CONNECTING THE DOTS: ECOLOGY, MOVEMENT & CONSERVATION OF LIONS ACROSS THE KALAHARI-KAVANGO LANDSCAPE

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Declaration

I declare that this thesis was composed by myself and that the work contained herein is my own except where explicitly stated in the text. The work has not been submitted for any degree or professional qualification except as specified.

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Abstract

Movement is a fundamental process that impacts an animal's fate, population dynamics and the structure of communities and ecosystems. In this thesis I consider open challenges and opportunities in how to model animal movement in the context of wild lion populations. I apply sophisticated modern statistical approaches from across the rapidly developing movement ecology field to long-term movement datasets from wild lions in Southern Africa to generate insights into connectivity between populations, local ranging behaviour and how lions respond to their thermal environment. Specifically, I evaluate how data inputs and approaches for modelling space use and connectivity perform in capturing lion movement (i) during dispersal across a landscape, (ii) at the home range scale and smaller, and (iii) how fine-scale animal movement can be linked to the environment and key climatic variables. As a whole, this body of work extends our understanding of the movement process in lions with particular application to spatial ecology for conservation research.

Research is what I'm doing when I don't know what I'm doing.

—Wernher von Braun

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Part I

PROLOGUE

1

Overview

THE MOVEMENT DECISIONS AN ANIMAL TAKES have a direct impact on its survival and recruitment opportunities. As a result, they can be a major contributor towards an animal's fate, population dynamics, and the structure of communities and ecosystems. For example, successful movement across a landscape is required to fulfil essential biological processes such as foraging, mating or dispersal. In order to best understand how to manage landscapes and the organisms moving through them, it is necessary to gain insight into the drivers and patterns of animal movement and how they respond to changes in land-use patterns and the environment.

1.1 MOTIVATION

The field of movement ecology has expanded rapidly in recent years, as have the analytical tools and the size of datasets available to ecologists. This rapidly developing field provides unprecedented opportunities to ask questions about where, why, and how animals choose to move — but also poses challenges in selecting appropriate tools, understanding which data inputs provide best inference, and how to evaluate model performance. This thesis centres around exploring these open opportunities and currently unmet challenges within movement ecology, using the African lion, *Panthera leo*, as a model system.

The African lion has decreased from an estimated 100,000 individuals to a figure closer to 20,000 within the last century (Bauer *et al.*, 2016). These declines have resulted in

extirpation from 80% of its historic range (Riggio *et al.*, 2013; Bauer *et al.*, 2015b), and represent a population reduction of approximately 43% over the past 21 years (Bauer *et al.*, 2016). Within much of its remaining range, the long-term persistence of wild lion populations is threatened by human activities and population declines continue. Expanding human populations coupled with habitat fragmentation has led to increased human-lion conflict due to shared space and prey consumption requirements.

Even when protected areas exist, lions will naturally move into surrounding areas due to their extensive home ranges. This is particularly common when these surrounding areas contain resources that attract carnivores. When communal farming areas border national parks, this can create landscapes of high anthropogenic mortality risk for lions (Woodroffe and Frank, 2005; Bauer, De Iongh and Sogbohossou, 2010; Loveridge *et al.*, 2017). As landscapes become increasingly fragmented, connectivity at a population level will increasingly rely on large-scale movement (i.e., dispersal). Much of this dispersal will fall outside of existing protected-area networks. Quantifying what factors have the largest impact on spatial decisions and how lions move through landscapes, at both a local and a larger geographic scale, is therefore critical to understanding how wild lion populations will respond and persist under changing environmental conditions and habitat modification.

This thesis makes use of spatial and demographic data from multiple wild lion populations across their range in Southern Africa. This will offer understanding on how lions move through and interact with their surroundings at multiple spatial scales, as well as across a gradient of land-use and environmental conditions. In doing so, the work will

also contribute insights into how this information, and the analytical tools available, can best feed into applied research on how to conserve vulnerable large carnivore populations.

1.2 THESIS STRUCTURE

My thesis begins with a general introduction to animal movement, landscape connectivity and the major challenges and opportunities in these fields, particularly in the context of wide-ranging large carnivore populations. I discuss key movement terminology and analytical approaches, and how they relate to my thesis as a whole. The introduction also includes an overview of the Southern African lion study system and core datasets.

My data chapters begin with a critical evaluation of the current status quo of understanding of landscape connectivity for lions, asking how well existing models capture observed dispersal events (Chapter 3). The subsequent chapters move to explore how we can improve our understanding of the external and internal factors that govern lion movement. This is approached by first considering how the structure (e.g., autocorrelation) implicit in movement data can impact the estimation of key space-use metrics (Chapter 4), then exploring how rates of movement vary in response to temperature and water availability in a highly seasonal, semi-arid system (Chapter 5).

The thesis concludes with a general discussion of the key findings and contribution to knowledge, contextualised in the broader field of movement ecology and its application to conservation. I also consider major limitations and constraints of the thesis data chapters, as well as the opportunities these provide for future research.

1.3 HOUSEKEEPING

My thesis was supervised by Professor David W. Macdonald, Andrew J. Loveridge and Samuel A. Cushman. Together, they provided oversight and advice on the thesis structure, methodological design, and gave comments on drafts. Full contributions to each data chapter are listed below.

Chapter 3: Comparing the Performance of Resistance Surfaces & Connectivity Models in Predicting Dispersal Trajectories of Wild Lions. Finerty, G.E., Cushman, S.A., Bauer, D.T., Elliot, N.B., Kesch, M.K., Macdonald, D.W. & Loveridge, A.J. In preparation for submission to Journal of Applied Ecology. GF and SC conceived the ideas and designed methodology; AL and DWM managed field research; AL, DB, NE, and KK collected the data; GF analysed the data and led the writing of the chapter. All authors provided comments on chapter drafts.

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2

General Introduction

SYNOPSIS This chapter provides the theoretical background and perspective that informs the rest of the thesis. It provides background to modelling animal space and movement, both at a landscape (with a focus on connectivity) and environmental (home range and within) scale. It considers the current status quo of knowledge, as well as open opportunities and challenges in the field, and how these relate to the study of African lions and the research addressed in the thesis. The final section describes the core study sites and datasets included in the data chapters.

2.1 LANDSCAPES & WILDLIFE

To be successful, an individual must fulfil certain life requirements — a minimum amount of resources must be obtained to satisfy its basic needs to survive and recruit to the next generation. For mobile organisms, movement is critical to this process at multiple spatial and temporal scales. Over their lifespan, individuals move to track daily and seasonal resource requirements, such as foraging or finding a mate (Dingle, 1996). At a population level, long-range movements (e.g. dispersal or migration) over tens of generations maintain genetic diversity and a population's ability to respond to long-term trends in environment such as climate (Frankel and Soule, 1981). Central to this process is the concept of connectivity.

> *Connectivity* can be defined as the degree to which the landscape facilitates or impedes movement (Taylor et al., 1993)

As development and extraction of resources continues, habitats are becoming increasingly fragmented, altering the extent to which landscapes are functionally connected. Smaller, more fragmented populations experience increased vulnerability to local extinctions via environmental and demographic stochasticity (Woodroffe, 2001) and increased disease susceptibility via loss of genetic diversity (Trinkel *et al.*, 2011). Identifying and protecting areas critical to maintaining connectivity has therefore become a central challenge in applied ecology and conservation. One avenue of connectivity studies that has received great interest is the generation of wildlife corridors.

> *"Corridor",* here, can be defined broadly as regions of the landscape that facilitate the flow or movement of individuals' genes (Chetkiewicz, St. Clair and Boyce, 2006).

They have become a cornerstone of modern conservation and are commonly implemented to connect fragments of wildlife habitat. This is particularly pertinent for species that undergo large-scale movements such as dispersal or migration, live at low density, or have large home ranges. In such cases, protected areas alone are unlikely to be sufficient to ensure the long-term viability of wild populations. Therefore multi-use zones, such as wildlife management areas and corridors between protected areas, are going to be central to maintaining connectivity in landscapes and managing meta-populations (Estes *et al.*, 2011; Tercek and Adams, 2013).

There is evidence that corridors perform a critical role in maintaining seasonal migrations (e.g. Powell and Bjork, 1995), one of the four categories of movement proposed by Ims (1995). However, the focus of this thesis is on large carnivores, specifically the African lion, who are not migratory. Therefore, for the remainder of the text, I prioritise discourse surrounding the role of corridors, and connectivity more broadly, in providing access to resources within a home range, or during dispersal — processes that form a fundamental role in the population dynamics of lions.

2.2 MODELLING CONNECTIVITY

Typical early efforts at connectivity models comprised largely of corridor design determined by simplistic, human-observed patterns of landscape structure (Beier and Noss, 1998; Vos, Baveco and Grashof-Bokdam, 2002). This form of connectivity is often termed "structural connectivity" (Francis *et al.*, 2021) and can be based on physical attributes i.e., the physical configuration of habitat patches alone without explicitly considering the movement of animals between patches. Although ecological processes such as habitat selection and movement were assumed to happen via corridors, process-based approaches to designing and planning corridors were lacking (Chetkiewicz, St. Clair and Boyce, 2006).

This created a mismatch between the process of connectivity (animal movement within the landscape) and the way corridors were implemented. This mismatch resulted in low corroboration between relevant biological metrics (e.g. immigration and colonisation rates) and corridor patterns (Beier and Noss, 1998). In their 2006 review, Chetkiewicz *et al.* highlighted integrating the behavioural process of habitat selection and movement into

the design of corridors as a key step in implementing landscape linkages in a more objective and effective manner.

A wide interest in—and conservation need for—understanding landscape connectivity, paired with advances in technology and quantitative methods, has led to a rapid proliferation of studies in generating connectivity models in recent years. It has now become common to use statistical tools such as path- or step-selection functions to describe habitats as probabilistic functions of landscape attributes for use in modelling connectivity (Cushman and Lewis, 2010; Elliot, Cushman, Macdonald, *et al.*, 2014; Zeller *et al.*, 2018). By linking the pattern (habitat composition and spatial configuration) and process of connectivity, the design and creation of corridors has now become more closely aligned to their intended purpose of describing the functional connectivity of landscapes.

> *Functional connectivity* here expands the concept of connectivity from a focus on contiguity of landscape features—i.e., *structural connectivity*—to how species respond to, or move through, different landscape features (Zeller et al., 2020).

While models that incorporate how animals respond to the landscape they move through confer clear benefits in linking connectivity to the movement process, they also require significant volumes of data to estimate the parameters. Animal movement and resource selection is context-dependent, and can vary in time e.g., between seasons (Zeller *et al.*, 2020), between life stages (e.g., Elliot, Cushman, Macdonald, *et al.*, 2014) or with the availability of resources (e.g., Morato *et al.*, 2018). Additionally high levels of heterogeneity in resource selection has been observed even within species (Bastille-Rousseau and Wittemyer, 2019). As a result, large volumes of data from a wide range of individuals and

environments are required to capture this variation. In contrast changes in structural connectivity are more easily quantified and observed. Functional connectivity is also intrinsically species-specific i.e., a landscape that is functionally connected for some species, is not necessarily for others. Unless there is data available for a broad suite of species that represent the combined needs of the species in an area, it is unlikely that single species models will prove sufficient for all focal biota; whereas a connected network of natural wilderness is likely to support movement for multiple species (Keeley, Beier and Jenness, 2021). Thus, structural connectivity alone can still provide useful information for recommendations for areas and species with a paucity of data, or where human infrastructure creates barriers that are likely to impact multiple species, such as roads or major fencing efforts. As large movement datasets (from GPS collars) have been collected for African lions across their range in southern Africa, facilitating the estimation of functional connectivity, I focus on this for the remainder of the section.

Modern connectivity approaches can now be used to assess functional connectivity of a landscape, given a species' population size, dispersal ability and landscape resistance patterns (Cushman *et al.*, 2013). They comprise of three core components: a resistance to movement surface (hereafter, resistance surface), source (and destination) points, and a connectivity algorithm that links the two together.

2.2.1 Resistance to Movement Surfaces

Resistance surfaces now form the foundation for most contemporary connectivity models, representing the landscape between populations as a continuum wherein low resistance represents ease of movement, and high resistance represents restricted movement or, in some cases, total barriers.

> *Resistance* values represent the willingness of organisms to move across a specific environment, the physiological cost or reduction in survival of doing so, or a combination of these things (Zeller, McGarigal and Whiteley, 2012).

Resistance surfaces provide quantitative estimates of how environmental and anthropogenic parameters impact organismal movement via a spatial layer with a resistance value assigned to each map cell. These can help us to better understand the movement of individuals through a landscape and between populations (i.e. dispersal), and how this relates to relevant environmental factors (e.g. Elliot *et al.*, 2014).

Resistance surfaces can be generated using a wide variety of input data (e.g., expert opinion, detection, relocation, pathway, or genetic data) and analytical approaches (e.g. resource selection functions, point or home range; reviewed in Zeller et al. 2012). Studies evaluating the differences between data inputs for resistance have found that empirical data generally outperformed expert opinion (Clevenger *et al.*, 2002; Shirk *et al.*, 2010), that genetic distances between individuals produced similar surfaces to those developed using movement paths (Cushman and Lewis, 2010), and that, on average, models based on GPS collar data, genetic data, or a combination of the both, outperform resistance surfaces based on opportunistic presence-only data (Zeller *et al.*, 2018).

However, until recently, compared with the number of studies generating surfaces, validation and rigorous comparison of resistance inputs remained rare (but see Poor *et al.*, 2012; LaPoint *et al.*, 2013; Cushman, Lewis and Landguth, 2014; Zeller *et al.*, 2018 for examples), creating a major gap in knowledge for producing accurate and defensible foundations for connectivity models. Developments in frameworks to evaluate the

performance of different data inputs as well as connectivity approaches in modelling observed biological processes (McClure, Hansen and Inman, 2016; Zeller *et al.*, 2018) have provided a road map to facilitate this, and I return to discuss this in section 2.2.3.

2.2.2 *Connectivity Algorithms*

Once a resistance surface has been created, a connectivity algorithm (most commonly based on either cost-distance or circuit theory) can be applied to create a corridor and/or connectivity surface in which each cell quantifies some measure of the relative probability of movement between source and end points across the resistance landscape.

Each connectivity model has its own assumptions about how animals move through the landscape and consequent strengths and limitations. Cost-distance models, e.g. least-cost corridors (Adriaensen *et al.*, 2003), act to minimize the trade-off between travel distance and travel over unsuitable habitat. For example, least-cost paths offer the shortest cumulative cost-weighted distance between source and destination points across a land resistance surface and represent optimal travel routes. An implicit assumption of these source-destination models (Cushman, McKelvey and Schwartz, 2009) is that animals have complete knowledge of the landscape in order to select and use the optimal paths. Other implementations, such as the resistant kernel method (Compton *et al.*, 2007) are non-directional, and measure cost distance from sources without regard to destination. Circuit theory (McRae *et al.*, 2008) treats the movement of individuals through a landscape like the flow of charge through electrical circuits. Models based on circuit theory assume that individuals have no prior knowledge of the landscape beyond their immediate surroundings. However, in most applications, they do assume at least partial knowledge of

where an individual will end up—if not perfect knowledge of the optimal routes to get there—via the specification of a priori destination points.

2.2.3 *Evaluation of Models*

Approaches for evaluating the performance of connectivity models to date have included comparison of outputs, and more rarely, the gold standard of validation — using an independent dataset to test how much of the target biological approach is captured by candidate models. Comparative approaches have particular appeal in evaluating the sensitivity of connectivity models to different inputs (e.g. Zeller *et al.*, 2016) or altering connectivity model parameters, e.g. the incorporation of varying dispersal thresholds (Cushman *et al.*, 2015).

Independent movement datasets have been used to generate insights into the performance (and sensitivity of) models based on multiple data inputs and connectivity approaches in predicting processes such as road crossings in bears (Cushman, Lewis and Landguth, 2014) and dispersal movements in wolverines (McClure, Hansen and Inman, 2016) and pumas (Zeller *et al.*, 2018). The latter study made significant progress in providing a standardised framework for assessing the combined performance of multiple connectivity models and data inputs.

Comparisons of different algorithms and inputs have value in helping to understand which approaches will be most effective in generating accurate maps for conservation efforts, but also in generating ecological insights into the mechanisms driving dispersal across systems. For example, dispersal in a highly connected landscape might give rise to simple patterns of isolation by distance (e.g. Koopman, Hayward and McDonald, 2007), whereas in systems where dispersal is influenced strongly by a gradient of

environmental variables, more complex patterns of isolation by resistance might appear (Cushman *et al.*, 2006). Therefore, evaluating connectivity across a range of species and environments may be critical in understanding how the dispersal process may change under future scenarios of environmental change.

2.2.4 *Open Challenges, Questions, and Opportunities: Modelling Landscape Connectivity*

Despite the popularity of connectivity models, there is still a lack of consensus on the most accurate data sources and analytical methods for providing the best inferences about population connectivity. This is a not a trivial task, as generating a connectivity surface is a multi-stage process, with a wide range of methods and data inputs available at each step. Additionally, landscape connectivity is constructed based on information about how animals select their habitat and how they perceive their surrounding landscape, and thus is likely to be species- and process-specific. To move forward there is a need for rigorous comparison and validation of each analytical fork in the road across multiple species and study systems to address key questions such as (a) how sensitive are connectivity approaches to different data inputs and connectivity algorithms, (b) how generalisable are connectivity models across space and between species, and (c) what biological implications do differences in model outputs have? In this thesis I address the question of how data inputs from different demographic groups and two commonly used connectivity algorithms perform in predicting the biological process of dispersal in African lions (Chapter 3). This directly contributes towards (a) and (c), as well as providing a case study to add the growing literature addressing these questions in other species (e.g. McClure, Hansen and Inman, 2016; Zeller *et al.*, 2018) a necessary step towards answering (b).

2.3 LOCAL SPACE USE & CONSERVATION

Globally, landscapes are changing in a way that restricts animal movement (Fahrig, 2007; Tucker *et al.*, 2018), and the climate and environment that wildlife exist in are changing rapidly. We are currently in the midst of the sixth mass extinction; with the loss of thousands of populations of critically endangered vertebrate animal species over the last century, there is clear indication that the sixth mass extinction is human caused and accelerating (Ceballos, Ehrlich and Raven, 2020). As well as requiring space to allow for dispersal between populations (section 2.1), there is a critical need to understand space and energy requirements for resident populations to understand how much space is required for populations to persist and how the conditions present will impact population viability. In a system like the Kalahari, for example, where there are large swathes of connected habitat in the form of the 52,000 km^2 Central Kalahari Game Reserve, lion prides are likely well connected within this system, but face other challenges, such as the impact of human activity at the edges of the reserve, and human-induced climate change. Climate change may affect lions directly, for example via the impact of heat on physiological tolerance or performance, on indirectly, via effect on their key resource base of prey.

2.3.1 Species area requirements

Central to understanding resident population space requirements is the concept of the home range, defined by Burt (1943) simply as:

> *"The area, usually around a home site, over which the animal normally travels in search of food."*

In this influential paper, Burt highlights the importance of understanding fundamental behavioural patterns in the management of wild animal populations, a challenge

researchers are still addressing today. Understanding species' area requirements is of key interest for area-based conservation, to answer the critical question of how much space is needed to maintain stable, interconnected populations that will persist in the long-term. This is particularly relevant in increasingly human-dominated landscapes, as species extinction rates have been shown to correlate with both reserve size and human presence (Brashares, Arcese and Sam, 2001) and habitat loss and fragmentation are some of the principle threats to terrestrial biodiversity (Brooks *et al.*, 2002; Wilson *et al.*, 2016).

2.3.2 *Movement in response to climatic variables*

Movement and space use at a finer-scale (for example daily distance travelled) can also provide insights into an animal's use of its environment, short-term resource needs and energetic budgets (Carbone *et al.*, 2005). This is closely linked to animal fitness via the impacts it can have on survival and recruitment opportunities as animals trade-off time spent foraging and seeking mates, with the cost of moving to acquire these things. In the face of global change, there is a clear need to understand the sensitivity of animal performance, such as movement, to changes in the environment, to predict how species such as large mammals will respond to future environmental change (Fuller *et al.*, 2016). By linking animal movement and climatic variables experienced in natural systems, particularly those at the hotter, more arid end of the spectrum, we can describe how animals respond to the variation in environment currently experienced to understand existing plasticity in movement.

Additionally, the movement capacity of animals is strongly linked to home range behaviour, with faster moving animals having larger home ranges (Tamburello, Côté and Dulvy, 2015). Movement within a home range governs the way animals use their habitat,

interact with conspecifics, obtain food, and negotiate human-modified landscapes. Understanding the implications of changing environments for wild populations will require understanding the fundamental links between the ways animals move at different scales, and ultimately the role they play in an individuals' fitness.

2.4 APPROACHES TO MODELLING THE HOME RANGE

A common approach to answering how much space animal require is to begin with home range analyses. From an ecological perspective, estimated home ranges can be fed into downstream analyses to explore variation in space, time, or between groups and individuals. Home ranges have also been used widely in conservation, for example to feed into recommendations on the size of reserves (Linnell *et al.*, 2001) and on land-use systems (Johansson *et al.*, 2016; Farhadinia *et al.*, 2018).

Although a commonly-used technique in ecological and conservation, the majority of studies use conventional home-range estimators (e.g. kernel density estimators; KDE), which are based on the assumption of independent and identically distributed data (IID; Fleming *et al.*, 2015). In contrast to this, most modern tracking data is strongly autocorrelated (Noonan, Tucker, *et al.*, 2019). Failing to account for autocorrelation in tracking data has been demonstrated to result in substantial under-prediction of space use (Fleming *et al.*, 2015), with conventional KDE producing significantly negatively-biased estimates of home range area across a range of species (Noonan, Tucker, *et al.*, 2019). This arises as a result of the fact that when data is autocorrelated, the total number of data points no longer reflects the total amount of information in the data, and thus the "effective" sample size is smaller than expected (Fleming and Calabrese, 2017). Negative bias of space use has potential consequences in the context of conservation, as underestimation could

lead to failed conservation initiatives (Brashares, Arcese and Sam, 2001; Gaston *et al.*, 2008) or exacerbate negative human-wildlife interactions that are often present at reserve boundaries (van Eeden *et al.*, 2018).

Additionally, a recent meta-analysis found that the autocorrelation-induced bias is greater for larger species, as a result of larger home range areas and crossing times (Noonan *et al.*, 2020). This is the result of the negative relationship between home range crossing time and effective sample sizes. Home range scales positively with body mass (Jetz *et al.*, 2004); as one of the largest terrestrial carnivores, this makes autocorrelation an especially pertinent consideration for the study of large carnivores, such as lions, something that has not been considered in studies on lion home range behaviour to date, despite the fact that the concept of autocorrelation in tracking data, and its relevance to home range estimation, is not a new idea (Swihart and Slade, 1985; Fieberg, 2007; Fleming *et al.*, 2015).

2.4.1 Open Challenges, Questions, and Opportunities in Modelling Animal Movement and Space Use

Ecologists today have access to a wide range of tools and methodology, especially via the commonly used statistical environment, R, including methods to account for autocorrelation in tracking data (e.g. the ctmm and CRAWL packages, among others). Modelling autocorrelation in movement is an active field, and there have been methods developed (such as the autocorrelated kernel density estimator; AKDE) specifically for home range area estimation, that can model not just autocorrelation structure, but also locational error, and a wide variety of specification of continuous movement models. Despite the slow uptake in the carnivore conservation field, these represent a significant opportunity to revisit classic studies of home range behaviour and provide additional insights. In Chapter 4, I apply a continuous time movement modelling approach to explore

the impact of structure in movement data, such as autocorrelation and non-stationarity, on commonly used estimates of animal space use: home range area and distance travelled.

2.5 UNDERSTANDING THE RESPONSES OF LARGE MAMMALS TO TEMPERATURE AND WATER AVAILABILITY

Free-living large mammals use both physiological and behavioural modifications to buffer themselves against thermal and water stress (Fuller *et al.*, 2016). Examples of behavioural modification include the selection of cool microclimates (such as shady areas), a shift to foraging more nocturnally or increased time at rest, or moving at a slower rate. As climate change progresses, mammal populations will increasingly be exposed to not only a warming climate, but also more frequent and extreme weather events such as heat waves and droughts (Diffenbaugh and Field, 2013; Parmesan, Root and Willig 2000). Increasing temperatures will mean greater head loads of animals, with the only way for mammals to lose heat being evaporative cooling (Tattersall *et al.*, 2012). Aridity, combining both high heat loads and a shortage of water—as is predicted under future climate change—is likely to pose a significant challenge to mammal populations.

2.5.1 *Open Challenges, Questions, and Opportunities in Modelling Animal Thermal Performance*

There is clear relevance in today's world to understanding how species perform under different climatic regimes; yet there is little known about the phenotypic plasticity of carnivores in response to temperature and aridity with a large bias towards herbivores in studies addressing the response of large mammals to changing climates (Fuller *et al.*, 2016).

Thermal performance curves (TPCs) describe organismal performance across a range of temperature conditions to understand how species respond to environmental variables. While laboratory studies have revealed valuable insights into how species

respond to temperature, they are not sufficient to predict accurately how animals respond under natural conditions (Fuller *et al.*, 2014). Although TPCs are typically assessed under laboratory conditions, they have recently been derived from field data to assess thermal performance in the wild (Payne *et al.*, 2016; Childress and Letcher, 2017; Nowakowski *et al.*, 2020). This represents an exciting opportunity to quantify thermal traits and understand mechanisms underlying temperature effects on movement in wild systems. In chapter 5, I assess how locomotory performance, measured by maximum capacity for hourly displacement, responds to a temperature gradient, and how this is impacted by life history differences and access to water. By studying thermal performance in free ranging lions, it is possible to obtains insights on the physiological capacity of large carnivores to cope with temperature and how this interacts with water availability. This is particularly relevant given the geographic focus of the thesis in the semi-arid Kalahari basin.

2.6 THE KALAHARI-KAVANGO ECOSYSTEM AND AFRICAN LIONS

2.6.1 Geographical focus of the thesis

The movement data used throughout this thesis were collected from wild lions across the central Kalahari region of Botswana and into the adjacent area of Zimbabwe (**Figure 2.1**). Long-term movement data was provided from core study sites located in and surrounding Hwange National Park (HNP), Zimbabwe, and Khutse and the Central Kalahari Game Reserves (KGR and CKGR), Botswana. Data from these locations were provided by projects with long-term lion monitoring programmes (see 2.5.5), facilitating long time series and a wide variety of individuals from the populations. Both sites can be classified as semi-arid climatically, but together represent an environmental gradient of increasing productivity within this.

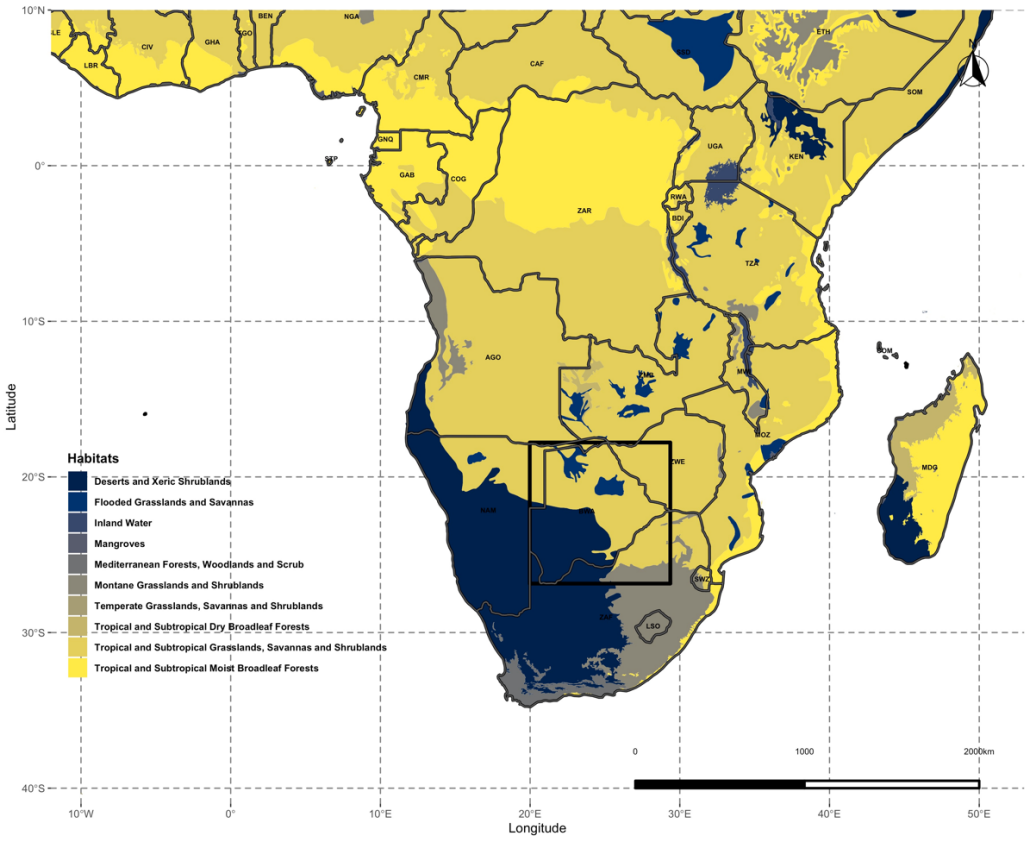


Figure 2.1 *Terrestrial Ecoregions for the Afrotropic biogeographic realm (Olson et al., 2001) with main geographical focus of the thesis overlaid as a black rectangle.*

2.6.2 *Kalahari Ecosystem*

The Kalahari is an extensive, elevated, flat, sand-covered plain that stretches across South Africa, Botswana, and Namibia (Thomas, 2002). The geological unit of the Kalahari Sands covers 2.5 million km^2 (Thomas and Shaw, 1990), forming one of the world's largest continuous stretch of sand. The natural flora is well adapted to low water and nutrient availability (Skarpe, 1990), growing in soils that are predominantly deep, structureless and lacking in Nitrogen, Phosphorus and organic matter (Skarpe and Bergstrom, 1986; Dougill, Heathwaite and Thomas, 1998).

2.6.3 *The Central Kalahari Game Reserve complex*

The Central Kalahari and adjoining Khutse Game Reserves are located in central Botswana (between latitudes 24.14°S and 20.67°S and longitudes 22.06°E and 25.80°E). The two reserves are contiguous with no fenced separation, as such hereafter we refer to them simply as the CKGR. Together the CKGR complex comprises approximately 55,000 km^2, forming one of the largest protected areas in Africa. Established in 1971, some pockets of the CKGR contain settlements inhabited by people from the Basarwa (San) and Bakgalakgadi tribes (Makhabu and Marotsi, 2012).

Climatically the area can be summarised as semi-arid, lying between 350 mm and 450 mm isohyets; rainy season falls between November and April, however there is considerable variation between years (Makhabu and Marotsi, 2012). The reserves are primarily covered with semi-arid shrub savanna and scrub, interspersed with large areas of open grassland, Terminalia sandveld, and smaller patches of Acacia woodland. The area is distinguished by the presence of clay pans that periodically contain water. There are also fossil riverbeds which mark the position of rivers that historically drained into the ancient Lake Makgadikgadi. The area is covered predominantly by deep Kalahari sands.

2.6.4 *Hwange-Matetsi complex*

The Hwange-Matetsi complex falls within the Kavango Zambezi Transfrontier Conservation Area (KAZA-TFCA), one of the world's largest terrestrial TFCAs comprising 36 national parks in a matrix of unprotected and communal areas. Hwange National Park (HNP; 19° 00′ S, 26°30′ E) itself covers approximately 15,000 km^2 of semiarid dystrophic savannah (with generally nutrient-poor soil) on Kalahari sands (Mbizah *et al.*, 2020). Mean annual rainfall is 600 mm with high variability (Loveridge *et al.*, 2016). There is a gradient of vegetation and water across the park, with the south more water limited

than the north. During the peak dry season, water is available only at artificially supplied water-points. Trophy hunting occurs in all adjacent land to the HNP, including communal lands, but not within the park (Loveridge *et al.*, 2016).

