on concluding thoughts on the role of wavelets as an important movement analysis tool that consolidates the different paradigms in movement ecology. We use Tinbergen's framework for animal behaviour study unite the analytical framework of the thesis to a theoretical one.

2 Concurrent use of fractals and wavelets for spatial-temporal analysis of animal movement patterns

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2.1 Introduction

Studies since the 1980's have stressed the importance of spatial and temporal scales in relation to animal behaviour and resource selection (Johnson et al. 2002; Johnson 1980; Levin 1992; Wiens 1989). Within the paradigm of animal behaviour studies, recent advances in telemetry techniques have enabled scientists to gather empirical evidence about movement ecology in particular (Brooks and Harris 2008; Fortin 2003; Weimerskirch et al. 2002). Detailed knowledge about the positional data of animals provides a huge repository to analyze movement patterns across a range of spatial and temporal scales (Weimerskirch et al. 2002). Since adjustments in animal movements are triggered by hierarchical spatial distribution of foraging resources and environmental factors (Bissonette 1997) in confluence with the physiological state of the animal, it becomes important that such movement adjustments and their triggers are studied at the right scale as perceived by the animal (Johnson et al. 2002). In this regard fractal and wavelet analyses have proved successful in analyzing movement across a range of spatial and temporal scales respectively (Fritz et al. 2003; Wittemyer et al. 2008). We therefore provide a novel and innovative method to explore cross scale movement pathways in spatio-temporal domains.

To efficiently identify behavioural processes and landscape patterns affecting movement, studies should be undertaken at the spatial and temporal scales at which the behavioural response is affected. Random or subjective choice of scales may result in failure to measure movement responses to variables relevant to a particular category of behaviour. For example, at a very fine spatial resolution variations in habitat types may result in disjointed patches, which in reality do not affect the movement of animals. While at a very coarse resolution, suitable and unsuitable patches may be clumped together also resulting in errors in interpretation (Milne et al. 1989). Thus, the complexity of factors affecting movement patterns might be masked or misinterpreted if not analyzed at the appropriate scale.

Techniques for analyzing movement patterns in space and time are constantly being updated. Investigating behavioural ecology studies shows that for decade's biologists have been analyzing animal pathways at different scales. However, they have relied on different data sources for different scales of analysis (Alerstam 1996; Fryxell et al. 2008). Therefore multiscale pattern analysis i.e. processes occurring across a range of spatial and temporal scales, are increasingly being recognized as an important feature for understanding dynamics in ecology. Looking at methods for multi-scale analysis of movement data it becomes apparent that most studies focus on

understanding the biology, but biologist often don't stress on methods (Laube 2010) that allow statistical analysis of multi scale studies.

The fractal dimension has been repeatedly used to quantify patterns in movement (Webb et al. 2009) since the time it was first used to characterize the tortuosity of animal pathways (Dicke and Burrough 1988; Seuront 2010). Fractal analysis has been widely used to describe movement patterns for a wide variety of organisms across a range of spatial scales (Salvatori et al. 1999). Mandelbrot (1982; 1977) was the first to use the term "fractal" to describe a geometric form that shows self similarity. Exactly self-similar geometric forms are perfect fractals at all spatial scales. Fractals in nature however do not show exact self-similarity and are therefore called statistical fractals (Doerr and Doerr 2004). They tend to show variable degrees of statistical self-similarity over a limited range of scales. This existence of stepwise behaviour (changes in fractal dimension when shifting between scales) implies that partial self-similarity is observed over limited ranges of scales separated by transition zones.

The divider method to measure fractals can be adapted to measure fractal dimension (D) over a wide range of scales (Krummel 1987; Nams 1996; Seuront 2010; Sugihara and M. May 1990). As mentioned earlier, because the driving processes acting on the organisms differ at different scales, the related fractal dimension of the trajectory shows the desirable property of being constant over a limited range of measurement scales (Seuront 2010; Wiens 1989). Such changes in value of the fractal dimension with scales, are useful to identify spatial scales associated with movement behaviours (Seuront 2010; Wiens 1989). Abrupt changes in the value of the fractal dimension with change in scale indicate that a new set of environmental or behavioural processes have become significantly important causing characteristic changes in movement patterns (Fritz et al. 2003). For example, the effect of home range behaviour, patchiness in the environment, or limited resource availability may cause abrupt changes in movement behaviour (Doerr and Doerr 2004; Sugihara and M. May 1990). This property has been widely used in animal movement studies to identify spatial scales where the environmental constraints acting upon organisms change rapidly (Fritz et al. 2003; Nams and Bourgeois 2004). Using this concept, Fritz et al. (2003) were able to apply fractals to identify various scales and boundaries between scales where wandering albatrosses (*Diomedea exulans*) changed their foraging search movements across five orders of magnitude (10 m to 1000 km).

As fractals are capable of identifying patterns across a range of spatial scales, models that incorporate temporal scaling range from complicated state space models to those that use the strength of first order autocorrelation in the

directionality of movement (Forester et al. 2007; Jonsen et al. 2003; Polansky et al. 2010; Wittemyer et al. 2008). An effective technique that successfully captures patterns of temporal auto-correlation across a range of temporal scales is the wavelet method (Time-frequency method). Testing the method on wild African elephant movement patterns, lions (*Panthera leo*) and African buffaloes (*Suncerus caffer*), Wittemyer et al. (2008) and Polansky et al. (2010) have provided evidence of temporal dependencies in movement patterns at multiple scales.

The concept behind using temporal auto-correlation in movement pathways as a statistical signature is that temporal correlations in movement data indicate periodic behaviours. Such periodicity in movement behaviour can be a product of repetitive environmental (e.g., light, temperature, and resource availability) and physiological (e.g., need for food and water, reproduction, and memory) triggers affecting the animal (Wittemyer et al. 2008). The time-frequency method of wavelet analysis is capable of providing compact summaries of temporal autocorrelation and therefore shows diurnal and seasonal based periodicities.

In ecological systems, non-stationary data are difficult to analyze with traditional time series methods (Cho and Chon 2006; Kim et al. 2006). Movement data such as time series of step length, turning angle, direction of movement and speed calculated from the tracking data of animals have non-stationary properties. The wavelet method is then extremely useful to analyze, visualize and manipulate such complex non stationary data (Schmidt and Skidmore 2004). Wavelets are capable of handling irregular data sets that are aperiodic, noisy and intermittent, representing complex structures without the knowledge of the underlying mechanisms and finding scale dependent regularities.

Although theoretical interpretation of movement patterns on a temporal scale has been undertaken in a spatial context and vice versa, most current techniques of animal movement analysis do not successfully incorporate an integrated analysis based on multiple spatial and temporal scales (Si et al. 2009b; Si et al. 2010). In this paper, a method is proposed to identify dominant spatial scales using fractals and to explore dominant temporal signatures using wavelets in each of these spatial domains. The patterns in spatio-temporal movement behaviour are explored using data collected on the Lesser Black-backed gull (*Larus fuscus*). The analytical framework was used to compare movements during the breeding and wintering seasons, concentrating mainly on foraging routines. The seemingly chaotic movement patterns of birds often have a distinct nested spatio-temporal pattern requiring logical statistical methods to be distinguished. Fractals and wavelets in combination can prove to be excellent tools in interpreting some of these

emerging patterns from the complex tracking data collected for a large numbers of animals.

The assumption is that movements associated with small spatial scales are associated with daily behavioural patterns, and can be expected to show daily temporal signatures using wavelet analysis. In contrast, movements in larger spatial domains (i.e., larger distances) are often associated with behavioural activities such as stopovers, and patch-to-patch movements, so can be assumed to show temporal signatures ranging from a few days to a few weeks.

Thus, the aim of this study was to develop a method of concurrently using fractals and wavelets to identify animal movement patterns across spatio-temporal scales.

2.2 Methods

2.2.1 Animal tracking data

The tracking data on the Lesser Black-backed Gull (*Larus fuscus*, hereafter gull) used for this study were provided by the Avian Research Institute, Wilhelmshaven, Germany and SOVON Dutch Centre For Field Ornithology, Nijmegen, The Netherlands. The gulls were tracked using GPS satellite transmitters as part of The European Space Agency Fly-safe Project (Ens B.J. 2008). In May-June 2007, 14 gulls (10 males and 4 females) were caught in Vlieland, The Netherlands, using a self-operating fall trap. Each bird was equipped with an Argos-GPS solar-powered Platform Terminal Transmitter (PTT; Microwave Telemetry Inc., Columbia, MD, USA). The Argos-GPS PTT's have an accuracy of ± 18 m. Two kinds of PTT's were used in this study. The 22 g PPT, which recorded only location, was fitted to six gulls, while the 30 g PTT, which also recorded the altitude above sea level (accuracy ± 22 m), heading (accuracy $\pm 1^\circ$), and ground speed (accuracy ± 1 km/h), was fitted to eight gulls (Ens B.J. 2008).

The Argos data for eleven of the gulls (9 males and 2 females) were used for this study, for the year 2007, which provided the maximum number of fixes. We analyzed and compared movement patterns only during the breeding and wintering seasons and not during migration. Since the attempt was to extract spatial scales around a central region and then test the temporal patterns within these spatial scales, the inclusion of the migratory section of the trajectory was not feasible in this study. We used the continuous position of the animal in time. Missing data values (due to lacking GPS fixes) were estimated using expected values from a Kalman smoothing algorithm (Stoffer

2008) obtained from a state space model. The smoothing technique was executed in R environment (R Development Core Team 2010) (Appendix A).

2.2.2 Fractal Analysis

We segregated the movement paths of individual birds into those associated with breeding and those associated with wintering and used 30 days in each season to analyze the movement pathways. Fractal Dimension (D) of these pathways was calculated for each season using the program Fractal 3.16 (Nams 2006). The employed fractal mean estimator uses the traditional divider method (Dicke and Burrough 1988). However it also incorporates replication by re-measuring the path multiple times with each divider size, beginning from randomly selected points along the path, thereby correcting for truncation in the measurement of gross distances (Nams 2006).

We applied the Fractal Mean Estimator to a series of narrow windows of spatial scale to estimate fractal D at various scales. To ensure that fractal D formed an effective measure of tortuosity (Doerr and Doerr 2004; Webb et al. 2009), the same range of spatial scales was used for all the birds, ranging from 0 to 400 km (maximum distance flown during the seasons). To estimate fractal D at each position of the window, $\log(\text{path length})$ was regressed versus $\log(\text{spatial scale})$. The $\pm$ window used for fractal was 0.25 at each scale. Window range is the width of a window on the spatial scale axis used for each fractal D estimate, and is expressed as a proportion. If the window range is 0.25, then the window of scales used ranges from a minimum of $[\text{middle scale} / 1.25]$ to a maximum of $[\text{middle scale} \times 1.25]$.

Plotting the fractal dimension for each sliding window led the detection of major and abrupt changes in fractal D with spatial scale (Fritz et al. 2003; Nams 1996). We then defined scale domain as the first significant break in the slope of relationship between path length and divider size (Fritz et al. 2003; Vilis and Maryse 2004) i.e. a broken line regression with two line segments was fit to the data to estimate the breakpoint of the domains (Vilis and Maryse 2004). This was used to define the scale dependent spatial domains where animals change their movement patterns (i.e. adjust path tortuosity).

Typically, the value of fractal D ranges from 1.0 to 2.0 but in some cases surpasses 2.0 D's. Values close to 1 indicate trajectories that resemble straight line pathways, while D equals 2 indicates a line so tortuous that it folds back on itself to completely fill a plane. $D > 2$ arises when the movement trajectory crosses itself a number of times creating an additional dimension through the overlapping of lines (Mandelbrot 1984; Webb et al. 2009) (Figure 2.1).

Figure 2-1: Interpretation of fractal dimension values in relation to the movement ecology of the Lesser Black-backed gull. Figure a) shows the trajectory of one Lesser Black-backed gull, figure b) depicts simplified graphic versions of parts of the trajectory with special emphasis on the patch structure of the environment, and figure c) highlights the approximate corresponding values of Fractal Dimension D to the movement patterns in figure b).

2.2.3 Wavelet analysis

Descriptive movement parameters (i.e., step-length, speed and net-displacement) were first calculated. Net displacement (displacement from a central location) formed an indicator of behavioural response. The net displacement data was segregated into two major spatial domains (which were identified by fractal analysis). To create a time series in the one spatial domain, displacement which occurred in that domain were retained and all other displacement was assigned null values. Wavelet analysis was then conducted to discern dominant periods and temporal patterning within each spatial domain.

Wavelet analysis allows for local estimation of dominant frequencies in time series X_n by employing functions (wavelets) that are dilated or contracted versions of an analyzing wavelet (function) ψ , translated across the time series. The continuous wavelet transform of the discrete time series X_n at scale a and time t_i is defined by

$$W[a, t_j] = \frac{1}{\sqrt{a}} \sum_{l=1}^N X_l \psi^* \left[\frac{(l-j)\Delta t}{a} \right] \quad \text{Equation 2-1}$$

Where ψ^* denotes the complex conjugate of the analyzing wavelet function ψ .

We used the Morlet mother wavelet. The Morlet wave function is a damped complex exponential wavelet. Being a complex wavelet, it provides information on both amplitude and phase, making it better adapted to analyzing oscillatory behaviour (Torrence and Compo 1998). The Morlet wavelet also suited this study because of its periodic property and the one to one relationship between its periods with scale (Polansky et al. 2010). For the Morlet, which has several smooth oscillations, the period is a well-defined quantity and it has the required property of showing changes with different analyzing scales (Torrence and Compo 1998). The Morlet wave function is defined as:

$$\psi(\eta) = \pi^{-1/4} \exp(-i\omega_0\eta) \exp(-\eta^2/2) \quad \text{Equation 2-2}$$

where ω_0 controls the oscillation frequency and was chosen to be 2π . The choice of scales (frequency) was chosen as a set of discrete values defined by $a_k = S_0 2^{k\Delta k}$, $k = 0, 1, \dots, K$, where $S_0 = 2\Delta t$, and Δk and K depend on the analyzing wavelet, length and resolution of the data (Torrence and Compo 1998).

The results of the wavelet analysis are represented in a scalogram or power spectrum. A scalogram is a data array of squared modulus values of the wavelet transform. High values in the scalogram array distinguish the time where the frequency of the time series X_n matches with the Morlet wavelet at a specific scale. Regions of the scalogram were deemed significant by a bootstrapped test. Significant scalogram values were defined as those that were greater than or equal to the 0.95 sample quantile of a 1000-bootstrapped scalogram of red noise null model fit to the data (Jevrejeva et al. 2003; Maraun and Kurths 2004; Maraun et al. 2007; Polansky et al. 2010; Torrence and Compo 1998). This procedure, known as the "area-wise test" (Maraun et al. 2007), removes spurious areas of significant scalogram values deemed insignificant by a bootstrapping test (Maraun et al. 2007; Polansky et al. 2010). The wavelet analysis and the scalogram values showed the temporal auto-correlation of the net displacement across different temporal

scales. Maximum and significant scalogram values were used to identify dominant temporal scales. These dominant temporal scales were related to ecological and spatial patterning in order to understand changes in behavioural modes. The wavelet analysis was done in the Matlab package for performing Cross wavelet and Wavelet coherence analysis (Downloadable from the site <http://www.pol.ac.uk/home/research/waveletcoherence/>).

2.3 Results

2.3.1 Fractal Analysis

Fractal analysis of the breeding and wintering trajectories of 11 individual gulls consistently exhibited an increase in the value of fractal D with scale, with apparent discontinuity (abrupt changes in the value of D). In this study, the value of fractal D ranged from 1 to 2.69 during the breeding season and from 1 to 2.74 during the wintering season (Figure 2.2). Two major changes in the value of fractal D (break in slope of the plot between the log of gross distance and the log of spatial scale) were identified during the breeding and wintering seasons, which defined transitional points separating the distinct nested domains. During the breeding season the first domain was identified at a spatial distance of 18.68 km ($\sigma = 7.51$ km) and a second domain from 18.68 km to 85.0 km ($\sigma = 24.27$ km) (Table 2 and Figure 2.2). The break points in the value of fractal dimension (D) during the wintering season were found to be centred at mean values of 19.91 km ($\sigma = 7.31$ km) and 87.09 km ($\sigma = 30.96$ km) (Table 2 and Figure 2.2).

Indistinct sub domains within these domains were also identified. Such sub-domains however did not show distinct temporal signatures and were therefore not considered for the wavelet analysis.

2.3.2 Wavelet analysis

Wavelet analysis of net displacement without segregating into domains did not reveal any distinct temporal signatures. Significant scalogram values from the wavelet analysis reveal time periods when the animal is mobile and away from the nest. Wavelet analysis of net displacement showed that the animals were active and mobile either once every 12 hours or once every 24 hours during the breeding and wintering season within the first spatial domain. These can be considered as cyclic a movement, that is 1, 2 cycles of movement per day (24 or 12 hour period). Thus, movement behaviour within the spatial scale categorized as Domain 1, during the breeding as well as the wintering seasons showed 1 or 2 cycles per day as seen in figure 2.3 and 2.4. Net displacement in domain 2 during the breeding season showed higher cyclic periods of 2 days or more (Figure 2.5). However, significant scalogram values in this domain were limited indicating only transient movement bouts

far from the nesting sites. Net displacement in domain 2 during the wintering season does not show very distinct temporal patterning at higher periods as seen in the breeding season (Figure 2.6). The figures also show individual variations in movements across multiple scales.

The distinct auto-correlative structure in the movement pathway is a function of the distance that the animal moves from a central location (net displacement) and it can be used to distinguish variations in movement modes. Diurnal movement patterns of birds probably indicate periods of resting and roosting followed by phases of feeding movement bouts. The significant scalogram values appear to be related to the time periods of movement bouts during the morning and evening hours. Evidence of this daily cyclic behaviour is reiterated by the box plot of step-length to time of day (time budget) for the breeding and wintering seasons (Figure 2.7). The time budget of step length of all the birds during the breeding as well as the wintering season shows cyclic periods of movement with longer step lengths followed by periods of rest (roosting). Although both seasons show at least two cycles of long movement bouts per day, there is variation in when they occur during the breeding and wintering seasons. These daily phases of movement during the breeding season occur from 5 to 10 am and from 3 to 10 pm. The wintering season also shows two cycles; from 9 am to 2 pm and from 6 to 10 pm. This corresponds to differences in movement seen in the wavelet analysis as well.

Table 2: Transition zones (T1, T2, T3, T4) and Domains (D I, D II) of movement trajectories of 11 birds (identified by the Bird Id Numbers) during the breeding and wintering season obtained through fractal analysis.