2.6.5 Lion Movement Datasets

Lion movement data for the Hwange-Matetsi complex was provided by the Trans-Kalahari Predator Program and is used in the analyses for Chapter 3. Data from the CKGR was provided for the thesis by the NGOs Leopard Ecology & Conservation and Kalahari Research and Conservation and are used in Chapters 4 and 5. My thesis was completed in partnership with Leopard Ecology & Conservation, and I contributed to the data collection of the movement dataset from this site as well as direct observation of the monitored lions. This fieldwork was granted ethical approval by the University of Oxford (reference code Zoology AWERB071116) and was covered under the research permits from the Ministry of Environment, Natural Resources Conservation and Tourism, Botswana EWT 8/36/4 XXVIII (9), EWT 8/36/4 XXVIII (26), ENT 8/36/4 XLVI (32), These cover the periods 30th April 2015 – 30th April 2017, 1st May 2017 – 31st December 2019, 4th September 2019 – 31st December 2024 respectively. Copies of the relevant permits and the ethical review document can be found in Appendix A.

Part II

DATA CHAPTERS

3

Comparing the Performance of Resistance Surfaces & Connectivity Models in Predicting Dispersal Trajectories of Wild Lions

Synopsis Evaluating connectivity and identifying corridors for protection has become a central challenge in applied ecology and conservation. The possibilities open to researchers for modelling connectivity have advanced considerably over the past decade, from the type and volume of empirical data available, through to the analytical techniques and software to implement them. However, as the options for modelling connectivity continue to develop, there remains a need for rigorous validation and comparison of how these approaches perform in capturing the biological process of interest. Understanding what data inputs are needed to make effective conservation inference is of particular relevance to conservation initiatives that involve high-effort activities such as collaring. In this chapter, I present a simple, repeatable method for delineating periods of dispersal in territorial carnivores. I apply this method to an empirical dataset of movement data collected from African lions (*Panthera leo*) to obtain movement trajectories of dispersing individuals across the Kavango Zambezi Transfrontier Conservation Area (KAZA), southern Africa. I use the observed dispersal trajectories to compare the ability of connectivity surfaces produced from three demographic-specific resistance surfaces (including those optimised using both home range and dispersal data), using both cost-distance and circuit theory approaches, to accurately capture movement during the dispersal process. I assess both comparative

measures of connectivity values at dispersal points across surfaces and the ability of the models to discriminate between observed and randomised paths. Results from the comparison show that, encouragingly, all connectivity approaches and resistance surfaces used perform, on average, well in predicting movements of an independent set of dispersing lions. I also discuss the challenges in thresholding what is considered as "connected" in delineating corridors and suggest how independent dispersal data can be used to guide this decision. Cost-distance approaches were generally more sensitive to resistance input than circuit theory, but differences in performance measures between resistance inputs were small across both approaches. These findings suggest that within this system, landscape is not highly limiting. Most of the dispersers traversed through landscapes that had minimal human settlement and are likely to be relatively highly connected by dispersal. I end the chapter by discussing how further research into limiting factors and dispersal abilities will be critical in understanding how populations might respond to increasing habitat fragmentation and human expansion over time.

3.1 INTRODUCTION

Wild animal populations are becoming increasingly isolated as a result of a growing human population and associated land-use conversion and fragmentation of habitat (Haddad *et al.*, 2015). Corridors that facilitate movement across a landscape are critical for the long-term viability of many populations as they ensure that key biological processes such as mating, dispersal and gene flow (Hilty *et al.*, 2019) can be achieved and that species maintain their ability to respond to changes in their environment, such as climate change (Chen *et al.*, 2011). This is particularly pertinent for the African lion (*Panthera leo)*, which has decreased from an estimated 100 thousand individuals to a figure closer to 20 thousand within the last century (Bauer *et al.*, 2016). These declines

have resulted in extirpation from 80% of its historic range (Riggio *et al.*, 2013; Bauer *et al.*, 2015a).

Smaller, more fragmented populations of lions experience increased vulnerability to local extinctions via environmental and demographic stochasticity (Woodroffe and Ginsberg, 1998) and increased disease susceptibility via loss of genetic diversity (Trinkel *et al.*, 2011). As landscapes become increasingly fragmented, connectivity at a population level will increasingly rely on large-scale movement (i.e. dispersal) to meet requirements for long-term population persistence (Björklund, 2003). For such wide-ranging species, much of this dispersal will fall outside of existing protected area networks and the identification of effective corridors to mitigate this will be key for maintaining population connectivity (Cushman *et al.*, 2015, 2018).

Dispersal is the key biological process ensuring movement of individuals between populations, and it logically follows that using dispersal data should be the most reliable approach to estimate resistance and model connectivity (e.g. Elliot, Cushman, Macdonald, & Loveridge, 2014). However, collecting these data is an extremely challenging task and has typically resulted in the return of small sample sizes (Fagan and Calabrese, 2006). To exemplify this, in a recent four-year study on wild dogs, only three of the 15 collared animals exhibited the expected long-distance dispersal movements (Abrahms *et al.*, 2017). While dispersal data is relatively rare, home range use data has been collected for many large carnivore species, and if adequate for capturing the dispersal process, would allow for relatively rapid functional connectivity assessment (Fattebert *et al.*, 2015).

However, there is an open question surrounding the capacity of home range use data to reveal functional connectivity for dispersing animals (Elliot, Cushman, Macdonald, *et al.*, 2014). This is a timely and important question to address given the

acute need for accurate and defensible connectivity models for conservation and the considerable challenges in obtaining dispersal movement data.

There is growing evidence that home range data can adequately capture habitat use and movement during the dispersal process for diverse mammalian species including leopards, desert bighorn sheep, kinkajous, brown bears and pumas (Newby, 2011; Fattebert *et al.*, 2015; Mateo-Sánchez *et al.*, 2015; Keeley, Beier and Gagnon, 2016; Keeley *et al.*, 2017; Zeller *et al.*, 2018). However, studies comparing corridors from dispersal data with those derived from other data inputs have shown substantial differences in the predicted connectivity for African lions, Iberian lynx and African wild dogs (Elliot, Cushman, Macdonald, *et al.*, 2014; Gastón *et al.*, 2016; Jackson *et al.*, 2016). A notable difference is that the former studies compared the ability of resource selection functions to predict observed dispersal habitat and movement, whereas the latter compared difference in connectivity outputs and not the ability of corridors to capture observed dispersal per se. Thus, it is unclear if the contrasting results are a consequence of species-specific differences or methods. I directly address this uncertainty for African lions by using an independent dataset on dispersal movement to validate the performance of connectivity models generated from demographic-specific resistance surfaces following the analytical paradigm of Zeller et al. (2018).

Zeller et al. (2018) assessed the performance of both multiple data types and connectivity algorithms in capturing the dispersal process for a species using three complementary metrics. This represents a substantial step forward in generating general recommendations regarding connectivity modelling by providing a standardised approach for assessing the performance of connectivity models in capturing biological processes. They tested two of the most used connectivity algorithms: cost distance (CD) and CircuitScape (CS). The two approaches use the

same resistance surface input as a foundation for modelling connectivity, with the main difference lying in the assumptions they make about an animal's knowledge of unfamiliar landscapes.

There are a variety of cost distance methods, some of which are non-directional, and measure cost distance from sources without regard to destinations, such as the resistant kernel method (Compton *et al.*, 2007), which calculates the incidence function of expected movement rate from a set of source locations synoptically through all pixels in the landscape. Other cost distance methods, termed source-destination models (Cushman, McKelvey and Schwartz, 2009), such as least-cost paths (Adriaensen *et al.*, 2003) and least-cost corridors, predict optimal, lowest cost paths and corridors between specified source and destination locations. These applications of CD assume animals will select optimal routes between pairings of source-destination points. In contrast, CS does not assume complete knowledge, but does assume a priori destinations.

In one of the only formal comparisons between CD and CS methods, Zeller et al. (2018) found clear support for higher model performance of source-destination CD than CS in predicting puma dispersal movement using their three performance metrics, based on those used in an earlier study by McClure et al. (2016). Furthermore, Cushman et al. (2014) found higher support for both non-directional resistant kernel and factorial least cost path modelling compared to CS in predicting locations where American black bear crossed a highway. These results, however, contrast with McClure et al. (2016) who found that CS outperformed CD models for wolverine dispersal data. The authors propose the differences in findings might be a result of the data input used for the wolverine models. The wolverine resistance surface was derived from a point selection function using data from VHF, rather than GPS telemetry data and had a long acquisition interval (points collected every 10 days). Combining the observation that

these data are relatively coarse, and that CS methods were less sensitive to data input, the conclusion was that CS may outperform CD where data are most like presence-only data. But it is also possible that this is a result of system- or species-specific ecological differences in the dispersal process.

By applying this validation approach to lion dispersal, using resistance data generated from GPS telemetry data in a path selection function (Elliot, Cushman, Macdonald, *et al.*, 2014), the results are more directly comparable. The findings will therefore contribute towards understanding how generalizable connectivity approaches and data inputs are across species. I also further develop this analytical paradigm by assessing how specific a connectivity surface is based on a spatial randomisation procedure first described by Cushman, Chase & Griffin (2010). This has particular relevance in understanding the specificity of a connectivity model and setting thresholds for delineating corridors – information that will be crucial for future conservation efforts, and to better justify the effort for collaring and prioritise which individuals in a population to target.

Despite the clear value in validating model outputs, studies using independent dispersal data to validate connectivity outputs have been limited, likely due to the challenges discussed above in obtaining data on dispersing individuals. An additional obstacle is the analytical difficulties associated with clearly identifying the segment of the path corresponding to dispersal movements. This is especially true for species such as lions that can exhibit prospecting searches outside their natal territory prior to eventual dispersal and may also exhibit secondary dispersal (Elliot, Cushman, Loveridge, *et al.*, 2014). As there is no obvious seasonal signature to the timing of lion dispersal onset, it can also be challenging to ensure that a collar is fitted just at the correct time to capture the departure phase. Combined with the reality that even once

dispersal from one range has occurred, the entire process from transience through to settlement can cover an extended period, means it is not to have paths that do not cover the entire period from natal range through to settlement. I present a simple, repeatable method (adapted from Weston, Whitfield, Travis, & Lambin, 2013) that makes use of readily available biological information on resident ranging patterns to identify dispersal periods and confirm its applicability to lions. While natal dispersers are likely the primary contributor to connectivity, lions also exhibit secondary dispersal. For example, when a male is displaced from an established territory and disperses again.

The primary aim of this chapter is to establish if the routes dispersing lions take can be predicted by various connectivity approaches, rather than to comprehensively describe the lion dispersal process. With this in mind, I do not distinguish between different types of dispersal events, and rather focus more generally on periods of transience as a way of capturing the routes lions take when moving between periods of range restricted, territorial behaviour. For simplicity, hereafter, I refer to individuals exhibiting the range of transience behaviours as "dispersers". Further discussion on the spectrum of movement behaviours I observed to occur outside of strictly range-restricted movements can be found in the final chapter of the thesis (see *Chapter 6 General Discussion*).

In summary, I use an independent, empirical dataset on lion dispersal movements to assess the performance of data from three demographic groups for estimating resistance and modelling connectivity, under two different algorithms. I use this to address the following research questions: (1) do connectivity surfaces created using dispersal data perform quantitatively better than those using male and female home range data? And (2) do source-destination CD or CS connectivity approaches best capture the observed routes selected by African lions during dispersal? Prior research

has demonstrated substantial demographic difference in connectivity for lions (Elliot, Cushman, Macdonald, *et al.*, 2014), that CS is less sensitive to data choice than CD, and that for path-based movement data the CD algorithm outperforms CS models (Zeller *et al.*, 2018). In line with these findings, I expect:

1. Across both algorithms, dispersal surfaces will out-perform those produced using home range data in capturing the observed dispersal process
2. CS will be less sensitive demographic differences in resistance surface values.
3. CD models will outperform CS models.

3.2 METHODS

3.2.1 Connectivity Modelling

Resistance surfaces

To create the connectivity models, I used three demographic-specific (adult females, adult males, and natal dispersers) resistance surfaces for African lions (*Panthera leo*) as defined by Elliot et al. (2014). The study extent falls within the Kavango Zambezi Transfrontier Conservation Area (KAZA-TFCA) and covers approximately 250,868 km^2. The extent is centred around the area for which I had independent movement data from those included in the original analysis, with an 100km buffer (Figure 3.1), and overlaps with the region used to parameterise the surfaces (Elliot, Cushman, Macdonald, *et al.*, 2014).

Resistance surfaces describe the cost of movement as a function of landscape features, with low values relating to ease of movement and high values to restriction (Zeller, McGarigal and Whiteley, 2012; Spear, Cushman and McRae, 2015). The resistance parameters for these surfaces were derived from path selection functions (Cushman and Lewis, 2010) based on GPS collar data (see Elliot et al., 2014 for further details). Although many different methods and input data can be used to create

resistance surfaces (for a review see Zeller, McGarigal, & Whiteley, 2012), those based on GPS collar data, particularly path selection functions, perform consistently well at capturing dispersal data (Zeller *et al.*, 2018). These, therefore, provide a suitable basis from which to explore the impact of other factors, such as demography, on animal behaviour and movement as a function of landscape features.

The surfaces from Elliot et al. (2014) model resistance as a function of eleven land use, habitat and anthropogenic variables known to influence lion movement. The relative resistance values across the study extent range from 1 – 5312 for dispersers, 3 – 10007 for adult males, and 2 – 23497 for adult females (Figure 3.3; step 1), with the variation in permeability driven largely by demographic differences in the strength of selection of protected areas, and avoidance of humans and agropastoral land (Elliot et al., 2014).

Connectivity modelling approaches

The connectivity approaches fall into two categories: those based on source-destination cumulative cost using least-cost corridors (cost distance; CD) and those based on circuit theory (CircuitScape; CS). I applied each connectivity algorithm across the three resistance surfaces between the start and end points of each dispersal event to produce animal-specific surfaces (as in Zeller et al., 2018). I ran CS using Circuitscape 5.0 (Anantharaman *et al.*, 2019) and CD using the gdistance R package (van Etten, 2017). The CS approach produces a cumulative current flow surface between the start and end points, and the CD approach sums the two cost distance kernels calculated on the start and end points, producing a surface whose values are the joint cost of moving through a given pixel from the start to the end of a movement path. This is also known as the least cost corridor between the start and end points (Cushman *et al.*, 2013).

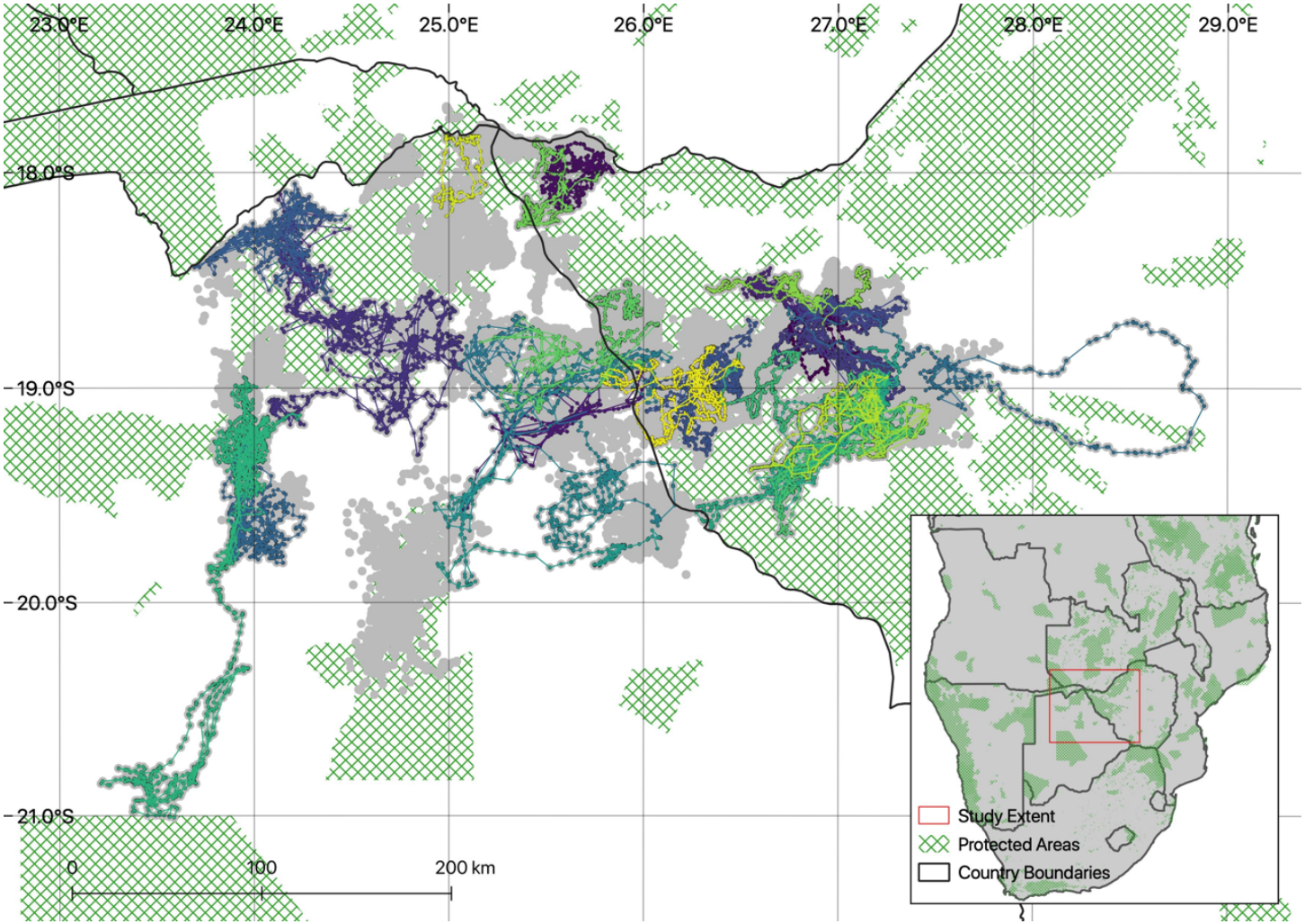


Figure 3.1 Map of the study area and lion GPS collar data.

Collar data was labelled as either resident or dispersing using a distance-threshold method adapted from Weston et al. (2013). Grey points represent the extent of the full GPS collar dataset, with points labelled as dispersing highlighted in colour. Green hatching represents National Parks and Game Reserves. All dispersal data presented here and used in the validation procedure were independent from the original dataset used by Elliot et al. (2014) to parameterise the resistance surfaces.

Both approaches use the same underlying landscape resistance data but differ in their assumptions about an animal's knowledge of the landscape. While source-destination CD approaches assume animal's will select optimal routes (non-directional CD approaches like resistant kernels, in contrast, assume no destination and no a priori knowledge of the landscape, but rather predict cumulative reduction in movement in all directions with increasing cost), a particular appeal of CS for predicting natal dispersal is that it is based on the concept of random-walk theory, and thus carries the implicit assumption that individuals have limited knowledge of the surrounding landscape (McRae *et al.*, 2008). However, as both implementations are based on a source-destination model, even for CS this implies some knowledge an animal's destination, if not perfect knowledge of the best way to get there. Thus, the comparison of methods allows us to contrast (a) perfect knowledge and known destination source-destination CD to (b) partial knowledge and destination CS.

Dispersal data

To create the validation dataset, I identified periods of dispersal from lions collared in Botswana and Zimbabwe as part of the Trans-Kalahari Predator Programme (Figure 3.1). I excluded any dispersal data used by Elliot et al. (2014) to parameterise the resistance surfaces to create an independent dataset on dispersal movement for validation purposes. I adapted a distance-threshold method from Weston et al. (2013) to estimate the point of emigration and settlement for individuals based on expected movement distances and excursion duration of dispersers in comparison to resident lions (**Figure 3.2**). As the question does not depend on the overall shape or size of this area, I defined home range simply as all the locations over a three-month period, and calculated distance as net displacement from the centroid of these locations. I based the distance thresholds on ranging distances of known resident lions in the study area

where individuals were recorded up to a maximum 26.13 km from the centre of their home ranges, but over 98% of observations were within 18.01 km. Based on these values, I assumed that a lion had dispersed if it was recorded over 26.13 km from the centre of its starting 'home range' and did not return to within 18.01 km for the following fortnight. The choice of a fourteen-day minimum excursion reflects the fact that the longest duration of excursion by resident lions was eleven days, with a mean of two. A biological justification for this time window is that a natal disperser would have to forage independently during an excursion of 14 days, and it is therefore an indication that they are likely moving independently of the natal group.

This method was developed to describe dispersal in juvenile golden eagles who were known to begin in their natal home range (Weston et al., 2013). However, the concepts are readily transferable to other territorial species, such as lions. To confirm this, I applied the proposed method to five subadult dispersers from Elliot et al. (2014), who were known to be still with their natal group at the start of their collar dataset, and where time of emigration had been determined by direct observations (full results of this comparison are presented in Appendix B). For three lions, the point of emigration fell within the window identified by Elliot et al. (2014) and for the other two, it fell shortly afterwards (within 10 days). This outcome is comparable to performance in juvenile golden eagles, where the method tended to estimate point of emigration slightly later than their reference dates (Weston et al., 2013). Although this results in the omission of some early dispersal movements, I can also be confident that all data included are from the dispersal period. The method has the added benefit of being simple to execute, repeatable, and based on easily obtained biological values from the species' movement behaviour.

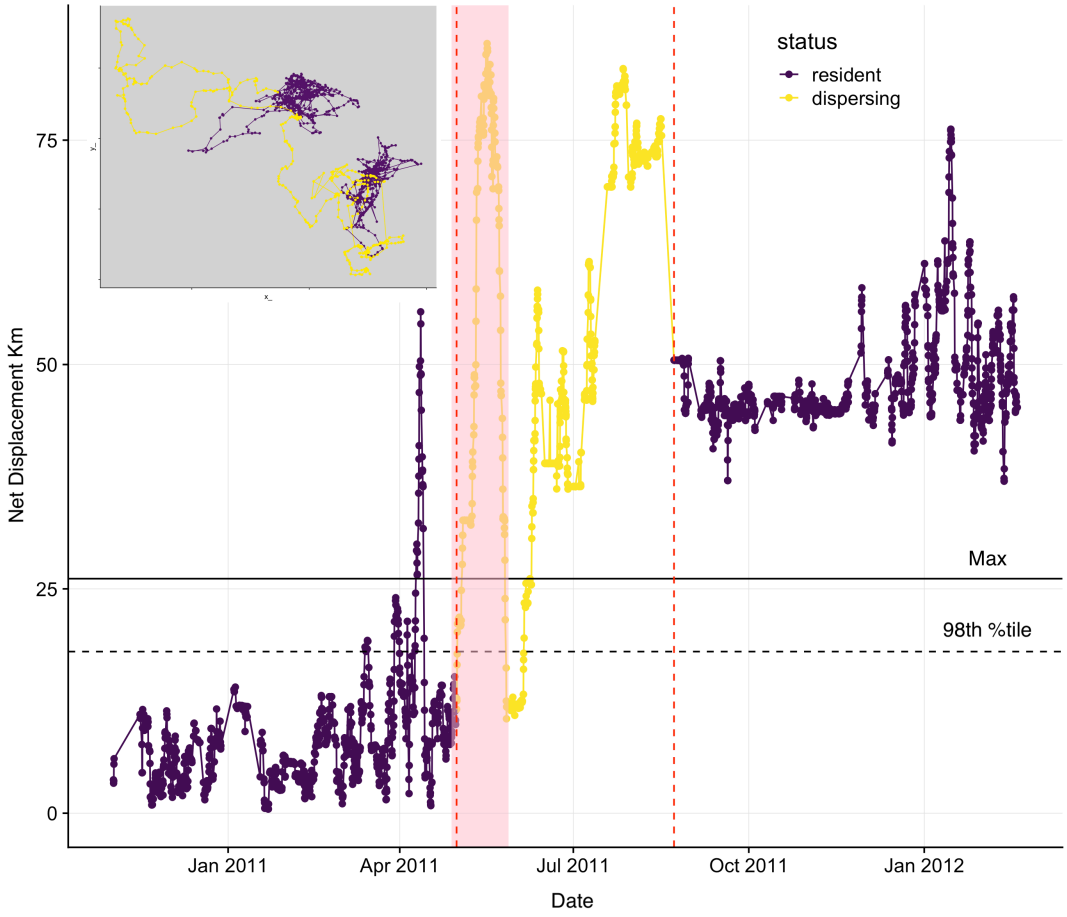


Figure 3.2 *Net displacement from the centroid of the first three months of data as a function of time showing labelled periods of residency and dispersal for one study animal. Vertical dashed lines represent point of dispersal and settlement, light red box indicates the window for dispersal estimated by field observation (Elliot et al., 2014). Inset graph shows a spatial representation of the same dataset.*

I created one further extension to the method to account for occasions where the start of a dataset occurs during the dispersal period, making the definition of dispersal onset based on a distance from initial home range irrelevant. In this case it was necessary to determine if the individual was broadly resident or not at the start of the dataset, and if not, when was the first time it was. To do this I used a moving window of three-months to find the first point in the dataset where a candidate disperser's mean ranging values from the centroid of the window was within the observed range for resident lions, then estimate a more precise date of settlement using the converse

criteria for dispersal. Specifically, for an animal to be classified as settled it must go below the maximum ranging threshold and then not go above the 98th percentile of ranging distances for more than 14 days. As dispersal may include short periods of temporary residence, I added the criteria that to be classified as having an established range, an animal must remain settled for at least three months (as in Elliot et al. 2014). All labelling of dispersal data was carried out in R (R Core Team, 2020).

This method identified a total of 28 dispersal events, with 19 examples of natal dispersal (13 males, 6 females) and nine of adult dispersal (3 males, 6 females). I extracted GPS locations from these dispersal periods (n=39,066). Median net displacement of dispersal events was 59 km (range 26 - 208 km).

3.2.2 Model Validation

Evaluating performance

Building on the frameworks presented in earlier studies (McClure, Hansen and Inman, 2016; Zeller *et al.*, 2018), I used five complementary measures of performance to evaluate each connectivity surface:

I. Mean connectivity value at observed dispersal points
II. Null resistance surface comparison
III. Null connectivity surface comparison
IV. Proportion of dispersal points in percentile corridors
V. Ranking in spatial randomisation procedure

Performance measures III and V were integrated into the methods described by Zeller et al. (2018) and McClure et al. (2016) from Cushman, Lewis and Landguth (2014), allowing me to directly compare the results to both approaches.

Performance measures (PMs) I to III centre on the mean connectivity values at observed dispersal points as a measure of how well the surface captures patterns of the biological dispersal process (represented here as GPS points from dispersal events). If a connectivity surface is performing well, observed dispersal points should fall on high connectivity values (PM I; Figure 3.3 step 2 b & f) — evaluating the performance of the entire surface. Additionally, connectivity values from surfaces generated using empirical resistance should be higher than those using a null, isolation-by-distance model (PM II; Figure 3.3 step 2 c & g). This isolates the performance of the resistance component of a connectivity surface by testing the null hypothesis that observed dispersal movement is unrelated to the resistance of the landscape (i.e., that animals travel without regard to habitat quality). I generated null resistance surfaces by running connectivity algorithms on surfaces where resistance is set to a value of one for all pixels.

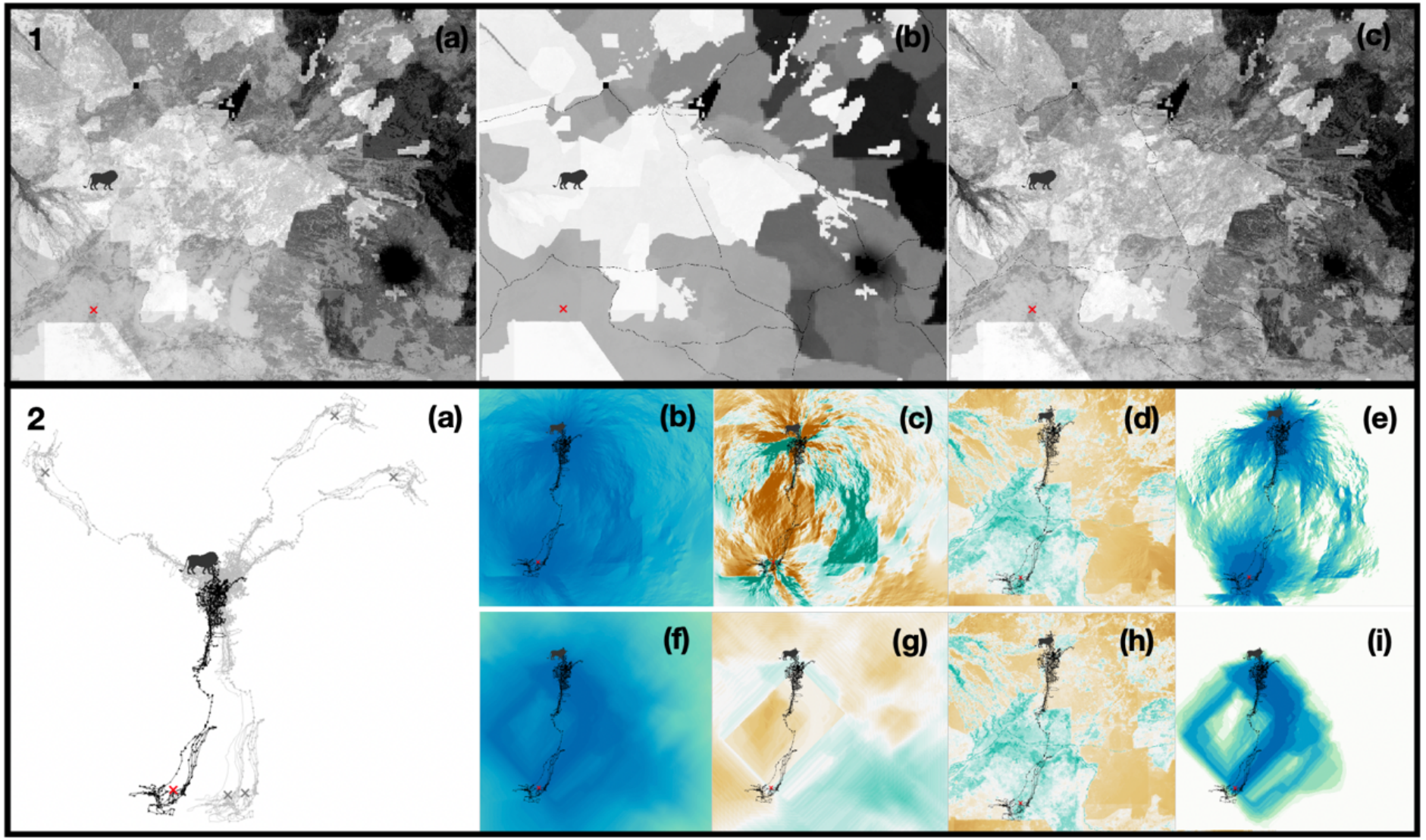
For the null connectivity comparison (PM III), I created neighbourhood average landscape resistance (NALR) surfaces by calculating the focal mean of landscape resistance using the neighbourhood of cells in a 5 x 5 matrix centred on the focal pixel. Given the resolution of the resistance surfaces (500 m x 500 m) this represents a buffer of 1 km around each pixel. I used the NALR surfaces to test the hypothesis that observed dispersal movement is driven largely by local resistance, rather than the wider pattern across the landscape (Cushman, Lewis and Landguth, 2014). This forms a counterpart to the null resistance comparison, this time isolating the connectivity component (Figure 3.3 step 2 d & h).

The proportion of points in corridors (PM IV; Figure 3.3 step 2 e & i) describes how much of the dispersal process would be captured by various percentile corridors (e.g. the 90th percentile, or the most traversable 10% of the landscape). Connectivity

models are often used to delineate corridors for wildlife management by taking an upper percentage of the connectivity values. A suitable connectivity map, for this purpose, should therefore encompass a high proportion of dispersal points within the upper percentile of connectivity values.

Finally, I used a spatial randomisation procedure to compare connectivity values obtained at dispersal points to values obtained at random samples of points (PM V). I generated random samples of points by rotating each observed path using the trajR package in R (McLean and Volponi, 2018) around its origin (by a value of radians drawn from a normal distribution) over 1 x 10^5 iterations (e.g. Cushman et al., 2010; **Figure 3.3** step 2 a). By comparing values at observed points to the distribution of values from the random samples I can obtain an estimate of the probability of the observed outcome given the data (Fortin and Dale, 2005), allowing us to test the hypothesis that routes taken during dispersal are unrelated to the predicted connectivity (Cushman, Lewis and Landguth, 2014). This is analogous to the second performance measure from McClure et al. (2016), I applied this spatial randomisation procedure to each of the performance measures (as described below in *Statistical analyses*).

Figure 3.3 Conceptual diagram representing (1) the inputs for connectivity modelling and (2) the validation process. Step 1 (a) - (c) depict resistance surfaces generated using dispersing individuals, adult females, and males, from left to right. Resistance is depicted from a gradient of low (white) to high (black). Overlaid are the start and end points of a single dispersal event represented as a lion and a cross, respectively. Step 2 (a) illustrates the spatial randomisation process, giving five examples (out of the total 100,000) of possible routes the same lion could have taken in grey, alongside the observed points in black. Step 2 (b) - (e) and (f) - (i) show the four performance measures for CircuitScape (top row) and cost-distance (bottom row) for the disperser surface inputs. Mean percentile value (b) & (f) are shown with high connectivity values gaining increasingly blue colours, as with the 90th percentile corridors (e) & (i). In the latter case, everything outside of corridor has been cropped. (c) & (g) represent the null resistance comparison, and (d) & (h) the comparison with neighbourhood average landscape resistance. Both comparisons are shown with negative values gaining increasingly brown colours, and positive values in blue. Shown on folowing page.


1
(a)
(b)
(c)
2
(a)
(b)
(c)
(d)
(e)
(f)
(g)
(h)
(i)

Statistical analyses

To test for differences in performance measures between connectivity approaches and resistance inputs I used a combination of generalised linear mixed-effects models and the rankings from the spatial randomisation procedure.

As performance measures I – III require direct comparison of the magnitude of values between connectivity approaches that generate values on very different scales, I used percentile rescaling to facilitate this, as suggested in previous papers (McClure, Hansen and Inman, 2016; Zeller *et al.*, 2018). Thus, the response variables for models describing PMs I-III represent mean percentile connectivity value and mean difference between percentile rescaled empirical and the two null surfaces (null resistance and NALR). For PM IV the response variables are proportion of points for each lion in the 90^{th} and 99^{th} percentile corridors.

To create the response variables for comparisons of the empirical surfaces to the two null surface specifications I calculated the difference at each dispersal point between empirical connectivity values and (a) surfaces with resistance set to one i.e. null resistance, and (b) NALR surfaces i.e. null connectivity. If values at the dispersal points are higher on an empirical surface compared to the null surface, then a positive difference will be obtained. This can be used to identify surfaces that significantly out-perform a null model. For the percentile corridors I calculated, per lion, the proportion of points in the top 10, and 1% of connectivity values, respectively. Repeating the analysis for two different percentile cut-offs allowed me to explore what impact the selection of threshold for what is considered a "corridor" has on inference about what connectivity models are most suitable for predicting dispersal.

I modelled each of these four validation response variables as a function of resistance type (male-, female-, disperser-, generated resistance)., connectivity approach (CD vs CS) and a categorical variable describing the length of the dispersal event as I expected longer paths may be more difficult to predict (particularly for cost distance approaches). I used 75 km as the threshold between short and long dispersal which, given an average home range in the region of 300 - 500 km^2, corresponds to moving across approximately 3 lion home ranges. Animal ID was treated as a random factor to account for repeated samples from each individual. I allowed for both random intercepts and random coefficients in the models. In the case of proportion of points, I used a binomial error distribution (with logit link). I used the package lme4 (Bates, Mächler, *et al.*, 2015) to fit the mixed-effects models in R (R Core Team, 2020).

In some cases, the maximal model (with the most random-effects components that is theoretically identifiable given the structure of the data) led to singular models. In these cases, I dropped terms where singularity occurred (as suggested in Barr, Levy, Scheepers, & Tily, 2013) and used the function rePCA from the R package *RePsychLing* to ensure that the complexity in the random effects structure is supported by the data to balance Type-I error rates with power (Bates, Kliegl, *et al.*, 2015; Matuschek *et al.*, 2017). Within each connectivity approach, the maximal fixed-effects specification included an interaction term to test for differences in the performance of each model at describing dispersal length categories and the sensitivity of each connectivity approach to resistance inputs.

I used likelihood ratio tests (of nested models) to provide an estimate of the statistical significance of each term and contrasts of estimated marginal means using the R package *emmeans* (Lenth, 2020) to assess statistical differences across and within factor

levels. I calculated marginal and conditional R_GLMM2 to describe the variance explained by the fixed effects and the entire model respectively (Bartoń, 2009; Nakagawa, Johnson and Schielzeth, 2017).

For PM V, I used the spatial randomisation procedure to compare both the mean percentile connectivity value (PM I) at dispersal points and the proportion of observed dispersal points (PM IV) in corridors for each surface to the distribution of mean values and proportion of points generated from the 1 x 10^5 iterations of random samples. To quantify this comparison, I recorded the proportion of instances, of 1 x 10^5 random samples, where a random draw of 39,066 points (total of observed dispersal points) produced a performance measure value higher than or equal to the value at the observed points. This allowed me to examine the specificity of the surfaces in capturing observed dispersal events. While PM I will tell us which surfaces produce, on average, higher connectivity values—or higher proportion of points in corridors—PM V tells us which surfaces produce higher values than we would expect *by chance* given the distribution of connectivity across the landscape.

Thus, together we are able to identify surfaces which have a good match between observed dispersal and high connectivity values (PM I), would capture a high proportion of dispersal events in percentile designated corridors (PM IV), identify how the separate components of connectivity are performing—resistance pattern or connectivity algorithm—(PM II & III), and what support there is that the observed dispersal is related to the underlying predicted connectivity (PM V).

Comparing connectivity values at dispersal points to the distribution from the random samples also provides a scale-independent means to compare surfaces without

rescaling, as values obtained at points from the random samples implicitly fall on the same scale (per surface) as observed points. This is advantageous as it avoids the need to discretise the continuous connectivity values into bins, generating a ranking that describes performance based on relative values of connectivity between the random and the observed points for each surface. We therefore repeated the spatial randomisation procedure for PM I, but directly using unscaled connectivity values to estimate the mean values. I included all connectivity surfaces—empirically-derived and null—in this ranking. This allowed me to examine how the process of discretising connectivity values (as is done in the generation of e.g., a percentile corridor) impacted the specificity of the surfaces.

When considering unscaled connectivity it is worth noting that the generated values (cost for CD surfaces, cumulative flow for CS surfaces, and neighbourhood average resistance for NALR surfaces) differ in their interpretation; with lower values conferring higher connectivity for CD and NALR, and the converse for CS. The response values used for the comparison of unscaled surface values were strictly positive, and right skewed - I therefore used the gamma and inverse gaussian families in the mixed-effects models as a good, flexible option for bounded data. I selected the family which best fit each resistance/approach combination by comparing AIC values. I used a "log' link function in both cases to ensure mu>0 and to aid interpretation of values (Dunn and Smyth, 2018). For proportion of points, I again used a binomial error distribution (with logit link).

3.3 RESULTS

3.3.1 *Mean connectivity value at dispersal points (PM I)*

For both CircuitScape (CS) and cost-distance (CD) surfaces, variation in mean percentile value at observed dispersal points was best described by an interaction term between resistance input and dispersal category (CS: $\chi^2(2)=168.12$, p=<2.2e-16; CD: $\chi^2(2)=751.2$, p=<2.2e-16). Indicating that the effect of resistance input on mean percentile connectivity was dependent upon which category of dispersal was being considered (i.e., long vs. short). Although statistically significant, differences between surfaces were small (<1 percentile value) and all surfaces predicted mean values of >97th percentile for all dispersal distance categories. The fixed-effects portion of both models explained a relatively small amount of the overall variation in mean percentile value at observed dispersal points (marginal and conditional R^2 values of 0.09 and 0.36 for CS, and 0.07 and 0.34 for CD, respectively).

For both CD and CS, the mean percentile connectivity value of observed dispersal points was much higher than the distribution produced from the spatial randomization procedure (PM V). The same pattern was observed using unscaled connectivity values, with the observed values performing well in comparison to the random sample, however the unscaled values showed a stronger difference (Table 3.1). It is worth noting when considering unscaled values, that for CD and NALR, lower values are indicators of better performance, whereas for CircuitScape (CS), the opposite is true, with higher values indicating better performance.

For percentile-scaled mean connectivity values, the relationship between the number of random draws (out of 100,000) that produced a mean of greater than or equal to the dispersal values and the resistance input differed between CS and CD approaches.

CD surfaces performed better for shorter distance dispersers, across all resistance surfaces, which was also true for male and disperser resistance under CS, but for female resistance the opposite was true (Table 3.1)

Connectivity Approach	Resistance Input	Dispersal Category	Comparison with Random Samples: Mean Surface Values: Unscaled	Mean Surface Values: %tile-scaled	Proportion in %tile corridor: 90th	Proportion in %tile corridor: 99th
CD	Disperser	<75 km	0	0	0.10122	0
		≥75 km	0	0.00184	0.00074	0
	Male	<75 km	0	0	0.16030	0
		≥75 km	0.00002	0.00330	0.00148	0
	Female	<75 km	0	0.00004	0.22352	0
		≥75 km	0.00067	0.01285	0.00006	0.00001
	Null	<75 km	0			
		≥75 km	0			
CS	Disperser	<75 km	0	0	0.18408	0
		≥75 km		0.00017	0.00001	0
	Male	<75 km	0	0	0.18260	0
		≥75 km		0.0001	0	0
	Female	<75 km	0	0.00041	0.09574	0
		≥75 km		0.00006	0	0.00016
	Null	<75 km	0			
		≥75 km				
NALR	Disperser	<75 km	0.00003			
		≥75 km				
	Male	<75 km	0.00054			
		≥75 km				
	Female	<75 km	0.01770			
		≥75 km				

Table 3.1 Ranking of mean values of connectivity and proportion of points in corridors in the distribution of means obtained from 100,000 random samples. Values are presented as proportion (out of 100,000) where a random draw performed equal to or better than the mean obtained at our dispersal points and can be interpreted as probability that observed movement is related to underlying landscape connectivity. Text in grey represents surfaces included only as null comparisons in the percentile-scaled performance measures.

For unscaled values, all CircuitScape (CS) and resistance combinations generated higher mean cumulative flow values at dispersal points than any of the randomised paths (**Figure 3.4**, row 3). For short distance dispersers, all CD and resistance combinations had mean cost values lower than all randomised paths (**Figure 3.4**, row 2). For animals travelling a longer distance (**Figure 3.4**, row 1), a small number of the random draws for

the female (67) and male (2) resistance inputs produced lower mean cost values than the observed dispersal points, with all observed values for disperser and null resistance inputs outperforming the random samples.

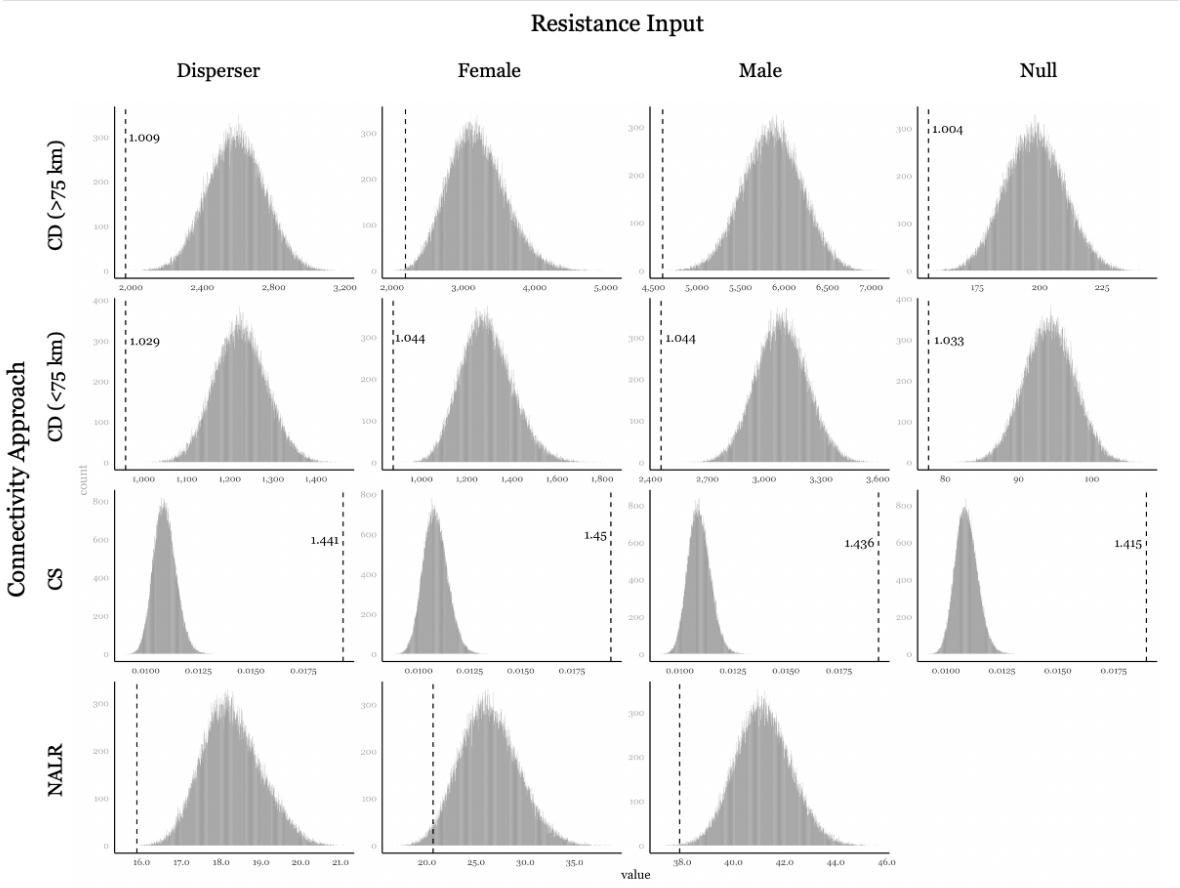


Figure 3.4 *Observed mean connectivity values from unscaled surfaces within distribution of mean values from randomised paths. Mean values of cost (rows 1-2), current flow (row 3), and neighbourhood average resistance (row 4) from 100,000 random samples of points are presented at histograms, with the mean value obtained at dispersal points shown as a dashed vertical line. Where the mean value at dispersal points outperformed all random samples, the times smaller (or larger, for cumulative flow) than the lowest (or highest) value obtained in the random samples is shown next to the line. When connectivity surfaces were unscaled, cost-distance (CD) surfaces were the only connectivity approach that indicated statistical support for the inclusion of a term describing the maximum displacement of dispersers (Disperser: $\chi2(1)=7.43$, $p=0.006$; Female: $\chi2(1)=5.208$, $p=0.007$; Male: $\chi2(1)=7.406$, $p=0.022$, Null: $\chi2(1)=8.787$, $p=0.003$).*

Under the neighbourhood average landscape (NALR) scenario (**Figure 3.4**, row 4), 3, 54, and 1770 random samples produced mean average resistance values lower (i.e., performed equal to or better) than those observed at dispersal points for disperser, male and female resistance inputs, respectively.

3.3.2 Difference between empirical - null surfaces (PMs II & III)

The data also supported an interaction term between resistance input and dispersal category in describing variation in the difference between empirical and null surface connectivity values for both connectivity approaches. (CS: $\chi^2(2)=443.63$, p=<2.2e-16; CD: $\chi^2(2)=14.326$, p=0.00078). Again, indicating that the effect of resistance input varied based on the type of resistance input used. No combinations of connectivity approach and resistance input produced estimated differences where the lower boundary of 95% confidence intervals fell above 0, i.e., no surfaces were identified that significantly outperformed a surface based on isolation-by-distance as measured by a higher percentile value on empirical surfaces under dispersal points. The only combination to produce a point estimate of >0 was CS, with male resistance input, for short distance dispersers (for context, estimated difference was 0.007). Again, marginal, and conditional R^2 squared values were low (CS: 0.04, 0.23; CD: 0.06, 0.19).

Conversely, all surfaces significantly outperformed those based on local resistance alone (neighbourhood average landscape resistance; NALR). Here there was no evidence to support inclusion of either an interaction term, or the main effect of dispersal category, i.e., the effect of resistance type was consistent across long and short dispersal events. Estimated marginal means (EMMs) for the CS and CD surface differences were 24, 20, and 30 for disperser, female and male surfaces, respectively. Contrasts between EMMs for

resistance inputs were all significant ($p<0.001$, p-value adjustment: bonferroni method for 3 tests).

3.3.3 *Proportion of points in percentile corridors (PM IV)*

At the 90th percentile cut-off threshold, all observed dispersal points in the <75 km category (bar two individuals on the CD-female surface combination) fell within the 90th percentile corridor, making modelling variation in the proportion of points redundant. Predicted proportion of points for >75 km category was >0.999 for all surface-connectivity combinations. At the 99th percentile threshold, the corridors still captured a high proportion of dispersal points, with the lowest combination (long distance category using female resistance and CD) predicting 72% of points in corridors. For short-distance dispersers, all combinations predicted 98% of points in corridors and above. For long-distance dispersers, the pattern with respect to resistance was consistent with surfaces optimised using dispersal resistance performing best (83 and 85% for CD and CS), followed by male resistance (80 and 85% for CD and CS), with female resistance capturing the lowest proportion of points (72 and 80% for CD and CS). The discrepancy between the top and bottom ranking combinations was larger for CD than CS (difference of 11 vs 5 %, respectively), and the difference between the top two CS surfaces was <1%. The difference in sensitivity of proportion of points in corridor to resistance input, based on the dispersal category, and the connectivity approach was reflected by support for a three-way interaction between connectivity algorithm, dispersal category and resistance input from the LRT statistic ($\chi^2(3)=135.27$, p=<2.2e-16).

For the spatial randomisation procedure, both CS and CD again performed very well for most combinations of approach, resistance input, and dispersal category in

capturing proportion of points falling into both the 90th and 99th percentile corridors with a high level of specificity. CD and CS for all three resistance inputs (disperser, male and female) performed very well in the long-distance category, with a proportion less than 0.002 of randomized paths producing a higher number of points within the 90th percentile corridor and close to none in the 99th percentile corridor (Table 3.1).

The short-distance dispersal category showed less discrimination in terms of proportion of points falling in percentile corridors compared with the distribution of the randomized paths, suggesting that short distance dispersal is less strongly linked to predicted connectivity across these resistance surfaces than is long distance dispersal. Using the CD method, the disperser resistance model performed better discriminating short distance dispersal values, followed by the male resistance surface, with the female resistance surface performing least effectively (Table 3.1). In somewhat of a contrast, for CS methods in the low dispersal distance category, the disperser and male resistance surfaces both performed less well than the female resistance surface (Table 3.1).

3.4 DISCUSSION

For both cost-distance (CD) and CircuitScape (CS) approaches, the observed mean value of actual dispersal points indicated higher connectivity values than the distribution produced from the spatial randomisation, based both on the unscaled and percentile rescaled connectivity values. The unscaled values showed a stronger difference between the observed and the distribution of randomised paths, but both indicate very high performance for both CD and CS. For the proportion of points falling in percentile corridors, both methods, again performed very well for most combinations of approach, demographic resistance input and dispersal category.

Long distance dispersal paths were captured well using CD and CS approaches, across all three (Disperser, Female, and Male) demographic resistance surfaces, with a proportion less than 0.002 of randomised paths producing a higher number of points within the 90th percentile corridor, and none in the 99th corridor. The short-distance dispersal category showed less discrimination in terms of proportion of points falling in percentile corridors compared with the distribution of the randomised paths, suggesting that short distance dispersal is less strongly linked to the predicted connectivity across these resistance surfaces than travel over longer distances.

My first expectation was that for both cost-distance (CD) and CircuitScape (CS) approaches, connectivity models built using dispersal resistance as an input will outperform those based on adult home range data in capturing dispersal movements. This was supported in many, but not all performance metrics and combinations of dispersal category and connectivity approach. Using the CD methods, the disperser resistance model performed better at discriminating short distance dispersal values, followed by the male resistance surface, with the female surface preforming least effectively – both in terms of the mean connectivity value at observed points, and the proportion of points in the 90th percentile corridors. In somewhat of a contrast, for CS methods in the short dispersal distance category, while the disperser and male resistance surfaces conferred greater specificity in mean value at dispersal points, both performed less well than the female resistance surface at discriminating dispersal values in the 90th percentile corridors. The same pattern was seen for long distance dispersers using CD methods, where although the mean value (both unscaled and percentile scaled) was better discriminated by disperser resistance, followed by male, then female resistance, once this was translated into a 90th

percentile corridor, female resistance scored more highly in performance against the random samples. It is worth noting that once the threshold for a "corridor" was increased to the 99th percentile, our expectations were met, with disperser resistance capturing a higher proportion of points than male resistance, with female surfaces capturing the least, across both CS and CD. While all combinations exhibited high ability to discriminate observed dispersal compared to the randomised paths, the female surface performed least well, particularly for long-distance dispersal events. Given the high overall predicted mean connectivity at dispersal points (>97th percentile) it is likely that an arbitrary cut-off of 90th percentile may not be sufficient to discriminate the most important routes for lions in this system, from those that are merely close by.

In general, there were smaller differences between the demographic resistance inputs for CS models, supporting the second expectation that CS would be less sensitive to differences in resistance surface values. Fundamentally though, the performance for all three empirical resistance inputs is very similar, with the main difference lying in the threshold required to discriminate dispersal paths more successfully than by chance, given the distribution of connectivity across the landscape. For both connectivity approaches, all resistance surfaces generated high connectivity values at dispersal points, and all were convincingly specific to points at dispersal. Together with the overall strong support that routes selected during dispersal are driven by landscape connectivity patterns, even for lower ranking combinations of resistance-connectivity, these results support the growing body of evidence that home range data can adequately capture the dispersal process (Fattebert et al. 2015; Keely et al. 2016; Keely et al. 2017; Newby 2011; Zeller et al. 2018).

It is also notable that none of the resistance-connectivity approaches outperformed the null resistance inputs. This is true considering both PM II (difference between empirical and null percentile values at dispersal points) and the distribution of mean surface values within the random samples (Table 1) where both CS and CD approaches with a null resistance input outperformed all 100,000 draws. This suggests that it is the connectivity algorithms (paired with known source-end points) that drive good fit in the models. One possible explanation for this is that in the study system dispersal may be driven to an extent by isolation by distance processes. The KAZA area I have modelled represents one of the remaining strongholds for lions, comprised of large areas of protected areas and it is possible that the dispersal events I have observed are through a system highly connected by dispersal. This is consistent with the findings of Cushman et al. (2011), who demonstrated that when a landscape is not highly limiting due to fragmentation the relative resistance values and predicted connectivity patterns are not different than isolation by distance. The same pattern was also shown in terms of the effects of dispersal on genetic differentiation, both in simulation (Cushman, Landguth and Flather, 2013) and empirical studies (Short Bull *et al.*, 2011; Vergara, Cushman and Ruiz-González, 2017). Where the landscape to contain greater variation in the permeability, and more constraint in the routes available to lions, it is quite possible that the pattern of resistance across the landscape would be a much greater driver of the emergent pattern of observed dispersal paths. It would be informative to compare these results across a gradient of landscape fragmentation — and highlights the need for large-scale replication of studies across the species' range, to determine the location and effects of limiting factors and how they affect movement patterns.

In contrast to this, for the null connectivity comparison, all resistance-connectivity combinations out-perform the NALR surfaces, both in specificity and in mean percentile value. This supports the hypothesis that dispersal routes are not driven by local resistance alone. The ranking of the NALR surfaces in the spatial randomisation procedure (Table 3.1) provide further insight as points used during dispersal were most strongly linked to the underlying neighbourhood resistance for the disperser surface (followed by the male surface, and finally the female). This supports the proposition that these demographic differences are biologically based, and one part of the story, but that once a connectivity algorithm has been applied, they are not the major driver of performance at the landscape connectivity level in these models, as supported by the strong performance of the null resistance connectivity model. This result is similar to that found in Barros et al. (2019) where range expansion and genetic diversity patterns in Egyptian mongoose populations were most consistent with a neutral model of uniform resistance. However, the conclusions regarding the relative importance of resistance in explaining emergent movement patterns is likely system- and process-specific. For example, Cushman et al. (2014) found substantial differences between two different empirically derived resistance surfaces for both resistant kernel and factorial least cost path approaches in predicting the location of road crossing in American black bears.

Although not included in the target methodology, in a subsequent post-hoc analysis after observing the strong relative performance in mean connectivity value of the null resistance input, I estimated the proportion of points that fell inside a 90th percentile corridor based on null resistance. While the proportion of dispersal points inside the corridors was comparable to the empirical surfaces, the null surface corridor did not

outperform even a single draw of random points — as all points, random or observed fell inside the corridor. In this aspect, empirical resistance confers a benefit in specificity. There is a clear need for further research on thresholding and optimising the delineation of corridors, which I return to below.

The final expectation that CD models will outperform CS models was not supported by the findings. Under the implementation I used to generate connectivity, both approaches performed equally well, both in terms of the mean percentile values predicted, the proportion of points in corridors, and the specificity of the models. In fact, CS models performed slightly better than CD models in this context. This contrasts with the results from Zeller et al. (2018) and partially supports those found in McClure et al. (2016). Given the differences of data inputs in the two studies above, it was difficult to parse out whether this might have given rise to the different conclusions. However, the resistance inputs for this study were based on path analyses of GPS telemetry data, consistent with the path analyses from Zeller et al. (2018). It is important to note that in the application of CD methods I used is functionally the least cost corridor which assumes a priori destination and pre knowledge of the landscape. This is fundamentally different than the applications of the CD method advocated for by Cushman et al (2010), which eschew the use of least cost corridors in favour of resistant kernels (Compton *et al.*, 2007), which do not presuppose an a priori destination or perfect knowledge of the landscape, but instead calculate the incidence function of expected movement frequency from source locations synoptically across all cells in the landscape (e.g., Cushman et al. 2010, 2012, 2018; Kaszta et al. 2020). Cushman et al. (2014) is the only evaluation I am aware of that formally compared resistant kernel applications of CD to other methods, including CS and factorial

least cost paths (Cushman, McKelvey and Schwartz, 2009), and found that resistant kernel and factorial least cost path methods of CD both outperformed CS in predicting road crossing locations of American black bears. Further research should evaluate the performance of resistant kernel approaches relative to CS and source-destination formulations of CD, particularly for movement at the population-level and overall connectivity.

The dispersal process in lions is a complex mixture of periodic, directed, and random movement (Elliot, Cushman, Loveridge, *et al.*, 2014). It is also a process that can occur over timescales ranging from months to years and might include temporary bouts of residency. Additionally, after some time spent a great distance away from the starting point, it is possible that the social landscape of resident prides and tenure will result in a destination for settlement that lies much closer to the start than most of the complete path. This generates some dispersal trajectories that are much less directed than the long-distance puma trajectories presented in Zeller et al. (2018). It is thus possible that species-specific differences in the underlying dispersal process - or the stage of the process selected - might underly the difference in conclusions regarding the best connectivity algorithm to describe this. I provide a validation of species-specific connectivity models, based on high-quality movement data for lion movement in this system – to generalise this to other lion populations, or other studies there is a clear need for replication. As more studies across species and study sites gather, this will be an important avenue for future research.

Given the complexity and the length of lion dispersal paths, it is also possible that the conclusions regarding the best connectivity algorithm may be result of the single source-destination approach I use to model connectivity. In recent years the options for

modelling synoptic connectivity across many combinations of source points (for both CS and CD approaches) has proliferated and evaluating the performance of these cutting-edge implementations will be an important development. The use of resistant kernels (Compton *et al.*, 2007), which relax assumptions about known destination points and include the ability to explicitly incorporate a biological threshold for dispersal ability may offer a particular improvement for cost-distance approaches (e.g. Cushman, Landguth and Flather, 2013; Wasserman *et al.*, 2013; Cushman *et al.*, 2015, 2018).

The ability to restrict the extent of a connectivity kernel to a biologically relevant distance has appeal in the light of the results surrounding proportion of points in a percentile corridor. All connectivity-resistance combinations would capture most points in a 90th percentile corridor — however, the random samples perform at least as well as the observed values in around 10-20% of the cases for short distance dispersers. As I increased the cut-off for the corridor to the 99th percentile, the proportion of dispersal points in the corridor remained high, but the difference between dispersal points and the random samples became more pronounced (Table 3.1). This suggests that selecting a threshold to consider a corridor may not be a trivial choice. Where available, using independent dispersal data, as I have, is one way to select an appropriate threshold. However, given the challenges of obtaining such data, explicitly including a dispersal threshold into the estimation of connectivity may also offer a powerful alternative. This may be particularly important in areas where the human population is expanding and the demand for land is at a premium and will be critical in advancing guidelines for creating corridors for conservation.

There were two additional insights that I had not included in the *a priori* expectations, regarding differential ability to predict dispersal events with long and short maximum displacement from starting location and the comparability of the results from unscaled and percentile-scaled connectivity. Across both approaches, surfaces were less specific in discriminating dispersal from the randomised points once connectivity had been rescaled — particularly for surfaces based on female resistance and for dispersers with high maximum displacement. This suggests that rescaling connectivity to compare between methods may require some careful consideration on the scale and method of rescaling and the implications for inference. Here I binned the continuous connectivity values into percentiles, however, a finer discretisation might be more appropriate as an approximation of a continuous scale. Regarding differential ability to predict dispersal events with short and long maximum displacement, the difference was most pronounced in the specificity of CD surfaces — however, in terms of practical use of the connectivity model, again high connectivity values were still observed for both categories of dispersal. It is possible that as dispersers move further from the specified start-end points their movements become less related to predicted cost kernels generated around these start-end points. It would be interesting to see if these results were consistent using surfaces generated taking a more synoptic approach to source points.

A final consideration of the results is that the models including resistance input and dispersal category produce low marginal R^2 values, with much of the variance encompassed by the random factor, individual. This suggests there are other differences that would explain variation in the selection of the landscape during dispersal, outside of demographic input data and the dispersal categories included here. Things to explore for the future could

include ways to capture more heterogeneity in individual movement choices, and variation in the dispersal process.