Breeding		Bird ID											
Transition zones (km)		41745	41749	41752	41757	41758	41762	41763	41764	41767	41771	41781	
T1	5	6	9.5	3	10.5	5	4	4	4	10	8	6.5	
	15	22	26	8.5	37	11	14	15	15	15	14	15	
	35	33	81	21.5	117	19	25	26	22.5	37	26	26	
	82	63	119	93	133	98	62	62	88	64	71	71	
D(I)	d1	11		7.5		3.0		10.5		6.500		2.6268	
	d2	11		26.0		11.0		37.0		18.682		7.5176	
	d3	11		98.0		19.0		117.0		41.500		30.0957	
	d4	11		71		62		133		85.00		24.269	
Wintering													
Transition Zones (km)		41745	41749	41752	41757	41758	41762	41763	41764	41767	41771	41781	
T1	6	6	16	3	5	5	5	10	10	12	4	11	
	12	24	37	18	10	14	17	23	20	22	22	22	
	33	62	69	19	20	24	31	34	38	72	28	28	
	61	78	129	93	96	63	80	67	85	155	51	51	
D(I)	d1	11		13		3		16		8.00		4.050	
	d2	11		27		10		37		19.91		7.314	
	d3	11		53		19		72		39.09		19.367	
	d4	11		104		51		155		87.09		30.963

Figure 2-2: Fractal D versus scales of movement trajectories for 11 birds over 3 years during the breeding (May, June, and July) and wintering season (November, December and January).

Figure 2-3: Wavelet scalogram of net displacement time series of 11 individuals during the breeding season in domain 1. Larger squared modulus values correspond to warmer colours (red, yellow) and smaller values correspond to cooler colours (blues). The thick black cone denotes the cone of influence outside of which modulus values are affected by zero padding and are not to be considered. Temporal regions of significant scalogram values are defined as those that lie inside the black closed lines.

Figure 2-4: Wavelet scalogram of net displacement time series of 11 individuals during the breeding season in domain 2. Larger squared modulus values correspond to warmer colours (red, yellow) and smaller values correspond to cooler colours (blues). The thick black cone denotes the cone of influence outside of which modulus values are affected by zero padding and are not to be considered. Temporal regions of significant scalogram values are defined as those that lie inside the black closed lines.

Figure 2-5: Wavelet scalogram of net displacement time series of 11 individuals during the wintering season in domain 1. Larger squared modulus values correspond to warmer colours (red, yellow) and smaller values correspond to cooler colours (blues). The thick black cone denotes the cone of influence outside of which modulus values are affected by zero padding and are not to be considered. Temporal regions of significant scalogram values are defined as those that lie inside the black closed lines.

Figure 2-6: Wavelet scalogram of net displacement time series of 11 individuals during the wintering season in domain 2. Larger squared modulus values correspond to warmer colours (red, yellow) and smaller values correspond to cooler colours (blues). The thick black cone denotes the cone of influence outside of which modulus values are affected by zero padding and are not to be considered. Temporal regions of significant scalogram values are defined as those that lie inside the black closed lines.

a)

b)

Figure 2-7: a) Time budget: step-length during each hour of the day during the breeding season averaged for 11 birds for three years (2007-09). b) Time budget: step-length during each hour of the day during the wintering season averaged for 11 birds for three years (2007-09). On each box, the central mark is the median, the edges of the box are the 25th and 75th percentiles, the whiskers extend to the most extreme data points that the algorithm considers to be not outliers.

2.3.3 Combined information from fractals and wavelets methods

Combined information from the fractals and wavelets methods can be visualized in figure 2.8. It represents the movement of a single bird during the breeding season, indicating the derived information on the bird's behaviour by combining fractal and wavelet analysis. The plot of fractal D versus scales shows two abrupt changes in the value of D with scale indicating distinct spatial domains where movement patterns change. A plot

of the positional data of the bird during the breeding season has been shown with circles indicating the two spatial scales where movement changes around the nesting site (from the fractal analysis). Wavelet analysis within each of these domains helps to identify the dominant temporal signature and infer behaviour associated with the spatial scales. Results from the wavelet analysis in the first domain show dominant movement cycles at 12 and 24 hrs; that is 1 or 2 cycles per day, 20 km around the nesting site, indicating close range foraging. Results from domain 2 indicate dominant movement cycles between 3 and 10 days. These movements in a range of 20 to 85 km around the nesting site are not daily movements and possibly indicate infrequent foraging bouts. Temporal analysis of movements beyond domain 2 (more than 85 km) did not reveal distinct temporal signatures and were therefore not useful for the interpretation of movement behaviour.

Figure 2-8: An example of trajectory analysis for a single bird using fractals and wavelets and the information that can be derived from it.

2.4 Discussion

The results indicate that given the large number of drivers that act as plausible trigger for movement in animals, the integrated approach using fractals and wavelets is useful for exploratory data analysis at scales where

behavioural processes and bio-physical factors could be affecting movement (Dalziel et al. 2008). These tools identify the spatial and temporal scales as perceived by the animal, rather than scales defined and perceived by humans (Ferguson and Elkie 2004).

The distinct changes in the fractal D 'transitions' indicate that the patterns of movement of the animal change across scales. The spatial range of an animal may be divided into regions, 'domains', where different aspects of the animal's biology are important. These changes in fractal D with scale suggests that the organisms change the way in which they view and interact with their environment at that scale. Searching for resources, traversing the home range or dispersing to new habitats are all likely to be very different types of movement conducted in different "domains" of scale (Wiens 1989). The fractal analysis shows that it is possible to test this idea and to identify transitions between domains and looking for abrupt changes (Nams 2005). This method defines scales at which constraints or behavioural decisions operate.

Fractal analysis provides an indication that movement modes change with spatial scale, but does not provide adequate knowledge to understand the movement behaviour in each domain. Testing the auto-correlative properties in movement pathways in the spatial domain is a straightforward and rapid method of identifying behavioural changes occurring in these domains. The time frequency method of wavelet analysis is effective in identifying significant periods of auto-correlative movement patterns versus random movements at each spatial scale. The theory behind such movement signatures is that highly repetitive movements may offer optimal utilization strategies for resource and space use when ecological conditions are seasonally static (Conradt et al. 2000; Weimerskirch et al. 2000). In these situations a high degree of auto-correlated movement results in risk reduction and energy conservation for various biological activities (Wittemyer et al. 2008).

The results from the wavelet analysis provided a statistical description of the auto-correlative patterns of movement in each spatial domain. In the first spatial domain, daily cycles of movement and rest periods were evident. Such behaviour is consistent with observations of Lesser Black-backed gulls made in the field and known behaviour for Lesser Black-backed gulls (Davis and Dunn 1976). Lesser Black-backed gulls are known to be pelagic with frequent trips to the open sea for foraging (Klaassen et al. 2012; Shamoun-Baranes et al. 2011). There is movement towards the feeding grounds during the early morning and evening hours followed by prolonged periods of roosting. There is however, variation in what time of the day they prefer to move during the two seasons. These variations probably are strongly related

to day length that varies in the course of the year. Daily cyclic movements could also be related to foraging activities in relation to tidal cues. In a study by Shamoun-Barnes, J. (2011), high resolution temporal data for the same species revealed that the gulls have an interesting behavioural pattern of sitting on the sea surface and drifting passively with the tidal currents.

Although the temporal signatures in the second domain were not consistent for all individuals, a strong inclination towards temporal signatures in the range of 2 days and more indicate that the gulls do make transient trips of more than 85 km distance. Lesser Black-backed gulls nesting on the island of Vlieland are known to make long distance movements away from the nest, which could correspond to the movement signature obtained in the second domain (Ens B.J. 2008). However, it is difficult to explain the exact behavioural implication of these long distant moving bouts and needs combined exploration into other factors such resource distribution, environmental factors and stage of migration. Studies from breeding colonies in Texel, The Netherlands, suggests that these directional movement far into the sea might be in relation to scavenging activities around fishing trawlers (Camphuysen 2013). Individual variation existed in the maximum distance travelled away from the nest as well; while some individuals were observed to travel only to the neighbouring mud flats of the Wadden sea area during the breeding season, others were observed to travel to as far as the United Kingdom, Belgium and the North of France (Ens B.J. 2008). Individual variations during the breeding season almost certainly depends on whether the birds have a nest with eggs or chicks or not (Klaassen et al. 2012). An interesting pattern worth mentioning is that some Lesser Black-backed gull have been observed to make frequent long range flights (upto 180 km)(Ens B.J. 2008) just before it embarks on its migratory flight known as pre-migratory trips and post migratory trips (Ens B.J. 2008; Klaassen et al. 2012). The reason for this kind of movement is unknown but could be governed by fuel deposition rates, flight mechanics and migration strategies of the birds (Alerstam 2001). Klaassen, R. H. G. et al. (in press) proposed that such movements were probably related to exploring sites for stopover, as some of the birds returned these sites on their return migratory journeys.

Due to changes in habitat on a seasonal scale and the physiological state of the animals, responses in movement patterns of the gulls based on the results presented allow the inference that the gulls switch between two spatio-temporal scales: 1) localized resource utilization (daily feeding bouts) 2) movement between habitat patches. The information obtained from such initial statistical analyses of movement pathways is critical for designing monitoring techniques over prolonged periods to garner information on foraging specialization, area restricted search patterns, and critical habitats for animals. For instance, the knowledge that Lesser Black-backed gulls are

making daily cyclic movements over a range of 0 to 20 km around a central location, corroborated with the knowledge about the general behaviour of the birds, can help deduce that this buffer area is mostly being used for the purpose of foraging and roosting. Context specific decisions can thus be made regarding scale for undertaking studies related to foraging strategy, socio-spatial processes and landscape properties: a scale as perceived and prioritized by the animal under study.

A limitation in the present study was that data at higher temporal resolution was not available. Such data could have allowed results that are more accurate on changes in spatial scales and temporal signatures in these spatial domains. However even high resolution data are not sufficient to predict precise boundaries in the spatial and temporal domains where behavioural modes change. An accurate breakdown into spatio-temporal domains will be attempted in further research and for that, it is essential that environmental covariates and expert knowledge about the species are supplemented and that these variables are as comprehensive as the trajectory data used.

3 Wavelet analysis of space-time movement trajectories for detecting animal behavioural change

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3.1 Introduction

Significant differences in the dynamic behaviour of moving animals can be explained by the animal's internal state, motion capacity, navigation capacity and the prevailing external condition (biotic and abiotic environment) (Nathan 2008). Individual animal movement models that attempt to capture these complex and dynamic movements can be difficult to generalize across diverse species. This is because animals use a continuum of strategies adjusting their decision based on the environmental factors such as availability of forage, biological interactions such as competition and predation as well as others factors like the stage of reproduction. Therefore, the question arises whether new models can factor in these variables without requiring subjective interpretation. One way of attempting this is to resolve movement behaviour into periodic cycles that reflect the animal's behavioural responses to the multidimensional variables affecting its movement. Empirical studies using periodic data sets are producing innovative results in movement ecology especially with the application of wavelets. It is a step forward towards the much required trans-disciplinary effort of mathematicians and ecologists to generalize techniques. This can help to quantify the statistical properties of moving animals and make conceptual advances (Giuggioli and Bartumeus 2010).

The challenges in analysing animal movement data has resulted in the adoption of sophisticated mathematical models showing statistical properties across different taxa (Giuggioli and Bartumeus 2010; Nathan 2008). The most common movement models are correlated random walk models (Bartumeus 2009; Bergman et al. 2000; Gurarie et al. 2009; Kareiva and Shigesada 1983; Nams and Bourgeois 2004; Shigesada 1980) which introduce step-length and turning angle distributions. Correlated random walk estimations have been effectively used to describe movements in relation to environmental and habitat variables (Gurarie et al. 2009). However, one problem in the use of these models is the difficulty arising due to gaps in tracking data, resulting in erroneous turning angle distributions (Block et al. 2005; Gurarie et al. 2009; Jonsen et al. 2007). In addition, when movement is observed over an extended period of time, heterogeneity in movement such as feeding, resting, and migrating, require more refined models that capture these movement types as a mix of behavioural modes. These are the Bayesian (probabilistic or likelihood) models which require some form of a priori information about the movement patterns and the ecology of the animal (Gurarie et al. 2009; Morales et al. 2004).

Diffusion and Levy walk distributions have also been used to describe search patterns and movement behaviour of animals which take spatial and temporal dimensions into consideration (Metzler and Klafter 2000). The Levy

walk theory is based on the premise that for an optimal search strategy for randomly distributed resources the animal uses a combination of short steps with intermittent long movement bouts, conforming to an inverse power law (Bartumeus et al. 2005; Viswanathan 1999).

Given the large number of factors influencing an individual and the complexity of parameter selection while modelling movement data, we propose a generalized technique of wavelet analysis to extract behavioural changes in movement data. Large numbers of periodic factors such as oscillations in light, temperature, resource availability and physiological state result in movement behaviours such as feeding, resting and migrating that have a temporal dependence and periodicity over a range of scales (Polansky et al. 2010). Standard statistical methods which assume spatial and temporal independence over time are unsuitable for analysis of periodic time series such as those produced by moving animals (Shumway and Stoffer 2011). Wavelet analysis has been demonstrated to be valuable in detecting these periodicities in animal behaviour (Wittemyer et al. 2008).

Time series data based on the notion of regularity and variations of the underlying phenomenon of interest over time, can be effectively analysed by wavelets that can track localized changes in signal. Wavelets are classes of wave like functions that can be used to capture signal features such as break-points and self-similarities (Bibian et al. 2001b). They can therefore track changes over time as well as over scales providing time-scale localisation of behavioural processes.

The wavelet transform of a time series decomposes the data using a wavelet function. The decomposition of the data series results in wavelet coefficients for each time stamp (Block et al. 2005; Ferguson and Elkie 2004). Scale in a wavelet analysis is generated by contraction and dilation of the wavelet function. Contraction or dilation changes the time window over which the wavelet function is applied (Polansky et al. 2010). Thus for each time stamp as well as each scale we obtain a wavelet coefficient value, thus providing information on changes in movement patterns over time as well as scale. As movement is a dynamic process, it often requires two variables to describe changes in behaviour. Therefore, in this paper we use a bivariate extension of the commonly used continuous wavelet transform. Cross wavelet and wavelet coherent analysis allows the use of two time series data together to explore the changes in movement behaviour in animals (Hudgins 1993; Maraun and Kurths 2004; Torrence and Compo 1998). While cross wavelet provides information about correlation between two signals, cross coherency exposes areas of strong local correlation and phase locked behaviour (Grinsted 2004). Since the technique has not been used for GPS tracked animal movement

data before, it provides an alternative and promising method of analysing multiscale movement data.

To demonstrate the use of bivariate extensions of wavelet analysis as a new technique to understand changes in animal movement modes, we first test our method on simulated trajectories following simple correlated random walks and Levy walks. We interpret the wavelet signatures associated with the simulated movements and see how different periodic movement behaviours evolve when analysed using wavelets. The wavelet method is then tested on empirical data using the tracking data of Lesser Black-backed gulls (*Larus fuscus*) to localise and visualise changes in movement behaviour over an extended period of time.

3.2 Methods

3.2.1 Wavelet analysis of movement data

The positional data or GPS fixes of the animals represents moves between successive displacements of each animal. The time interval between the successive moves is a fixed time interval. For each animal, estimates of movement parameters (speed, turning angles and step length) were calculated between moves which form the signal to be analysed. The continuous wavelet transform is suited for analysing movement data because it allows the analysis of such non-stationary signals that show transient patterns operating over a large range of scales. The aim of the wavelet analysis is to determine both the temporal variations in the signal and the frequency (or scale) content of the signal. Scales in the case of temporal data such as movement is represented in hours. However, in order to define movement behaviour more accurately it is beneficial to characterise it with more than one movement parameter.

Therefore, speed and turning angle were used to characterise the dominant movement behaviours in the trajectories. Speed and turning angle for moving animals are considered as coupled processes, where rate of change of speed and turning angle can characterise changes in behavioural patterns. For example, movement behaviours such as intensive and extensive search movements are essentially forms of search behaviour in animals and can be characterised using speed and turning angles. The amount of time that an animal remains in a region and also the intensity, in which it searches an area, can be characterized by the degree of directional correlation (or persistence) represented by the correlation in speed and turning angle. Therefore the stronger the correlation in changes in speed and turning angle the more intense the search (Dusenbery 1989; Zollner and Lima 1999) and vice versa.

3.2.2 Identifying dominant movement behaviour

To identify dominant movement behaviours we used a bivariate extension of continuous wavelet analysis, the cross wavelet analysis. The continuous wavelet transform of two time series x_n and y_n is defined as W^X and W^Y . The cross wavelet transform of these two time series is then defined as:

$$W^{XY} = W^X W^{Y*} \quad \text{Equation 3-1}$$

where $*$ denotes complex conjugate. The real argument of the wavelet power reveals regions of high common power while the complex argument reveals the phase relationship between the two time series (Grinsted 2004). Torrence and Compo (1998) give the theoretical distribution of the cross wavelet power of bivariate time series.

The steps used to identify these movement behaviours are as follows:

- i. A continuous time series of the positional data was constructed that had n total moves at a sampling interval of $d(t)$.
- ii. Speed and turning angle at each time step (moves) was calculated.
- iii. The speed between moves was transformed (for data of Lesser Black-backed gulls) by its square root. This improved the spectral analysis by stabilizing the variance.
- iv. The cross correlation wavelet analysis resulted in power spectrum values between speed and turning angle. Cross correlation of speed and turning angle showed the strength of correlation in the changes of speed with turning angle between each move.
- v. The cross correlation wavelet analysis of speed and turning angle was examined to distinguish maximum and minimum power spectral values that extend over a large number of moves.
- vi. Movement segments having maximum power spectral values were assigned as intensive search behaviour. This means that the two processes (rate of change in speed and turning angle) are strongly correlated processes that change rapidly indicating intensive search. Similarly, movement segments with no significant cross correlation or minimum power spectral values in speed and turning angle were assigned as extensive search behaviour (Newlands 2001; Newlands, Lutcavage et al. 2004).

3.2.3 Localising changes in movement behaviour

Another useful quantity to localise the correlation between speed and turning angle is the cross coherent wavelet analysis which identifies phase locked regions of high correlation or no correlation of the two variables. It is defined as the square of the cross-spectrum and normalised by the individual power spectrums of the two time series. The cross coherence between two time series x_n and y_n is defined by an equation which is similar to the traditional

correlation coefficient equation:

$$p(f) = \frac{|w^{xy}(f)|}{\sqrt{|w^{xx}(f)w^{yy}(f)|}} \quad \text{Equation 3-2}$$

where w^{xy} is the cross spectral density between the two signals x_n and y_n . $p(f)$ takes values between 0 and 1 depending on the correlation of the two processes locally. The significance level of cross coherence was determined using Monte Carlo methods.

Thus, the two movement behaviours identified by the cross wavelet analysis is localised and visualised by cross coherent wavelet analysis. Cross wavelet and wavelet coherence software was provided by A. Grinsted (2002-2004) used in the MATLAB environment.