The overall result that all of the assessed connectivity-resistance combinations perform well is encouraging in its implications for modelling corridors for conservation. It is also encouraging that the performance of connectivity models using resistance parameterised from home range data captures the observed dispersal movements well in this system — meaning that connectivity maps can be generated for multiple sites across the lions' range where these data already exist. For each new context, validation will still be a critical element of defensible connectivity maps, however given the range of species that this now has support for, the outlook is positive. Understanding how connectivity and dispersal varies across the gradient of environments where these wide-ranging animals exist will be important in understanding the population viability of this rapidly declining carnivore. Additionally, if resistance does not play a major role in determining the good fit of connectivity models, future work may be best placed focusing on how to best define source points and delineate thresholds for defining corridors, rather than on optimisation of resistance inputs. Conversely, if different estimates of resistance are found to be highly important when landscapes are highly fragmented and limiting (e.g., Cushman et al. 2011; Short Bull et al. 2011, Vergara et al. 2017) this suggests that accurate estimation of resistance surfaces is important, especially when landscapes are heterogeneous in ways that limit movement. That would, in turn, focus future work on quantifying when landscape features become limiting to movement (Short Bull *et al.*, 2011) and gene flow (Cushman, Landguth and Flather, 2013). Indeed, there is some evidence that this might be true for applied challenges such as predicting the locations wildlife will come into contact with

risky human features such as roads, with Cushman et al. (2014) finding that performance of connectivity predictions in this context was much more sensitive to resistance surface than connectivity method (in contrast to the results of this paper) in a highly heterogeneous and fragmented landscape.

Overall, the results provide important advances in understanding the performance of different connectivity modelling methods and the sensitivity of this performance to the resistance surfaces used. The results show that all connectivity modelling methods used, and all resistance surfaces employed performed quite well in predicting movements of an independent set of dispersing lions. This is highly encouraging. The results also suggest more attention be given to limiting factors, the relative importance of different resistance levels, and to evaluating a broader range of connectivity modelling methods (such as all-directional, dispersal limited modelling with methods like resistant kernels). Several studies have suggested that density, distribution, and dispersal ability of the study species dominates the effect of differential resistance on functional connectivity (e.g., Cushman et a. 2013b. Future work should therefore also evaluate the effects of different numbers and spacing of dispersal source points and different dispersal abilities on connectivity predictions. Finally, while this study benefits from using a large sample of independent movement data for a species of high conservation relevance, understanding the true performance of different modelling methods and data sources would benefit from employing a simulation approach that could more flexibly produce large sample sizes responding to known and controlled simulated processes (Cushman *et al.*, 2013), as has been instrumental in evaluating model performance in landscape genetics, for example (Landguth and Cushman, 2010; Shirk, Landguth and Cushman, 2018).

4

Sources of Bias in Modelling Movement & Space Use in African Lions

SYNOPSIS In the previous chapter I addressed the performance of a range of resistance inputs and connectivity algorithms in predicting the routes dispersing lions take when moving between resident ranges. In this chapter, I move to assess statistical frameworks for describing local space use and movement at the home range scale and below. To do this, I make use of a long-term movement dataset from lions in the Central Kalahari region of Botswana. I apply recent statistical advances in path segmentation and continuous-time stochastic process models to explore the impact of behavioural and structural features of the movement process—namely non-stationarity and autocorrelation—on estimates of home range area and distance travelled, as well as the ability of different statistical frameworks to capture observed patterns. The results of this chapter clearly demonstrate the utility of methods that explicitly model autocorrelation structure, such as continuous time movement models, in predicting future space use, and facilitating comparisons between and among populations. However, they also demonstrate the sensitivity of these types of models to non-stationary processes, a common feature in animal movement behaviour. Most efforts to date have focussed on how to discretise the data to meet the assumptions of stationarity imposed by current modelling frameworks. I suggest that there would be value in efforts that develop frameworks that can more flexibly model the

movement process and rather incorporate non-stationarity as a reality of how animals behave.

4.1 INTRODUCTION

There is much interest in modelling movement and space use of species both in studies of fundamental ecology and their application to the conservation sphere. Globally landscapes are rapidly changing in ways that restrict the movement of wild animal populations (Fahrig, 2007; Tucker *et al.*, 2018). As landscapes become increasingly human-dominated, it becomes ever more critical to understand how much space species require for long-term population persistence (Pe'er *et al.*, 2014). Additionally, as landscapes change, so might the distance animals have to roam to meet their energetic and reproductive needs. Energetic budgets play a large role in individuals' survival and recruitment rates, and therefore have direct links to population fitness. There is also evidence to support the proposition that human-modified landscapes alter the distances travelled (and rate at which these are covered) in African carnivores (Oriol-Cotterill *et al.*, 2015).

To effectively answer the questions prompted by this link between movements and conservation, it is a pre-requisite to quantify area and distance travelled accurately. Home range analyses are a commonly used tool to understand species' area requirements and provide a clear foundation for conservation actions, including recommendations on protected area size (Linnell *et al.*, 2001) and advocacy for land-tenure systems (Johansson *et al.*, 2016; Farhadinia *et al.*, 2018). Metrics related to mean-speed and distance can provide a quantifiable link between animal behaviour and energetics and daily distance has been used to, for example, make policy recommendations (Bartoń *et al.*, 2019). Quantifying variation in an animal's movement speed over time also provides important

insights into behavioural mechanisms and the link between animals' and their environment.

There has been a rapid proliferation of knowledge and methodologies in movement ecology over the past decade as a result of advances in tracking technology (Kays *et al.*, 2015). This has resulted in an unprecedent opportunity to explore how animals move through and interact with their landscapes, both environmental and social. However, with the increasing availability of finer-scale tracking data comes additional considerations in the methodological approaches used to analyse such data. Three major components of this include the continuous nature of the movement process, autocorrelation structure in the data, and non-stationarity in the movement process. Failing to account for these factors has been shown to produce biased estimates of animal space use and movement parameters (Noonan, Fleming, *et al.*, 2019; Noonan, Tucker, *et al.*, 2019; Fleming *et al.*, 2020; Noonan *et al.*, 2020). However, many commonly used metrics still rely on discrete binning of the movement process, the assumption of independent and identically distributed data (IID) or lack a clear diagnostic for stationarity (i.e., characterised by a specific mean and variance).

Many methods for home-range estimation (e.g., conventional kernel density estimation; KDE) assume IID (Fleming *et al.*, 2015). In contrast with this, there is often substantial autocorrelation present in tracking data. Autocorrelation in the data results in a discrepancy between the total number of data points and the information present in the data (i.e., effective sample size; Fleming and Calabrese, 2017). This has been shown to lead to underestimation in home range area when conventional KDE is used on autocorrelated data (Noonan, Tucker, *et al.*, 2019); a bias that scales to become greater for larger and more

mobile species (Noonan *et al.*, 2020). This bias is particularly critical when it comes to describing space requirements of threatened species as underestimation could result in failed conservation planning (Gaston *et al.*, 2008) or impact human-wildlife conflict at protected area boundaries.

Additionally, tracking data come in a wide range of formats, varying in locational precision and sampling schedule. Summing the straight-line distance (SLD) between discrete points is the typical way that distance travelled is quantified from tracking data. However, SLD methods are highly sensitive to the sampling schedule, movement tortuosity, locational error and have been shown to cause substantial bias in animal travel distance (Sennhenn-Reulen *et al.*, 2017; Noonan, Fleming, *et al.*, 2019). The advent of modelling movement as a continuous-time stochastic process (CTSP) has offered a solution to many of these limitations. Adoption of CTSPs has become increasingly feasible as user-friendly implementations, in statistical environments that ecologists are familiar with, have been developed (e.g. the R package *ctmm*; Calabrese, Fleming and Gurarie, 2016; Fleming and Calabrese, 2020).

Continuous-time implementations of the home range distribution (e.g., autocorrelated KDE; AKDE) and speed and distance estimation (CTSD) provide estimates that are scale-insensitive, robust to missing data, and can account for locational error and a wide range of autocorrelation structures in the data. The AKDE was developed as a generalisation of the KDE method to account for autocorrelation in tracking data (Fleming *et al.*, 2015; Fleming and Calabrese, 2017). CTSD uses a simulation-based approach to reconstruct paths, conditional on the observed data and a fitted movement model, to generate mean speed estimates sampled from the distribution of simulated trajectories. Both approaches

have the capability to account for locational error (Fleming *et al.*, 2020) and come fully equipped with confidence intervals. However, the accuracy of such methods will depend on how well the fitted model captures the structure present in the empirical data. Misspecification, both in terms of the error-model and the movement model selected, has been shown to result in inaccurate estimates, such as speed and distance (Noonan et al. 2020b).

The African lion (*Panthera leo*) is one of the largest terrestrial carnivores, is highly mobile, and exhibits home ranges in the order of thousands of square kilometres towards the arid extent of its range (Zehnder, Henley and Weibel, 2018). There has been substantial interest in describing home range size in lions over the years. However, to date as far as I am aware none of these studies has made use of recent advances in continuous-time approaches to modelling space use. Given the ecology of the species, it is highly likely that we could be substantially underestimating space use requirements for this vulnerable species. Additionally, lions exhibit substantial non-stationarity in their movement behaviour, which comprises active bouts of foraging and long periods of rest during the day. This has the potential to bias estimates of distance travelled if movement behaviour is averaged across these non-stationary periods.

In this chapter I use a continuous-time movement framework to address three main considerations in modelling space use of lions from GPS tracking data (1) the extent of autocorrelation structure in the data, (2) the impact of differential movement behaviour during resting and foraging periods, and (3) the impact of locational error (in a correctly specified movement model) on estimates of speed, distance, and home range size. My expectations are that:

- Movement models assuming no velocity or positional autocorrelation (IID; as assumed by conventional KDE methods and MCP) will perform worse in model selection criteria than those that account for velocity and/or positional autocorrelation
- Home-range area will be substantially larger and less biased for lions using methods that account for autocorrelation
- Speed and distances generated using the CTSD method will be larger than those found previously from SLD approaches
- Movement models that fail to account for non-stationarity in movement behaviour will produce biased estimates of speed and distance
- Error-driven bias will in general be small compared the biological scale of CTSD and home range sizes
- Error will play a much smaller role in the estimation of active speeds, where the magnitude of movement between relocations (in the scale of kilometres) is large in relation to device measurement error but will have a larger impact during resting periods where movements are likely to be small (in the scale of metres).

4.2 METHODS

4.2.1 Tracking Data

In this chapter I analyse tracking data generated by collar-mounted GPS satellite devices (hereafter GPS collars) fitted to 30 lions between April 2011 – September 2020 in Khutse and the southern Central Kalahari Game Reserves (CKGR), Botswana. The two reserves are contiguous, with no fenced boundary between them, and together form a protected area of approximately 55,000km^2. Three models of GPS collars from two common

commercial vendors in studies of large carnivores were deployed over the study period: Vertex Plus (n = 5) and GPS Plus (n = 19) from Vectronic Aerospace GmbH, and IR-Sat (n = 4) from Africa Wildlife Tracking. Some collars were deployed more than once, creating 61 unique collar-animal deployment combinations. Collar sampling rates varied from a minimum of 5 minutes to every 3 hours, with the vast majority of tracking data collected at an hourly rate. I accounted for variation in sampling rate between lions and within deployments of a single collar by, using a consistent single daily location for the range segmentation method (4.2.2), and via the use of implementations of the continuous-time movement models (4.2.3) that can account for irregularity in sampling regimes. All data represents high quality movement data in the context of estimating space use for large carnivores, and I evaluated the appropriateness of each time series for each methodology prior to inclusion in the analysis as described in the following sections.

GPS collars were deployed as part of a long-term monitoring project and the resulting time series vary in their duration, sampling rates, and the life history stages of the animals, providing a realistic sample of the kinds of data available to large carnivore movement ecologists and a variety of scenarios to explore bias in estimated quantities. Where different subsets of the data have been used to answer specific questions, this is noted in the relevant section below. Error-calibration data were collected for each model of collar either by leaving collars stationary in a fixed location or recovering periods of "opportunistic" calibration data from periods at the end of deployment where the animal was known to be stationary, e.g., as a result of a mortality event. These calibration data were used to estimate the devices' root mean square (RMS) user equivalent range error (UERE). RMS UERE is used as a device-specific proportionality constant to translate unit-

less dilution of precision (DOP) values into location error in metres (Fleming *et al.*, 2020) in an error-calibration process described in detail in Appendix C.1). After error calibration, I "cleaned" tracking data by screening for outliers in speed and core deviation (see Appendix C.2 for an example). All data were obtained under appropriate permits and based on Institutional Animal Care and Use Committee approved protocols (see Appendix A).

4.2.2 Range segmentation

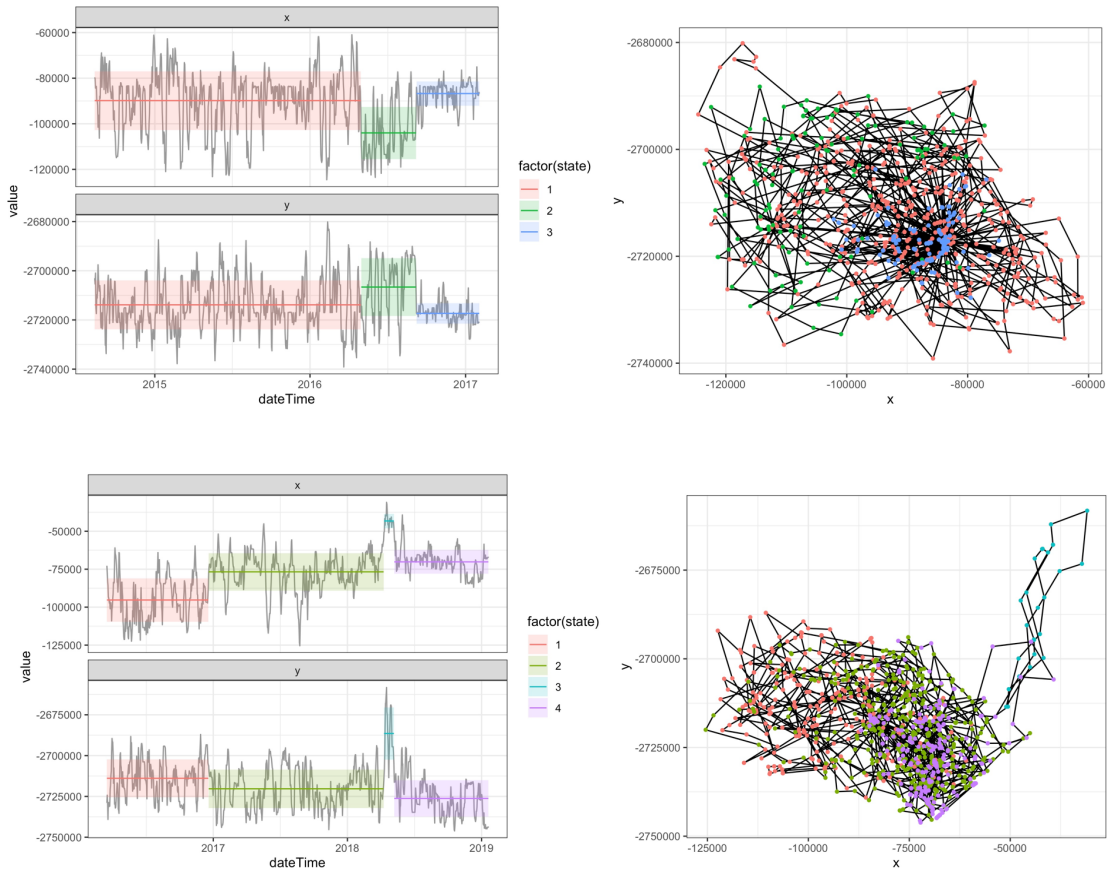
The Kalahari is a semi-arid, dynamic system, and even range-resident animals may shift their home range periodically (e.g. Valeix *et al.*, 2012) to track changes in their key resources (namely prey, and for males, females). Additionally, individuals might alternate between different movement strategies (e.g., range-resident, nomadic or dispersal) associated with different (transient or resident) ranges over their life history and in response to social perturbations. To avoid confounding large-scale changes in range with diurnal non-stationarity in movement behaviour, I used a segmentation method implemented in the R package *segclust2d* (Patin *et al.*, 2020) to identify the start and end point of range shifts characterised by a specific mean and variance in XY coordinates.

Before segmenting, I resampled the relocations to a single daily fix, retaining only the record closest to midday. Using a daily fix rate is common for identification of large-scale processes such as home range shifts, or transitions between movement strategies (e.g., Bastille-Rousseau *et al.*, 2015; Patin *et al.*, 2020) as it acts to reduce the noise caused by fine-scale movements. I ran the segmentation analysis with a minimum segment length of 14 days and the default maximum number of segments (75% of maximum value). Time series that were shorter than 29 days (i.e., the minimum segment length x 2) were excluded

from the analyses as they would be too short to identify a stationary period under the criteria set. I selected the minimum segment length to avoid classifying an area exploited only for a few days (such as might occur at a large kill site) as a distinct range, while still identifying periods where the animal exhibits atypical ranging behaviour (such as an extended foray outside the usual range). Such forays could bias home range estimation (which assumes the current movement behaviour will continue indefinitely into the future) and likely have an underlying movement process distinct from usual range-restricted behaviour. For a broadly transient individual, this might also identify periods of temporary residency. Figure 4.1 shows example outputs of this process.

The range segmentation produced time series that varied in their duration. When estimating home ranges, there is no single threshold for length of timeseries required for reliable estimation of area, as this inherently is dependent upon the size of the range and the time it takes an animal to cross it. This might vary between and within individuals, even within the same species. Thus, instead of setting an absolute criterion for minimum duration, or imposing a consistent length a priori, I rely on assessments of appropriateness of each dataset, based on effective sample size, as described in the following section (4.2.3).

Figure 4.1 *Output for two individuals from the range segmentation analysis. The segments identified are highlighted by different colours. The left column shows the mean (horizontal line) and variance (transparent band) for each segment. The right column shows the daily XY locations, also coloured by segment. The top row shows an example where the female dispersed from her natal range (in red) to an overlapping range (in green), followed by an instance of irruptive nomadism (blue), where two periods of residency were punctuated with a long-distance movement unrelated to season or life-stage (Teitelbaum and Mueller, 2019). The bottom row demonstrates first a shift in mean (from red to green), followed by a range contraction (shift in variance rather than mean location; green to blue). Given the timing of the shift, this was likely associated with the start of rainy season and aggregation of prey at a waterhole near the centre of the range. Figure shown on following page.*



4.2.3 *Bias in Movement and Space Use*

To explore possible sources of bias in modelling animal space use and movement, I fit a range of continuous-time movement models (CTMMs) under different assumptions of autocorrelation structure and error specifications. I then fed these into downstream analyses to assess their impact on point estimates of two common metrics, home-range area and daily distance travelled. CTMMs treat animal tracking data as a continuous-time stochastic process (CTSP). CTSPs confer the benefit of separating the continuous-time movement process from the discrete-time sampling process, are robust to irregular sampling, and can account for a wide range of autocorrelation structures (Calabrese, Fleming and Gurarie, 2016), making them ideal for this purpose. I implemented all

analyses, unless stated otherwise, in the R package *ctmm* (Calabrese, Fleming and Gurarie, 2016; Fleming and Calabrese, 2020).

Non-stationarity in the movement process

Lions are predominantly active during the night and dawn/dusk times, while remaining at rest for most of the daytime hours. To delineate night and day sections of the data, I used the function *annotate* to calculate the sine of the sun's altitude for each relocation, which is proportional to solar flux during the daylight hours (Fleming and Calabrese, 2020). I then labelled all times where this value was equal to, or greater than, 0.6 as "day" and the rest as "night." This corresponds to approximately the hours of 10 am – 4 pm; 4 pm – 10 am, although it varies with time of the year. For simplicity throughout the chapter, I refer to these periods as day and night, but in practise by night, I mean the period where lions are more active/foraging, and by day, I refer to the period lions are mostly at rest. While I acknowledge there may be other periods, unrelated to time of day where lions exhibit long periods of rest or limited movement, for example after a large kill or while mating, this represented a simple way to account for a significant component of non-stationarity in lion movement behaviour.

To explore non-stationarity in the underlying movement process, I first estimated the autocorrelation structure in each segment of tracking data for the full dataset, then for night and day relocations separately (hereafter average, night, and day models, respectively). To achieve this, I fit a series of range-resident continuous time movement models (CTMMs) to each subset of the data then used model selection to identify the best model fit, given the data (Fleming *et al.*, 2014b) following the workflow described by Calabrese et al. (2016). Although CTMM is capable of fitting endlessly diffusing models

(without range residency), I opted to fit range-resident models for two reasons. Firstly, the AIC values for range resident and endlessly diffusing models cannot easily be compared (Fleming and Calabrese, 2020) so at present selection between the two would rely on visual comparison of the fit of the top model against the empirical variogram. Second, the fit of the model at short lags (critical for speed and distance estimation) should not be impacted by an assumption of range-restriction, and where this is important, i.e., home range analyses, I set criteria based on visual diagnostics of the variogram to limit analyses to range-resident individuals anyway (discussed further below).

All models were fitted using correctly specified HDOP-informed error models (as selected in Appendix C.2). Once I had selected the top models for active, resting, and the average model, I examined the impact of non-stationarity in the autocorrelation structure of the data in several ways related to home range area and speed and distance estimation described below in section *Impact of downstream analyses*.

Locational Error

To explore the impact of accounting for error when modelling movement and space use in African lions, I re-ran the model selection process under five scenarios: (1) Calibrated error model (as above); (2) Assuming homoscedastic errors; (3) Assigning a plausible RMS UERE (10m); (4) Homoscedastic errors with a plausible RMS UERE (10m); (5) No error model.

Understanding the sensitivity of movement parameters, the range distribution, and CTSD estimates under the above scenarios will help in making informed decisions when a dataset has no DOP values (2), no calibration data exists (3), or neither are available (4 & 5). As the archiving and best practise guidelines improve, ecologists should be faced with

these scenarios less and less frequently. However, it is still useful guidance to be able to use older datasets where any of these (or all) limitations may apply. Additionally, it can be reasonable and practical to ignore error in studies where the movement between fixes is much larger than the scales of error (Fleming *et al.*, 2020). Testing the impact of error in individuals where I have the highest level of error information available allows us to better understand how critical locational error is in modelling the movement of African lions. Additionally, the collars I use here (Vectronic Aerospace GmbH and African Wildlife Tracking) are commonly used brands in large wide-ranging carnivores, and thus the findings will be of relevance to other studies.

Impact on downstream analyses

Before inclusion in downstream analyses, I set certain criteria for each segment to ensure data were appropriate and of sufficient quality. For home-range analyses, I only proceeded with segments that showed a clear asymptote in their variogram and had DOF (effective sample size) for area of >5. Effective sample size for area of a given movement dataset is based on the number of observed range crossings, rather than the number of sampled locations (Fleming *et al.*, 2019). The animals that fulfilled these criteria are here after referred to as the range-resident subset.

Variograms provide a way to visualise the autocorrelation structure in tracking data by presenting the semi-variance as a function of increasing time lags (Fleming *et al.*, 2014a). At long lags, clear asymptotes area diagnostic of range-residency, whereas at short lags, increasing upward curvature suggests autocorrelation in velocity (i.e., on average how long the animal moves in the same direction at the same speed). The asymptote in a variogram of a range-resident individual is proportional to home range size; if a time series

fails to show a clear asymptote with increasing time lags, this indicates either the time series is too short to reveal the home range extent, or that there is non-stationarity in the mean process (Calabrese, Fleming and Gurarie, 2016). These criteria therefore ensure that the segments represent appropriate data for home range analysis, with enough home range crossings to derive produce area estimates of reasonable precision to explore the impact of autocorrelation-induced bias.

For home-range estimation, I applied an error-informed autocorrelated kernel density estimator (AKDE) with weights to mitigate for irregular sampling as some collars changed sampling schedule during deployment (Fleming *et al.*, 2015, 2017, 2018). The method accounts for error by teasing apart variance due to movement and error, and the data are first Kriged to reduce location error before placing the kernels (Fleming et al., 2016, 2017). Autocorrelation is handled via a generalisation of the Gaussian reference function KDE, where autocorrelation is structure is first estimated, then conditioned upon when optimising the bandwidth (Fleming *et al.*, 2015).

To assess autocorrelation-induced bias in home-range area estimates, I used block cross-validation of the point estimates for area from AKDE and conventional KDE (cKDE) range distributions assuming that the data were sampled from an IID process, as in Noonan *et al.* (2019). Home-range estimators extrapolate space use into the future, based on the current focal movement process. It therefore follows that an unbiased estimate generated at the 95% area over a given time period should contain 95% of the locations from a subsequent time period, given a consistent movement behaviour and minimal autocorrelation between cross-validation blocks. I used the first 50% of an individual's locations for the first time period (T1) and the second 50% for the subsequent time period

(T2). Inclusion of consistently higher than 95% of subsequent locations would indicate positive bias, and vice versa for negative bias.

Although the range segmentation was aimed at ensuring each segment was piecewise stationary in locational mean, it is possible some changes in movement behaviour remained undetected. Therefore, following recommendations from Noonan *et al*. (2019) I used the Battacharryya distance (BD, Battachaaryya, 1946; Winner *et al.*, 2018) to test whether the mean and covariance parameters of the fitted models' distributions from T1 and T2 differed significantly. BD acts as a measure of dissimilarity (ranging from 0 – Inf) between the gaussian distributions corresponding to the two fitted movement models; where the CIs on this distance contained zero the two distributions were assumed not to differ significantly. This ensured that any cross-validation failure is related to bias in the point estimate, rather than unmodelled changes in movement behaviour.

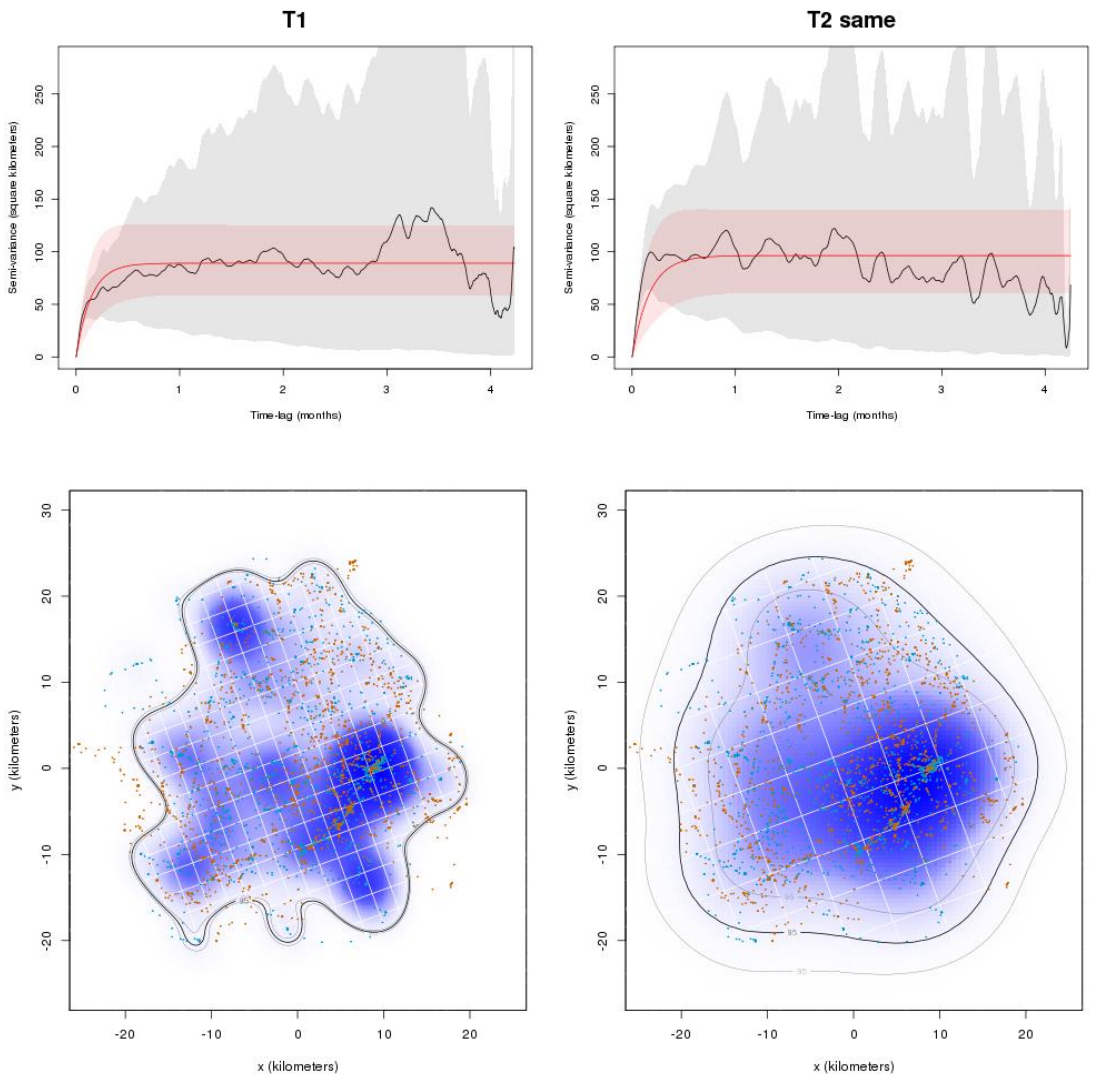


Figure 4.2 *Representation of the cross-validation procedure for a single individual. The top row depicts the selected fitted movement models for T1 and T2 plotted over the empirical variogram. Note the similarity in the height of the asymptote (σ; 89 km² and 96 km², respectively). The lower 95% confidence interval (CI) of the Battacharryya distance estimate contained 0 (estimate [95% lower – upper CIs] = 0.0005 [0 – 0.002]). The Euclidean distance between the mean location (in square kilometres) of the two distributions is also very close (0.14 [0 – 19.36]). This individual was therefore included in the block cross validation. The bottom row shows home range distributions (in blue) generated from first half of the dataset (KDE on the left, AKDE on the right). The black line delineates the estimated 95% home range area (95% CIs around this shown in grey). Locations from T1 are plotted in blue, with those from T2 in orange.*

The block cross-validation provides four response variables (proportion of points in 95% AKDE and KDE, and 50% AKDE and KDE) which I fed into a beta regression model, implemented via the R package *glmmTMB* (Brooks *et al.*, 2017). I selected a beta family (with logit link) for the distribution as proportion of points is bounded 0 – 1. The proportion of points in 95% AKDE contained three values of exactly 1, therefore I rescaled using the formula (y(n-1) + 0.5) / n to bound [0,1]. I fit the effective sample size as a fixed effect, and after inspection of model residuals as term in the dispersion model to account for heteroskedasticity. I explored fitting a random intercept to account for multiple segments from the same individual, but the variance components 'estimated' were small, leading to convergence issues, thus I proceeded with fixed effects only. Model residuals were interrogated using the R package *DHARMa* (Hartig, 2020). This allowed us to extract the mean proportion of points captured per approach for core (50%) and 95% area and test for a relationship with effective sample size, which is expected from Noonan et al. (2019).

For home range area estimation, the most important features to capture for a CTMM are the height of the asymptote (σ) and the home range crossing timescale (τp). Therefore, for home-range analyses, I did not expect diurnal non-stationarity in activity to have a substantial impact on the area estimates. However, to test the assumption that night and day datasets were generated from the same process I used the same logic described above for the cross-validation blocks, using the BD as a measure of similarity between the mean area and covariance parameters of the night, day, and average CTMM fits.

For speed and distance estimation I used a continuous-time speed and distance estimator (CTSD) that accounts for both location error and tortuosity (Noonan, Fleming,

et al., 2019). The key parameter to derive reliably for CTSD is the timescale for velocity autocorrelation (τv). This can be interpreted as the time, on average, that an animal moves at the same speed, in the same direction, and is akin to tortuosity in a discrete framework. If the data are too coarse to retain any signature of the animal's velocity (typically when the sampling interval is $> 3\tau v$), a correlated velocity model (CVM) will not be selected. I excluded these segments from CTSD analyses, as the data contains insufficient information for accurate speed and/or distance estimation of any kind (Noonan, Fleming, *et al.*, 2019).

To assess the impact of diurnal non-stationarity on CTSD, I estimated the mean speed (in km/day – effectively daily distance) for each segment using day, night, and average models. I compared mean speed for night periods conditioned on the night CTMM to night speeds conditioned on the average model, and the same for day periods using the day and average CTMMs.

4.3 RESULTS

4.3.1 Extent of Autocorrelation Structure and Diurnal Non-Stationarity in Tracking Data

For all segments of tracking data, and all periods of time, models assuming independently and identically distributed (IID) data performed significantly worse at describing the observed movement processes (differences in AICc between selected CTMM and IID models ranged from 1652 – 196,434, 319 – 75,635, 982 – 120,115, for average, day, and night models, respectively; see Figure 4.3 for example).

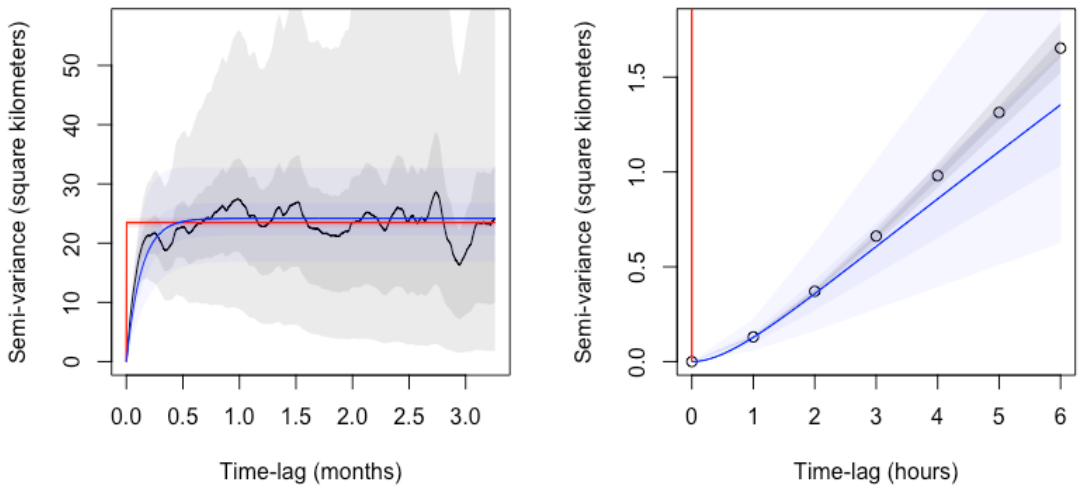


Figure 4.3 Comparison of fitted IID and top selected CTMM (in this case OUF) for the average model of a single individual. For both panels, the empirical variogram is shown in black (with 50 and 95% CIs in grey shading) and IID and OUF model fits (plus 50 and 95% CIs) are plotted in red and blue. The left panel shows the behaviour of the SVF at intermediate to long lags, while the right panel shows the fine-scale behaviour. At short time lags, the IID model fails to capture the velocity autocorrelation indicated by the upwards curvature (τv estimated as 38 minutes [36 – 41] in this example); at intermediate lags there is discrepancy as a result of positional autocorrelation, that gradually "dies off" over some time period (τp estimated as 3.9 days [2.6 – 5.8]). Taken as a whole, the IDD model resulted in an AICc value 33,113 higher than the selected movement model that captures these features.

All segments across all time periods selected a correlated velocity model (CVM), bar a single night segment, where the data were at a 3-hour sampling schedule. Point estimates of the velocity autocorrelation timescale (τv) from the average models ranged from 20 – 120 minutes. This can be interpreted as, on average, the period that the animal moves in the same direction at the same speed. The range for night-only positions (15 – 93 minutes), was similar to the average models, whereas τv ranged from and 11 minutes – 39 hours for day positions (Figure 4.4).

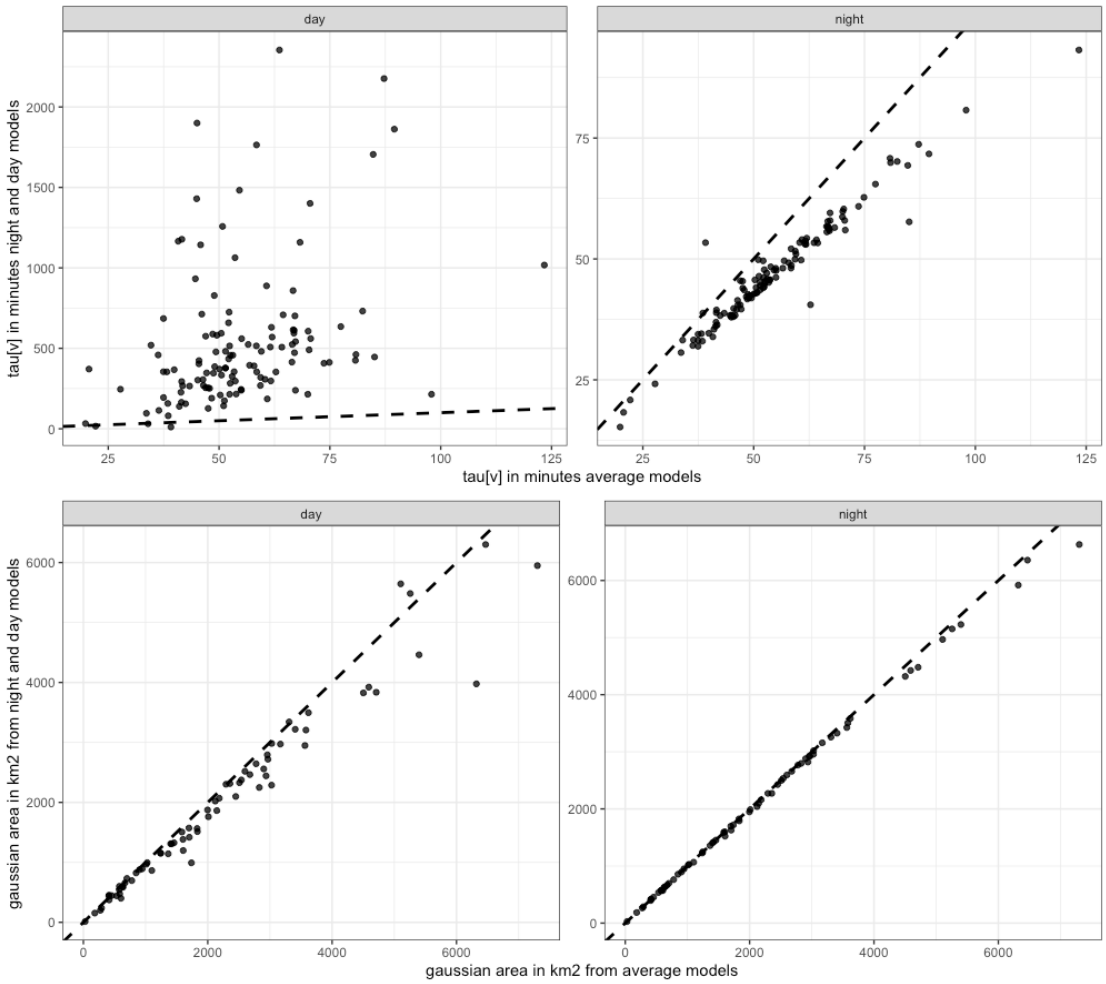


Figure 4.4 Point estimates for velocity autocorrelation and gaussian area parameters from continuous-time models based on day and night only positions as a function of average model point estimates. The dashed line represents a one to one ratio.

For the range-resident subset of the data (n=73) in all cases, models with positional autocorrelation (τp)– or home-range crossing timescale – were selected. The home-range crossing timescale can be thought of as the time it takes for positional autocorrelation to die off and for locations to become independent. Point estimates for τp were similar between models based on the full dataset, and night/day subsets, but exhibited a wide range between segments from just under a day to over a month (average model: mean = 7.38 days, range = (0.79 – 41), night: 8.04 (0.55 – 33), day: 4.96 (0.65 – 32).

Similarity in home-range behaviour between average and night- day-segmented models were echoed by the results from the Battacharryya distance (BD) measures, where 100% of the lower confidence intervals for the night-average comparison contained 0, and 58% of the day-average. For the remaining 42% all BD point estimates were below 0.06, and the Euclidean square distances between the distributions' mean locations were all below 5 square metres. Although I did not run kernel density estimates for night- and day segmented models, the gaussian area point estimates from the fitted CTMMs (shown in Figure 4.4) show high levels of convergence between day, night, and average models.

4.3.2 Home-Range Area Estimates

All the cross-validation models supported a term for effective sample size (N_{eff}) in the dispersion model, based on AIC criteria and likelihood ratio tests (LRT; listed in Appendix C.3). N_{eff} had a significant positive effect on predicted bias (Table 4.1; Figure 4.5), measured as proportion of points from T2 captured by the T1 home range in models based on the 95% and 50% KDE (KDE_{95}; KDE_{50}). In contrast, N_{eff} was not a significant predictor of bias in either AKDE model ($AKDE_{95}$; $AKDE_{50}$). While $AKDE_{95}$ and $AKDE_{50}$ produced predicted values of 94% and 55%, KDE_{95} and KDE_{50} predicted values varied with sample size, giving values as low as 73% and 33% at small sample sizes (Figure 4.5).

Model	Parameter	Conditional model			Dispersion model		
		Est	SE	Δ AIC	Est	SE	Δ AIC
$AKDE_{95}$	Intercept	2.53	0.12		2.24	0.43	
	N_{eff}				0.03	0.01	5.6
$AKDE_{50}$	Intercept	0.18	0.09		0.76	0.44	
	N_{eff}				0.04	0.01	6.6
KDE_{95}	Intercept	0.66	0.21		1.41	0.45	
	N_{eff}	0.02	0.004	6.12	0.04	0.01	3.8
KDE_{50}	Intercept	-0.86	0.17		1.15	0.45	
	N_{eff}	0.01	0.002	9.96	0.05	0.01	7

Table 4.1 Model outputs from beta regression of proportion of points in T2 captured by home-ranges from T1 as a function of effective sample size (N_{eff}). Δ AIC denotes the difference in AIC when model term is omitted.

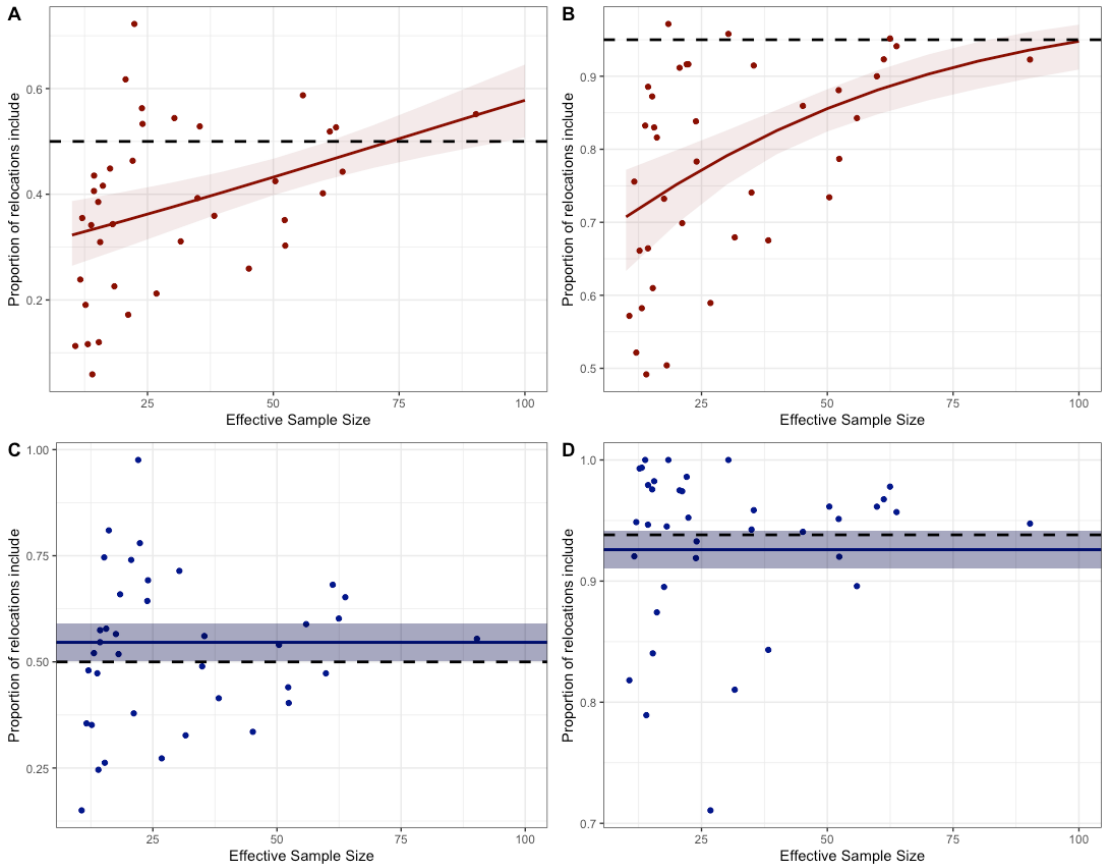


Figure 4.5 Scatterplots depicting the proportion of locations from the second half of the data included in 95% an 50% home ranges estimated from the first half of the data, as a function of effective sample size for KDE (A & B) and AKDE (C & D) approaches. Solid lines represent predicted values from beta regression models (+/- 95% CIs). The dashed lines represent the values at which these estimates should cross-validate – the line in panel D is adjusted from 0.95 to match the scaling of the input variable for $AKDE_{95}$ described in the methods.

Home range area 95% point estimates were, on average, 707 km² larger when estimated using AKDE compared the KDE under the IID assumption (means of 2058 and 1320 km², respectively, extracted from a linear mixed model accounting for repeated samples from individuals presented in Appendix C.3). This difference became increasingly pronounced as data quality (i.e. effective sample size) decreased – at the lower end of the spectrum KDE produced estimates of approximately half that of those produced by AKDE

(Figure 4.6, panel A). Additionally, while the magnitude of the confidence intervals in relation to the point estimates grew smaller with effective sample size for AKDE – as one would expect with increasing information – the relationship for KDE was much less convincing (Figure 4.6, panel B).

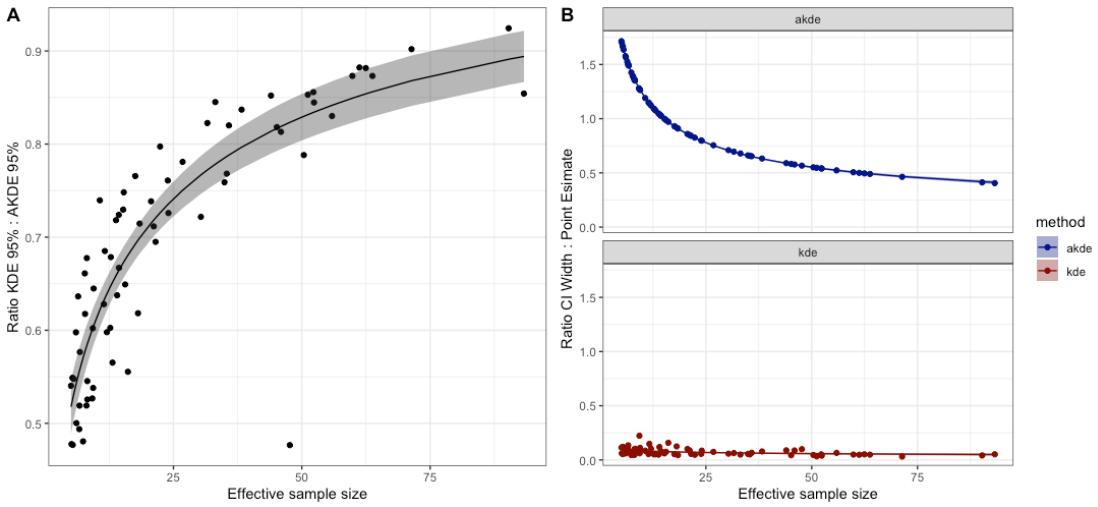


Figure 4.6 Scatterplots depicting the relationships between (A) the ratio of 95% KDE area : 95% AKDE area, and (B) the ratio of the width of confidence intervals : area estimate for the two methods. Solid lines represent predicted values from the non-linear models (see Appendix 5.4), with 95% confidence intervals around these.

Differences between home-range area point estimates from the fully calibrated error model (scenario 1) and the other error specifications for each home range segment were in general very low, with a mean absolute difference across all four scenarios that represented < 0.2 % change. For scenarios that assumed homoscedastic errors, either using calibration data (2) or a plausible RMS UERE of 10 m (4) the maximum absolute difference was < 3 km^2 (or 0.08% change). For scenarios that either ignored error (5) or used a plausible RMS UERE of 10 m with heteroscedastic error based on dilution of precision (DOP) values (3), all but four segments changed < 1%. Four segments experienced larger differences in the range of 30 km^2 - 100 km^2 but these differences were still substantially

smaller than the width of the confidence intervals around the original point estimates for these segments, which were of the magnitude of between 561 km^2 - 2327 km^2.

4.3.3 Speed and Distance Analyses

Mean speeds during the day and night were clearly sensitive to the models and input data they were based on (Figure 4.7, panels A & B). Mean speeds estimated for movement during the day using models conditioned on daytime tracking data were an average of 6 km/day slower than those estimated over the same dataset using the average models ($t = -19.73$, $p = <2e^{-16}$). Mean speeds from the night models were on average only 2 km/day faster than those from the average model ($t = 3.45$, $p = 0.00066$). For night speeds, the difference was more pronounced the smaller the value for τv, i.e. for more tortuous movements (Figure 4.7, panel C). For day speeds, the difference initially increased with τv before decreasing again for models that estimated long periods of consistent velocity at time lags of > 500 minutes/8 hours (Figure 4.7, panel D).

Average differences in mean speed estimates between the fully calibrated error model and the other error scenarios was small (0.0003, 0.007, 0.0005, and 0.02 km/h for scenarios 2, 3, 4, and 5). The largest of these is smaller than the mean confidence interval (CI) width (0.04) for daytime speeds under error scenario 1. Figures for night speeds error models were similarly small (0.0008, 0.006, 0.0004, 0.009 km/hr for scenarios 2, 3, 4, and 5) compared to a mean CI width of 0.06 km/hr.

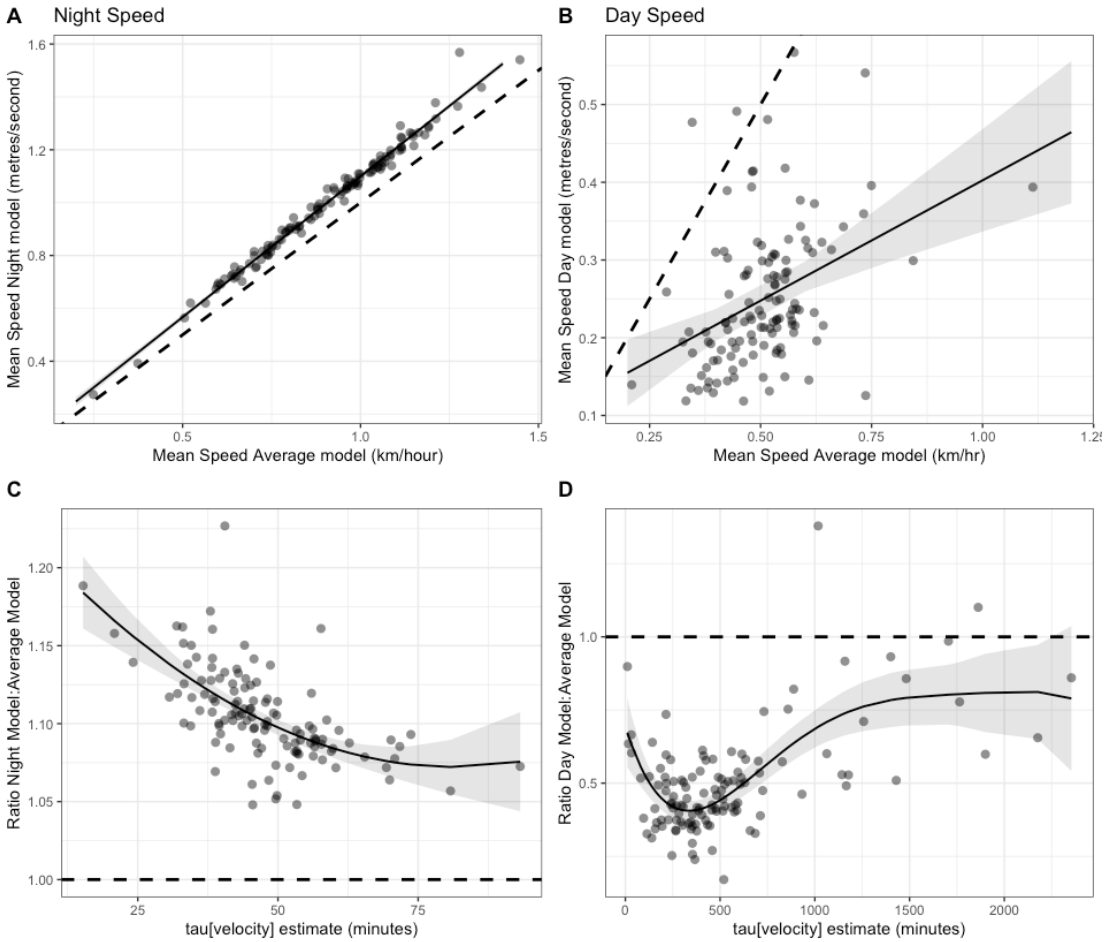


Figure 4.7 Scatterplots showing mean speed (km/h) during the night (A) and day (B) models as a function of the mean speeds from the average models. The solid lines represent fitted slopes (with confidence intervals) from a linear regression and have a value of 1.06 and 0.31, respectively. Panels (C) and (D) demonstrate how the extent of the difference varies with the autocorrelation timescale estimated from the day/night segmented models. Solid lines are fitted values (with confidence intervals) from a linear regression with polynomials of order 2 and 4, respectively. Dashed lines represent the values you would expect if speeds from the segmented models were equal to those from the average models.

4.4 DISCUSSION

Lions exhibited substantial positional and velocity autocorrelation in their movement behaviour. Estimates for the characteristic timescale of velocity autocorrelation (τv) were generally in the range of minutes to hours, whereas the home range crossing timescale (τp) ranged from days to months. This was reflected in the wholesale rejection of movement models assuming independently and identically distributed (IID) data based on

information criteria, supporting my first expectation that models allowing for the estimation of autocorrelation structure will provide a better fit given the observed movement process. The sampling schedules in the datasets ranged from hourly – 3 hourly fixes and are a good reflection of the frequency of sampling common in modern tracking data on large carnivores.

As a results of its persistence in time, τp has been indicated as a key parameter in home range estimation (Fleming and Calabrese, 2017) and represents the timescale over which autocorrelation in position decays; historically the point at which τp decays beyond statistical significance has been referred to as the time to independence (Swihart and Slade, 1985; Worton, 1989; DE Solla, Bonduriansky and Brooks, 1999). In this way τp can be thought of as approximately the time lag or sampling interval at which data would meet the IID assumption. The results from this study indicate that, first, it would be hard to determine a priori what an appropriate sampling interval might be, given the variation in the range of τp estimates, and second, that for many individuals data would need to be thinned to an infeasible degree to meet the assumptions of IID models. Although some studies have a labelled autocorrelation as a red herring (Fieberg, 2007; Kie *et al.*, 2010), these were carried out on datasets where the extent of autocorrelation present in the data were low compared to modern tracking data (Noonan, Tucker, *et al.*, 2019).

Although lions exhibit high levels of positional autocorrelation, rather than being an obstacle to home range analyses, harnessing this autocorrelation using continuous-time movement models (CTMM) and autocorrelated kernel density estimator (AKDE) allowed for less biased predictions of future space use compared to conventional KDE with a Gaussian reference function bandwidth optimizer (cKDE). As expected, home-range areas

from AKDE were also substantially—and consistently—larger than cKDE, indicating that results from studies prior to the availability of these methods have likely underestimated space requirements for lions. For very long-term datasets, where the duration becomes much larger than τp, the results of this study support previous findings that AKDE and cKDE estimates will converge –however, the longer the duration time the more likely it is for the movement process to become non-stationary and thus the number of appropriate datasets of sufficient length for robust cKDE home-ranges may quickly become quite restricted.

Additionally, τp is linked to the effective sample size of a dataset for area estimation, with datasets with durations much larger than τp having larger degrees of freedom related to increased independent information on the current ranging pattern. At the upper end of the scale for Kalahari lions this would require a minimum of four – five months of data to capture enough home range crossings to achieve five degrees of freedom (DOF) for area. Therefore, even though, for example monthly home ranges biologically might exist, statistically there is insufficient information to accurately estimate these. Where a monthly home range is estimated, using methods such as those implemented via the *cttm* package will at least ensure that information around the uncertainty around parameter estimation is produced and is reflective of the effective sample size of the dataset.

If the interest is in space use variation at a smaller temporal scale, then other methods, such as resource selection in a point, step, or path framework (e.g., Cushman and Lewis, 2010; Elliot *et al.*, 2014; Zeller *et al.*, 2016) might prove more fruitful and less likely to produce spurious inferences. These methods rather than asking how much space an animal requires (i.e., the home-range concept), rely on being able to answer where the

animal was, over the sampling period. This can equally be modelled in a continuous-time framework as the occurrence distribution (Fleming *et al.*, 2016) providing a probability distribution function corresponding to our understanding of where the animal was located over the sampling period, given the data, the movement model, and optionally a location error model (Fleming *et al.*, 2016, 2020). This can be easily combined via raster multiplication with information on corresponding habitat, environmental and landscape features to obtain covariates describing "used" resources. This provides a natural extension to current path-level analyses, and may alleviate some of the issues related to sensitivity of sampled covariates to sampling schedule (e.g. Zeller *et al.*, 2014) as well as accounting for autocorrelation in tracking data time series, which can be extensive but can also provide key information on the underlying movement process that would be lost by thinning the data (Cushman, Chase and Griffin, 2005, 2010; Elliot, Cushman, Loveridge, *et al.*, 2014). Indeed, examination of the signature of autocorrelation structure present in the data—and certainty around where the animal was located—could provide key criteria to allow an informed decision of whether to use , for example, point, or path analyses, at what temporal scale to define a path, and how you can interpret your inference of what resources are "used" or "available."

τv can be thought of as, on average, the time period over which an animal moves in the same direction, at the same speed, and is related to the discrete metric of tortuosity, with trajectories with high τv being more tortuous and vice versa. There was variation in τv, both between individual datasets, and between night and day periods. As a general rule, tracking datasets retain signature of τv when the sampling schedule is $< 3\ \tau$v (Noonan, Fleming, *et al.*, 2019). For the night periods, where lions are generally more active, the

values obtained for τv suggest that a minimum sampling schedule of an hourly fix, or below, would be needed to ensure this criterion was met for all individuals. This is exemplified in one of the segments at a 3-hourly sampling schedule where a correlated velocity model was no longer selected for the night period. Increasing the sampling frequency of GPS tracking datasets comes at a cost of decreasing collar battery lifetime and thus the total duration of the dataset (important for home-range analyses to obtain enough home range crossings). The balance in determining which of these is most important will depend on the intended biological question at hand, although technological advances in collar battery life increasingly make this trade-off moot.

The variation observed between τv from the segmented night/day models, translated into differences between mean speeds estimated using a model that averages over these differences and the segmented models. In this case, I did not have an absolute "truth" of the mean-speed/distance travelled over the datasets to use as a reference point, but at the very least it demonstrates that τv from CTMMs, and thus CTSD, estimates are highly sensitive, in a consistent way, to non-stationarity in the movement behaviour, particularly when animals exhibit long periods of rest. In this way, the data support the suggestion that failure to account for non-stationarity can have implications and introduce bias into CTSD estimates. In addition to the mean-speed over the sampling period, it is also possible to generate instantaneous speeds using the *ctmm* package (see Noonan, Fleming, *et al.*, 2019 for how these are derived). By averaging these over the hours of the day, it is possible to examine where major differences arise (Figure 4.8).

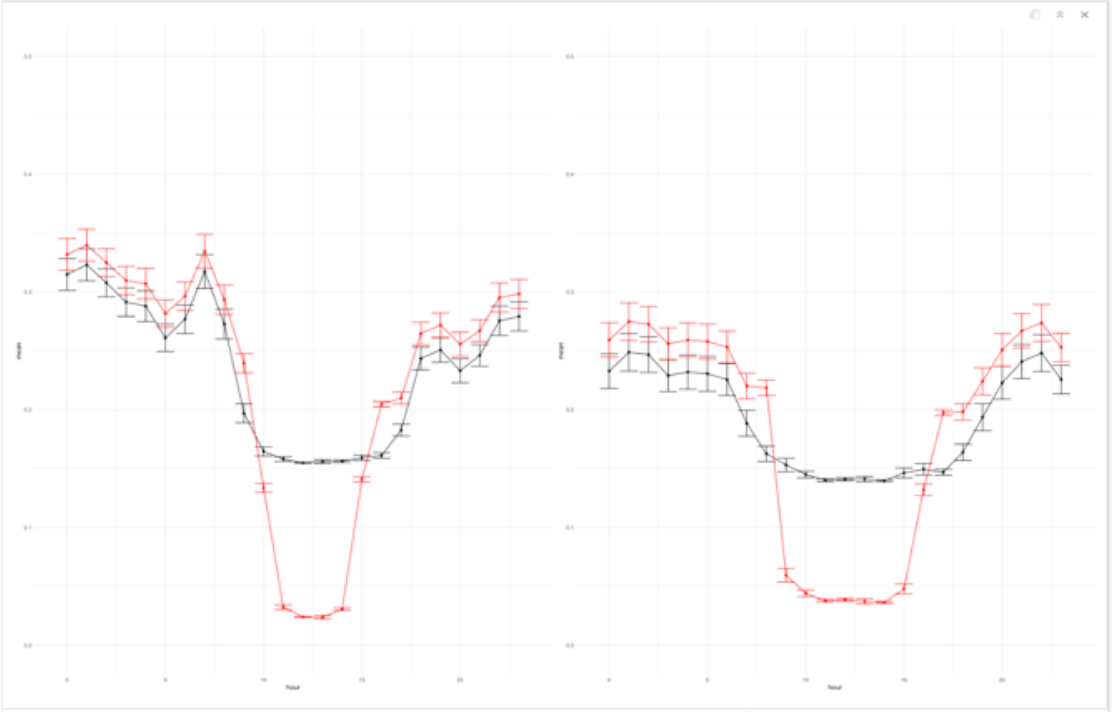


Figure 4.8 Instantaneous speeds point estimates, averaged over each clock hour, for two datasets. The red lines represent values merged from night/day segmented models, with values from the average model shown in black. While night speeds are on average slightly higher from the segmented model, the difference in day speeds is more dramatic. These values highlight how identical movement datasets can produce different values dependent upon identification of a correctly specified movement model. Additionally, the period of the day over which lions are active may vary from individual to individual, meaning bias may not even be consistent within a given study.