3.2.4 Simulated movement data

Simulated trajectories were used to test the wavelet analysis on two movement models. Movement trajectories were simulated in the R (cran) environment, using package 'adehabitatLT'. Two types of movement trajectories were simulated as a correlated random walk and as a Levy walk. Based on Kareiva and Shigesada (1983), the correlated random walk trajectory is built iteratively. At each step of the simulation, the orientation of the move is selected from a normal distribution of turning angles where r is the concentration parameter for wrapped normal distribution of turning angles, while the length of the move is drawn from a chi distribution multiplied by $h(\sqrt{dt})$ (where h is a scale parameter and dt is the time interval). In order to make the trajectory similar to a discretized Brownian motion the distribution is multiplied by $\sqrt{dt}$ (Calenge et al. 2009). In this simulation the variables r and h were chosen randomly for purpose of demonstration as $r=0.6$ and $h=5$.

Levy walks are probabilistic search patterns, which are specialized random walk models. They have diffusive properties, consisting of short walk clusters separated with intermediate long moves. This kind of pattern is followed at all scales creating fractal like trajectories. For simulating the Levy walk, move steps are drawn from a probability distribution with a power-law tail:

$$P(l_j) \sim l_j^{-\mu} \quad \text{Equation 3-3}$$

where l_j is the move-step length and μ is the power-law (Levy) exponent (In the equation ' $\sim$ ' means distributed as). Levy coefficient range from $1 > \mu \geq 3$. The simulation is done by sampling a random relative angle from a uniform distribution $(-\pi, \pi)$ for each step, and a step length generated by

$dt(l_0(\text{runif}(1)^{\frac{1}{1-\mu}}))$ (Calenge et al. 2009). To demonstrate the use of wavelets on a simulated levy walk trajectory, the power law coefficient was randomly selected as $\mu = 2.5$.

The choice of parameter values for the simulated trajectories was chosen to approximate initial analysis of the empirical data of the Lesser Black-backed gulls. The analysis of the trajectories as shown in figure 3.1, gives an indication of the levy coefficients for a sample of individuals tagged under the project.

Figure 3-1: (a) Time series of movement step length of a single Lesser Black-backed gull (id number 41781) for one year (b) Move step length frequency distribution for the same data. Inset graph and list: Normalized log-log plot of move step frequency to move step length, giving Levy exponent μ ($\mu=2.68$) within ideal limits. List shows bird id and levy exponents less than 3. For the remaining birds, the Levy exponent was greater than 3 and thus followed super diffusive correlated random walks (Viswanathan 1999) or a combination of Levy walk and correlated random walk.

3.2.5 Tracking data of Lesser Black-backed gull

To demonstrate the use of wavelet in understanding empirical data, the tracking data of a Lesser Black-backed gull (bird id 41781) for the year 2008 (January to December) was used for the current study. The choice of the study period and the gull identified for this study was based on the period with minimum number of missing fixes and maximum positional data so that the time series extracted from it was a credible representative of a moving bird. It was fitted with a 30 g Platform Transmitter Terminal (PTT). The Argos-GPS PTT has a locational accuracy of ± 22 m, heading accuracy of $\pm 1^\circ$ and ground speed accuracy of ± 1 km/h (Ens B.J. 2008). The duty cycle for the transmitter was as follows:

Bird id 41781: fixes from 5:00 – 22:00, 1 hour steps (18 fixes per day)

The Argos data for the Lesser Black-backed gulls was found to have missing fixes. Missing GPS fixes in the data was estimated using expected values from a Kalman Smoother filter obtained from a state space model (Shumway and Stoffer 2011). This smoothing technique was chosen such that it did not create artificial time dependency (Polansky et al. 2010).

Data for three seasons (breeding, wintering and migration) were segregated. The last date that the bird was found in the breeding site coordinates was defined as the departure date for migration. The period when a bird remained sedentary at the wintering site was regarded as the wintering period.

3.3 Results

3.3.1 Visualization and interpretation of wavelet analysis of simulated correlated random walk and Levy walk trajectories

The simulated bird trajectories were analysed using wavelet analysis to provide a baseline from which empirical movement data could be interpreted.

Figure 3.2 (a), depicts two models of simulated trajectories; namely correlated random walk and Levy walk. For cross wavelet as well as cross coherent analysis, a wavelet power spectrum is plotted as function of time and period (or temporal scale) in a two-dimensional graph. The wavelet analysis in figure 3.2 (b) of speed and turning angle of the two trajectories show a range of power spectrum signals across temporal scales (Y axis) and along time (X axis). Both trajectories were analysed over a temporal scale of 150 hours. Larger power spectral values correspond to warmer colours (red, yellow) and smaller values correspond to cooler colours (blues). Arrows show the relative phase angle relationship of speed and turning angle, with in

phase pointing right, anti-phase pointing left, speed leading turning angle by 90 degree pointing down and turning angle leading speed by 90 degree pointing up.

From the cross wavelet analysis, movement segments having maximum cross correlation values were identified as intensive search patterns and segments with minimum cross correlation values as extensive searches. For this paper, these were identified as cross wavelet power spectral values between 0.7 and 1 as intensive search behaviour and between 0 and 0.3 as extensive search behaviour. In this analysis, the phase angles did not show strong scale dependence and were therefore not very relevant for the interpretation.

The correlated random walk (CRW) model corresponds to a succession of random steps where movement has a directional persistence. It assumes a unimodal symmetrical distribution of turning angles (about zero) (Dray et al. 2010). The simulated random walk trajectory assumes that distinct behavioural phases such as intensive or extensive searches should not show periodicity along time (X axis) because the parameters governing the movements remain uniform in time and space. In addition since the trajectory is modelled as a stationary process, when viewing the movement from different temporal scales, it should not show a distinct trend. Cross coherent wavelet analysis as shown in figure 3.2 (b), between speed and turning angle helps to visualise the correlation of two coupled signals along time over different temporal scales. As seen in the figure, the two kinds of search behaviour, intensive and extensive searches do not show any regular trends in time or at different temporal scales. This implies that wavelet decomposition of speed and turning angle should display regions of high correlation punctuated with regions of low correlation, unevenly dispersed along the x axis (time) over all scales of temporal observation. High power spectral values from wavelet coherency are therefore erratically spread in the time frequency space (shown as dotted circles in figure 3.2(b)).

Levy walk patterns show distinct phases in behaviour (James et al. 2011). The Levy walk hypothesis suggests that when an animal does not resort to knowledge based search rules (such as memory and knowledge of landscape properties), the fractal properties of a Levy walk could improve the chances of locating the optimal feeding grounds (Bartumeus 2009). For example, a forager may start by carrying out an area restricted search with short steps and frequent change in directions characteristic of intensive search behaviour. After some time, if this attempt is not successful, it may abandon the area and move over a longer distance with relatively little change in direction until it reaches a favourable patch to conduct another intensive search (Plank and James 2008). It is analogous to saying that Levy patterns

occur when periods with a high rate of change of speed and turning angles are interspersed with periods of low rate of change of speed and turning angle. Levy walks also follow a fractal like behaviour (Bartumeus 2009), which implies that similar patterns of movement will be noticeable at different scales under study. The cross coherent wavelet analysis of levy walks will therefore show a regular periodicity along time and since Levy walks are scale invariant; these periodicities are repeatedly seen at higher temporal scales. As shown in figure 2(b), the power spectral values of wavelet coherency show maximum values at scales of 8, 16, 32 and 64 hours, as indicated by dotted lines. This means that the animal shows intensive search behaviour every 8, 16, 32 or 64 hours.

Figure 3-2: a) Simulated correlated random walk and Levy walk trajectories. b) Cross wavelet and Cross coherent wavelet analysis of speed and turning angle of the two trajectories (CRW and Levy walk models). The dotted circles in cross coherent analysis of simulated CRW indicate an example of intensive search movement spread randomly across a range of periods or temporal scales. The dotted lines in cross coherent analysis of simulated Levy walk indicate dominant periods or dominant temporal scales where intensive search is predominant. The blue regions in the figure are indicative of regions where correlation between speed and turning angle is low, indicative of an extensive search patterns.

3.3.2 Case study: Lesser Black-backed gull full Trajectory

Cross-correlation wavelet analysis of speed and turning angle of the full trajectory of a single Lesser Black-backed gull shows similar correlation

properties of speed and turning angle as studied in the simulated trajectories (Figure 3.3). Two behavioural modes were distinguished by the rates of change of speed and turning angle. Intensive search patterns were demarcated by cross wavelet power spectral values between 0.7 to 1 and extensive search from 0 to 0.3.

The cross coherent wavelet power spectrum shows switches in movement behaviour of the gulls resolved over time and temporal scales (Figure 3.4). Signal peaks with maximum power spectral values of wavelet coherency indicate intensive search patterns (in warmer colours of red and yellow) which occur frequently between 1 and 6 hours. Similar periodicities are also seen every 24 to 48 hours and every 5 days (indicated by dotted lines in figure 3.4). The results may be interpreted as an example of a gull moving between two food sources once every day, and at each food source showing intensive search behaviour; the wavelet coherence of such a signal will show one cyclic pattern of intensive movement every 24 hours. If the same animal moves from this cluster of patches to another patch cluster every 5 days, then a high power spectral value will periodically occur at a temporal scale of 5 days. Changes in movement modes through the year as viewed from these three frequencies (24, 48 hours and 5 days) is shown in figure 3.5.

Figure 3-3: Cross correlation wavelet analysis of speed and turning angle for a Lesser Black-backed gull (bird id 41781) from January 2008 to December 2008 showing 2 dominant frequencies. Dotted circles indicate examples of intensive and extensive search modes drawn from the values of the power spectrum values in each mode (as shown in the legend).

Figure 3-4: Cross coherence wavelet analysis of speed and turning angle for a one year trajectory of a Lesser Black-backed gull (id 41781). The regions in red (high spectral power) indicate movements analogous to intensive search and those in blue (low spectral power) indicate movements analogous to extensive search behaviour. The dotted lines highlight periods (or temporal scales) where intensive search is predominant.

Figure 3-5: Time spent in each mode of movement (intensive/extensive) in each month of the year at three different frequencies: every 24 hours, every 48 hours and every 5 days.

3.3.3 Case study: Lesser Black-backed gull breeding wintering and migratory trajectories

Wavelet analysis of speed and turning angle during the breeding, migration and over-wintering periods demonstrates the variation in movement patterns in different stages of migration of a gull. We considered 30 day trajectories during the breeding and over-wintering phases and full trajectories during the migratory phases. Figure 3.6 shows that during breeding and migratory seasons, the gull shows frequent intensive searches every 8 and 16 hours. In addition there is an increase in intensive movements at temporal scales of 64 hours (2.6 days). This is consistent with tracking and field studies done on the population of Lesser Black-backed gulls breeding in the North Sea islands of the Netherlands. It is observed that daily trips occurred around an area of 80 km of the nest and the mean trip duration is about 8 hours (Shamoun-Baranes et al. 2011). In addition exceptional long foraging trips were recorded in active breeding gulls. Some of these trips were associated with commercial fishing trawlers where the gulls are active scavengers (Shamoun-Baranes et al. 2011). The over-wintering season did not show a strong association with a single period but rather a continuous period of intensive search with a periodicity of 0 to 32 hours (1.3 days).

Figure 3-6: Cross coherent wavelet analysis of Speed and turning angle of individual 41781 during the breeding, migration and wintering season. The dotted lines in cross coherent analysis highlight periods or temporal scales where intensive search is predominant. The blue regions in the figure indicate regions of extensive search.

3.4 Discussion

In this study, temporal periodicities between speed and turning angle were used as signatures to visualise the dynamic behaviour of simulated movements, which were then confirmed using empirical data from gulls. The strength of using mathematical techniques such as wavelets is that analysis is similar to non-parametric techniques where hypothesis testing and prior knowledge about the movement of the animal is not necessary. Although wavelets have been used to analyse non-stationary statistical properties in movement (Polansky et al. 2010; Wittemyer et al. 2008), the novelty in our approach is the use of bivariate extensions of continuous wavelet analysis namely cross wavelet and cross coherent wavelet analysis to improve understanding of empirical movement data.

Behavioural changes in movement, also known as behavioural intermittence (Bartumeus 2009), are modulated by the internal state of the animals as well as external cues and results in changes in the directional inertia of an

organism. These velocity and directional changes result in variations in search patterns of an organism. Recent theoretical work on pure random movements (or stochastic processes) in animals show that success of even a random search pattern relies on the reorientation between two behavioural changes (Bartumeus 2009). Therefore, it is crucial that behavioural changes are captured using robust properties of the trajectories that can be generalised for all animals. Since such changes in behaviour are bound to have periodic signatures, wavelets are ideal to explicitly visualise and explain the mechanistic links between different behavioural modes and statistical properties of the trajectories.

3.4.1 Movement analysis of simulated trajectories

The cross wavelet and cross coherent wavelet analysis of the simulated trajectories showed that the wavelet power spectral maps and two kinds of search behaviours (intensive and extensive) were able to characterise transitions and changes in movement patterns over time and scale. When cognitive and environmental information are sufficient, animals rely on search rules based on stochastic processes, rather than deterministic processes. This results in random movements. Wavelet analysis of such processes will have an inherent randomness over all scales of temporal analysis. In the case of correlated random walk movements, there is a persistent change in direction. Therefore a wavelet analysis of only turning angle may depict a regular periodicity. However when turning angle is correlated with speed, intensive and extensive searches can be identified in the time frequency space.

Levy walks were simulated as destructive foraging behaviour, where the same feeding grounds are not utilised more than once. Instead, after an intensive feeding bout, the animal in search of randomly distributed resources moves in a straight path (ballistic movement) until it finds food again (Plank and James 2008). Such movements have two important characteristics, namely, distinct change in behaviour from intensive movements to extensive movements over time, as well as self-similarity over multiple temporal scales. The results show that both these characteristics can be distinctly visualised in the cross coherent wavelet analysis of the simulated Levy walk. The multiscale processes in movement are intrinsically correlated to the inner dynamics of the organism and the structural properties of the environment around it. In the context of mobility of an animal, searching for food can be assumed to be analogous to searching for patches and stopover sites, although at different scales. This scaling information obtained from wavelets can be analysed further to understand interrelated processes.

3.4.2 Movement analysis of empirical trajectories

Animal movement in real life is much more complex than these simulated trajectories and involve a continuous change in movement strategy over time and scale. Speed and turning angles are two key attributes of movement trajectories that can be used to explain these behavioural changes. Usually each species tend to show characteristically similar signatures of these attributes (Dodge et al. 2009).

Wavelet analysis of a yearly trajectory of a single Lesser Black-backed gull was used to explain behaviour of the bird as a combination of intensive and extensive search patterns. The results (Figure 3.4 and Figure 3.5) indicate that time spent in each mode of movement (intensive/extensive) for each month of the year varies with the temporal scale from which it is viewed. For example if movement trajectories are sampled every 24 hours, one is more likely to find the bird undertaking an intensive rather than an extensive search. These movements are related to feeding cycles, movement to roosting places and bathing bouts.

The time spent at three different frequencies (viz. every 24 hours, every 48, hours and every 5 days) varies through the year and can be better understood when viewed separately during the breeding, wintering and migration period. The wavelet analysis during the breeding season showed signal peak of intensive searches every 6 hours and less than 16 hours. This is supported by field observations by Camphuysen (2011) showing non-interrupted periods spent at the nest averaging 6.0 ± 5.5 hours for males and 3.7 ± 3.6 hours in females. Short trips associated with intensive moving in a localised area is related to feeding, roosting and bathing trips occurring once or twice every day. A signal peak of intensive search occurs every 64 hours, which is indicative of long distance foraging trips to feeding, sources given that the species is known to travel long distances away from the nest. For the population under study, some foraging trips went as far as the United Kingdom, Belgium and North of France from their breeding site in Vlieland, The Netherlands. The birds made repetitive trips to the mainland from the breeding site on the island Vlieland. However, these long movements were made only periodically.

Lesser Black-backed gulls are known to cover large distances and achieve high speeds during migration (Ens B.J. 2008). Individuals are known to cross large water bodies such as the Bay of Biscay and individual average daily speeds during the migration ranged from 11.4 to 175 km/hour (Klaassen et al. 2012). The variation in speed and turning angle during the migratory phases was because the bird travelled for more than 1000 km on some days and on others travelled shorter distance in and around the stopover sites (Klaassen et al. 2012). Lesser Black-backed gulls in general are also known

to be able to alter their flight modes frequently, using a combination of flapping flight (Shamoun-Baranes and van Loon 2006) , thermal soaring (Alerstam et al. 2007), ridge soaring (Kerlinger 1989) and dynamic flight (Klaassen et al. 2012). Being generalist feeders they also find ample feeding grounds during their migration and tend to stop often to achieve energy efficiency (Klaassen et al. 2012). In this study, the longer flights were relatively straight with low turning angles while the shorter distances were more tortuous. This shows that even at high scales the same kind of Levy patterns is visible where there is movement analogous to intensive search at stopover sites while there is movement analogous to extensive search on migratory days. On stopover days the birds flew little, except for feeding early in the morning and movement between roosting sites. Spectral analysis of the migratory movement shows the same results. During the autumn migratory journey the bird moved with low speed and a higher rate of change of turning angles, demonstrating intensive movements (Figure 3.6). This is indicative of time spent at an early stopover site. Once the migration began (after a time interval of 10 days) spectral peaks appeared to significantly diminish at lower frequencies and appeared mostly at 24 hour periods and predominantly every 64 hours. The spring migration however showed predominantly extensive search patterns with local power spectral values showing maximum values at temporal scales of 16 and more pronounced at 64 hours. This shows that while migrating long distances, birds tend to undertake intensive searches less frequently, in this case occurring every 64 hours. Spring migration in particular is faster with less number of stops as the birds strive to reach the breeding grounds earlier to find profitable nesting sites.

During the winter, there is more movement compared to the breeding season and intensive searches are equally interspersed with extensive movements (Figure 3.6). Winters are largely spent feeding at inshore and offshore sea lagoons, large lakes, rivers, canals, and dumpsites. The species, being opportunistic omnivores, move between a variety of feeding sites but come back to a central roost. Such movement between distant feeding sites and intensive search patterns in the feeding grounds, results in the spectral signature seen in figure 3.6.

3.5 Conclusion

The use of wavelet analysis as a data mining function to discover changes in movement modes in a trajectory was successfully tested. The technique amplifies temporal periodic properties inherently embedded in movement trajectories. Testing wavelet analysis on simulated trajectories as well as empirical datasets shows that complex behaviour at multiple scales can be visualized and understood. It is evident that wavelet analysis, based on

robust mathematical foundation, is an ideal tool to explore these signatures without prior assumption. There are two major limitations in using wavelet analysis for movement trajectories. Firstly, the ecological interpretation of the time frequency graphs is a demanding process in order to understand the frequency content of the resolution together with the time variable. Second, hard boundaries at which behavioural modes change must be distinguished. Further research in defining time bound changes in movement modes will help in segmenting movement trajectories into a combination of movement strategies.