Although the way I segmented the data was fairly crude, given the ecology of lions, at least for the daytime period, this is likely to represent a fairly considerable proportion of non-stationarity in τv. Future studies could extend this to use path segmentation methods (Edelhoff, Signer and Balkenhol, 2016) to more sensitively separate out periods of foraging and rest and examine the impact of this in a more fine-tuned manner. Additionally, reference points for known speed and distance travelled could be obtained. This could be achieved either by direct follows of animal tracks, by setting a high frequency sampling schedule, such that the straight-line distance between points will approximate true distance (although in this case, a good handle on locational error is likely necessary), or perhaps

most simply by simulating paths of known length, based on values from empirical lion tracks that emulate biologically informed foraging and resting behaviour. Estimates obtained from the day and night models in this study for mean-speed over the sampling period would translate to approximately a mean travel distance of 18.6 km/day (16.9 over the night period of approx. 17 hours by my definition, and 1.7 over the 7-hour day period). These are nearly double that reported from the same system using summed straight-line distances (Büttner, 2019: 9-10 km/day) – and are much closer to values obtained from lions using direct follows (Stander, 1998: 19 km/day). Given the greater congruence between these values, it seems likely that CTSD estimates are a more realistic representation of the travel distance than those based on straight-line distances, which rather represent a minimum, and one that has been shown to be biased by both tortuosity and sampling schedule. Across all my down-stream analyses, models were relatively insensitive to locational error, at least in terms of the biological impact of differences, and the magnitude compared to the width of the confidence intervals around the point estimates for area and mean-speed. At the hourly scale therefore, it is unlikely that error-driven bias will be much of a concern for lions.

There are many reasons that synthesising existing datasets is a valuable exercise, for example, to ask questions at a larger geographic scale than is possible from a single study site and understand the variation and plasticity in movement behaviour present in lions. The methodological advances that CTMMs provide, creates a good framework for achieving this—additionally the fact that estimates from AKDE and CTSD analyses come equipped with appropriate confidence intervals would suggest that these might be particularly good candidates to analyse in a meta-analysis framework, where uncertainty

around the response variable can be accounted for. Although I did not directly test for this, CTSD estimates have been shown to be robust to different sampling schedules (Noonan, Fleming, *et al.*, 2019). This confers an additional benefit over using straight-line distances, facilitating easy comparison across study sites and over time, given the caveat of the minimum data quality needed to derive τv.

Overall, this chapter demonstrates the utility of modelling movement for wide-ranging carnivores in a continuous-time framework, as well as some of the concerns about the continuation of modelling various space use metrics under the assumptions of IID data or stationarity without first assessing the extent of this, and impact on downstream analysis. Although I use lions as a case study, the findings regarding home range area estimation are likely to be equally applicable to other large, wide-ranging carnivores, such as leopards or wild dogs. The study is based in the semi-arid Kalahari, where movement is known to be at the extreme of what is observed for lions across their range, except perhaps the Namibian desert populations. It is therefore likely that differences between AKDE and conventional KDE methods will be more apparent here than in systems with smaller home ranges, where many range crossings can be observed over a shorter sampling duration. However, with global change, and predicted differences in the environments animals will be exposed to, it is particularly important to understand species area requirements across this range of environments they can persist in, to adequately manage space for future populations. Additionally, non-stationarity in behaviour is a feature common not just in lions, or large carnivores, but across animal species, who often show distinct diurnal patterns. The results here suggest that care should be taken when modelling space use to account for this, rather than averaging across distinct processes. Here I focus on ensuring

that the data and methods are appropriate to generate robust estimates of a stationary home-range process, however, it is worth noting that non-stationary in both the mean and variance of positions was a major feature across many of the individuals in this study across all life stages, and likely represents a biological reality of life in semi-arid systems. There is a rising interest in viewing movement strategies as part of a continuum, rather than segmenting the data into discrete stationary phases, applying this to the concept of the home range is an aspect for future research that I feel would be particularly relevant in this system.

5

Lions exhibit water-dependent thermal performance when moving through a semi-arid savannah

SYNOPSIS The global climate is changing. To best understand how species will be impacted by these changes, we need a clear theoretical and empirical underpinning to link species performance and the climatic environment they experience. A common approach to this is the use of thermal performance curves (TPCs) to describe how fitness-related performance measures vary across a range of thermal values. Thermal traits, assumed to mediate organismal responses to changing environments, can be derived from these curves and have been used to predict how species will respond to emerging environments. To date empirical studies on thermal tolerance using this approach are heavily biased towards ectothermic organisms and data collected under laboratory conditions. In this chapter, I construct TPCs based on hourly movement rate to describe thermotolerance in locomotory performance for free-ranging African lions in the Central Kalahari region, Botswana. I assess how locomotory performance in response to temperature varies between sexes and under different surface water availability conditions. There are clear differences in TPCs between sexes, and during periods of restricted water availability, with lions exhibiting maximum locomotory performance at higher temperatures when surface water is widely available. Males had a higher maximum rate of performance than females, with the top 20% of performance values operating over a narrower range of temperatures. This difference was particularly distinct during peak rainy season. To my knowledge, this

is the first study to apply this approach to large carnivores and opens several pertinent lines of enquiry for understanding mechanistic links between predator behaviour, physiology and responses to local climatic conditions. Lions in the Kalahari are a particularly interesting system to study response to temperature and water, given the semi-arid environment and the diurnal and seasonal range of climatic variables and extent of movement animals in this system exhibit. Much of Africa is predicted to experience increased temperatures and changes in patterns of rainfall, making this a critical element of fundamental predator ecology to understand if we are to predict long-term viability for lion populations following climate change.

5.1 INTRODUCTION

Animals move in response to their environment at various temporal and spatial scales. The choices they make are driven by a wide range of factors including the environment available to them and physiological (metabolic or thermodynamic) constraints (Wilson et al., 2015). At an hourly timescale, animal movement may be restricted by the temperature experienced or the range of habitats within their immediate mobility reach; at a longer timescale, and wider spatial extent, movement is shaped by broad-scale patterns of spatial variation and seasonality of the environment. Movement can thus be viewed as the unifying process that ties together animal space use in both geographic (home ranges and distribution) and environmental (habitat use and selection) dimensions (Van Moorter et al., 2016). In order to fully understand the spatial dynamics and requirements of populations it is necessary to understand how animals respond to variation in their environment across the full range of these timescales.

To date, spatial ecology in African lions has focussed primarily on variation in, and correlates of, home range size (e.g. Spong, 2002; Loveridge *et al.*, 2009; Valeix, Loveridge and Macdonald, 2012; Tumenta *et al.*, 2013; Laizer, Tarimo and Kisui, 2014; Tuqa *et al.*, 2014; Zehnder, Henley and Weibel, 2018) and habitat preference/selection (e.g. Davidson *et al.*, 2012; Elliot *et al.*, 2014; Davies *et al.*, 2016). These have generated important insights surrounding the space and resource requirements of these highly mobile large carnivores, how they vary temporally and between key demographic groups. There have also been critical developments in our understanding of how lions perceive and respond to spatial and temporal variation of risk in human-dominated landscapes (Valeix *et al.*, 2012; Oriol-Cotterill *et al.*, 2015; Loveridge *et al.*, 2017). Information on the extent and distribution of home range areas, the overlap with human activity, and how lions respond to key resources in the landscape have clear conservation applications in terms of conflict management at the edge of reserves (Loveridge *et al.*, 2010) and population connectivity (Cushman *et al.*, 2015, 2018).

However, movement and space use can also be viewed at a finer scale. For example, the daily distance travelled by individuals represents short-term space requirements. This is reflective, in part, of food and other resource needs and can provide an important indicator of an animal's use of its environment (Carbone *et al.*, 2005). Movement within a home range governs the way animals use their habitat, interact with conspecifics, obtain food, and negotiate human-modified landscapes. In addition to this, energetic budgets play a large role in individuals' survival and recruitment rates, and therefore have direct links to population fitness. Modelling the movement process in this way also allows for a more fluid approach to linking movement and climatic data, and can provide important insights

into the variation in movement patterns present (Elliot, Cushman, Loveridge, *et al.*, 2014) that may be missed when aggregated at the home range-scale.

Studies that address movement at the sub-home range scale in lions have found that movement patterns vary at the individual- and group-level in resident, dispersing (Elliot, Cushman, Loveridge, *et al.*, 2014), and reintroduced lions (Yiu *et al.*, 2015). Changes in mean-speed have been related to different movement strategies and life history events, with tenured males generally moving faster and further than both resident females and nomadic males (Hayward *et al.*, 2009; Elliot, Cushman, Loveridge, *et al.*, 2014). Dispersing lions also moved faster, and further, and in a more directed manner, during the transient stage than pre- or post-dispersal (Elliot, Cushman, Loveridge, *et al.*, 2014).

For territorial males, the increased travel distance is likely related to increased investment in patrolling their home-range and was also correlated with a lower per diem food intake than other demographic categories (Hayward *et al.*, 2009). For nomadic males, increased movement is likely an adaptive mechanism to avoid competition and harassment from territorial males, and was also associated with increased movement during the day period compared to the night (Hayward *et al.*, 2009). While there is a cost to territorial defence, a switch to moving during the warmer day time hours also has potential fitness costs. For example, West and Packer (2002) found that excessive body temperature has a strong negative impact on lion sperm quality, therefore nomadic males may have reduced likelihood of fertilisation, where mating opportunities arise.

Lions have been shown to adjust their mean and instantaneous speed in response to climatic variables, such as rainfall (Elliot, Cushman, Loveridge, *et al.*, 2014; Oriol-Cotterill *et al.*, 2015), human presence (Valeix *et al.*, 2012; Oriol-Cotterill *et al.*, 2015), and

key landscape features, such as waterholes (Valeix *et al.*, 2010). There is also evidence that an individuals' response to these variables maybe be context dependent and may vary between demographic groups. For example, studies have found that in general lions move at a slower rate with increased precipitation (Oriol-Cotterill *et al.*, 2015), but that this effect is strongest for territorial females (Elliot, Cushman, Loveridge, *et al.*, 2014). Mean speed has also been correlated with seasonal cycles inside protected areas across both sexes (Valeix *et al.*, 2012). Climatic variables have clear links to African lion demography (Celesia *et al.*, 2010), however explicit modelling of lion movement in response to this is relatively rare (but see Tuqa *et al.*, 2014 and above studies).

Thermal performance curves (TPCs) describe how an organism performs across a range of conditions—in this case temperature—to understand how species respond to environmental variation. Typically, performance is maximised under a range of optimal temperatures, and declines to zero just beyond the upper and lower critical temperatures, which define the thermal tolerance range. Multiple thermal traits can be derived from TPCs which can be used to understand organism-temperature relationships (Huey and Stevenson, 1979). They are typically assessed under constant temperature regimes in a lab-based setting, however it also possible to derive them from field-based data (Payne *et al.*, 2016; Childress and Letcher, 2017), including GPS data (e.g. Nowakowski *et al.*, 2020). They can be fit to a wide range of physiological or ecological performance variables, including temperature-dependent movement, as a relatively easy to measure metric which has been linked to proximate determinants of fitness (e.g., Miles, 2004). While less common than lab-derived TPCs, field-derived TPCs confer the benefit of describing the behaviour of organisms under natural conditions and provide realistic circumstances for

exploring how additional constraints on performance, such as water limitation, can alter the shape of the curve.

Lions in the Kalahari must move large distances to satisfy their basic requirements, ranging widely to gain access to widely dispersed clumps of resources such as food, and mates. Although there are some hotspots of resources around waterholes, in general prey distribution is dynamic and ephemeral in the Kalahari system, thus the capacity to move is a key determinant of success in this arena. Movement is also closely linked to energetic budgets, as one of the major trade-offs lions expend energy on in this system. As a result, movement is closely linked to lion fitness via its impact on survival and recruitment opportunities. For male lions, this also includes capacity to move to defend extensive territories both to secure mating opportunities and protect cubs from intruders.

More generally, there is a bias toward herbivores in studies examining the responses of large mammals to changing climates, and little is known about phenotypic plasticity of carnivores in response to temperature and aridity (Fuller *et al.*, 2016; but see Trethowan *et al.*, 2016, 2017 for recent examples of insights from the study of thermobiology in lions). In this study, I combine movement and temperature data from animal-borne devices to explore how movement performance in lions responds to temperature, sex, and varying surface water availability. Lions are top predators who must hunt to access foods, and range widely to defend the resources in their territory. Understanding how changes in temperatures may affect lion movements will provide a central clue in understanding how predators might respond to changing climate. I first ask: what are the spatiotemporal gradients in temperature and precipitation present in the study system? I then move to

explore how lion movement performance responds to these environmental variables at the population level, and how this varies between males and females using a TPC framework.

Mammals, as endotherms have a more complicated relationship with external temperature than ectotherms and have the capacity for both behavioural and physiological modifications in response to fluctuations in temperature. Given the differences in life history, social and ranging behaviour, and sexual dimorphism present in male and female lions, I expected differences in the relationship between movement performance and temperature between the sexes. I expected males to exhibit higher, on average, maximum displacement because of their larger body size, and greater need to cover distance in defence of females. Males have greater need to prioritise territoriality and so may pay other physiological (and risk) costs to maintain dominance of their territory of females. I also expected this as a function of the fact that females both carry offspring during pregnancy, which is energetically costly, and have their movement constrained (limits how far and how fast they can move) when they are in the company of very young cubs. Additionally, evaporative cooling plays a critical role in how large mammals respond to heat load (Fuller *et al.*, 2016), and a shortage of water has been shown to impact mammalian capacity to regulate their internal temperature, resulting in higher maximum daily body temperature in dehydrated mammals (Fuller *et al.*, 2014). Once physiological options for thermoregulation are exhausted, the only remaining option is to adjust behaviourally. Thus I expected that I would observe differences in movement performance during periods where water availability was high, compared to more arid periods, with specifically higher thermal performance when water is not limiting. Female lions have been shown to exhibit increased homeothermy during gestation (Trethowan *et al.*, 2016) and I expected this may

make them more sensitive in their response to temperature, particularly when water supplies are limiting. I conclude by considering what impact future land-use and climatic changes might have for African lions in the Kalahari, and what the key future avenues are for linking movement to population processes. Many of the remaining strongholds for lions occur in southern Africa in semi-arid, water limited systems, that are experiencing climatic change. These regions represent a model ecosystem to adequately describe and understand mechanistically how animals respond to environmental constraints such as water availability and temperature fluctuation.

5.2 METHODS

5.2.1 Study Area and Lion Movement Data Collection

The study area is located between latitudes 24.14°S and 20.67°S and longitudes 22.06°E and 25.80°E (**Figure 5.1**) within the central Kalahari region, Botswana. The study is centred on the Khutse and Central Kalahari Game Reserve complex; together the two reserves form one of the largest protected areas in Africa, covering approximately 54,768 km^2. The two reserves are adjacent, with no fenced separation, and as such, I hereafter refer to them simply as the CKGR. The northern, eastern, and south-eastern boundaries of the CKGR are delimited with fences. However, these have been shown to be largely permeable to predators (Kesch, Bauer and Loveridge, 2013, 2015).

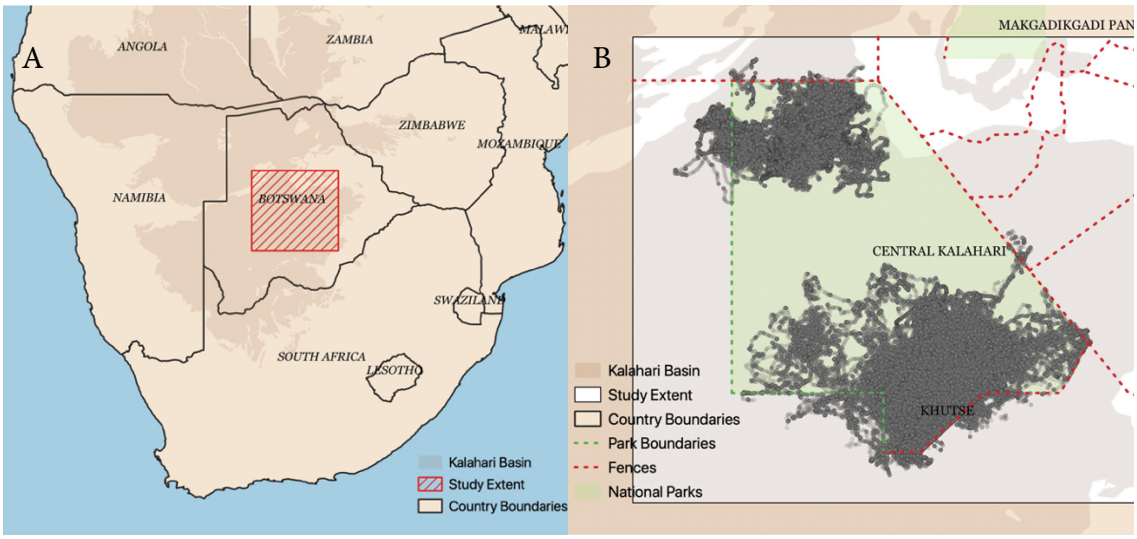


Figure 5.1 *Map of the study area within Southern Africa (A) and the spatial distribution of movement data within the study extent (B).*

The CKGR falls within the wider Kalahari ecosystem and is characterised by semi-arid savanna, with a flat terrain covered predominantly by a mixture of open herbaceous and open scrubland vegetation (Mishra *et al.*, 2015). While the vegetation in the region is relatively homogenous, climatically the Kalahari experiences pronounced seasonality with high interannual variability in rainfall levels (Nash and Endfield, 2002). The rainfall regime within the annual climatic season is confined to the summer months (November to April), and over a longer period can be defined by extended wet and dry seasons, centred around January and July respectively (Nash and Endfield, 2002).

Between 2004 - 2020, collar mounted GPS units were deployed on 51 lions from the CKGR population (**Figure 5.2**). For this chapter, I selected data from the period October 2009 onwards as movement data prior to this was largely female biased and generally of lower quality in precision and resolution. This resulted in a total of 43 individuals from a range of ages, sexes, and life-history stages. All animal handling procedures followed institutionally approved protocols.

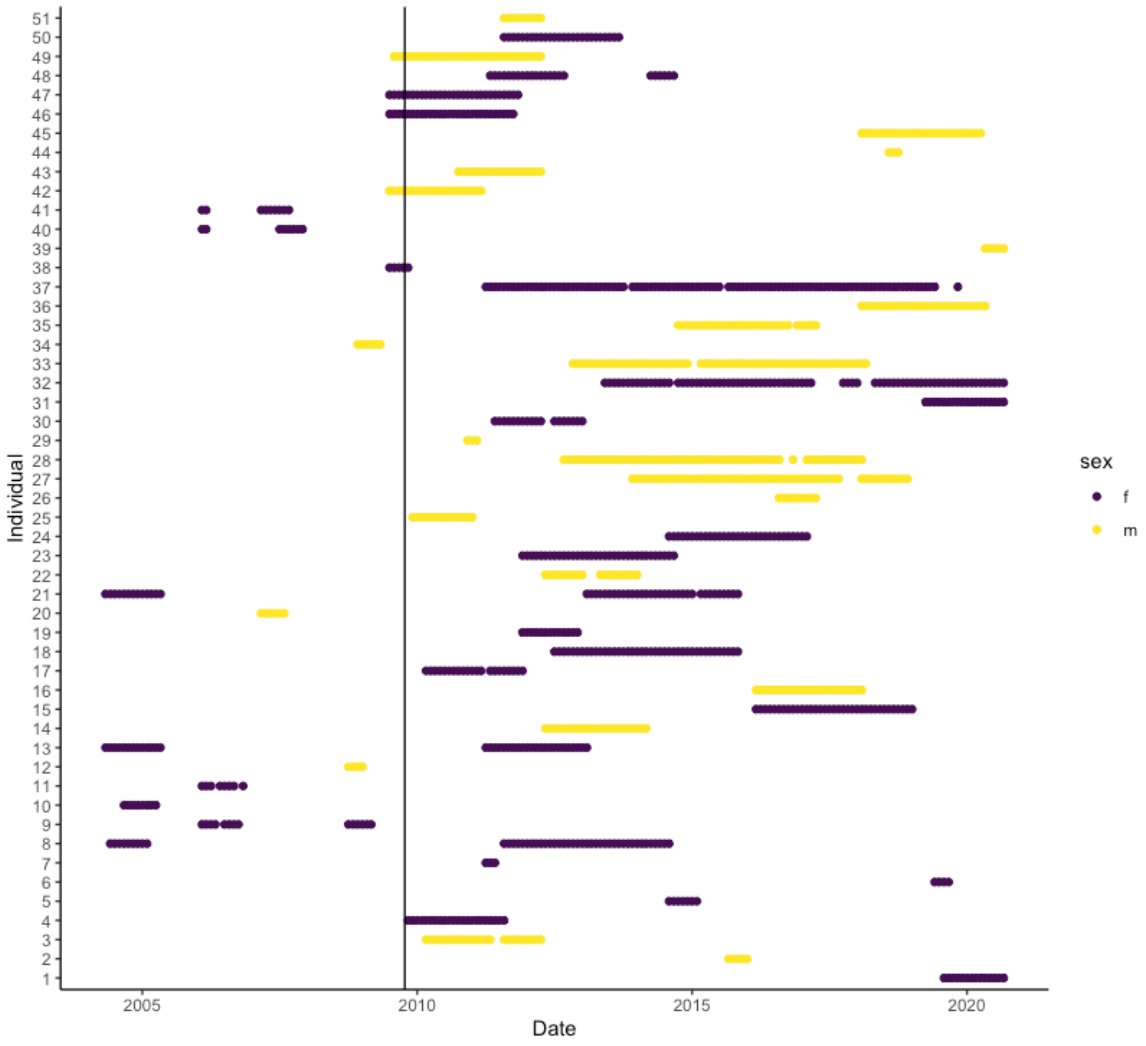


Figure 5.2 *Temporal distribution of movement data over the study period. Months where individuals were collared are represented by coloured points (males in yellow, females in purple) with the cut-off for inclusion represented by the vertical line.*

5.2.2 *Spatiotemporal Variation in the Kalahari Environment*

I used two freely available remote sensing products to describe precipitation and temperature across the extent of the study area between the eleven-year period January 2009 – December 2019 (Figure 5.3). For rainfall I used the Climate Hazards Group InfraRed Precipitation with Stations dataset (CHIRPS v2.0) which provides monthly precipitation estimates at 0.05° resolution between 1981 to the current day, based on blended station and satellite data (Funk et al., 2015). For temperature, I used the ERA5-

Land monthly average data, which is a reanalysis dataset combining model data with observations across the world to provide a globally complete dataset of the temperature of air in Kelvin at 2m above the surface of land, at a 0.1° resolution, from 1981 to present. I subsequently converted these values to degrees Celsius.

To provide context for the physical environment that lions experience in the Kalahari, I first extracted monthly values of precipitation and temperature, averaged across the study extent from our remote sensing datasets to examine what broad-scale patterns of variation in precipitation and temperature exist over the study period. I then applied the Seasonal-Trend decomposition procedure (STL) to decompose each time series into overall trend, seasonal and remainder components based on a locally weighted regression smoother (Cleveland *et al.*, 1990). Plotting rainfall values across the year over the study period, showed two clear periods of varying water availability (see Appendix C.1). While dry and rainy season onset varied between years, the months of December – February consistently included peak rainfall over the study system, where water would be widely available at pans; whereas June – August were consistently the driest months, where water is restricted to few locations with solar-pumped waterholes. I therefore selected these two time periods to test if restricted access to water acts as a limiting factor on lion thermal performance.

5.2.3 Fine-Scale Data on Ambient Temperature

To provide fine-scale information, at the timescale of the movement data (hourly resolution) I used instantaneous data from temperature loggers integrated into GPS collars. For each locational fix, the fitted devices also recorded a value for temperature that can be used as a proxy for ambient temperature.

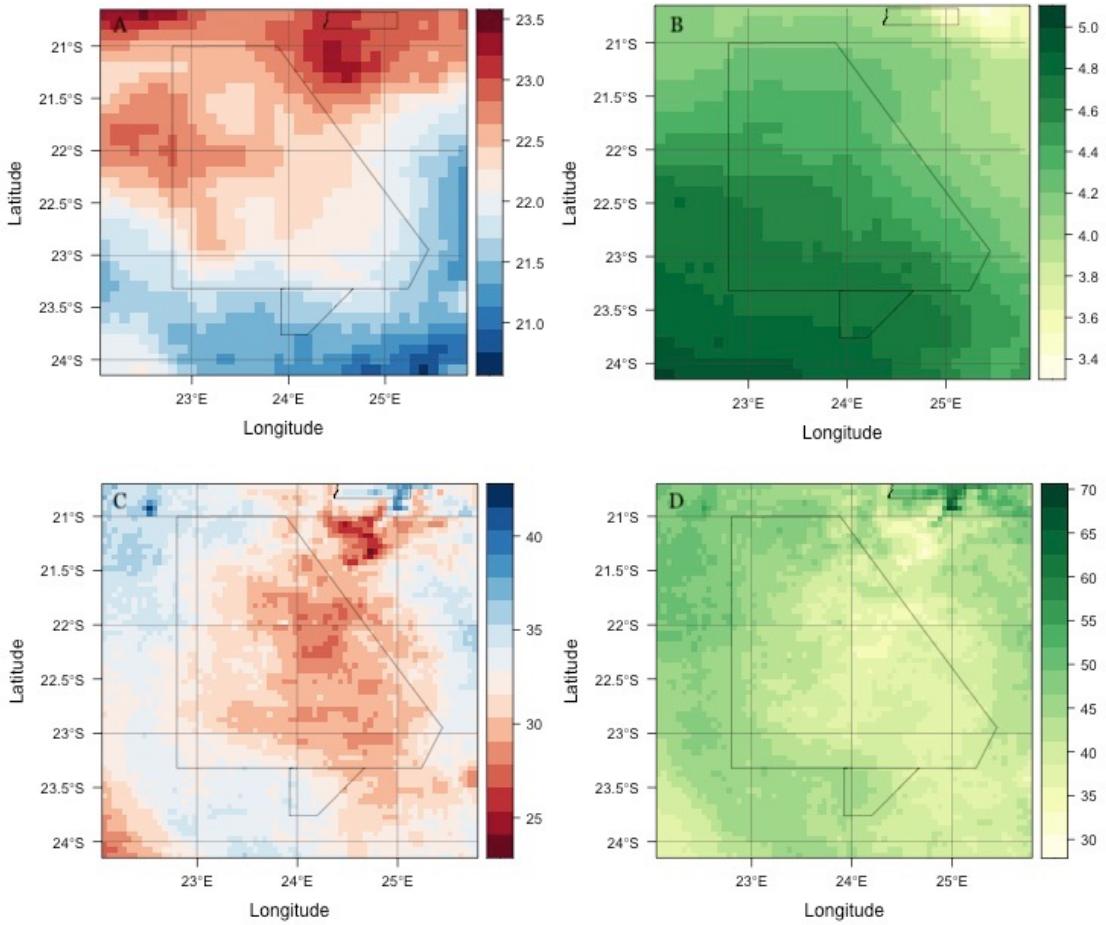


Figure 5.3 Spatial representation of mean (A & C) and standard deviation (B & D) of climatic variables temperature (A - B) in degrees Celsius and precipitation (C-D) in mm/month across the months January 2009 - January 2019. Temperature values are derived from the ERA5-Land monthly averaged dataset (Hersbach et al. 2020), and precipitation from the Climate Hazards Group InfraRed Precipitation with Stations dataset (CHIRPS v2.0; Fun et al. 2015). The mean annual precipitation and temperature per pixel of the study area between the years 2009 - 2019 ranges from 24 - 42 mm/month, and 21 - 23 degrees C, respectively. Across the study area, there is a gradient of increasing mean temperature (A) from the south-east to north west, while the variability (B) is greatest in the south-west and decreases as you move north-east. The variability in precipitation (D) is greatest in the wetter regions of the map (C), with drier regions experiencing a smaller variability across the months of the study period. For both temperature and precipitation values, the standard deviation over the course of the study period (includes both intra- and inter-annual variability) is greater than the range in the overall mean, suggesting high levels of seasonality and interannual variation. Figures demonstrating the spatial distribution of mean and variability in environmental variables averaged across the years for each month can be found in Appendix C1.

The temperature recorded by these collar-mounted sensors is generally a combination of ambient, circuit-generated, and animal body temperature (Thaker *et al.*, 2019). The sensors are located in electronic housing, and the values recorded are related to ambient temperature, but also impacted by the animal's body temperature, heating of the housing from solar radiation, and the cooling effects of wind (Vectronic Aerospace GmbH Vertex Plus Manual). While this makes it challenging to link the temperature value absolutely to the ambient temperature, it provides a fine-scale relative measure of the temperature experienced by the animal at a resolution relevant to the movement recorded. Stationary tests of collars at my field site (data not presented) showed a close qualitative match between patterns in temperature between the weather station at camp and values recorded by collar devices, which match findings from Thaker et al. (2019), who found that collar-derived temperatures were predicted well by ambient temperatures. In practice, air temperature is only one factor that impacts heat load in mammals facing climate change, and is relatively minor compared with other sources of heat exchange including radiant heat and "forced" convective heat transfer from wind (Mitchell *et al.*, 2018). In this aspect, the sensors, which respond to the same sources of heat transfer, provide a more realistic measure of the experience of the animal than air temperature alone.

5.2.4 *Thermal Performance Curves*

I fit curves to the maximum movement rate at each degree temperature to characterise the upper capacity for movement performance. Movement rate here is defined as the straight-line displacement (SLD) between sequential fixes per unit time, and is measured in km/h. Movement in this context serves to act as a measure of whole-organism performance and has been used as metric in field-based studies of thermal performance (e.g. Nowakowski *et al.*, 2020) linked to proximate determinants of fitness (Miles, 2004).

The Kalahari is a highly heterogenous landscape, and animals moving through it balance trade-offs such as the energetic costs of movement, with the need to search for food, water, and mates, and thus optimise their fitness as a result of movement decisions. Temperature is likely to mediate these movements by impacting key axes of the movement ecology framework described by Nathan et al. (2008), namely internal motivation to move, and physiological constraints on movement. By linking local movement and organism performance, TPCs based on movement datasets describe a fundamental process linking fitness and species distributions, by integrating elements of thermal biology and spatial ecology.

The collars were programmed to collect locations at an hourly resolution, with some periods of finer-scale data and a small proportion of missing fixes that created longer gaps. As SLD estimated speeds are sensitive to the sampling resolution (Noonan, Fleming, *et al.*, 2019), I excluded any sequential time steps where the gap was greater than an hour (with a tolerance of 10 mins; approximately 6% of the data) and resampled the periods of finer-scale data to an hourly resolution. This resulted in a sample size of 563,321 data points from 43 individuals (21 females, 22 males). I matched estimates of movement rate with the start of the time step such that they reflected the temperature experienced at the start, rather than the end of the accumulated displacement.

To compare TPCs between sexes and seasons, I split the data into four categories: an orthogonal combination of sex (male/female) and seasonal precipitation (dry/rainy). I calculated the maximum movement rate per degree of temperature for each lion, then summarised as the population mean (with associated standard deviation) for each of the four datasets. I then fit TPCs to this mean rate, incorporating variation in rate values, by

using weighted non-linear least squares (NLLS) regression. I applied weighting using the optimal 1/standard deviation. To fit the NLLS models, I made use of a recently available pipeline in R that facilitates reproducible fitting of a wide range of TPC model formulation (Padfield, O'sullivan and Pawar, 2020); the associated R package *rTPC* contains helper functions to select starting values for NLLS parameters, and provides a wrapper to the package *nls_multstart* which uses an iterative approach combined with Akaike information criterion (AIC) model selection to overcome issues in the sensitivity of NLLS regression models in R to choice of starting parameters. I then used high resolution predictions of the fitted models to estimate thermal traits associated with TPCs. Namely critical thermal minimum and maximum (CTmin/CTmax), the maximum rate (Rmax), the optimum temperature (Topt) and thermal performance breadth (breadth), which is defined as the range of temperatures over which a curve's rate is at least 0.8 of Rmax.

TPCs can be fit using a wide range of non-linear formulas/model specifications; I used a model selection approach (based on AIC with correction for small sample sizes; AICc) to select the most supported model for each dataset from a subset of all possible options, curated based on the thermal traits of interest and statistical properties of our performance rate (see Appendix C.2).