Contemporary research on movement ecology is characterized by a wide range of techniques to analyse changes in movement patterns and behaviour over time (Holyoak et al. 2008; Nathan 2008). Rapid development of telemetry devices has allowed the tagging of diverse species of free ranging animals generating very large and detailed data sets (Andrews et al. 2008; Block et al. 2005; Ferguson and Elkie 2004; Gurarie et al. 2009; Ropert-Coudert and Wilson 2005). Since the tagging of a few individuals does not represent the population or the behaviour of the species as a whole, analysis of such telemetry data is trending towards Lagrangian mode of analysis (individual based) instead of the more popular Eulerian mode of analysis (population based). Therefore, for individual movement analysis, automated statistical methods such as the wavelets are innovative spatial analysis tools that can convincingly pick out ecological signals from theoretical and real data sets of moving animals.

4 Change detection in animal movement using discrete wavelet analysis

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4.1 Introduction

The study of animal movement patterns reveals fundamental information about their behaviour, habitat and ecology (Turchin 1998). Animals use an environment that is patchy and heterogeneous (Fritz et al. 2003). Every part of this complex environment may be perceived as a patch or inter-patch at different scales of observation and with movements in a changing landscape (Barraquand and Benhamou 2008; Fauchald and Tveraa 2003; Wiens 1989; Wiens et al. 1995). For example, animals may spend more time in a nesting or resting place and show only limited movement. In contrast, other places are used intermittently for foraging, where animals may show more dynamic movements. Segregation criteria for such composite movements are difficult to draw up in such a continuum of space and time, though it is also a necessary step towards understanding the habitats used for the different biological needs of an organism and the modes to reach these habitats.

The multi-scale and non-stationary nature of animal movement requires rigorous statistical methods to detect change points in their movements. While the definition of change varies with different scenarios, we used Sharifzadeh et al.'s definition of change as points in time where the local trend of data values change (Sharifzadeh et al. 2005). Here we propose a method using discrete wavelet analysis to identify discontinuity in time series data representing different movement behaviours in animals. However, we did not deal with the notion of degree of change, but instead focused on localizing time stamps, at which the properties of movement changed abruptly, but before and after which the properties remained constant. With an increasing repository of telemetry data available, much attention has been paid to the paradigm relating to research on moving animals. The "first passage time" (Fauchald and Tveraa 2003) is one of more straightforward methods, where first crossing duration is calculated at the perimeter of a circle of radius (R) centred at a relocation point. The methods, though effective, involve subjectivity in the choice of the dimension ' R '. More automated methods with less subjectivity are the Hidden Markov models (Morales et al. 2004) and State Space models (Fryxell et al. 2008). These identify hidden movement modes but require a prior choice of the movement model as some form of correlated random walk (Johnson et al. 2008; Morales et al. 2004). Change detection using the properties of the trajectories were demonstrated by Gutenkunst (2007) using local path straightness, as well as by Tremblay et al. (2009) by fractal analysis using the self-similarity in trajectories.

Barraquand and Benhamou (2008) proposed a method of segmenting trajectories and change point detection based on 'residence time' or the time spent near each location. This method is more generic than other methods of

segmentation and combines calculating an ecologically relevant parameter with a robust statistical method of change detection. It proposes the statistical processing of a new signal composed of the residence time at each point of the animal's relocation. The approach is similar to the first passage time, which computes how much time an animal takes to cross a circle of a given radius(R), with the centre at the relocation point. The residence time is biologically more appropriate because it calculates the first passage time at each relocation, plus the passage time that occurred in this circle before or after the current relocation. The qualification to this is that the animal does not spend a time greater than maximum time (max_t) before re-entering the circle. The segmentation of the trajectory and change points are calculated using the statistical method proposed by Lavielle (Lavielle 1999, 2005).

Lavielle's method can also be used to detect change points in the movement trajectories using a movement focus variable other than the residence time, for example step length, speed, acceleration, or change in direction. Lavielle's method allows non-parametric segmentation of a time series using the penalized contrast method. This method finds the best segmentation of a time series of focus variables (e.g. residence time or step length) into K segments. It searches the segmentation for which a contrast function (measuring the contrast between the actual series and the model underlying the segmented series) is minimized.

Since it is statistically robust, we adopted Lavielle's method for analyzing two variables: step length and residence time. In addition, we used a more widely tested approach to analyze time frequency changes, namely wavelet analysis (Addison 2002; Bibian et al. 2001a; Nason and Sachs 1999), on step length and residence time.

We propose a new and efficient approach towards detecting change points in animal movement time series data by exploiting the properties of discrete wavelet analysis. Wavelets have been well defined in change point detection (Yu et al. 2008) in fields such as the medical sciences, economics and geology, and its use has been well documented. In addition, wavelet analysis has been recently used to detect regime shifts and non-stationary properties of moving animals (Gaucherel 2011; Polansky et al. 2010; Wittemyer et al. 2008). The novelty of the method we propose in this paper lies in adapting the use of discrete wavelet transform (DWT) on animal movement data, instead of the continuous wavelet transform (CWT) that is widely used in this field. Although CWT is useful in signal processing at all scales, it generates a large amount of data and further analysis of the wavelet coefficients becomes cumbersome. DWT is a more suitable alternative for analyzing scales and positions based on powers of two (dyadic scales). DWT avoids the redundancy in data characteristic of continuous wavelet analysis. This is

important because the redundancy in CWT is indicative of the correlation of wavelet coefficients: these are intrinsic to the wavelet function rather than the time series, which makes the interpretation of the coefficients dependent on the chosen scale and the specific problem in question (Cazelles et al. 2008a). Therefore, DWT makes further analysis of coefficients more efficient and is just as accurate (Mallat 1989).

An important characteristic of wavelet analysis is that it does not assume stationarity of the data (Pittiglio et al. 2011) and animal movement is formed of temporal signals containing numerous non-stationary or transitory characteristics. Thus, these characteristics form movement signatures that can be identified and localized using wavelet analysis across a range of temporal scales. The discrete wavelet method consists of decomposing the signal into a hierarchical set of low frequency content (called the approximations) and high frequency content (called the detail). The Mallat algorithm is used for the fast wavelet transform of the signal. While the low frequency content of the signal gives the identity and global trends of the signal and coarse variations over time, the high frequency content is generally composed of the finer nuances and has the information needed to detect change points and frequency breakpoints. Since the 1990s, a large number of methods have been proposed for the use of wavelet transform to detect change points in different fields. However, the underlying idea is essentially based on the theory that change points are detected by finding large values of wavelet coefficients at different scales. The methods differ mainly on the quantification of how large the values need to be in order to be deemed a significant change point (Yu et al. 2008). The choice of threshold has varied from the maximum absolute value of coefficients (Wang 1995) to extreme values over a certain threshold based on a pareto distribution (Raimondo and Tajvidi 2004). Other statistical details such as standard deviation and variance from a normal distribution of the coefficients can also be considered for threshold selection (Bibian et al. 2001a).

Here we use empirical data from the GPS tracking of Lesser Black-backed gulls (*Larus fuscus*). The change points with respect to their movement may show smooth transition while moving between proximal patches, for example, from the nesting site to the roosting site or while exploring for better resources. These would be represented as low coefficient values of the wavelet transform in the movement parameters. Sharp transitions in movement parameters such as step length or speed in the case of Lesser Black-backed gulls are apparent when the birds make long distant movements to the open sea for feeding, or sudden migratory movements (often more than 100 km) from the breeding, wintering or stop-over sites (Klaassen et al. 2012). These would be represented as high coefficient values in the wavelet transform of the movement parameter used for analysis.

Our aim was to test the effectiveness of a new, efficient, change detection method using discrete wavelet analysis for segmentation of the movement trajectories. Two focus variables, namely step length and residence time, were used to demonstrate the method, which we then compared with trajectory segmentation using Lavielle's method.

4.2 Methods

4.2.1 Gull data

Adult Lesser Black-backed gulls were mounted with Argos-GPS solar-powered Platform Terminal Transmitters (PTTs) from Microwave Telemetry Inc., Columbia, MD, USA (Ens B.J. 2008) in Vlieland, one of the Wadden islands in the Netherlands. The tracking data of one bird (bird ID 41781) for the period May 2007 to May 2008 was used for the study. This period was chosen because it contained the maximum number of fixes. The gull was fitted with a 30 g PTT. The Argos-GPS PTTs had a locational accuracy of ± 22 m, a heading accuracy of $\pm 1^\circ$ and a ground speed accuracy of ± 1 km/h (Klaassen et al. 2012). Fixes were recorded from 05:00 – 22:00 hrs, in 1-hour steps (18 fixes per day). 3,751 fixes were collected during the study period. Missing GPS fixes was estimated using expected values from a Kalman Smoother (Shumway and Stoffer 2006) obtained from a state space model. This smoothing technique did not create artificial time dependency (Polansky et al. 2010).

The continuous position of the gull in time t , obtained as spatial coordinates $x(t)$ and $y(t)$, was used to construct a time series $X_n = (X_0, \dots, X_n)$. The step length was calculated as the distance between the current point and the next one in the data set (i.e. N , and $N+1$, where N was the current record).

4.2.2 Calculation of the residence time

Computation of the residence time $\tau_R(i)$ was done by calculating the number of times the path crossed the perimeter of the circle centered on a location, both forward and backward. The duration of the path within each circle was then calculated as (Barraquand and Benhamou 2008):

$$\tau_R(i) = [F_{1,R}(i) - B_{1,R}(i)] + \sum_{v=1}^{V(i)} [F_{2v+1,R}(i) - F_{2v,R}(i)] + \sum_{w=1}^{W(i)} [B_{2w,R}(i) - B_{2w+1,R}(i)]$$

Equation 4-1

where $F_{1,R}(i)$ and $B_{1,R}(i)$ are the forward and backward first passage time defined by Fauchald and Tveraa (2003). The differences $F_{2v+1,R}(i) - F_{2v,R}(i)$ and $B_{2w,R}(i) - B_{2w+1,R}(i)$ for the increasing iteration indices v and w represent the extra time spent while going forward and backward from the circle. V and

We represent the maximum values allowed for v and w at each location i . By taking into account the relevant time spent within the circle, the residence time is less sensitive to the choice of the radius R (Barraquand and Benhamou 2008). The radius of the circle should be biologically relevant, representing for example, range of perception, spatial cognition, or resource density (Barraquand and Simon 2008). Since such data are not easily available for our target species, we used one of the criteria suggested by Barraquand and Benhamou (2008), where the radius is equal to a multiple of the average step length and the radius is such that residence time was calculated for all relocation positions.

When the radius is small, the residence time yields a more focused overview of the trajectory, whereas when a large radius is used to calculate the residence time, the results show drastic changes at each step and the exact transition points are lost. However, the choice of residence time depends solely on the aim of the study. Since we wanted to focus on the transition points, we chose a small radius of 25m (mean step length for the entire period was 25.8 m). Once the residence time was calculated and a new signal was obtained, it was segregated using Lavielle's method (Lavielle 1999, 2005) and then discrete wavelet analysis.

4.2.3 Segmentation methods for change detection

4.2.3.1 Lavielle's method

Let Y_i be the value of the focus variable at time i , then it is assumed that the data is generated by the model:

$$Y_i = \mu_i + \sigma_i \epsilon_i \quad \text{Equation 4-2}$$

Where μ_i and σ_i are the mean and the standard deviation of Y_i respectively. ϵ_i is a sequence of random variables with zero mean and unit variance. Here we used mean as the contrast function. The segmentation model is based on the hypothesis that the parameters are constant within a segment but change between successive segments, and $\sigma_i = \sigma$ for all segments. For a series build of K segments, the difference between the observed series and a given segmentation model is measured by the function:

$$J_k(Y) = \sum_k G_K^1(Y_{i \in k}) \quad \text{Equation 4-3}$$

Where $Y_{i \in k}$ represents the observations in each segment k and

$$G_K^1(Y_{i \in k}) = \sum_{i=t_1^k}^{t_n^k} (Y_i - \bar{Y}_k)^2 \quad \text{Equation 4-4}$$

Here $\bar{Y}_k$ is the mean of the samples, while t_1^k and $t_{n(k)}^k$ are the first and last observations in each segment k . The two focus variables, namely step length and residence time, were used for change detection at migratory scales. Lavielle's method of change detection was performed by the `adehabitatLT` package of R open source statistical software (Calenge 2006; R Development Core Team 2010).

4.2.3.2 The wavelet method

Discrete wavelet transform (DWT) allowed the quantification of the main periodic components of the movement data and detected the points in time when the signal changed abruptly. Discrete wavelet transform (DWT), $\rightarrow Wf$ corresponds to wavelet function, ψ , decomposing a signal S across scales x and time locations t . DWT actually involves sub-sampling of $Wf(x, t)$, at dyadic scales, $x = 2^j$ (for each level $j = 1, 2, \dots, L$). By the discrete wavelet transform, the signal is successively passed through high pass and low pass filters. The movement parameters, such as step length or speed, constitute high frequency content (detail information) and low frequency content (coarse approximation). This can be written as:

$$S = a + d_j \quad \text{Equation 4-5}$$

Where a represents the approximation at the highest level of decomposition, d represents the detail and $j = 1, 2, 3, \dots, L$ is the levels of decomposition. The low frequency content will show the general structure of movement, but is unable to pinpoint the exact change points in the movement. This information lies in the high frequency content of the signal, which is shown as the 'detail' part of the signal. At each level of transformation, the resolution of the frequency content of the signal becomes more precise and is therefore more likely to show change points accurately. This is because there is a stage of down-sampling involved at each level of transformation, in which the output of the filtering is decimating by two. As a result, the uncertainty in frequency is reduced by half and the resolution of the frequency is doubled (Gokhale and Khanduja 2010).

The choice of a small wavelet allows local discontinuities to be identified. However, the movement data also contains noise, which complicates the identification of discontinuities. Discrete wavelet transform eliminates noise in the 1st and 2nd level decompositions and the discontinuity in the signal becomes visible in the 4th or 5th decompositions. To identify the change points in a data set, we need a regular wavelet that can detect the smallest discontinuity : we know that for the Daubechies dN wavelets, the regularity of the wavelets increases with the order of the dN series (Misiti et al. 1997). We therefore used the Daubechies D4 wavelet, which has two vanishing

moments. Thus, for both constant and linear signals, the coefficients of the wavelet transform were zero (Addison 2002). The two choices, one of the mother wavelet and the other of the level of decomposition, facilitated the detection of prominent change points and considerably reduced the correlation of coefficients, respectively.

The main issue in analyzing the coefficients of wavelet decomposition is selecting a function that can extract features such as abrupt changes in movement patterns. To detect change points from the wavelet coefficients we modelled extreme values by assigning thresholds. The thresholds were assigned using the 3-sigma rule on the normally distributed coefficients. This was done by calculating the Z scores:

$$Z = \frac{d_{i,j} - \overline{d_{i,j}}}{sd_{dj}} \quad \text{Equation 4-6}$$

where $d_{i,j}$ is a coefficient i at level of decomposition, j , $\overline{d_{i,j}}$, represents the mean and of the coefficients, and sd_{dj} the standard deviation at level j of decomposition. This means that the wavelet coefficients were divided into three segments where 68% of the values drawn from the normal distribution of the coefficients were within one standard deviation (1 sigma) from the mean, representing moving bouts; 95% of the values lay within two standard deviations (2 sigma) from the mean, representing short stops, and 99.7% were within three standard deviations (3 sigma) from the mean, representing long stops. We assumed that the coefficients with the lowest values ($-1 \geq Z \leq 1$) represented normal moving signals, while abrupt changes were represented by coefficients values that lay 2 standard deviations ($-1 < Z > 1$) from the mean, these were classified as short and long stops. The coefficients from the chosen level of decomposition were used to reconstruct the signal. The time at which the discontinuities occurred were identified as in Lavielle's method (by matching the coefficients showing change points to the time stamp). In addition, change points were characterized into short and long stops representing the abruptness of the change. The trajectory was then plotted with the change points to show their spatial spread. The wavelet analysis was performed in MATLAB 7.1, The MathWorks, Inc., Natick, Massachusetts, United States.

In summary, we tested two change detection methods (Lavielle's method and the wavelet method) and for each method, we used the two focus variables (step length and residence time).

4.3 Results

4.3.1 Lavielle's method

4.3.1.1 Focus variable: step length

Lavielle's method is based on the calculation of a contrast matrix (Lavielle 1999, 2005). We assumed a priori that the mean of the segments would change and set the maximum number of segments ($K_{\max}$) as 10, since we were studying migratory scale change points and given the resolution of the data collected. Note that the choice of $K_{\max}$ affects the calculation of the optimal number of segments (K_{opt}). It has been reported that assuming $K_{\max}$ to be 2 – 4 times the expected number of segments gives the best results (Barraquand and Benhamou 2008; Calenge 2006). The value of the contrast matrix J_k to the number of segments changed abruptly at 5 segments (Figure 4.1a and 4.1b). According to the rule proposed by Lavielle, this means that K_{opt} for the time series of step length is 5. The change points on the plot of the time series are shown as red line breaks (Figure 4.1). Table 3 shows segregation of the step length time series of a gull (ID 41781) into five segments, detailing the exact date of change as well as a biological interpretation of segments using expert knowledge. The segments clearly show that the movement trajectory has been divided into the breeding, wintering and migratory phases (Figure 4.2). Since the data starts in one breeding season and ends in the next, it shows five segments: part of the 2007 breeding season, autumn migration of 2007, wintering in 2007 – 2008, spring migration of 2008, and part of the 2008 breeding season.

In computing the contrast values, when $K_{\max}$ is increased, the results are still identical. The segments still represent the breeding, wintering and migratory parts of the trajectory because of the resolution of the data collected.

4.3.1.2 Focus variable: residence time

The residence time was calculated with a small radius of 25 m. The computation of the residence time ensured that it was less sensitive to the selection of the radius and was more likely to represent statistically stationary values of residence time for a given radius and where the animal performed uniform movement (Barraquand and Benhamou 2008). Lavielle's method was then used to detect change points as an effective, non-parametric segmentation method. The optimal number of segments was calculated as six. Segregation of residence time series of the gull using Lavielle's method, with exact dates of change and biological interpretation of the segments, is shown in Table 4. The segments formed as a result of changing movement patterns represent the breeding, migratory and

wintering periods. In addition to the segments identified by using step length as the focus variable, residence time allows the spring migration to be distinguished as two separate phases.

a)

b)

Figure 4-1: Lavielle method of change point detection: Analysis of step length time series of a gull (ID 41781) from May 2007 to May 2008. a) Plot of step length with time (as no. of relocations). The red lines indicate the change points. b) Plot of value of contrast function (J_k) to the number of segments (K). A clear change in the value of J_k at 5 shows that the optimum number of segments is 5.

Table 3: Segregation of step length time series of a gull using Lavielle method

Focus variable: Step length				
Segment	Biological interpretation of segments	No. of points	Date Begin	Date End
Segment 1	Breeding period (year 2007)	1405	6/12/2007	8/9/2007
Segment 2	Autumn migration	97	8/9/2007	8/13/2007
Segment 3	Wintering period	5572	8/13/2007	4/1/2008
Segment 4	Spring migration	302	4/1/2008	4/14/2008
Segment 5	Breeding period (year 2008)	1407	4/14/2008	6/11/2008

Table 4: Segregation of residence time series of a gull using Lavielle method

Focus variable: Residence time				
Segment	Biological interpretation of segments	No. of points	Date Begin	Date End
Segment 1	Breeding period (year 2007)	1448	6/12/2007	8/11/2007
Segment 2	Autumn Migration	52	8/11/2007	8/13/2007
Segment 3	Wintering period	5574	8/13/2007	4/1/2008
Segment 4	Spring Migration Phase 1	255	4/1/2008	4/12/2008
Segment 5	Spring Migration Phase 2	47	4/12/2008	4/14/2008
Segment 6	Breeding period (year 2008)	1407	4/14/2008	6/11/2008

Figure 4-2: Segments of change in movement patterns of a Lesser Black-backed gull (ID 41781), identified using the Lavielle method: Time series used are step length and residence time. The segments have been categorized in the legend using prior knowledge of the ecology and movement behaviour of the bird. Change points are indicated by red stars.

4.3.2 Wavelet method

4.3.2.1 Focus variable: step length

Discrete wavelet transformation of time series of step length involved hierarchical decomposition of the signal by passing it through a set of high and low filters with down-sampling at each level. The high frequency content of the signal was decomposed to four levels (Figure 4.3). Level 4 detail (d4) showed prominent abrupt discontinuities, which were better localized in time than the other levels, and it was therefore used for further analysis (Figure 4.4a). The histogram of the coefficients of the detail at level 4 was plotted with a normal distribution. In figure 4.4 b, the area within the grey lines accounts for 68% of the decomposed set, while the yellow line divides the distribution at the 95% mark, and the pink lines at the 99.7% mark. The Z scores were used to index the values of the coefficients into three segments (representing moving, long stops, and short stops, respectively). The

reconstructed signal and the corresponding coefficient values resulted in a time-stamped indexed series (plotted in figure 4.6).

4.3.2.2 Focus variable: Residence time

The residence time indicates those geographic areas where the animal spends more time. The discrete wavelet decomposition of the time series of residence time data results in high frequency and low frequency content of the original signal. The high frequency content provides detailed information about the changes in the residence time and is important to identify frequency breakpoints or to detect change points. The detail at level 4 shows the sharp change points (Figure 4.5). The lowest frequency content of the reconstructed detail signal is associated with the resting phases, while the highest frequency content is the movement phase (Figure 4.6).

Figure 4-3: Decomposition of step length time series using discrete wavelet transform. The Debauchies wavelet 4 (Db4) was used followed by reconstruction of the signal at each level as shown in the plots above. D4 shows the sharp transition points and was chosen for further analysis.

a)

b)

Figure 4-4: Analysis of decomposed time series: a) Reconstruction of detailed signal at level 4 from the discrete wavelet transformation of step length time series of a Lesser Black-back gull. b) Histogram and normal distribution fit to coefficients of detail at level 4.

Figure 4-5: Decomposition of residence time series using discrete wavelet transform: The Debauchies wavelet 4 (Db4) was used followed by reconstruction of the signal at each level shown in the plots above. d_4 shows the sharp transition points and was used to find transition points between different modes. A higher value of residence time corresponds to intensive use of resources and longer stay, and vice versa.

Focus variable: Step length

Focus variable: Residence time

Figure 4-6: Movement trajectory showing change points using discrete wavelet transformation of step length and residence time series. Moving bouts are shown in grey, long stops are shown in pink, while short stops are shown in yellow. The breeding site is marked by a blue star.

4.3.3 Method sensitivity

To test the methods' sensitivity we simulated a composite behavioural trajectory of uncorrelated random walks and Levy walks in the R software. The trajectory was composed of 50 steps, measured at regular time intervals. The first 25 steps were modelled as an uncorrelated random walk followed by 25 steps modelled as a Levy walk. The uncorrelated random walk was modelled using an iterative process. For simulation, the concentration parameter for wrapped normal distribution of turning angles was taken as zero. The move lengths were drawn from a chi distribution. For simulating the Levy walk, move steps were drawn from a probability distribution with a power-law tail $P(l_j) \sim l_j^{-\mu}$, where l_j is the move-step length and μ is the power-law (Levy) exponent. The Levy exponent μ was selected as 2. We used step length of the trajectory as the signal S to test the sensitivity of the discrete wavelet analysis in detecting change points. Fig. 7 shows the trajectory, with red marks indicating the start and finish points and the blue mark indicating the change point at 25 steps. The discrete wavelet transform

of the step length time series, using Db4 wavelet, showed distinct change points at level 1 of decomposition. The reconstruction of the signal, followed by analysis of the coefficients by the discrete wavelet analysis method proposed here, revealed seven significant change points. The Z scores allowed detection of abrupt signals from the long movement bouts of a Levy walk. The segment of the trajectory modelled as uncorrelated random walk did not show any change points. It is interesting to note that although the method is sensitive in detecting large coefficients, one of its disadvantages is its localization. Since the wavelet analysis might provide several large coefficients for a single change, precision in localization of change is poor. In this regard, another method called the wavelet footprint has been more successful: it removes overlap among support intervals of wavelet coefficients at different levels (Sharifzadeh et al. 2005).

Figure 4-7: Decomposition of step length time series of simulated trajectory using discrete wavelet transform. a) Composite simulated trajectory showing starting and end points as red marks and the change point from an uncorrelated random walk to the levy in blue. b) Reconstruction of the signal using detail coefficients at level 1 following a discrete wavelet transform of the signal S (where S is the time series of step length between relocation points). c) Histogram of the coefficients at level 1. d) Plot of step length versus time of the original signal, with change points detected using discrete wavelet analysis marked as red points.

4.4 Discussion

Movement ecology is a new field of ecological studies and has recently attracted attention because of the availability of large datasets from telemetry data. However, the tagging of a few individuals results in a very biased dataset, which is in no way representative of the behaviour of the entire population. Therefore, the trend in this field is towards a Langrangian mode of analysis (which emphasizes individual behavioural studies) rather than an Eulerian mode of analysis (population-based studies), which is the most conventional method of studying behaviour at the moment (Turchin 1998). The Langrangian approach to analyzing movement, focusing on individual movements, is going through an evolutionary shift towards ecoinformatics, in which advanced statistical techniques and processes are being applied to datasets collected from cutting edge telemetry devices (Nathan et al. 2008). Descriptions of these methods do not always use a large number of animals, but rather one or a few individuals (Gurarie et al. 2009; Polansky et al. 2010; Thiebault and Tremblay 2013). However, ecologists are asking whether the use of these technologies is resulting in a better understanding of ecological issues (Hebblewhite and Haydon 2010). The answer lies in the momentum of improvement in analysis techniques for movement studies. The results of our study show that application of concepts from the field of statistics can advance our understanding of movement data comprising a large number of relocation points. While Lavielle's method was found to be appropriate for a preliminary examination of relocation points of an animal, the discrete wavelet analysis, already known for its proficiency in time series analyses from studies in other fields, was found to be adept in detecting change points in movement trajectories and providing much more detailed ecological information. Since most methods used for change detection in animal movement are difficult to apply when the modes of movement, ecology, and thresholds for change are unknown, the use of non-parametric methods, such as the discrete wavelets analysis, will become valuable for objective analysis.

4.4.1 Segmentation method: Lavielle's method

For a bird like the Lesser Black-backed gull, the range of movement patterns is wide: it breeds in the Netherlands and winters in Portugal. These gulls are known to demonstrate a generalist flight strategy (Rayner 1988), showing a variety of movement modes such a flapping flight, thermal soaring and dynamic soaring (Klaassen et al. 2012). These birds are known to show sudden and swift migratory movements from the breeding to wintering sites, with intermittent stopovers along the migratory route (Klaassen et al. 2012). Four obvious change points are expected while transitioning from the breeding or wintering season to migratory movements, and vice versa. Precise segmentation methods should be able to identify movements

associated with stopover sites, principal wintering locations, and breeding sites, because when a bird is at a central place and is less mobile (such as at a nesting or stopover location), it makes very short steps and has low speeds. However, when moving from resting places to other patches of importance (feeding or roosting sites), its movements are characterized by longer steps. The migratory movements are the longest steps, with speeds ranging from 11.4 to 175 km/hr for this species (Ens B.J. 2008).

Figures 4.1 and 4.2 show the change points using Lavielle's method. The movement trajectory clearly shows four change points, segregating it into the categories for breeding, migratory and wintering phases. The breeding site was located on the island of Vlieland, the Netherlands, the migratory journey encompasses a trajectory through Netherlands, Belgium, France, Spain and Portugal, and the wintering sites were located in the south of Portugal. As the variation in step length and speed are high during the three phases, in the case of these gulls, the change points were more accurately predicted by Lavielle's method. However, when the changes are less abrupt, as in the case of slow-moving terrestrial animals, Lavielle's method may not be able to predict the exact changes in space and time. In our case, for the gulls it was also not able to predict any of the stopover locations. The method is therefore useful for the preliminary exploration of the movement data only.

In a heterogeneous environment, animals spend more time at locations that are biologically more profitable (Barraquand and Simon 2008). This also depends on the stage of their life history, migratory stage, and prevailing needs. Thus, analysis of a time series of residence time can give key information on how time utilization varies in contrast to the well-known concept of space utilization in habitat analysis studies. As shown in our results, the segmentation of the residence time series using Lavielle's method showed a distinct stopover site during the spring migration, providing five distinct tipping points. It should be noted that although Lavielle's method is parameter-free, the calculation of the residence time requires a choice of a radius. To ensure reliability and consistency in the change detection, it is best to perform the analysis and test the results with different radii (Barraquand and Benhamou 2008).

4.4.2 Segmentation method: Wavelet method

The discrete wavelet decomposition of step length time series was capable of detecting numerous change points. We hypothesize that when coefficients of a discrete wavelet transform are normally distributed, the change points will be located in the tail of the distribution. The choice of the function relies on the fact that it focuses on the general content of a wavelet coefficient at the selected band of decomposition, while highlighting extreme values over

certain thresholds. By selecting thresholds using the 3 sigma rule, we avoided the bias of selecting absolute maximum coefficient values as change points. In the empirical study, large numbers of change points were detected, resulting in numerous segments. The change points characterized as short and long stops were classified and named from prior knowledge of the gull and the abruptness of change. In the study of the Lesser Black-backed gulls, the main stopover sites, wintering locations and places where the animal rested for a short time while migrating can be easily detected. Transitions from breeding to migration to wintering and vice versa were regularly identified by the latitudinal shifts in different seasons in the birds. The details in the changes in movement patterns during these periods can be picked up by the wavelet signals (Figure 4.8). The results show that stopover locations and short stops are concentrated closer to the breeding site and occur mostly during the autumn migration. The spring migration shows fewer stops. This is relevant as the birds are known to fly faster during the spring migration, probably in order to find the most beneficial nesting sites (Klaassen et al. 2012). Since they are generalist feeders, these migrating gulls find plenty of feeding habitats along their migration journey and therefore show many stops and slow migrating speeds (Klaassen et al. 2012).

Discrete wavelet transformation was used to decompose the time series of residence time showing the same stopover site, breeding site and wintering site as revealed by Lavielle's method on the residence time. In addition, the discrete wavelet transform method was capable of showing more precise tipping points, even indicating less important resting sites and areas intensively used during the breeding and wintering seasons. It must be noted that differences in step length and residence time are commonly used for localizing intensive and extensive search patterns, but when using discrete wavelet analysis, the differences are used to identify frequency breakpoints for changing movement patterns rather than movement modes.

The discrete wavelet transform was used to find transitions at a coarse migratory scale. For this purpose, several decompositions were conducted using the empirical data spanning different mother wavelets, decomposition levels, and threshold analysis. The level of decomposition was also tested by using the best wavelet selection algorithm of the wavelet packet. For different objectives and different resolution of movement data, change detection using discrete wavelet analysis may involve using different levels of decomposition and a different mother wavelet. The Haar wavelet has been found to achieve some success in different fields for change detection.

Since new movement data now being collected are becoming progressively more detailed with larger numbers of fixes, change detection is becoming increasingly difficult to define. To avoid false detection, we can use the

discrete wavelet method to effectively remove noise from the dataset. When large numbers of coefficients are close to zero, it indicates that there are insignificant changes in the signal at most times. By setting these coefficients to zero followed by an inverse DWT, the signal can be de-noised and subsequently analyzed (Cho and Chon 2006). The threshold method we propose here acts in a similar way by characterizing the low coefficient values as regular movement bouts and highlighting the large coefficients as abrupt changes. In addition, the advantage of using DWT of ecological time series is that it is less sensitive to irregular data, by adapting the wavelet shape in sampling gaps and boundaries (Cazelles et al. 2008a).

4.4.3 Biological relevance

In our empirical study of the Lesser Black-backed gulls, the similarities and differences as a result of different focus variables and different change point detection methods are shown in figure 4. 8. It shows the latitudinal shift of the gulls through time. Figure 4.8 illustrates that Lavielle's method applied to step length as well as residence time in fact under-predicted the autumn migration period to a mere 4 and 2 days, respectively (Tables 4.1 and 4.2). This is because during the autumn migration, the birds were moving much more slowly with more stops than during the spring migration (Klaassen et al. 2012). These segments of the migratory journey, with a large number of stops and slow movements, were segmented as parts of the breeding season or wintering season. The spring migration was divided into two phases by using residence time. This is because the first phase of the migration is relatively slow (mean speed 7.54 km/hour) compared to the second phase (mean speed 21.30 km/hour). This can be explained from a biological point of view by the fact that the birds arriving earlier at the nesting grounds might well have a better choice of nesting sites and they therefore tend to fly faster as they near the nesting location to reduce the competition in finding a nesting site.

However, the wavelet analysis was able to predict the main moving periods, stopover periods and resting periods in more detail by using step length as well as residence time (Figure 4.8). While residence time has an added biological importance, since optimizing the time spent in different patches increases the fitness of the animal (Charnov 1976), step length and speed are powerful quantitative measures of movement to test mechanistic hypothesis such as environmental cues affecting movements (Turchin 1998). Figure 4.8 shows that in the use of both focus variables, the breeding site located at Vlieland, the Netherlands, was predicted accurately. In addition, for both focus variables, the wavelet analysis predicted common long stops, which include a stopover site in France (autumn migration) and the wintering

sites in Portugal. The difference between the methods was mainly seen in the short stops.

Figure 4-8: Plot of latitudinal movements against time of a Lesser Black-backed gull: The tipping points and segmentation of the trajectories by different methods on two time series (step length and residence time) are shown using the colour coding described in the legends.

4.5 Conclusion

The movements considered in this paper were global and at large scales, based on the frequency of data available. Lesser Black-backed gulls are predicted to have an energy-minimizing strategy for migration and to show great variations in their routes, daily speed, and stopover sites (Klaassen et al. 2012). For such birds, the use of methods of segmentation of trajectory, where thresholds have to be defined a priori, is demanding because collecting eco-physiological data at each time stamp is challenging. The discrete wavelet analysis is an excellent choice for analyzing movement trajectories of animals where individual variations are expected. It provides exciting possibilities for automated detection of changing movement patterns in the analysis of animals that show cryptic behaviour. The change points in the movement patterns can provide the baseline from which complex multifactorial interactions between multifactorial processes, such as the effect of climate change on animal behaviour, can be studied in detail. The choice of

the focus variable is important depending on the aim of the study. Although discrete wavelet analysis is a novel method of detecting variation in movements at different scales, this analysis alone is not able to explain the ecological reasons behind the segmentations, or the physical and biological interactions that result in different movement patterns. We have shown that discrete wavelet analysis does provide a tool to speculate about such interactions, which then need to be carefully interpreted using expert knowledge and field studies.

5 Mining periodic behaviour of moving animals in relation to environmental cues

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5.1 Introduction

With the increasing availability of telemetry data from animals, movement studies have evolved from ecology centred modelling to more statistical approaches that quantify the trajectory itself. Quantification has resulted in understanding individual animal movement and their causes which sets a precedent for population based studies (Turchin 1998). However, three difficulties have emerged in the application of individual based movement analysis. First is explaining the role of different environmental variables that effect movement behaviour (Giuggioli and Bartumeus 2010). Second is the notion of scaling up, wherein results obtained from analyzing individual moving animals should provide insight into large scale organism-environment interactions (Hawkes 2009; Schick et al. 2008). To understand the application of basic movement models at a landscape level, it is essential to assess whether the same patterns and processes at one spatial or temporal domain scale up to the next level as well (Schick et al. 2008). Thirdly, there is the notion of models with increasing behavioural complexity. As animals move through increasingly complex environments, it becomes challenging to extract the influence of individual environmental controls across different spatio-temporal scale.

Multiscale processes occur in ecological systems (Wiens 1989). Studies related to different biological aspects of animals such as foraging (Fritz et al. 2003), dispersal patterns (Blums et al. 2003), competition (Rutten et al. 2010) and population dynamics (Lewis 1993) have been made at specific scales, which are typically chosen according to the availability of habitat and climate data, or are even defined arbitrarily (2002). The problems of single scale studies are that they limit ecological understanding and they do not reflect the hierarchical way in which the animals respond to their environment over several spatial scales (Bissonette 1997). There is a requirement of stratifying movement strategies according the scale at which changes in behaviour occur.