I used non-parametric bootstrapping as a robust way of computing parameter and model prediction confidence intervals (CIs). Bootstrapping entails resampling each dataset iteratively and re-fitting the model to reconstruct a relatively unbiased sampling distribution of parameters, from which confidence bounds can be constructed. This allowed me to calculate CIs for both estimated and derived parameters from the NLSS model fits. I performed case-resampled bootstrapping using the *Boot()* function from the

R package *car* (Fox, 2006). While overlapping CIs do not imply anything about statistical significance, the inverse—non-overlapping CIs—can be used as an indication of differences between estimated quantities when calculated appropriately. Given the relatively large sample size of our TPCs, I cautiously used non-overlapping confidence intervals of parameters between different TPCs for inference.

5.3 RESULTS

5.3.1 *Spatial and Temporal Trends in Study Environment*

As expected from the climate of the study area, results from the seasonal trend decomposition procedure suggested strong seasonality in both rainfall and precipitation, but also an upwards trend in average temperature over the study duration (**Figure 5.4**).

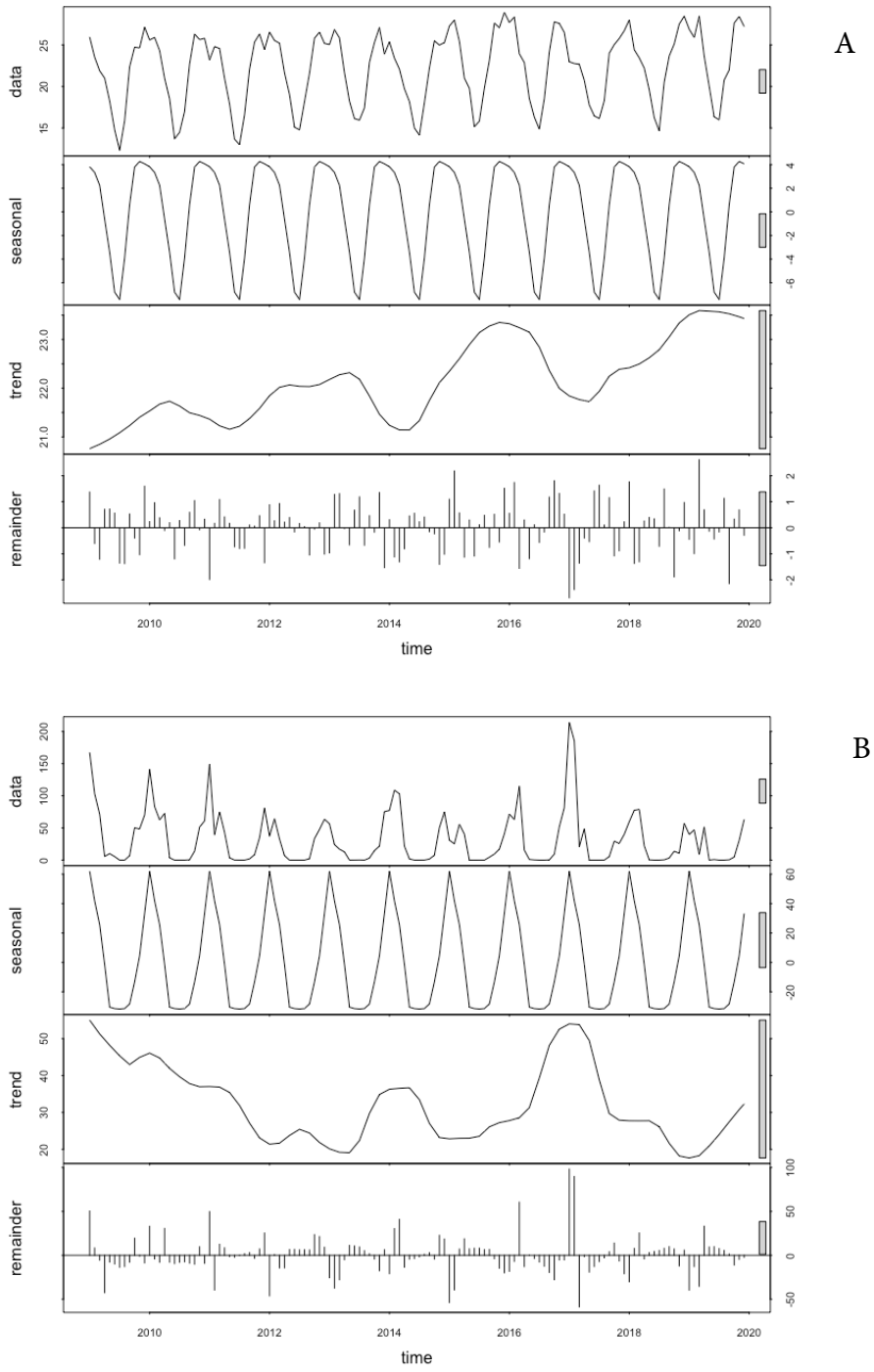


Figure 5.4 *Output from the seasonal decomposition trend procedure (STL) for temperature (A) and precipitation (B). The timeseries for each climatic variable is presented as (from top to bottom) the raw input data, the seasonal and trend components, and the residual variation.*

5.3.2 *Thermal Performance Curves*

The movement datasets from peak rainy season (December – February) for both males and females were best described by a thermal performance curve (TPC) based on the gaussian model formulation. During the dry months (June – August), female movement was best described by a modified gaussian curve, and males by the O'Neill model. A full account of relative support for each TPC modelled is provided in Appendix C2. The resulting TPC fits demonstrated clear differences in movement performance between the sexes, and across seasons (**Figure 5.5**).

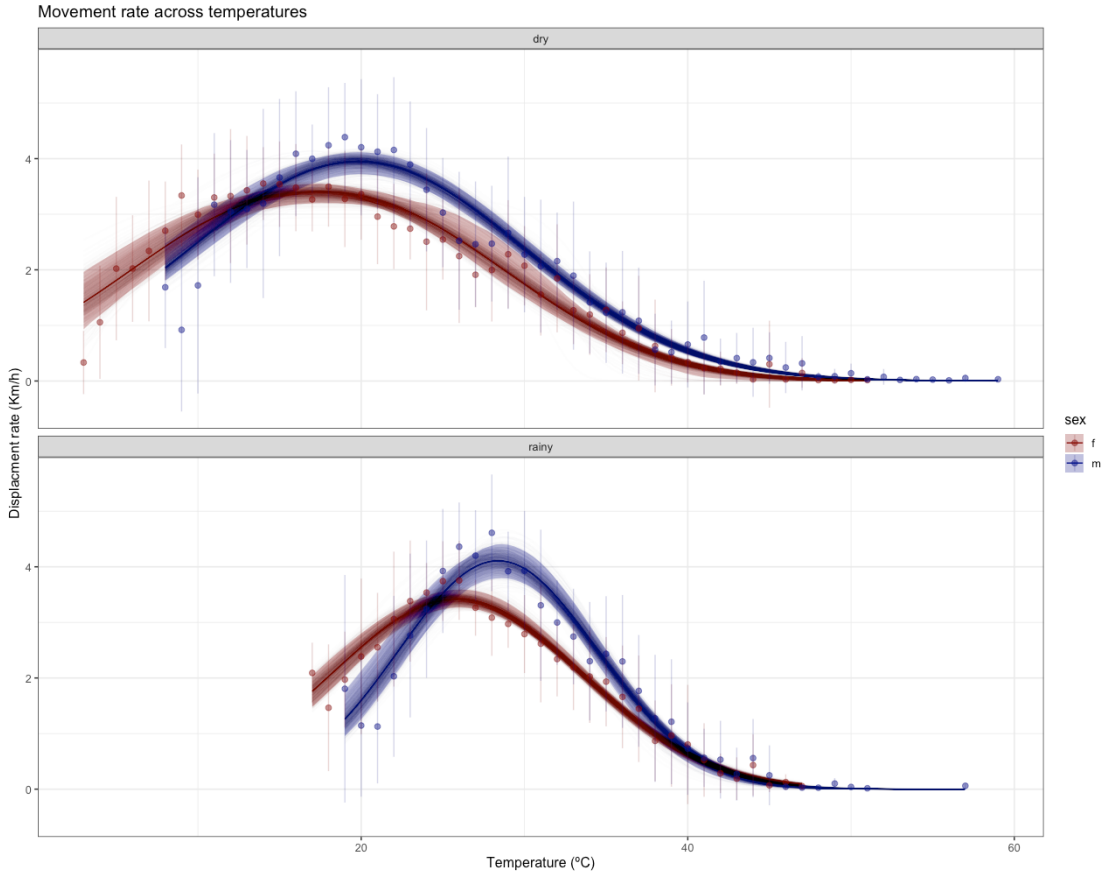


Figure 5.5 Thermal Performance Curves *for male (m, dark blue) and female (f, dark red) lions during the dry months of June – August (top row), and rainy months December – February (bottom). The average rate input data for models is presented as points, with the standard deviation around the mean shown by vertical lines. The solid lines represent predicted values of maximum speed per degree Celsius from non-linear least squares regression models. Confidence intervals around each curve from case-resampled bootstrapping are shown as transparent ribbons, alongside the individual bootstrapped predictions.*

5.3.3 *Sex- and season-related differences in peak-movement performance traits*

Across both seasons, males had a higher estimated maximum rate of movement (Rmax) than females (dry season: 3.4[3.23, 3.59] vs 3.95[3.72, 4.12]; rainy season: 3.42[3.28, 3.62] vs 4.11[3.8, 4.42]), and their movement rate peaked at a higher temperature (Figure 5.6). The difference between the optimal temperature (Topt) was more distinct during the rainy season (males: 28.39[27.69, 29.04] vs females: 25.86[25.25, 26.46]) than the dry season (males: 19.8[18.76, 20.7] vs females: 17.33[16.12, 19.22]).

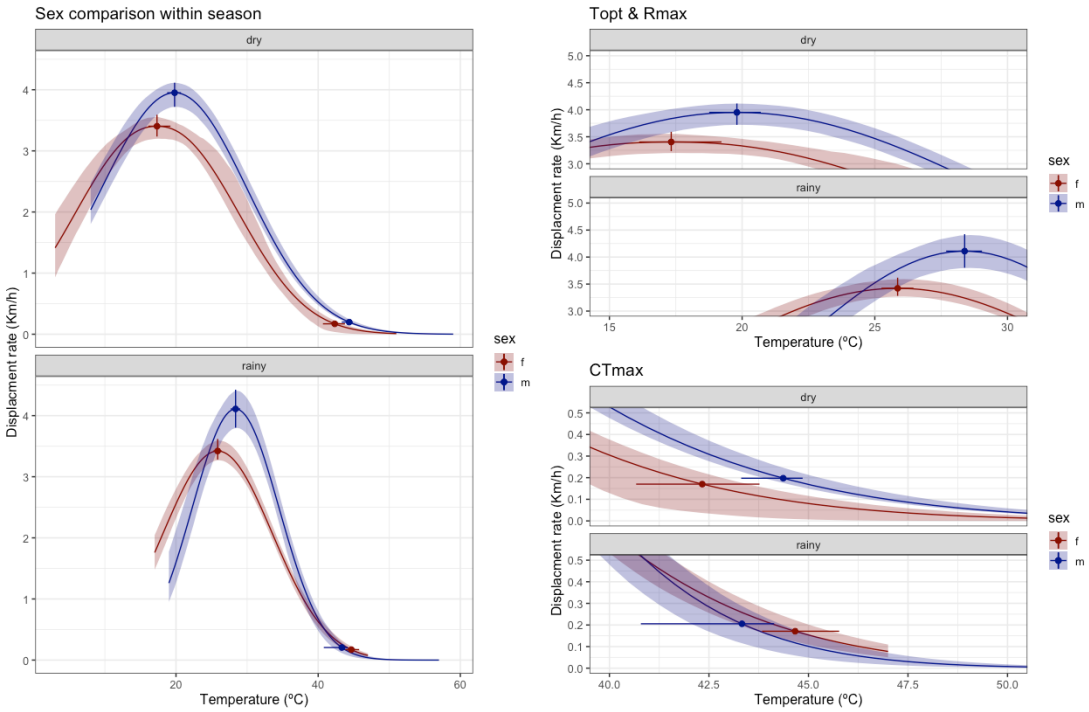


Figure 5.6 Sex-related differences in thermal performance traits between the dry and rainy seasons. Solid lines, and surrounding ribbon provide predicted values and bootstrapped CIs as in previous figure. Solid points show estimates for the thermal traits Topt and Rmax directly estimated by NLLS models, alongside case-resampled bootstrap upper and lower CIs. On the right the relevant area of the curve is displayed zoomed in for Topt & Rmax (top) and CTmax (bottom) to better display variation around these estimates. Topt represents the temperature where the largest rate value occurs, while Rmax is the value of the maximum rate.

CTmax was more similar between the sexes for both seasons, with females having a lower CTmax (42.33[40.67, 43.77]) than males (44.37[43.31, 44.85]) during the dry season, and

the converse in the rainy season (females: 44.67[43.84, 44.77] vs males: 44.33[40.79, 44.14]).

For both sexes, Topt was higher, and associated with a steeper curve during the rainy season (Figure 5.7). The difference in Rmax between seasons was far less pronounced, particularly for females (Figure 5.7 top right). In contrast, the seasonal difference in CTmax was larger for females, who saw a reduction during the dry season, compared to males who exhibited similar CTmax values for both seasons (Figure 5.7 bottom right).

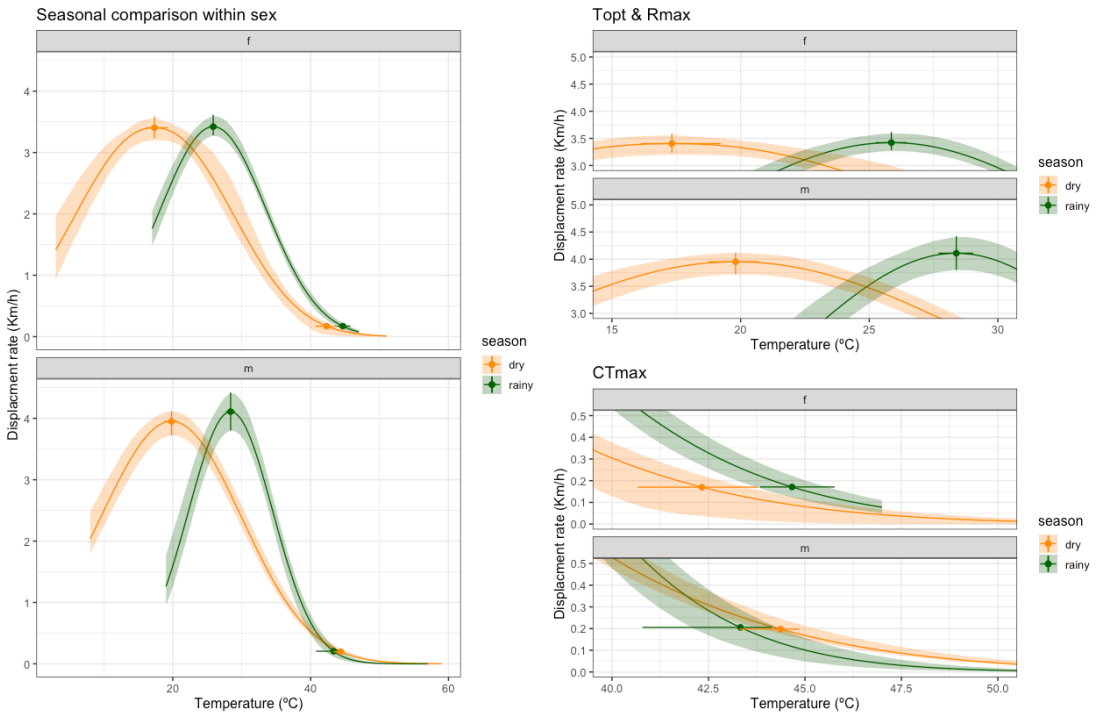


Figure 5.7 Seasonal differences in thermal performance traits. TPCs from above are here shown grouped by sex to better display difference in Topt, Rmax & CTmax between seasons.

5.3.4 *Sex- and season-related differences in other derived movement performance traits*

TPCs can be described by their skewness, with negative values indicating typical left skew where the slope after the optimal temperature is steeper than before. All TPCs provided negative estimates for skewness, but only females during the dry season had CIs that did not overlap 0 (Figure 5.8 middle row). As can be seen in the curves in Figure 5.7, the range of temperatures at which animals performed close to their maximum rate was much more narrow during the rainy season (Figure 5.8 top left), there was also a greater difference between the sexes during rainy season (Figure 5.8 top right). A similar pattern can be seen for thermotolerance (Figure 5.8 bottom row).

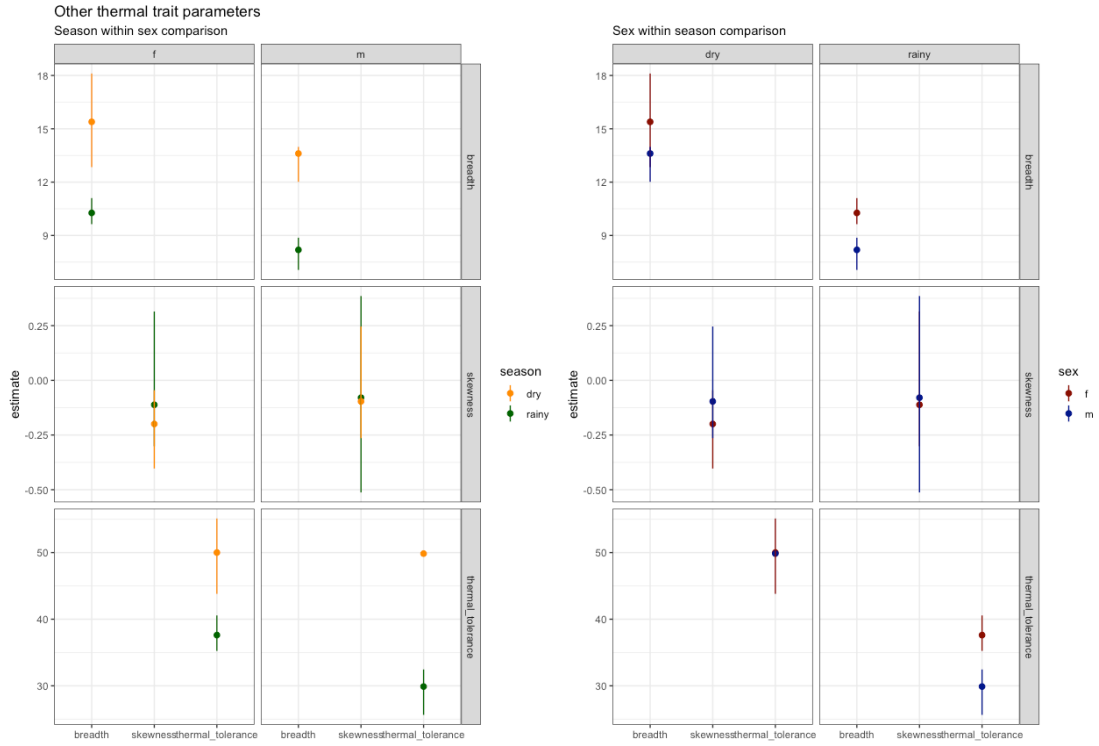


Figure 5.8 Derived thermal performance traits thermal performance breadth (breadth, top row), skewness (middle row), and thermal tolerance (bottom row). Points display estimated quantities, grouped by sex (left) and season (right), with case-resampled bootstrapped CIs given alongside. Breadth is calculated as the range of temperatures over which a curve's rate is at least 0.8 of the peak. Skewness is related to the activation and deactivation energies of a TPC, and are calculated by fitting a modified-Boltzmann equation to all raw data above (or below, respectively) the optimum temperature. Thermal tolerance is calculated as CTmax – CTmin. As predicting zero from the curve formulas used is impossible, CTmax/min here represents the temperature where the rate is 5% of the maximum.

It is worth noting that the curves I fit to describe the movement are not formulated to directly estimate skewness or thermotolerance, or rather the performance parameters underlying their calculation (CTmax, CTmin, Activation Energy/e, Deactivation Energy/eh). Thus, some caution should be applied in their interpretation, compared to Rmax, Topt and breadth, which were the main focus of this chapter.

5.4 DISCUSSION

Climate change and habitat alteration are creating novel thermal environments for species. Predicting how populations will respond to these emergent conditions relies critically on understanding how temperature exposure at a fine spatial and temporal scale results in performance change, and how this interacts with other limiting factors such as increased aridity or anthropogenic-induced stress. I show here that GPS tracking data and collar-mounted temperature sensors can generate data to readily characterise TPC from movements in the field, allowing direct insights into thermal traits in lions across ecological and life history contexts.

The results presented demonstrate clearly that temperature-movement relationships in lions are modified by rainfall, and vary between periods of high and low surface water availability. There are also sex-related differences in the functional relationship between movement performance, temperature, and water availability. This serves to highlight the dependence of thermal traits on ecological, life history and landscape contexts. It also demonstrates that TPCs derived from GPS movement tracks in the field can provide ecologically relevant estimates of thermal performance and provide an informative framework for unifying elements of thermal biology and spatial ecology.

Field-derived TPCs allowed me allowed me to characterise optimal temperature (Topt) under natural conditions, which is an important thermal trait for assessing vulnerability to climate change (Huey *et al.*, 2012). These methods open avenues to study how thermal traits vary across season, years, habitats, and individuals, that are not as easily studied with laboratory measured TPCs. Movement through heterogenous landscapes involves balancing energetic costs with search for food, water and mates, as well as interactions with conspecifics (Cushman and Huettmann, 2010); using field-based data allows for the incorporation of such constraints on movement performance which can fluctuate over time (e.g. food availability, precipitation, biotic interactions) resulting in thermal parameters that are more closely aligned with the realised thermal niche for the organism. However, it also makes it more challenging to tease apart different drivers than in controlled laboratory settings.

Here I show clear differences in thermal traits, but elucidating the mechanisms underlying these is a clear next step in the process to ask: what is different for females? What physiological and behavioural adjustments result in the observed changes in whole-organism movement performance? Fundamental ecological knowledge of the system can provide some hypotheses, and additional data on internal response to temperature and behaviour at a fine resolution would allow us to empirically test these. Threthowan *et al.* (2017) showed that dominant males visited waterholes twice as often as females, and suggested this might be an adaptive mechanism to increase water uptake to facilitate evaporative cooling to compensate for increased heat load from possessing a mane. Water is (ephemerally) available at salt pans spread widely across the Kalahari during the rainy season, providing greater opportunity to replenish water/electrolytes during evaporative

cooling. This is one possible mechanism by which lions may be able to operate at higher temperatures during periods of high rainfall. Linking the movement performance metrics estimated here to space-use and behaviour around pans and waterholes may allow future insight into this.

Other crucial data would include access to internal core temperatures to explore variation in heterothermy in lions i.e., storing heat load during the day to dissipate at night. This has been explored in arid-dwelling species, such as oryx, which switch from gaining heat during the day to dissipating heat at night when the environment is too dry to use evaporative cooling (Ostrowski, Williams and Ismael, 2003). There is significant variation in night and day temperatures in the Kalahari, and this is another physiological mechanism to cope with heat load in large mammals that might be available. Lions have been shown to display increased homeothermy during pregnancy (Trethowan *et al.*, 2016), if lions display greater degrees of variation/extent in heterothermy outside of this, that could explain why males and females respond differently to fluctuations in temperature and aridity, as females would have left flexibility during periods such as gestation. There may also be other life history events, such as dispersal, that limit movement performance as a result of fewer microclimate refuges available during long-distance displacements outside of core areas (e.g. Fuller *et al.*, 2014). Finally, fine scale accelerometery could be used to describe other activities that may be related to heat loss, such as increased time spent in seeking shade, in heat reducing postures, or cooling activities such as bathing.

While thermal traits such as optimal temperature and thermal performance breadth appear to be plastic in the Kalahari lion population, critical thermal maximum was far more similar across comparisons, suggesting this trait is constrained and that there may

be limited potential for change via acclimation or selection as climates get warmer. It would be informative to look more closely into individual variation in thermal traits within this system and across other populations to better understand plasticity and the amount of free-standing variation present for adaptive capacity.

The results of the skewness metric suggest that during all seasonal and sex combinations, lions generated left-skewed performance curves (but with caveat that I did not chose models that optimise estimation of this parameter). However, this is similar to what Nowakowski *et al.* (2020) found for movement in desert tortoises and would support empirical examples from other species that suggest that temperature-dependent mechanisms generate left-skewed TPCs across biological scales from heart rate (Sinclair *et al.*, 2016), whole-organism movement performance (Navas, Gomes and Carvalho, 2008) long-term space use (Nowakowski *et al.*, 2020), scaling right up to population growth rates (Deutsch *et al.*, 2008). Fully understanding the implications of climate change for large carnivores will likely require deeper investigation of how they respond across these time and spatial scales. How does the frequency of long-distance movements, or home range size change alongside the amount of time spent at optimal temperatures? What long-term population impacts of changing climates can be seen in survival and recruitment rates? How does this interface with other environmental and anthropogenic stressors?

Climatic variables, such as temperature and precipitation have a clear link to both species distributions and the demography of large carnivores. They have been linked to the phylogenetic structure of carnivore communities across Africa (Kamilar, Beaudrot and Reed, 2015) as well as broadscale patterns in demographic parameters (Celesia *et al.*, 2009). However the impact of high temperatures on fitness-related events, such as mortality, is

poorly documented in wild animals, particularly carnivores. Recent studies in wild dogs provide support that both pup and adult mortality are linked to high ambient temperatures (Woodroffe, Groom and McNutt, 2017; Rabaiotti *et al.*, 2021). The findings of these studies indicate that the species is not only likely more vulnerable to climate change than would be predicted by the traits usually used, but also that climate vulnerability via high ambient temperatures interacted with anthropogenic risk of mortality (Rabaiotti *et al.*, 2021). The wider Kalahari-Kavango ecosystem represents significant strongholds for a number of large carnivore species, and understanding how animals behave and perform in these systems is not only important in the context of maintaining these populations, but also in understanding how populations in other regions across the range might respond to increasing aridity and novel climates.

Large carnivores—including lions—but also mammals more generally are facing not only increased heat loads, but also reduced and more variable water and food availability, particularly in semi-arid regions of their range. Although not the most sophisticated climate analysis, the temperature and precipitation quantification included in this chapter show large, and fast changes, over what is climatologically a relatively short period of time. Both insufficient water and food can act to narrow the ambient temperature range over which mammal body core temperature is held relatively constant, and can lead to increased risk of physiological malfunction and death (Fuller *et al.*, 2021). My findings indicate that lions are sensitive to temperature in their performance, and that the functional relationship of this is dependent upon the availability of sufficient water. Additionally, lions in the Kalahari are in a resource-poor environment where limited food is a common occurrence, placing additional stress on the already large energetic

constraints wide-ranging carnivores in this system face. This has implications for the way we manage landscapes for wildlife in these systems, including the provision of water, for example via artificially-bored waterholes.

Greater collaboration between movement ecologists and climatologists would allow for matching of animal behaviour and performance with modelled future climate scenarios and is likely a critical step in accurate predictions of species response to climate change. The vulnerability of species to changing environments is dependent upon their exposure and sensitivity to environmental change, their resilience to disturbance, and the underlying potential to adapt (Huey *et al.*, 2012). Organisms have various options to respond to changing environments, they could shift their range, or remain but adapt, either through change in genetic composition or as a result of phenotypic plasticity. For lions, especially those living in human-dominated landscapes, range shifts are an unlikely option. There is therefore a clear need to understand what capabilities, and plasticity in physiology and behaviour, exist to adapt to avoid extirpation.

Part III

EPILOGUE

6

General Discussion

SYNOPSIS The overarching aim of this thesis is to use spatial and demographic data from wild lions across the Kalahari-Kavango landscape to better understand how lions move through and interact with their surroundings at multiple spatial scales, across a gradient of land-use, and environmental conditions. The front matter of the thesis provides a general introduction and background to the literature on lion spatial ecology in the context of research into modelling landscape and local space use for conservation. The body of the thesis addresses the thesis aim by evaluating how data inputs and approaches for modelling space use and movement perform both at the geographic scales of the landscape (*Chapter 3*), and the home range scale and smaller (*Chapter 4*); and how animal movement can be linked to the environment and response to key climatic variables (*Chapter 5*). The concluding section of this thesis summarises the key findings and limitations of each chapter, as well as future research directions and extensions. The key findings are placed in the context of the wider body of work this thesis contributes to, and the extent to which they fulfil the overarching thesis aims.

6.1 KEY FINDINGS & CONTRIBUTION TO KNOWLEDGE

6.1.1 Comparing the performance of resistance surfaces & connectivity models in predicting dispersal trajectories of wild lions

The findings from my first data chapter highlight the appropriateness and high performance of landscape connectivity models in predicting the routes that dispersing

lions take across the Kavango-Zambezi Transfrontier Conservation Area (KAZA). All resistance inputs (both from home range and dispersal data) and connectivity algorithms (source-destination cost distance, CD and CircuitScape CS) tested generate connectivity surfaces that scored highly at observed dispersal points. Observed dispersal routes were strongly linked to predicted connectivity, as indicated by near perfect performance in the spatial randomisation procedure. Dispersal trajectories were more closely linked to landscape connectivity than local resistance alone, indicating a role of cumulative decision-making in the generation of long-distance movement patterns across the landscape. This is encouraging for the use of connectivity models in lion conservation and land-use planning, as home range data is widely available at many sites across the lions' range.

Another key message was that unscaled connectivity values were more closely linked to the dispersal movement trajectories than after percentile-rescaling. This serves to remind that these surfaces are continuous outputs—making them into binary corridors or thresholding arbitrarily reduces their information and performance (McGarigal and Cushman, 2005; Cushman *et al.*, 2010). At the same time, delineated corridors are often the desired output for end users/conservation practitioners, and thus the generation of these remains a critical step in the process from a practical perspective. To my mind, there are a couple of key considerations to address between what I have modelled and moving forward. These revolve around the way source (and destination) points have been specified, how dispersal movement has been modelled, what the best uses for dispersal data to provide connectivity inference are, what successful connectivity looks like beyond movement, and how generalisable local models are at the scale of the lion's range.

Under the current models, we use known start and end points to generate connectivity surfaces per lion for validation; however, this is unrealistic from two perspectives: a lion likely does not have awareness of its destination, and as modellers we are unlikely to be aware of the destination either. A natural extension to this is to model connectivity synoptically using, e.g. resistant kernels (Compton *et al.*, 2007) to generate expected functional connectivity for every pixel in the study area across many different source points. Two previous studies have addressed connectivity in lions in this system using such an approach (Cushman *et al.*, 2015, 2018).

Beyond repetition of the validation methods described in the chapter, the independent dispersal dataset could be valuably applied to optimise how we select dispersal thresholds in these models. Relevantly, Cushman et al. (2015) used the dispersal resistance surface evaluated in this chapter to assess changes in connectivity (resistant kernel) across nine landscape change scenarios, under eight different potential dispersal abilities. Understanding what the current status quo of dispersal ability is currently could be critical in predicting the impact of future land use change, as Cushman et al (2015) shows the outcome of this is dependent on the dispersal ability of the species.

Another consideration of the current work is that much of the dispersal data is from animals that moved within sparsely settled or even protected areas, which presumably has a profound effect on their movements. Two exceptions to this can be seen in the most eastern and western examples of dispersal identified (see Figure 3.1). Both these trajectories extend further from protected areas, are more linear than those within the national parks, and in fact both animals were killed during dispersal as a result of conflict with humans. This highlights two avenues of food for thought. First, that it would be

informative to contrast dispersal events through areas of generally low resistance/high protection with those that cover long distances between core areas. Second, the movement process of dispersal is only one aspect of the biological process as a whole; for genetic connectivity to be maintained, an individual must not only be able to reach a location, but also survive to reproduce there. With this in mind, it would be valuable for future studies to compare movement connectivity with models of genetic connectivity in overlapping regions (e.g. Cushman and Lewis 2010; Dures *et al.*, 2020).