In order to confront these challenges we propose a statistically robust method to explore changes in movement patterns due to environmental covariates over a range of temporal domains. The concept is to extract distinct patterns in the trajectory of a moving animal that is significantly linked to an environmental cue. One way to extract distinct patterns in moving animals is to explore repetitive cyclic behaviour. In case of animals, repetitive or periodic behaviour can be expected to be a result of periodic cues from nature such as temporal oscillations in temperature, precipitation, light, wind, forage etc. as well as the animal's circadian rhythm. The periodic movement pattern associated with environmental cue is likely to have a degree of temporal correlation and also operate at multiple scales (Polansky

et al. 2010). Since the period (the regular time intervals in a periodic motion) that is affected by different cues is an unknown parameter, one needs a signal processing method that automatically detects periodicity in the data. Among the different period detection techniques that can be applied to signal processing, wavelet transform can be directly applied to movement data (Ropert-Coudert and Wilson 2005) and results in exploratory analysis of the auto-correlative properties of the GPS data. However, animals do not repeat the same behaviour at the exact same time and place. In addition, there could be several periodicities existing at the same time. Therefore, certain assumptions and uncertainties have to be accounted for. To account for these two issues the following steps were followed:

1. First, important locations that can be designated as “reference spots” are defined, from where the periodicities can be viewed. The idea of reference spots lets us detect the periodicity associated with a particular location. This also allows for detection of multiple periodicities associated with each reference spot.
2. Second, multiple periodicities can be detected using wavelet transforms. Wavelet transform gives a concise visualization of periodic behaviour over different temporal scales.
3. And thirdly, cross wavelet analysis is applied. This bivariate extension of wavelet analysis allows the examination of two time series together (such as a movement variable and an environmental variable) that is expected to be correlated to each other. The cross wavelet analysis introduced by Hudgins et al. (Hudgins 1993) that examines two time series together has already been applied to various problems in climatology such as the ENSO-Monsoon system (Torrence and Webster 1999), and is ideal to explain the correlation of environmental cues with the movement of animals.

It is important to emphasize the significance of cross wavelet analysis that allows scale, periodicity and behaviour to be modelled in a single visualization. Such an overview essentially provides the corner-stone for using data for detailed analysis at the appropriate scale. For instance in case of sea gulls, different periodic movement behaviours such as daily feeding, patch to patch feedings, deep sea foraging, and so on, are triggered by different environmental factors. Daily foraging for sea gulls is most strongly influenced by tidal waves, temperature and local humidity of the place. However, patch to patch foraging probably occurs when the weather is appropriate for long distance travelling and is most likely dependent on wind speed, wind direction and temperature. Similarly, deep sea foraging is also likely to be primarily dependent on wind speed and direction. Thus visualizing and exploring these periodic behaviours and their triggers at the right temporal scale is critical for modelling movement.

Thus the aim of this study is to test whether cross wavelet analysis is a suitable method to detect periodic movement patterns in animals as a result of environmental cues. Polansky and Wittemyer et al (2010) used wavelet analysis to study auto correlative properties of movement data and acknowledged the limitation of deductive ecological interpretation of wavelet statistics. Linking environmental co-variables to periodic movements is therefore an important step forward towards improved biological interpretation of movement data using spectral analysis. We use empirical data of GPS tagged Lesser Black-backed gulls (*Larus fuscus*) to assess our method. Three questions were tested in this chapter: Are diurnal movement in gulls correlated to environmental variables. Do these periodic patterns in gulls owing to environmental changes show variations at different temporal scales? And can cross wavelet analysis be used to study individual variations as well as group patterns?

5.2 Methods

Cross wavelet analysis was applied in two phases:

1. Step length during the breeding season of a single gull (ID 41781) was tested against three environmental variables, namely temperature, precipitation and wind speed.
2. Step length of 12 gulls during the breeding season was tested against temperature to illustrate individual variations and group behaviour.

5.2.1 Tracking data

The tracking data of the Lesser Black-backed Gull (hereafter gull) used for this study was provided by the Avian Research Institute, Wilhelmshaven, Germany and SOVON Dutch Centre For Field Ornithology, Nijmegen, The Netherlands. The gulls were tracked using GPS satellite transmitters as part of The European Space Agency Fly-safe Project(Ens B.J. 2008) . Each bird was equipped with an Argos-GPS solar-powered Platform Terminal Transmitter (PTT; Microwave Telemetry Inc., Columbia, MD, USA). The Argos-GPS PTTs have an accuracy of ± 18 m. For this study the gull with the PTT id 41781(sampling interval 1 hour) was used to test the effect of animal movement with different environmental variables at different temporal scales. Data from twelve gulls (PTT id's 41742, 41749, 41752, 41757, 41758, 41762, 41763, 41764, 41767, 41771, 41775, and 41781) were used to demonstrate the use of cross wavelet analysis in analyzing individual variations and group pattern of gulls with temperature as the environmental variable. We selected the month of May, 2008 during the breeding season to test our methods.

Continuous position of the animal were obtained at time t as spatial coordinates $x(t)$ and $y(t)$ to construct time series $X_n = (X_0, \dots, X_n)$. There were missing data values in X_n which were estimated using predicted values from a

Kalman smoothing algorithm (Stoffer 2008). The Kalman smoothing algorithm is adapted from a state space model. The smoothing technique was executed in R environment (R Development Core Team 2010). Subsequently the movement parameter used for the study namely step-length or distance travelled between two GPS fixes was calculated.

5.2.2 Reference Spots

Animals with periodic behaviour commonly have a central location that they visit repeatedly. These are termed "reference spots"(Patterson et al. 2009). Reference spots can be obtained by different kinds of density based clustering methods. We adopt the method used by the MoveMine moving object data mining system (Patterson et al. 2009). It is an adaptation of the widely used kernel density method of estimating the home range of an animal (Benjamini et al. 2010). The kernel function is based on the quadratic kernel function described in Silverman (1986, p. 76, equation 4.5). Figure 5.1 shows the reference spots identified from one year data of the gulls (2007-2008). Through prior knowledge of the species three important reference spots were identified; the breeding site, the wintering site and a major stopover site. Each of these reference spots is associated with different periodic movements which can be visualized by the Fourier analysis of a movement parameter like step length. In the present study we use the breeding site as the main reference spot to further analyse the effect of environmental variables on behaviour of the gulls.

Figure 5-1: a) Three reference spots identified from the gull data set used shows the breeding site, stopover site and wintering site. Each of these reference spots is associated with different periodicities and therefore cannot be analyzed together. b) Plot of all the gps fixes from the tagged Lesser Black-backed gulls (2007-2008)(Ens B.J. 2008)

5.2.3 Environmental Data

To test the application of cross wavelet analysis for mining periodic behaviour of the gulls in relation to environmental co-variables, we use the movement parameter, step length during the breeding season, as well as three environmental variables: temperature, precipitation and wind speed. Data for the breeding season was ideal because there is a well-defined reference spot (the nesting site), from where changes in movement patterns can be easily interpreted. Environmental data was downloaded from the Royal Netherlands Meteorological Institute, Station Vlieland. Mean hourly data for temperature, precipitation and wind speed were used for the study.

5.2.4 Cross wavelet analysis

The wavelet transform of a time series decomposes the data using a wavelet function resulting in a time-scale representation of a temporal pattern (Gaucherel 2011). Scale in a wavelet analysis is generated by contraction and dilation of the wavelet function. Contraction or dilation changes the time window over which the wavelet function is applied on the time series. Increasing the size of the window increases the scale at which the wavelet coefficients are calculated. The parameter scale in the wavelet analysis can be paralleled to scales used in maps. Corresponding to high scales in maps, in wavelet analysis higher scales (or periods) represent global view of the

signal that usually spans the entire signal and low scales (or periods) correspond to a detailed view that relatively lasts a short time. Thus, wavelet coefficients are obtained for a series of scales and at each time stamp. We use the Morlet wavelet for this study defined as

$$\psi(\eta) = \pi^{-1/4} \exp(-i\omega_0\eta) \exp(-\eta^2/2) \quad \text{Equation 5-1}$$

The continuous wavelet transform of the discrete time series X_n at scale a and time t_j is defined by

$$W[a, t_j] = \frac{1}{\sqrt{a}} \sum_{l=1}^N X_l \psi^* \left[\frac{(l-j)\Delta t}{a} \right] \quad \text{Equation 5-2}$$

where ψ^* denotes the complex conjugate of the analyzing wavelet function ψ .

A local power spectrum of a wavelet transform is the square of the wavelet coefficient $|W_n^X(s)|^2$ for each scale and at each time stamp. Cross wavelet transform (XWT) of two time series x_n (movement parameter) and y_n (environmental parameter) can be defined as $W^{XY} = W^X W^{Y*}$, where $*$ indicates the complex conjugate. As the cross wavelet transform gives complex values, it can be decomposed into amplitude and phase angles. The phase angles describe the delay between the two signals at a time t on a scales.

Thus cross wavelet transform exposes regions with high common power between the two time series and further reveals information about the phase relationship. If the two series were physically related we would expect a consistent or slowly varying phase lag. The circular mean of the phase angles can be used to quantify the phase relationship. In the visualization produced phase arrows can be interpreted as:

- right: in-phase
- left: anti-phase
- down: X leading Y by 90°
- up: Y leading X by 90°

Regions of significant scalogram values were defined by the "area wise test" (Maraun et al. 2007) which is a bootstrapping test. Regions of modulus values greater than or equal to the 0.95 sample quantile of 1000 bootstrapped scalogram of red noise null model fit to the data were considered significant and marked in black contour lines (Bartumeus 2009; Maraun and Kurths 2004; Maraun et al. 2007; Polansky et al. 2010; Torrence and Compo 1998). An interpretation of cross wavelet analysis is shown in figure 5.2. Cross wavelet and wavelet coherence software were provided by

A. Grinsted and Aslak Grinsted (2002-2004) and used in the Matlab environment.

Figure 5-2: Interpretation of Cross wavelet analysis: a) On the time-series of speed during a day of a gull a Morlet wavelet with scale (period) $s = 2$ hours and $s = 6$ hours are superimposed at time position $t = 13:00$ and $t = 16:00$ hours, respectively. (b) Wavelet power spectrum is plotted as function of time and period in a two-dimensional graph where larger squared modulus values correspond to warmer colours (red, yellow) and smaller values correspond to cooler colours (blues). (c) Cross wavelet analysis of speed and temperature (i) and cross wavelet analysis of speed and precipitation (ii) showing areas of common power and phase relationships.

5.3 Results

a) Cross wavelet analysis of step length and temperature

b) Cross wavelet analysis of step length and precipitation

c) Cross wavelet analysis of step length and wind speed

Figure 5-3: Cross wavelet transform of time series of movement parameter step length and environmental variables. The 5% significant level against red noise is shown as a thick contour. Larger squared modulus values correspond to warmer colours (red, yellow) and smaller values correspond to cooler colours (blues). The relative phase relationship is shown as arrows.

Figure 5-4: a) Cross wavelet analysis of step length and temperature of twelve gulls during the breeding season (May 2008). b) Average power spectral values from cross wavelet analysis of step length and temperature of all the individuals.

5.3.1 Interpretation of cross wavelet analysis

Interpretation of cross wavelet analysis is made by analyzing regions of high common power and the phase relation between the two time series under consideration. The results in figure 5.3 show diurnal movement patterns in the gulls related to three environmental variables and variations at different temporal scales. Cross wavelet analysis of step length and temperature, precipitation and wind speed reveals strong diurnal cycles with specific

periods of high common power. For example, step length and temperature show consistent high powers at a scale or period of 24 hours. Higher powers are also seen beyond 96 hours (4 days) but these areas are not significant. In addition, step length showed consistent 6 and 24 hour cycles with precipitation and 24 hour cycles with wind speed.

For two time series to be related, areas with consistent or slowly varying phase lags should be considered in the regions of high common power. The phase angles give an indication of the lag between the two time series. In figure 5.3(a), where step length is analyzed with temperature in the 24 hour period, both time series are in-phase over the entire breeding season. This suggests that a daily activity of one cycle per day is a result of daily oscillation in temperature. The 5% significant areas of high power are phase-locked suggesting a strong link between the two time series. For shorter cycles (periods), the phase angles are not consistent and show that that hourly movement is probably not significantly dependent on the temperature and is affected by other factor. The average phase angle for the 24 hour period is $24 \pm 15^\circ$ and proves that step length of movement essentially mirrors temperature and does not have a significant lag between them.

Cross wavelet analysis of step length with precipitation in figure 5.3(b) showed an average angle of $169 \pm 15^\circ$ demonstrating that movement and precipitation are predominantly in anti-phase. The average phase angles in the significant regions of higher power movement and precipitation indicates that movement is inversely related to precipitation. At higher periods phase angles gradually varies from anti-phase to precipitation leading movement by 90 degrees. Cross wavelet analysis between step length and wind speed showed that movement was mainly in-phase at a period of 24 hours. However at higher powers (64 hours or 3 days) the phase angles gradually varies from in phase to anti phase.

Figure 5.4(a) shows individual variations using cross wavelet analysis of step length with temperature. Consistent common high powers show diurnal cycles in all individuals but also shows heterogeneity in time periods of movement bouts and resting phases. The power spectral values from cross wavelet analysis of all individuals were stacked into a 3D matrix and averaged for each time stamp and at all scales in figure 5.4(b). The result shows that correlation between distance moved and temperature was not continuous across time for the temporal scale 24, thereby showing a distinct pattern in the sample under study that can be further linked to other ecological and social factors.

5.4 Discussion

Wavelet analysis is a powerful tool for time series analysis of animal movement data (Gaucherel 2011). Here, the use of cross wavelet analysis reveals a correlation between two time series whose interaction is not clear a priori. We have illustrated the use of wavelet analysis in interpreting multiscale, non-stationary movement data and feature extraction from a complex data set.

The cross wavelet analysis is used for exploratory data analysis as a first step towards modelling moving animals. The traditional methods of visually analyzing trajectories of animals tagged with telemetry devices are replaced with mathematical models and statistics. Advanced data mining techniques can process large amounts of telemetry data in a conceptually standardized way. The method proposed serves as the first step towards understanding the organism-environment interaction, and is the basis for choosing the right environmental variables at the right scale for detailed modelling.

The results show that periodicities at a central location can be explained by periodicities in the environmental variable. The method allows exploration of periodic movement behaviour invoked by environmental cues through a range of temporal scales.

The wavelet approach as a statistical approach however does not provide answers to the underlying processes of the movement behaviour. The interpretation of the spectrograms is based on basic knowledge of the species. For instance if the wavelet analysis were to be used on nocturnal animals, it most probably would provide similar results with 24 hours periodicities; however interpreting the results would depend on the knowledge about the ecology of the animal– in this case that it is active at night. Therefore it is essential that cross wavelet analysis is applied with good ecological understanding of a species (Grinsted 2004).

While the study uses only a few environmental variables, it illustrates that it can easily be replicated to test for a large range of variables and in doing so we can identify parameters that are capable of explaining cyclic behaviours. This is essential for segregating complex variables into categories such as limiting factors, or into factors that affect the cognitive senses of the animal etc.

Most studies that examine animal behaviour with environmental variables are not able to account for the fact that different components of the environment are important to animals at different scales (temporal scales). Identifying when or for how long a particular environmental cue triggers a specific

behaviour is the first step towards explaining why and when animals move to certain parts of their range. However, this important step is often skipped due to lack of sufficient data at the right scale or tools to identify the scales according to the species under study. Incorrect definition of scales, relative to the perception of space by an animal may result in the failure to measure response to variables and variation relevant to the process of interest.

Further research can focus on using the spectral signatures in cross wavelet studies to extract exact points where the periodic behaviour changes. These can be defined as tipping points and provide knowledge about the triggers, which cause sudden changes in movement behaviour.

6 Synthesis

6.1 Synthesis

This thesis is a compilation of application of wavelets as a quantitative approach for describing the dynamic and complex patterns in animal movement data to increase the accuracy of ecological interpretations. In order to understand the advantages of developing this line of analysis in movement ecology we need to delve a little into the history and theory of quantitative and behavioural ecology.

6.2 Historic background of quantitative ecology

In the early 20th century, ecology was often described as “scientific natural history” because it intertwined natural history to natural philosophy through practical scientific research (Elton 1927). The term now has little importance except to emphasize that it was once extremely novel to combine natural history with scientific rules of nature such as distribution of species, structure of the ecosystem and physical attributes of a species (Kingsland 2004). This evolution in ecology in the 18th and 19th centuries to include quantification and scientific analysis was largely due to the advancement of Newtonian science in different fields such as life sciences and sociology (Hankins 1985). One of the pioneers of this was Alexander Humboldt (1769-1859) (often considered the father of ecology) who advocated that the basis of all scientific understanding was the use of quantitative methods and mathematical analysis with the most modern instruments and techniques available (Cannon 1978; Dettelbach 1999). Although criticized for his romanticism of nature, his methods inspired ecologist like Charles Darwin whose experiment and critical analysis aimed at discovering unexpected patterns, lead to the development of the evolutionary theory (Kingsland 2004). For a long time the technology for measurements were crude and therefore there was a tendency to formulate theories based on assumptions, observations and limited experimental work (Ludwig and Reynolds 1991). But the recent impetus of technology has allowed collection, storage and handling of large datasets (Ludwig and Reynolds 1991). However now that precise data on various ecological processes is available, there is reluctance in pursuing mathematical options in ecology. Traditional ecologists still rely on descriptive ecological methods and tend to show wariness towards using mathematical techniques to develop theories (Weiner 1995). This is seen by a simple review of articles in pure ecological journals as well as the recent emergence of new applied ecological journals that provide a niche for such articles.

In the case of movement ecology, some ecologist have noted that the genesis of animal movement as a field in ecology is largely due to the modern application of concepts borrowed from statistical physics and new techniques of measurement (Giuggioli and Bartumeus 2010). I observe, that the use of mathematics, concepts from physics and statistics in ecology, to

formulate hypothesis and theories, is not a new phenomenon, but revival of an old idea of an interdisciplinary approach that resulted in some of the fundamental theories in ecology such as concepts of biogeography, theory of evolution, laws of thermodynamics to understand biogeochemical cycles and the idea of ecosystems. Since then however empirical ecology and theoretical ecology has developed tangentially (Codling and Dumbrell 2012). Codling and Dumbrell (2012) in their paper on mathematical and theoretical ecology noted that empirical ecologists conduct numerical analysis without consideration to underlying theory, while theoretical ecologists sometimes pursue mechanistic mathematical models without validation in the real world. They suggest an iterative approach where mathematical models be tested with data and numerical analysis lead to theoretical development. Since this thesis is based primarily on advancing the field of movement ecology by developing and using statistical analysis of empirical and simulated data, I will endeavour to link these developments to broader ecological theories.

Jacob Weiner indicated in 1995 that the science of ecology has been in the doldrums for the last three decades because of lack of generation of testable theories and the Popperian notion of refutability which says that scientific advancement requires updating of theories (Weiner 1995). He suggests that improvement in ecological studies requires a new paradigm with predictive models and testable theories, greater appreciation of the role of natural history and need for new approaches with diverse application. For theories to be formulated we need to discover patterns in nature and apply constructive and deductive mathematics to understand them. The data collected using telemetry devices form an ideal collection of information that can advance the ecological theories of movement. These data sets are unique in the sense that ecological data for animals has never been so accurate and detailed. Presently the use of movement data from telemetry devices is largely being used for specific empirical studies or causal narratives. There is need for simple robust mathematical formulae that can range in their uses among species and applications and also contribute to the testing and formulation of theories. In lieu of this requirement, this thesis brings together the application of wavelets as a mathematical approach to study animal movement as a behaviour that can be tested and theorized upon by discerning patterns.

6.3 *Animal movement as a behaviour*

Movement is an essential part of lives of animals that affect their behaviour in most ecological processes. Traditionally studying movement as a behaviour has mostly involved evolutionary contexts like dispersal and decisions to dispersal (like con-specific interactions) as the main focus (Léna et al. 1998). The actual process of movement that causes dispersal has not received

significant importance (Liedvogel et al. 2013). However it is important that evolutionary history of movement such as dispersal is studied along with proximate causes of movement as is the recent trend in other aspects of behavioural ecology (Liedvogel et al. 2013). Proximate causes for movement would involve incorporating knowledge about environment, space use, habitat as well as biological factors such as biophysical conditions, neuro-sensory conditions and breeding success. I propose that animal movement itself can be considered in the context of behaviour ecology that is affected by evolutionary and proximate factors and show distinct characteristics.

Studying movement within the framework of behaviour ecology will help ecologists link the analytic framework described in this thesis to understand the mechanism, function and significance of movement. In the introduction of this thesis, two questions were highlighted namely, 1) Can wavelets be used as a mathematical tool to analyze temporally localized statistical properties of movement trajectories to derive ecological answers? and 2) Can animal movement be explained as transitions between different modes of movement with multiscale properties? The first question has been sufficiently demonstrated in the chapters 2, 3, 4 and 5. The second question has been dealt with in chapter 2 and 3. We now provide a theoretical depth to these questions by showing that wavelets can be used to analyze behavioural questions in animal movement within the traditional framework of behaviour ecology.

6.4 *Traditional framework of behaviour ecology: Tinbergen's 4 questions:*

This is the 51st year of Niko Tinbergens seminal paper (1963) "On the aims and methods of ethology". The paper has withstood the test of time and even today the framework he proposed for the study of behaviour ecology is still intact (Bateson and Laland 2013), although a more nuanced application is seen given the new wave of detailed data. He proposed that for an all-inclusive study of behaviour requires four important questions to be answered: What is the survival value of the behaviour (adaptation)? What is the mechanisms that cause the behaviour (mechanism)? How does the behaviour develop during the lifetime of an individual (ontogeny)? And how did the behaviour evolve (phylogeny)? While mechanism and adaptation are current problems, ontogeny and phylogeny are historic. While further discussion will show how the analytical framework of this thesis helps in answering the current problems, it also throws light on line of research required in the historical problem.

In a simple but important example of a theory development, I note that Darwin realized that nature's patterns arose from the activities of organisms connected to each other in myriad ways. I reason that activities of animals,

especially birds, connected to each other are also dependent on the temporal patterns in nature and within an organism. Taking movement as behaviour, I theorize on their repeated temporal patterns using Tinbergen's questions as a theoretical framework, using wavelets as an analytical framework and data of the Lesser Black-backed gulls as empirical evidence (Figure 6.1).

Figure 6-1: Theoretical and analytical framework for analyzing movement under the purview of Tinbergen's framework for "Methods in Ethology".

6.4.1 Survival Value

Tinbergen (1963) devoted a substantial part of his paper to the section of survival value or current utility of a behaviour. The principle questions being the function of a particular behaviour and how does the behaviour impact on the animal's chances of survival, reproduction or fitness? Periodicity in animal movement is a commonly occurring behaviour frequently linked to the circadian rhythm of an animal (Dray et al. 2010). Periodic behaviour as described in the introduction chapter is repeating a particular activity after regular intervals of time. These repetitive patterns were affirmed to be an understudied phenomenon by Wittemyer et al (2008) and they stated that "Treating cyclic (strongly repetitive) patterns of movement as behaviour signals can offer new insight into the factors impacting population organization and the spatial ecology of animals". This thesis deals with the

cyclicity in movement by using wavelets to analyze temporal periodicity. Cyclicity in movement at different temporal scales have been attempted to be explained with respect to environmental variables, spatial distribution of resources, sensory and associative memory inputs (Block et al. 2005; Fagan et al. 2013; Phillips et al. 2004; Wittemyer et al. 2008). There is no denying that animals rely on these inputs (as shown in figure 6.1) to a large extent. However the survival value of repetitive patterns in movement is proven by the fact that although these external inputs are important, new search theories show that periodicity in movement may increase the fitness of an organism, given all other factors remain considerably static (Bartumeus 2007).

New search theories suggest , for example, that when all other factors remain unchanged, and perceptual cues are minimal, fitness of an organism increases when explorative movement follow at least three main components 1) directional persistence, 2) multiscale fractal like movement and 3) super-diffusive movement (Bartumeus 2007; Maye et al. 2007). This can be visualized as a movement mode that is a combination of intensive and extensive search patterns, with a fractal like pattern. We show in chapters 3 that the wavelet model is able to pick out these kinds of patterns in the movement of the Lesser Black-backed gulls. We show that search patterns of the birds show similarities to Levy probabilities, with self similarities occurring at higher temporal scales. This kind of movement is considered to optimize the random search strategies when perceptual cues are strongly reduced. Frederick Bartumeus (2007), suggests that such properties in movement are perhaps an adaptive strategy towards stochastic search patterns and are not just individual nuances but leading to ecosystem level processes such as macroscopic diffusive properties of motion, and population level encounter rates.

In the figure below (Figure 6.2) we see the movement of a Lesser Black-backed gull, colour coded, to show intensive and extensive movement as discussed in above paragraph. This is a view of the movement every 6 hours and shows the variation in intensive and extensive searches with time and space. During this breeding period a combination of systematic and random search patterns are seen that influences the fitness of the individual. Systematic searches are performed when the animal has prior knowledge about a location as for this individual is located in and around the nesting site and the foraging sites on the tidal breaks located at the edges of the island, where the animal regularly travels. Random searches can be seen in the long distance foraging trip. The patterns in these random foraging trips also show multiscale variations and fractal properties, which begs the question whether there is an associated adaptive strategy that increases the foraging fitness of the animal. These questions require in depth study of energy balance and are

beyond the purview of this thesis. But it is important to note that these questions arise because wavelet analysis discussed in chapter three of the thesis provides the information from which such research questions could be answered. The analysis in this chapter not only shows the individual periodicity in movement across different temporal scales, but also helps in characterizing the movement as intensive and extensive movements to locate optimal foraging sites and resting places.

Figure 6-2: Space time visualization of intensive and extensive movement patterns of a Lesser Black-backed gull, during the breeding season, studied at a periodicity of every 6 hours.

6.4.2 Mechanism

The mechanistic basis of a behaviour has a plurality of fields which was explained and discussed by Tinbergen (1963). The questions about the mechanism of a behaviour can range from how both behaviour and psyche "function" on the molecular, physiological, neuro-ethological, cognitive and social level, as well as what the relations between the levels look like? The overall question about the mechanism of periodic movements in animals is what are the stimuli that elicit the response and what are the level of complexity associated with these stimuli.

Periodic movements of birds are a result of endogenous and exogenous factors influencing them (McKenzie et al. 2009). While endogenous factors such as circ-annual rhythm probably control the coarse temporal scale of decisions, the finer temporal scale of decisions appears to be dependent on the meteorological conditions, resource availability and stored energy. In chapter 5 of the thesis, we discuss the usefulness of wavelets in detecting the

periodic movement of birds in relation to environmental stimuli. The chapter shows how long distant moving birds such as the Lesser Black-backed gulls, face a wide variety of environmental factors that determine when, where and how they move. For successful migration and foraging, birds need to experience availability of suitable habitat and environmental conditions (Smith and Deppe 2007) which influences movement strategy as well as movement routes (Alerstam et al. 2003). For example, the effect of wind influences the timing and energetic in many birds (Hedenström et al. 2002) and wind patterns have an important influence on the evolution of bird migration routes (Alerstam 2001). Dynamic atmospheric conditions, such as wind, precipitation, temperature, and cloud cover impact movement patterns (Gauthreaux Jr et al. 2005) directly through their influence on movement direction and speed (Gauthreaux and Able 1970) and indirectly through their impact on birds' activity budgets and energy balance, which in turn determine flight range and overall movement speed (Berthold 2001). These external stimuli work in tandem with endogenous characteristics, such as fat load, muscle mass, and water content, which influence movement behaviour by altering the energy dynamics (Moore and Aborn 1996; Smith and Deppe 2007). It can be deducted that the precise outcome of this interaction is mediated by the bird's physiology and results in very specific movements at specific time. In addition the effect of these stimuli act at different scales and produce layering of behavioural responses in accordance to the temporal or spatial scale at which they are acting. These layered behavioural periodicities are affectively picked by cross wavelet analysis, linking the movement variables to different external stimuli.

For example periodicity due to external stimuli is starkly demonstrated during the breeding season of the Lesser Black-backed gulls when human fishing activities and fishing discards from fishing trawlers effect their movement at regional scales. It is a proven fact that when fishing trawlers operate, scavenging birds show site fidelity to certain foraging grounds with intensive search movements, while in the absence of fishing trawlers birds tend to move long distances with extensive search movements (Bartumeus et al. 2010). Cyclic fluctuations in chick growth were also studied in the Lesser Black backed gulls on the island of Texel in Netherlands, based on periodicity in fisheries discard from fishing vessels (Camphuysen 2013). Patterns in commercial fishing vessels at a distance of 80 km from the colony were show to have a weekly cycle that correlated to growth patterns in chicks. Thus, there are a complex set of factors affecting movements at various scales. Using wavelets, we can study each of these factors in isolation and try to understand their effects at multiple temporal scales.

6.4.3 Ontogeny¹

Tinbergen is credited with opening the debate on ontogeny or behavioural development through the life of an organism (Tinbergen 1963). The main questions are how does the behaviour change with age, and what early experiences are necessary for the behaviour to be shown? Which developmental steps and which environmental factors play a role. Although we do not analyse the ontogeny of behaviour in this thesis, it is important to note its importance and discuss how the behaviour of adult birds can provide insight into their development. The ontogeny of behaviour is not just controlled by genetic inheritance. Social learning, parental effects, behavioural traditions also play an important role. In chapter 2 of the thesis we discuss the spatial and temporal scaling in movement of Lesser Black-backed gulls. In the spirit of the ontogeny question, we will discuss some of the developmental steps and historic account of how the characteristics of movement discussed in the chapter may have developed (Cramp and Simmons 1983). Fractal analysis was used to identify two spatial domains around a central resting place, 0-20 km and 20-80 km, where changes in movement patterns occurred. Within each of these spatial domains, there were variations in temporal periodicity of movement. The birds tended to move with a periodicity of one or two cycle around a distance of 20 km from the nest and showed long distant movement only at intervals of 10 days.

Keeping this in mind we will speculate how at different stages in life of a Lesser Black backed gull, movements vary around a central location. During the breeding season, the female bird arrives at the nesting site before the male and claims a territory. Pairs are generally monogamous for several years, and following an elaborate courtship ritual, the eggs are laid. 25 days prior to egg laying, the female bird starts food-begging, which results in courtship-feeding by the male, wherein the male presents solid or regurgitated food to the soliciting female. It can be deduced from this that the males tend to show frequent movements further from the nesting area during this period, in order to provide food for the female. Courtship feeding diminishes considerably after the eggs are laid and the males as well as the females develop long distant feeding bouts. However there is rampant conspecific aggression in this species and there are high levels of chick predation (Davis and Dunn 1976) . As a result one of the parents generally stands guard over their clutch. In this respect it will be interesting to note how movement of a breeding pair varies using tracking technology. During this period both parents also show movements related to collection of nest building material. Once the young are born they remain in the nest for a few days before making small excursions to neighbouring areas. Young chicks are

¹ The ecology and ontogeny of Lesser Black-backed gulls is adapted from the detailed chapter on the species in the book 'Birds of the Western Palearctic' (Cramp and Simmons 1983), volume 3, Oxford University Press, London

fed by the adults near or close to the nest. Other territory owners peck chicks that stray from the territory and many movements in the nesting site are related to aggressive behaviour and defence tactics especially by the males. The duration of parent-young caring is not precisely known and therefore further knowledge about their dispersion and movements can be deduced from observations of the birds in and around the nesting sites. The off duty breeding birds often move outside the colony, usually to the edges of the water nearby, where they roost with immature, non-breeding and failed breeders. They form a group of what can be called as a "club" of roosters. Movement related to feeding and nest relief is usually highest in the early morning, minimum in the afternoon (when temperatures are high) and again increases towards the evenings. These cyclic trends in movement were visualized using the wavelet analysis in chapter 2. Long distance movement is exhibited by both sexes and could be related to feeding bouts in relation to fishing trawlers that have been known to be operating at least 5 days a week within a distance of 80 km from the nesting site. Outside the breeding season there is no evidence that the bond of the pairs exist or that of the young ones. They either migrate or feed during the migration and wintering seasons singly or in small flocks. The movements during these periods vary considerably with the availability of food sources. Thus, all of details shows how behaviour changes with age and are affected by early experiences resulting in a definite pattern of movement throughout the life of an individual.

Another aspect of the movement and its temporal cyclicity of the birds is the effect of photoperiod. Photosensitivity and photo-stimulation causes physiological changes in the body of birds which influence the movement of the juveniles as well as the adults (MacDougall-Shackleton and Hahn 2007). Changes occur in the form of fat deposits and feather moults and determine the range and type of flight. The medial-basal hypothalamus has been acknowledged to be the physiological centre in the brain that controls the effect of photoperiod, time management and regulation of reproductive physiology due to external stimuli and in essence controls the periodicity in movement during the lifetime of an animal (MacDougall-Shackleton and Hahn 2007).

6.4.4 Phylogeny

The main issues related to the phylogeny or evolution of a behaviour are how does the behaviour compare with similar behaviour in related species, and how might it have arisen through the process of phylogeny? Why did structural associations evolve in this manner and not otherwise? The questions about evolution about behaviour as foreseen by Tinbergen (Tinbergen 1963) was mostly related to the aspect of natural selection. But

recent advances in genetics have also put greater importance to chance events such as genetic drift and founder effect (Bateson and Laland 2013).

In order to understand the evolutionary history of periodic movement with varying temporal scales, I begin by mentioning two very interesting laboratory studies. First is an experimental and mathematical modelling done on *Escherichia coli*, which proves that the processes of motility and taxis although coupled at present times, evolved from separate genes (Wei et al. 2011). The paper proves that the genes for motility evolved before the genes for taxis. They hypothesized and prove that undirected motility (not related to taxis towards a stimulus) is an adaptation for the bacteria to disperse away from one another and improves the chances of obtaining better resources in a physically structured environment. The second is a study done on *Drosophila* fruit fly to analyze how behaviour can be independent of sensory inputs and stimuli, in a paper titled "Order in spontaneous behaviour" (Maye et al. 2007). The basic law related to all kinds of movement studies is that movement is a response to deterministic environmental variables. Any movement that is not the result of external stimuli is considered residual movement that until now was considered to be random. However studies done on tethered fruit flies, in the absence of external stimuli, shows that this residual movement is in fact not random but is inherently fractal and shows Levy flight probabilities. The authors conclude that such movement behaviours are evolutionary and a result of specialized brain circuits.

These studies, although not falling within the confines of movement ecology, are extremely important in the context of the analytical framework of this thesis. The benefits of using wavelets to explain variation in movement, is that it exposes patterns and change points from the trajectory of the animal without considering external stimuli, as well as being scale independent. The possibility that animals might show movements due to inherent genetic coding, and variations thereof, emphasizes the importance of an analytical framework that does not require information on external stimuli. The studies also show that when animals are insufficiently informed and lack the cognitive skills to find adequate resources, they tend towards an adaptive form of movement that increases fitness. Like in the case of the fruit flies, which showed fractal and Levy flight patterns, conceivably such movement behaviours may have been adopted in higher forms of life as well.

In chapter 4 of the thesis, we discuss the use of discrete wavelets analysis to find changes in movement during migration. We use wavelets to detect change points in movement behaviour along the migratory route of Lesser Black-backed gulls. I follow the contents of chapter 4 to discuss how migratory journey of the Lesser Black-backed gulls might have evolved and

how it relates to the patterns found in the chapter. One school of the evolutionary study of bird migration suggests that sedentary birds started moving within their ancestral distribution, in response to influences such as resource crunch, natural selection of improved feeding and breeding habitats, or due to changing climate (Berthold 2001; Rappole 1995). Such genetic tracking of resources in due course is hypothesized to have evolved into long distance predictable movements; better known as migration. The overall migration to the wintering site or to the breeding site for birds can be said to be goal directed. It is reasonable to assume that ways of attaining that goal will be more profitable in terms of say taking less time, making fewer errors, or conserving energy. Therefore individuals have to make decisive journeys, reacting to environmental cues and its internal state with some set of behavioural rules. The results from the chapter show that Lesser Black-backed gulls tracked in the study used a large number of stopovers during their migratory journey. This is also true for the other birds tagged from the same breeding colony and each of them shows a different migratory route. A study by Klaassen et al. (2012) shows that the Lesser Black-backed gulls do not follow the shortest route during the migratory journey, but use a large number of stopovers and detours and have a tendency to follow the coast. Given their scavenging habits and generalist flight patterns it would be probable that the birds would be able to migrate faster using any optimal flying conditions and stops to re-energize anywhere. However this is not true for the Lesser Black-backed gulls. Klaassen et al. (2012) hypothesize that the birds have unusually slow migrating speeds because they do not minimize time of travel but rather adopt an energy minimizing strategy. An optimal migration strategy commonly assumes a time minimizing strategy and most birds tend to follow this rule (Lindstrom and Alerstam 1992). It is therefore interesting to ask how the gulls have evolved with an energy minimizing strategy of migration. In addition is this energy conservation true for all scales of observation? Although this discussion is beyond the realms of this thesis, it is interesting to note that tracking data of birds and mathematical models are now being able to pick up these unusual patterns that are constantly testing traditional theories of optimal flight strategies. These unusual patterns set the scene for alternative explanations using evolutionary hypothesis. In addition, the experimental genetic studies such as those discussed above are proof that these studies need to be incorporated into evolutionary studies of movement ecology.

6.4.5 Concluding remarks on movement ecology and Ethology

The focus of the thesis is on the use of rigorous statistical analysis to elaborate discrete behavioural aspects of movement. The customary method in ecology for hypothesis testing of an ecological problem is largely missing.

Instead informative mathematics has been used to infuse new information in the field of movement behavioural. I believe that certain patterns and unexplained phenomenon are projected because of such robust mathematical techniques, which would not have been detected if analysis were conducted for standard hypothesis testing. As discussed earlier, the process of model building and theory development has to be an iterative process, where a theory contains a model that depicts a relationship between constructs and permits conjecture. Thus using wavelets, data of the Lesser Black-backed gulls and simulated data, I have constructed an informative movement models and then attempted to organize the knowledge gained into theoretical constructs. This paves the way for new avenues of research in each of these fields through a parsimonious choice of the most informative mathematical model.

6.5 Movement ecology and conservation value

The investment in ecological studies such as those related to tracking animals are often justified by the fact that knowledge about animals will help preserve them (Bograd et al. 2010). A large number of projects have been initiated to track animals and scientific projects including sophisticated mathematical analysis, have been developed (Hebblewhite and Haydon 2010). It is therefore ironic that as our knowledge about the ecology of animals expands, the global biodiversity contracts (Ferraro and Pattanayak 2006; Stedman-Edwards 1998). Improved understanding about the ecology, habitat and dispersal of animals has only proved that a large number of factors responsible for the increased extinction rate of animals are attributed to anthropogenic factors. Landscape fragmentation and urbanization have resulted in changes in ecological systems including dispersal and movement of animals (Van Dyck and Baguette 2005).

Although not proportionate to the gravity of biodiversity loss, funding on a regular basis is injected into projects that help acquire data on movement, physiology, behaviour etc of animals (Block 2005; Hebblewhite and Haydon 2010; James et al. 1999). There is hope that scientific knowledge gained from these projects will help in the conservation problem (Caro 1998). However sometimes scientific solutions are not as easy to implement. International boundaries, laws and regulations, political barricades and limited resources make the simplest of recommendations difficult to implement (Daily and Matson 2008; Victor et al. 1998).

Policies regarding conservation are based on years of knowledge accumulated by researchers (Sutherland 2008). Willian J. Sutherland (1998) makes an extensive list of 20 subjects in animal behaviour studies that can be significantly used in conservation practices. One of the direct impact of

movement data and movement ecology is identification of critical habitats (Bograd et al. 2010). In addition there is direct use of movement data related to understanding spread of diseases and human wildlife conflict regions (Pittiglio et al. 2014; Si et al. 2009a). Exploring movement data have helped ecologists to understand the spatial and temporal dynamics of populations and their interaction with the environment (Nathan et al. 2008). Since conservation efforts require an integrative approach, continuous monitoring of behaviour and its trends with respect to different variables will essentially help in appropriate planning. The importance of animal telemetry is that individual variations in behaviour can be monitored. Individual variations are progressively being considered within the realms of conservation modelling because it suggests how far an animal is willing to deviate from a “mean” response (DeAngelis and Mooij 2005). As discussed in the introduction chapter of the thesis, key aspects of an animal’s life activities are a product of movement and its interaction with the environment. Cook (2008), in his exhaustive review on the advantages of telemetry for conservation practices deftly summarizes “To stem the loss of biodiversity and aid in the recovery of endangered animal populations, there is need for innovative and interdisciplinary research, monitoring programs and research initiatives to inform decision makers. It is clear that biotelemetry and bio-logging are not a panacea; however they are valuable tools available to conservation practitioners”.

6.6 Future niche

The informative movement models, as presented in this thesis, has myriad applications like when and what resources can be used by animals, what are the limiting factors affecting movement at a particular scale, understanding fitness of an animal and other complex multi-factorial and multi-scale processes. There are theoretical models for these studies such as optimality and functional responses that can be tested using GPS location of animals, even so, the information on other variables on the physiology, habitat, environmental variables, con-specific and inter-specific interactions are not available or available at different frequencies. One of the first recommendations for the analytical framework proposed in this thesis would be to develop a line of research that can input information from wavelet analysis into habitat and resource utilization studies. This line of research is required to gain a more detailed and faceted assessment of temporal patterns. For example, significant scalogram values from a wavelet analysis can be linked to unique habitat to locate principle foraging sites. In addition, using wavelets can help us forecast behaviour patterns at different scales. The use of spectral analysis for forecasting is a mature field (Schlüter and Deuschle 2010; Wong et al. 2003); nevertheless using it on biological studies will entail a complex model that can assimilate expert knowledge. There has

been some success in forecasting traffic flow using dynamic wavelet neural networks and there is a possibility that such models can be adapted for ecological movement studies as well (Jiang and Adeli 2005). In addition, there is scope to analyze the altitude readings of the PTT tags with wind speed and directions using wavelets to understand the flight pattern of the birds. The detailed analysis of time related to different behaviour was also not attempted in this thesis because of the frequency of the data available for analysis was not dense enough to provide accurate hard boundaries. The time for which a specific behaviour occurred at each scale can be calculated by the scalogram values of the wavelet analysis (Wittemyer et al. 2008). Although the use of wavelets to analyze auto correlative properties in animals has been tested in other studies, as detailed in the introduction, I recommend a comparative study to test the robustness of methods such a cross wavelet analysis, on animals of different taxas. Lastly as discussed in the section on ontogeny of this chapter, it will be interesting to tag a breeding pair of birds to see their interactions, movements in relation the reproductive efforts and contact, if any, during the non breeding season. In the end it should be noted that wavelet analysis be used first as an exploratory analytical framework rather than a confirmatory study design to extract information without a prior hypothesis. The results can then be used to ask new questions, improve the sampling design and answer specific ecological questions like temporally linked foraging patterns.

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Appendix

Appendix A: Kalman smoothing

The continuous position of the animal in time t obtained as spatial coordinates $x(t)$ and $y(t)$ were used to construct a time series $X_n = (X_0, \dots, X_n)$ with fixed time intervals. The missing GPS fixes in X_n were constructed using Kalman smoothing (Shumway and Stoffer 2000). Latitudinal and longitudinal were obtained from state space models:

$$\begin{aligned} lat_{obs}(t) &= lat_{true}(t) + w_t, & lat_{true}(t+1) &= lat_{true}(t) + v_t \\ long_{obs}(t) &= long_{true}(t) + w_t, & long_{true}(t+1) &= long_{true}(t) + v_t \end{aligned}$$

Where w_t and v_t are random variables that are normally distributed with mean 0 and a variance of σ_{obs}^2 and σ_{proc}^2 respectively. This model was initially developed and used in the space tracking field where the state equations were used to define the motion of the spacecraft from its positional data $x(t)$ and $y(t)$. The Kalman smoothing were computed with the R (cran) statistical programming language with the package `sspir` (Dethlefsen and Lundbye-Christensen 2005; R Development Core Team 2010)

Appendix B: Definitions

Scale: The word "scale" has many meanings but in general it refers to the resolution at which patterns are measured, perceived or represented (Bissonette 1997)

Scale of Observation: The spatial and temporal scales at which observations of natural systems are made. (Bissonette 1997)

Hierarchical system: "a system organized as a system of systems within systems. The dynamics of a hierarchical system can be ordered along a spectrum of frequencies. Higher frequencies belong to lower level subsystems; lower frequencies belong to higher level organizations. Subsystems of similar frequency belong to the same level of organization within the hierarchy." (Bissonette 1997)

Movement is the process by which individual organisms are displaced in space over time.

The terms entity and trajectory refer to a point object and the representation of its movement, respectively (Turchin 1998)

Movement patterns "in a data refer to (salient) events and episodes expressed by a set of entities. In the case of moving animals, movement patterns can be viewed as the spatio-temporal expression of behaviours. Only formalized patterns are detectable by algorithms. Hence, movement patterns are modelled as any arrangement of sub trajectories that can be sufficiently defined and formalized. It furthermore starts and ends at certain times (temporal footprint), and it might be restricted to a subset of space (spatial footprint)" (Gudmundsson J 2008)

Movement statistics:

- *Steplength:* the distance between the current point and the next one in a data set of positional data(as N , and $N+1$, where N is the current record)
- *Turning angle:* the absolute angle between the previous step and the next step in a data set of movement data (as the angle between points $N-1$, N , and $N+1$)
- *Net displacement:* the distance between a central location such as the nest (for an individual) and the current record

Summary

In an age when unbridled movement among humans is making the world seem more compact, it is appealing to examine how movement among living entities is and has been moulding the ecological framework of this planet. In fact, this beguiling field has especially fascinated ecologists for many years, who acknowledge that movement takes a focal part in most ecological and evolutionary processes in animals. Most animals show a range of movements associated with critical functions of survival such as feeding, mating, migration, dispersal, avoiding predators etc. Such a diverse array of movement can now be visualised and analysed due to an upsurge in the technological advancement in GPS tracking of animals. Large repositories of movement data are now being collected from a range of species, ensuing a renewed interest in improving multidisciplinary techniques in studying animal movement under the purview of the field called movement ecology. Movement behaviour is however not easy to analyze. Firstly animals moving through a complex environment, change their movement patterns frequently. Such transitions from one movement behaviour to another are a result of multiple factors such as weather, habitat and inter-specific interactions occurring either individually or in tandem changing at multiple temporal and spatial scales. In addition, behavioural responses are difficult to characterize without prior knowledge about the species. Lastly, even though extensive data from tracking animals is available, there is no consensus in an analytical framework that can be used to analyse such multidimensional data. Understanding where and when changes in movement occur is the first step towards understanding the limiting or key factors acting at different scales. In this dissertation, I therefore aim to address the current problems in methods in movement ecology using empirical data of Lesser Black-backed gulls (*Larus fuscus*) and an analytical framework incorporating wavelets to address those problems.

I use wavelet analysis to explore temporal periodic properties in movement of the birds from the positional data of animals. For example, in chapter 2, temporal information from wavelet analysis is concurrently used with fractal analysis of the trajectory, to build a model, which indicates switches in movement patterns of the birds between spatio-temporal scales. The aim was to efficiently identify spatial and temporal scales at which behavioural responses in animals are functional. In the next two chapters, new methods are derived using variations of wavelet analysis, to segment movement trajectories based on search patterns and migratory movement behaviours. When the modes of movement, and thresholds for change are unknown quantities, segmenting trajectories based on movement behaviour is difficult. These chapters showed that the use of non-parametric methods, such as the wavelets analysis, are extremely valuable in objectively detecting transition

points in movement based on properties of the trajectory . A key challenge in understanding animal behaviour from movement data has been explaining the role of environmental cues. This is because animals moving through complex environments, influenced by multifarious factors, and it becomes challenging to extract the influence of each environmental control at the right scale. To understand the decision making process during animal movement triggered by organism–environment information fluxes, there is a need to link environmental data with statistics of animal movement. For this purpose, in chapter 5 of the thesis, a bivariate extension of the wavelet transform is used to extract periodic patterns in moving animals in relation to environmental cues.

This thesis is based primarily on advancing the field of movement ecology by developing and using statistical analysis of empirical and simulated data. Therefore, in the Synthesis, I endeavour to link these developments to broader ecological theories. The theoretical and analytical framework for analyzing movement is discussed under the purview of Tinbergen’s framework for “Methods in Ethology” and how the mathematical informative model presented in this thesis effectively links these frameworks. I surmise that the methods proposed in this thesis for deconstructing animal movement provide a new line of research in the field of animal movement and has the potential of answering a myriad of ecological questions.

Samenvatting

In een tijdperk waar door ongebreidelde verkeer onder mensen de wereld meer compact lijkt, is het aantrekkelijk om te onderzoeken hoe het verplaatsingspatroon tussen levende wezens daadwerkelijk is en het ecologische kader van deze planeet heeft gevormd. In feite heeft dit interessante onderwerp vooral ecologen voor vele jaren gefascineerd, die erkennen dat verplaatsingen een focale deel in de meeste ecologische en evolutionaire processen bij dieren inneemt. De meeste dieren vertonen een scala aan verplaatsingspatronen die zijn gekoppeld aan kritieke overlevingsfuncties zoals voeding, paring, migratie, verspreiding, vermijden van roofdieren enz. Deze veelzijdige verplaatsingen kan nu worden gevisualiseerd en geanalyseerd als gevolg van een toename van de technologische vooruitgang in het volgen van dieren met behulp van GPS. Grote hoeveelheden verplaatsingsgegevens worden nu verzameld voor een scala van soorten, waardoor een hernieuwde belangstelling is ontstaan voor het verbeteren van de multidisciplinaire technieken bij het bestuderen van verplaatsing bij dieren onder de discipline 'verplaatsingsecologie'. Verplaatsingsgedrag is echter niet eenvoudig te analyseren. In de eerste plaats verplaatsen dieren zich in een complexe omgeving en hun verplaatsingspatronen veranderen regelmatig. Dergelijke overgangen vanuit één verplaatsingsgedrag naar de andere zijn het gevolg van meerdere factoren zoals weer, habitat en inter-specifieke interacties, die, hetzij individueel of samen, kunnen wijzigen op meerdere temporele en ruimtelijke schalen. Bovendien, gedragsveranderingen zijn moeilijk te karakteriseren zonder voorafgaande kennis over de soorten. En tot slot, ondanks dat er uitgebreide gegevens van het volgen van dieren beschikbaar is, er is in een analytisch kader geen consensus dat kan worden gebruikt om dergelijke multidimensionale gegevens te analyseren. Begrijpen waar en wanneer wijzigingen in verplaatsingsgedrag optreden is de eerste stap naar het begrijpen van de beperkingen of belangrijke factoren die op verschillende schalen belangrijk zijn. Daarom wil ik in dit proefschrift de huidige problemen in de methodologie van de verplaatsingsecologie met behulp van empirische gegevens van de kleine mantelmeeuw (*Larus fuscus*) duidelijk maken en een analytisch kader ontwikkelen waarin wavelets zijn opgenomen om die problemen aan te pakken.

Ik heb wavelet-analyses gebruikt in het verkennen van temporele periodieke eigenschappen van verplaatsingen bij vogels, om het gedragspatroon van de positionele gegevens van dieren uit te leggen. Bijvoorbeeld, in hoofdstuk 1 is temporele informatie uit wavelet-analyses gelijktijdig gebruikt met fractal analyse van het traject, om een model te bouwen, die de omslag in verplaatsingspatronen van de vogels tussen ruimtelijke-temporele schalen aangeeft. Het doel was om zo efficiënt mogelijk ruimtelijke en temporele

schalen te kunnen identificeren waarin de verschillende verplaatsingsreacties bij dieren functioneel zijn. In de volgende twee hoofdstukken zijn nieuwe methoden ontwikkeld zowel door het gebruik van variaties in wavelet analyses als door het gebruik van segment verplaatsingstrajecten, gebaseerd op zoekpatronen en migratie. Wanneer de mate van verplaatsing, ecologie en drempels voor verandering onbekend is, is het moeilijk om trajecten gebaseerd op verplaatsingsgedrag te segmenteren. Deze hoofdstukken toonden aan dat het gebruik van niet-parametrische methoden, zoals wavelet analyses, uiterst waardevol zijn in het objectief opsporen van overgangspunten in verplaatsingen, gebaseerd op eigenschappen van het verplaatsingstraject. Het begrijpen van de rol van de omgevingsfactoren is een belangrijke uitdaging in het begrijpen van dierlijk gedrag met behulp van verplaatsingsgegevens is. Dit is omdat dieren, die zich door een complexe omgeving bewegen, beïnvloed worden door vele verschillende factoren, en het is een uitdaging om de invloed van deze factoren op de juiste schaal te begrijpen. Om het besluit-makend proces tijdens de dierlijke verplaatsingen, veroorzaakt door veranderende organisme-omgevingsinformatie, te begrijpen, is het noodzakelijk deze omgevingsgegevens te koppelen aan statistische informatie van de dierlijke verplaatsingen. Daarom wordt in hoofdstuk 5 van dit proefschrift een bivariate extensie van de wavelet transformatie gebruikt om periodieke patronen tijdens het verplaatsen van dieren met betrekking tot omgevingssignalen te extraheren.

Deze thesis is voornamelijk gebaseerd op het bevorderen van het gebied van verplaatsingsecologie door het ontwikkelen en het gebruik van statistische analyse van empirische en gesimuleerde gegevens. In de synthesis probeer ik deze ontwikkelingen te linken aan bredere ecologische theorieën. Het theoretische en analytische kader voor het analyseren van verplaatsingsactiviteiten wordt besproken onder de bevoegdheid van Tinbergen zijn kader voor "Methoden in ethologie" en ook hoe het wiskundig informatieve model gepresenteerd in dit proefschrift deze kaders effectief aan elkaar koppelt. Ik verwacht dat de in deze thesis voorgestelde methoden voor het ontrafelen van de dierlijke verplaatsingen een nieuwe ingang biedt voor onderzoek op het gebied van dierlijke verplaatsingen en de potentie heeft om een groot aantal ecologische vragen te beantwoorden.

Author's biography

Maitreyi Sur was born on 24th March 1985, in Allahabad, India. She was raised in a small industrial town of Durgapur, where she completed her high school in 2003. As a school topper, to follow her academic pursuits, she moved to the Indian capital, Delhi for her undergraduate studies in Zoology from the University of Delhi, from where she graduated in 2006. Due to her avid interest in ecology and animal behaviour studies, she took up Masters

in Environmental Studies course from The Energy and Resources Institute (TERI University), New Delhi, India. It is here, that she got the opportunity to work on a number of projects on ecology and animal behaviour studies while pursuing her academic studies. Some of these experiences supplemented her academic career with practical experience. One such project was at Nandan Kanan sanctuary, Orissa, India on "Mass nesting of Openbill Storks". The others being with Hindalco Industries on a project on restoration ecology of red mud and culminating in a six month project in the ecologically diverse region of Terai, India and thesis research on "Conservation issues of sourcing of timber from the Terai Arc Landscape and relevance of forest certification in the Pilibhit forest region" with World Wildlife Fund (Forestry division, India). Soon after accomplishing her master's degree in 2008, she received the European Commission, Erasmus Mundus scholarship for her doctoral research, under the supervision of Professor Andrew Skidmore, at the University of Twente, The Netherlands. She moved again in pursuit of her education, to Netherlands in 2009, where she started her PhD which resulted in this thesis and the following publications:

Sur, M., Skidmore, A. K., Exo, K. M., Wang, T., J Ens, B., & Toxopeus, A. G. (2014). Change detection in animal movement using discrete wavelet analysis. *Ecological Informatics*, 20, 47-57.

Sur, M., Skidmore, A. K., Wang, T., Exo, K. M., J Ens, B., & Toxopeus, A. G. Mining periodic behaviour of moving animals in relation to environmental cues. In proceedings of "*Measuring behaviour, 2014*", the 9th International Conference on Methods and Techniques in Behaviour Research, Wageningen, The Netherlands. (Accepted)

Sur, M., Skidmore, A. K., Exo, K. M., Wang, T., J Ens, B., & Toxopeus, A. G. Wavelet analysis of space-time movement trajectories for detecting animal behavioural change. *In review: Ecological Complexity*.

Sur, M., Skidmore, A. K., Wang, T., Exo, K. M., J Ens, B., & Toxopeus, A. G. Concurrent use of fractals and wavelets for spatial-temporal analysis of animal movement patterns. Presented in the Young Researchers forum on '*Moving objects and knowledge discovery*', University of Ghent, Belgium, 2011. *In preparation* to be re-submitted as a journal article.

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