Finally, there is room to explore greater incorporation of the scale of decision making and individual heterogeneity during the dispersal process into the evaluation of the connectivity models. In this study, I only consider the scale of the entire dispersal path, but lions likely evaluate their choices at a much finer scale in space and time. Additionally, while I account for individuals statistically, there could be value in exploring differences in performance between individuals. Drawing closer together the logic of models and the behavioural ecology of decision making by individual lions is a challenge, but also important for generating fundamental insights into the dispersal process.

6.1.2 *Sources of bias in modelling movement & space use in African lions*

The overwhelming take home message from this chapter is that autocorrelation was ubiquitous and substantial in the data analysed, and that methods that fail to account for this are likely to produce biases—at a biologically relevant magnitude—in estimates of lion space use. This is in line with previous studies that have demonstrated similar phenomena in a range of species (e.g. Noonan, Fleming, *et al.*, 2019; Noonan, Tucker, *et al.*, 2019; Noonan *et al.*, 2020). Studies that focus on home range area in lions are common (e.g. Spong, 2002; Loveridge *et al.*, 2009; Valeix, Loveridge and Macdonald, 2012; Tumenta *et*

al., 2013; Laizer, Tarimo and Kisui, 2014; Tuqa *et al.*, 2014; Zehnder, Henley and Weibel, 2018), yet the vast majority of these are based on methods that have been shown to underestimate space use requirements, and produce unrealistically small confidence intervals as a result of a mismatch between effective and assumed sample size. This has implications for conservation recommendations, and the ability to robustly compare variation in home range behaviour between and among individuals and populations.

The discussion around how to handle autocorrelation in movement data is not a new endeavour, neither is the recognition that the characteristic timescales of autocorrelation can, in fact, provide useful biological context to aid in the interpretation of animal decision making. Early reflections on such analyses, (e.g. Macdonald, Ball and Hough, 1980) used the concept of home range crossing time to filter data to a time length which would represent independence in animal choice, on the logic that if they have remained in a given area for longer than the timescale on average for crossing the home range, this would reflect choice, rather than an artefact of previous location. Since this work, methodology has advanced allowing increasingly sophisticated models that can accommodate a range of described autocorrelation structures common in tracking data (e.g. the ctmm and CRAWL packages in R); one of the challenges will be how to ensure these translate into applied research.

There are numerous reasons that the uptake of new analytical approaches in the applied field of conservation research can be slow; including inaccessibility of the methods, greater familiarity with more well-known methodology, or because the results are hard to interpret. However, it is also clear that understanding the structure present in movement data, and how this relates to the underlying biology of the species can be crucial to

obtaining accurate estimates of animal space use. Especially in wide-ranging carnivores such as the African lion, as I demonstrate in this chapter. Throughout the chapter text, I highlight how continuous-time movement models can be used as a flexible option for modelling movement across a range of timescales. Alongside my findings, I present a clear workflow for using a continuous-time movement approach to describe animal movement, with detailed discussion of the decisions and considerations taken along the way. The analytical approaches presented in this chapter have great potential for inference about space-use requirements and energy allocation in species of conservation interest; here I pull them together to explore a range of quantities of interest to conservation practitioners and aim to provide a road map to making informed decisions about modelling space use. While this goes some way towards emphasising the clear need for such considerations, it is also true that the analytical minutia of the methodology may be at odds with facilitating immediate uptake by practitioners. A plausible future step towards this might be the publication of a technical end-user focused digest of such research.

Another theme that runs throughout the chapter is non-stationarity in movement processes. I explicitly address this in the context of diurnal changes in activity, however it is equally as implicit in ranging behaviour at the home range scale. In this chapter, I handle non-stationarity in mean location via segmentation of the data into approximately homogenous sections, however this results in a somewhat unsatisfying reduction of lion behaviour to simple categories that may not match the underlying behavioural process. Lions in the Kalahari exist in a structurally homogenous (open pans surrounded by a matrix of scrub), but temporally rather dynamic system. The process underlying home range behaviour is reminiscent of the drifting territoriality observed in red foxes

(Doncaster and Macdonald, 1991), or the multi-range tactic (e.g. Couriot *et al.*, 2018). While the advances in technology to capture and model animal movement have changed remarkably in the last fifty years, major analytical advances in home range analysis centre around how to more sophistically model fundamentally the same thing (i.e., how to best meet assumptions of a fixed mean location). This is in contrast to the ideas that lie at the centre of the home range concept (Burt, 1943), which are remarkably more nuanced and flexible. For many species there is no fixed and immutable home range, rather it is a multi-scale nonstationary quantity that varies over space and time. There are a number of potential approaches one might explore in modelling this, including state-switching models (e.g. Michelot and Blackwell, 2019) and models that allow home ranges to emerge mechanistically from individual movements (e.g. agent based models). Whatever the route, there is a clear need for a new non-equilibrium, non-stationary paradigm of home ranges and it is likely to represent an exciting development for spatial ecology over the coming years.

6.1.3 *Lions exhibit water-dependent thermal performance when moving through a semi-arid savannah*

My final data chapter uses collar-borne GPS devices with inbuilt temperature loggers to match high resolution (hourly) information on animal movement and their thermal environment to explore thermal performance—measured as whole organism movement—in a semi-arid population of lions. The findings demonstrate that the relationship between lion peak movement performance and temperature is clearly context-dependent and varies between seasonal availability of water and sex. While the approach I have taken (thermal performance curves; TPCs) is widely used in ectothermic species, and under laboratory conditions, studies measuring performance in natural systems is far rarer. This is likely partially since collecting sufficient data to test such hypotheses in natural systems requires

extensive long term data collection including many individuals in the population and a long enough time to cover the range of temperatures experienced in the wild. To my knowledge this is the first time the methodology has been applied to large mammals, something that was made possible by, and highlights the incredible value of, long-term monitoring projects, such as the Hwange Lion Project and Leopard Ecology & Conservation, who have both contributed data to this thesis.

While the measurements I use in this study for movement rate and the temperatures experienced by animals have caveats, the patterns observed are clear and closely match ecologically grounded hypotheses about lion movement biology. The approach is also widely applicable to other species where movement data and information on temperature is available, providing great potential for exploring how species e.g., across trophic levels might differentially respond to changing environment, something that will be important for understanding how ecosystems as a whole might fare under forecasted future conditions. Studies have recognised that climatic variables are important drivers in the demography of lion populations (Celesia *et al.*, 2009), we add to this story by showing how whole organismal performance in the context of animal movement is limited by temperature and water. In this chapter, I consider thermal performance at the population level, but to better understand underlying intraspecific variation a valuable extension would be to explore individual heterogeneity in thermal traits. What plasticity exists in the optimal temperature for movement performance in lions and their upper capacity for movement at high temperatures, or under drought limiting circumstances?

6.2 RUNNING THEMES AND CONCLUSIONS

The capacity of animals to move, in the context of global change is something that will interact with habitat fragmentation and landscape connectivity (the focus of earlier chapters in the thesis) as animals must both be able to reach suitable habitat and persist once they arrive there. It also has clear links to human activity, via the additional stress proximity to human activity places on animals, which may in turn have physiological and behavioural implications that interact with how species perform under environmental stressors. Understanding long term viability for wild populations will require an integrated understanding of each of these factors, as well as how they interact. This thesis contributes pieces of the story towards our understanding of these themes in lions, but also opens up a number of avenues for future research.

Throughout the thesis, one message is clear: that to make sound inference about spatial ecology, especially when these inferences are intended for management purposes, you need rigorous interrogation of the methodological approaches (Chapter 4), as well as independent validation of model outputs, bearing in mind the end-use and the biological process they are intended to capture (Chapter 3). Sufficient validation of models has been labelled the "Achilles' heel" of connectivity modelling (Laliberté and St-Laurent, 2020) but is clearly necessary if we are to build defensible land management plans, and have confidence that they will provide the services intended for wildlife.

One major roadblock in achieving this is to ensure we have sufficient data from enough locations and individuals to be able to perform such evaluation of models. Long term research sites provide incredible access to this and need to be valued appropriately for the insights they can generate and their importance to research and conservation

purposes. This means dedicated funding to support long-term research sites, and recognition of the resource they provide. Not only is this data important for evaluation of models, but also allows for insights into fundamental ecological processes, as they provide data that ranges across the environmental variation present both intra- and inter-annually in natural systems, something I made use of in my final data chapter (Chapter 5). This is not something that would be possible to generate from data collected on the average time scale of a PhD or funding call.

A further challenge is to ensure that cutting edge methodology and gold standards in research practice are translated into use in applied research. As mentioned above in section 6.1.2 there can be a number of barriers to this. However, encouragingly there are groups, with strong statistical backgrounds, working towards making these methodologies easier to implement for a wider range of ecologists, with different backgrounds. One example of this is the development of the ctmmweb app (https://ctmm-initiative.github.io/ctmmwebdoc/). This is built upon the eponymous R packages, and provides point and click functionality to upload tracking data and carry out sophisticated analyses following a pre-defined work flow and advice for visual diagnostics of the data. Efforts such as this that reduce the learning curve and reduce the barrier to uptake of new methods provide an invaluable resource for applied researchers. Another avenue likely to lead to improvements in this arena would be greater dissemination of results across a wider range of platforms. Even in remote field sites, access to the internet is improving, and easily digestible blogs, with clear messages are likely to be more convincing than very technical research papers – as well as imminently more accessible, given the lack of paywall.

Another clear message that comes out of the research in this thesis is the value in, and need for, metareplication of studies. Here I generate insights into lion ecology from multiple sites across their range in the Kavango-Kalahari ecosystem. However, there remains much need to evaluate how response of wildlife to change in the context of different landscape structures, water, human footprint and productivity regimes. Understanding how populations behave at the extremes of their niche is interesting from a fundamental ecology perspective, and can shed light on the plasticity of behaviours present in species, but would be best complimented with comparison from across their ranges. Something that will be key for understanding what free-standing variation and capacity for adaptation exists in wildlife faced with todays changing world.

In this thesis I make use of established approaches that lie at the heart of applied spatial ecology, such as home range analyses, connectivity models and animal displacement. But I also pair these with approaches from other fields (such as thermal biology; Chapter 5) and developed on different study species (e.g., the dispersal threshold method from an avian species; Chapter 3). Wildlife populations worldwide face a multitude of challenges and threats, both directly from humans and indirectly as a result of human-induced global change. To understand the impacts these have on wildlife and mitigate against them, we are going to need to work between disciplines and take an integrated approach to research and conservation planning. One example of this is the advent of climate connectivity models (Keeley *et al.*, 2018), that recognise the emerging challenge of connectivity design, specifically to facilitate movement in response to climate change.

For me personally, I have felt that I have gained a lot from exposure to researchers working in very different biological fields to me, via collaborative efforts and more informal discourse with other researchers. Both in terms of the expertise available out there to complement your own research, and the types of approaches that are out there. As part of my DPhil project, the NERC DTP at Oxford, and my involvement with the wildlife and research community in southern Africa, I have been exposed to researchers working across a range of species from ant communities to plants to large mammals, and disciplines such as climate and physical sciences, earth sciences, and statistics, as well different research groups. This is something that has without a doubt influenced my research. I think more broadly the types of challenges we face in modelling and understanding complex natural systems are something that we must approach collaboratively and make use of the hive mind of expertise that exists worldwide. This is something I feel strongly will benefit the field of applied research and ensure we have the knowledge and the tools required to best manage species and land for wildlife, and also future human generations.

7

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A

Permits & Ethical Review for thesis fieldwork

A.1 ETHICAL REVIEW APPLICATION FOR AWERB

Introduction and Background

Leopard Ecology & Conservation (LEC) was established as a non-profit conservation organisation in 2000 by Monika Schiess-Meier, to promote research and the long-term conservation of leopards (Panthera pardus) in Khutse Game Reserve (KGR) and the southern regions of the Central Kalahari Game Reserve (CKGR), Botswana. In 2005, the increasing conflict between lions and livestock owners led to the expansion of the project to include lions (Panthera leo). LEC have now collected ten years of scientific data, including observations, blood samples and GPS collar data on the lion population in the KGR and CKGR. There are currently 10-12 individual lions collared at any one time.

The lion project remains on-going and towards the end of 2014, LEC finalised its five-year research and work plan "to make a meaningful contribution towards the long-term conservation of large felid predators as key components of a healthy, functioning ecosystem in Botswana". This proposed DPhil project will be completed in partnership with LEC and forms part of their lion research. It will help to support their five-year aim, via contributing towards the following project objectives:

- Monitor lion demographic trends within KGR and southern CKGR as well as neighbouring communal grazing areas.
- Improve understanding of habitat requirements of lions within existing protected

areas, using KGR and CKGR as study areas.

- Improve understanding of predation and habitat selection patterns of lions within communal grazing areas outside protected areas.
- Investigate appropriate strategies to reduce and mitigate human-predator conflict and enhance the conservation opportunity within the study area.

This project aims to better understand how lion populations move through and interact with their landscape and how this interfaces with human-wildlife conflict issues. A thorough understanding of these processes will lead to the development of more informed conservation management strategies and will thus provide benefit for both the resident lion populations and human inhabitants surrounding the protected areas.

Work Components

My involvement in this project involves only observational study, combined with statistical and modelling techniques in order to get the most out of the existing datasets. Although Oxford University (WildCRU) does not have primary responsibility for this lion research (i.e., this trapping and handling would take place anyway) I will use the collar data (GPS positions and activity score) to create models that describe how lions move through their landscape and how their activity varies in different land-use types. For example, by simulating alteration to the permeability of the landscape, I will replace the need to actually alter the landscape, thus eliminating the potential impact on the population.

Animal Handling: Collaring procedure

Lions are collared by LEC as part of a long-term monitoring program with the permission of the Department of Wildlife and National Parks (DWNP, permit number EST 8/36/4 XXIX (42)). This has been ongoing since 2005, and is expected to continue into the future for at least the next five years. It is LEC policy that at least one male and one female from

each group of lions are collared. By visiting these collared animals once a month, this allows LEC to observe the majority of individuals in the study area on a regular basis. The lifespan of the collars LEC use varies between 1.5-2.5 years depending on the settings of the collar. As mentioned above, between 10-12 lions are collared at any one time. In order to maintain this, animals are caught and collared when the battery life is at an end. Per year, this means approximately 6 animals will be caught and collared. This collaring is performed in accordance with the 2012 ethical approval given to Paul Trethowan and Andrew Loveridge by AWERB. All procedures are undertaken with the permission of the DWNP and are performed by a skilled veterinary practitioner in compliance with all local regulations and international standards.

In order to minimise undue stress and maximise safety, darting is carried out when the lion is relaxed and presents a clear target (either on the rump or shoulder). Small dart needles (1.5 x 25mm) are used to reduce the risk of injury to the animal in case the dart strikes outside of the desired large muscle groups. In order to minimise the risk of this, LEC employs a highly experienced veterinary practitcioner who has been darting wild felids for many years. During the procedure lions are monitored carefully (temperature and breathing) and are placed in a shaded area to reduce the risk of the lions becoming hyperthermic. Additional precautions, such as keeping water nearby to cool the animal are undertaken. There have been no complications arising from the collaring procedures in any of the 21 lions LEC have immobilised for collaring. After the procedures are completed the lions are monitored for the duration of their recovery process in order to ensure the animal's safety while its ability to protect itself from other lions or predators may be compromised by latent drug effects.

Animal Observation

The collars currently deployed (Vectronics GPS Plus Iridium; 1.4kg i.e. <2% of an average adult female lion's weight) return one GPS location per hour and an averaged measure of acceleration every 64 seconds on two-axis. From the next collaring event, they will also have a small (approximately 60g) external biologger attached with tri-axial accelerometer functions, to measure Overall Dynamic Body Acceleration (ODBA). This will provide even finer-scale activity measurements, recording tri-axial acceleration at a sub-second resolution. In order to link these activity scores to actual lion behavoiurs e.g. walking, hunting, sleeping, some ground-truthing is required based on observation.

In order to observe the lions I will be downloading their last known GPS location remotely and then driving out to observe focal individuals directly through binoculars. I will then record their behaviour and use this to label known time-sequences of output from the collars. This will greatly add to the value of the existing dataset as models can then be trained, using the labelled output, to recognise different activities from the collar output alone. These models will reduce the need for further observation and interference in the future, as they can be applied to future activity data in order to interpret the collar output without the need for direct observation.

In addition to behavioural data, I will also visually assess and record body condition and belly-fat score on a scale of 1-5 to give an indication of the health of the animal and time since their last meal. I will be using Vibrissae (whisker) spot patterns to individually identify lions, a method used widely and successfully. Existing facial and other scars, ear notches, nose colour and scarring and mane colour, shape and size will also be used in conjunction with whisker spots. Although this requires a large amount of rather time

comsuming preliminary work, it will mean that no other physical marking procedure will be needed to identify lions.

LEC employ a number of indigenous San trackers, who are well known for their outstanding animal tracking abilities (Stander et al. 1997) and assist in the process of finding and observing lions. The trackers working in this study have spent most of their lives in the CKGR as hunters and gathers, following a tradition of tracking and interpreting spoor. They are very familiar with the landscape and the behaviour of the wild animals, and using their expertise allows us to reduce the amount of time spent locating and/or potentially disturbing the lions.

Ultimately, my individual work causes no additional direct intervention with lions. I rely on procedures agreed by AWERB in 2012 for trapping / sedating / handling protocols. There have been no adverse effects due to processing or tracking lions since this 2012 permission was granted.

A.2 RESEARCH PERMITS

PRIVATE BAG BO 199
GABORONE
BOTSWANA
REFERENCE: EWT 8/36/4 XXXIX (54)

TEL: (+267) 3914955
FAX: (+267) 3951092

REPUBLIC OF BOTSWANA

MINISTRY OF ENVIRONMENT, NATURAL
RESOURCES CONSERVATION AND TOURISM

6th April, 2017

Stephen R. Henley
Leopard Ecology Conservation
Private Bag BR7
Gaborone

EXTENSION OF RESEARCH PERMIT – KALAHARI LEOPARD AND LION ECOLOGY AND CONSERVATION IN KHUTSE GAME RESERVE AND THEIR CONFLICT WITH HUMANS

We are pleased to inform you that the research entitled: "**Kalahari leopard and lion ecology and conservation in Khutse Game Reserve and their conflict with humans. (EWT 8/36/4 XXVIII (26)** is extended from the **1st May 2017** to **31st December 2017**.

The following individuals are covered under the extended permit:

1. Dr Stephen Henley-Principal Researcher
2. Ms Monika Schiess-Meier
3. Mr Fritz Schiess
4. Mr Philip Schiess
5. Ms Genevieve Finerty
6. Mr Tshoganetso Gagosimologe
7. Mr Pagiso Ithuteng
8. Mr Kagiso Malefo
9. Mr Mosepele Mamou
10. Mr Supula Monnaanoka
11. Mr Phalatsa Nkadima

Our Mission: *To protect the environment; Conserve the country's renewable and natural resources; Derive value out of environment for the benefit of Botswana*

BOTSWANA

12. Mr Keitumetse Ngaka
13. Mr Keolebetse Otukile
14. Mr Sokwa Puridaroma
15. Mr Bontle Raseme
16. Mr Ongaletswe Segwaba
17. Mr Tshepho Tsito

Kindly note that veterinarians have been excluded but can be endorsed on capture permits as and when necessary to do so.

Please note that conditions of the above permit (as extended) still apply.

Yours faithfully

Dr Michael Flyman
FOR/ACTING PERMANENT SECRETARY

cc: Director, Department of Wildlife and National Parks

Our Mission: *To protect the environment; Conserve the country's renewable and natural resources; Derive value out of environment for the benefit of Botswana*

BOTSWANA

TELEPHONE: 3914955
TELEGRAMS: MEWT
TELEX:
TELEFAX: 3914861
REFERENCE: EWT 8/36/4 XXVIII (26)

REPUBLIC OF BOTSWANA

MINISTRY OF ENVIRONMENT,
WILDLIFE AND TOURISM
PRIVATE BAG BO 199
GABORONE
BOTSWANA

ALL CORRESPONDENCE MUST BE ADDRESSED TO
THE PERMANENT SECRETARY

13th November 2014

S.R. HENLEY
PRIVATE BAG BR 7
GABORONE

Email: leopardecology@gmail.com

REQUEST FOR RENEWAL OF A RESEARCH PERMIT: KALAHARI LEOPARD & LION ECOLOGY & CONSERVATION IN KHUTSE GAME RESERVE & THEIR CONFLICT WITH HUMANS : EWT 8/36/4 XXVIII (9)

Your request for renewal of the above permit received on the 16th October 2014 refers.

Approval is given for the renewal of your permit from the **30th April 2015 to the 30th April 2017.**

Please note that the conditions of the above permit still apply.

Thank you

Yours Faithfully

G. Tapeng
FOR/PERMANENT SECRETARY

cc. Director, Department of Wildlife and National Parks

Our Mission: *To protect the environment; Conserve the country's renewable and natural resources; Derive value out of environment for the benefit of Botswana*

BOTSWANA

PRIVATE BAG BO 199
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BOTSWANA

TEL: (+267) 3914955
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REPUBLIC OF BOTSWANA

MINISTRY OF ENVIRONMENT, NATURAL RESOURCES CONSERVATION AND TOURISM

REFERENCE: ENT 8/36/4 XLVI (32) **3rd September 2019**

Research Coordinator
Leopard Ecology & Conservation
Private Bag BR7, Gaborone
Botswana

Email: s.henley@leopardecology.com
p.kegakilwe@leopardecology.com
monika.schiess@ieu.uzh.ch

Dear Sir,

RESEARCH PERMIT: KALAHARI LEOPARD AND LION ECOLOGY AND CONSERVATION IN KHUTSE GAME RESERVE AND THEIR CONFLICT WITH HUMANS.

We are pleased to inform that you are granted permission to conduct research, for a study entitled **"KALAHARI LEOPARD AND LION ECOLOGY AND CONSERVATION IN KHUTSE GAME RESERVE AND THEIR CONFLICT WITH HUMANS."**

The research will be conducted in these areas – **Khutse Game Reserve, southern Central Kalahari Game Reserve and neighbouring grazing lands.**

This permit is valid from **4th September 2019 to 31st December 2024.**

This permit is granted subject to the following **conditions**:

1. The permit does not give authority to enter premises, private establishments or protected areas. Permission for such entry should be negotiated with those concerned.
2. You conduct the study according to particulars furnished in the approved application and / or proposal.
3. You shall, where necessary to do so, duly consult communities in or around the study sites to explain the purpose of your research.
4. Government of Botswana shall be duly acknowledged in all research outputs.

5. Copies of research outputs from the study shall be deposited directly with the Ministry of Environment, Natural Resources Conservation & Tourism HQ and other institutions as designated on the application form.

6. This permit is not transferable.

7. Failure to comply with any of the above conditions may result in the immediate cancellation of the permit.

8. This permit covers the following individuals:

Alessandro Araldi
Genevieve Finerty
Tshoganetso Ernest Gagosimologe
Tefo Gabanapelo
Stephen Henley
Pogiso Ithuteng
Mosepele Mamou
Rosemary Miles
Gana Moisapodi
Dikgang Mokgweba
Sebula Monnaanoka
Keitumetse Ngaka
Phalatsa Nkadima
Keolebetse Otukile
Sukwa Poditaroma
Fritz Schiess
Philipp Schiess
Monika Schiess-Meier
Meno Tshiama
Mpho Tshiama
Sena Tshiama
Tshepho Tsito

Yours Faithfully,

Dr Michael V. Flyman
FOR / PERMANENT SECRETARY

MINISTRY OF ENVIRONMENT, NATURAL RESOURCES CONSERVATION & TOURISM
RESEARCH & DEVELOPMENT UNIT
04 SEP 2019
TEL: +267 3914955
BAG BO 199, GABORONE

Mission: *The Ministry exists to protect, conserve and derive value out of natural and cultural resources and to promote a sustainable environment for the benefit of the nation.*

BOTSWANA

PRIVATE BAG BO 199
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BOTSWANA

TEL: (+267) 3914955
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REFERENCE: EWT 8/36/4 XXXX (140)

REPUBLIC OF BOTSWANA

MINISTRY OF ENVIRONMENT, NATURAL RESOURCES CONSERVATION AND TOURISM

14th December 2017

Field Coordinator
Leopard Ecology and Conservation
Khutse Game Reserve
C/o Private Bag BR7
Gaborone

Dear Dr Stephen Henley,

EXTENSION OF RESEARCH PERMIT EWT 8/36/4 XXVIII (26) – KALAHARI LEOPARD AND LION ECOLOGY AND CONSERVATION IN KHUTSE GAME RESERVE AND THEIR CONFLICT WITH HUMANS

We are pleased to confirm the following amendments to your Research Permit Ref. EWT 8/36/4 XXVIII (26), as previously amended by EWT 8/36/4 XXXIX (54)):

1. Validity of the research permit is extended from **1st January 2018** until **31st December 2019**.

2. The extended permit covers the following individuals:

   Dr Stephen HENLEY
   Monika SCHIESS-MEIER
   Keitumetse NGAKA
   Tshepho TSITO
   Fritz SCHIESS
   Philip SCHIESS
   Genevieve FINERTY
   Tshoganetso GAGOSIMOLOGE
   Pagiso ITHUTENG
   Kagiso MALEFO
   Mosepele MAMOU
   Supula MONNAANOKA
   Phalatsa NKADIMA
   Keolebetse OTUKILE
   Sokwa PURIDAROMA
   Bontle RASEME
   Ongaletswe SEGWABA

3. Please note that conditions stipulated in the original permit still apply.

Yours faithfully,

Dr Michael V. Flyman
FOR/PERMANENT SECRETARY

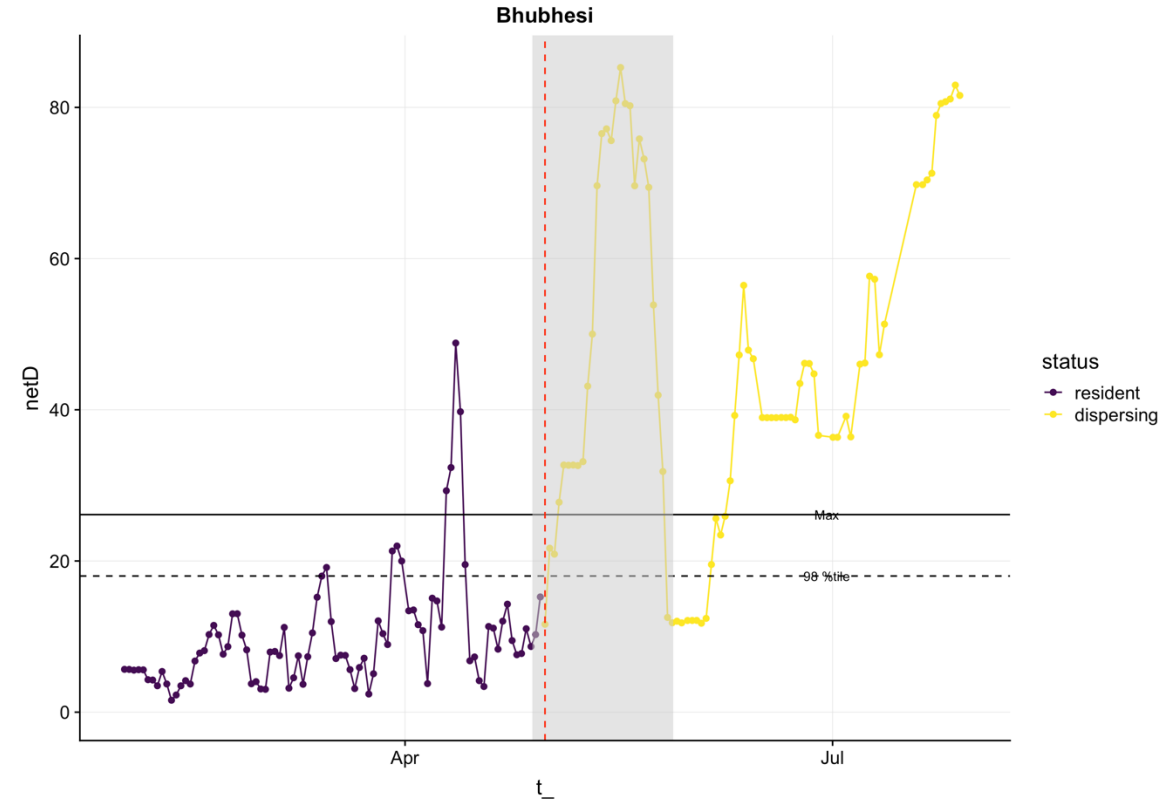
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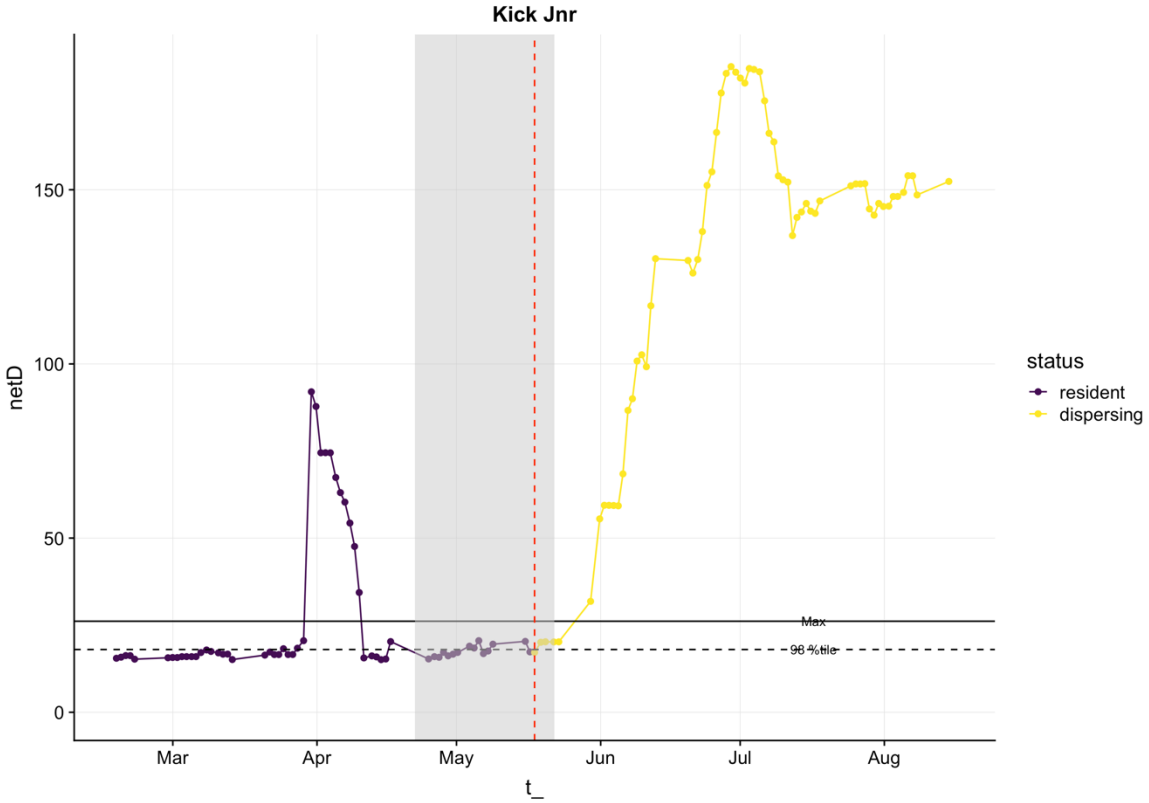
cc. Regional Wildlife Officer – South Central
Director, Department of Wildlife and National Parks

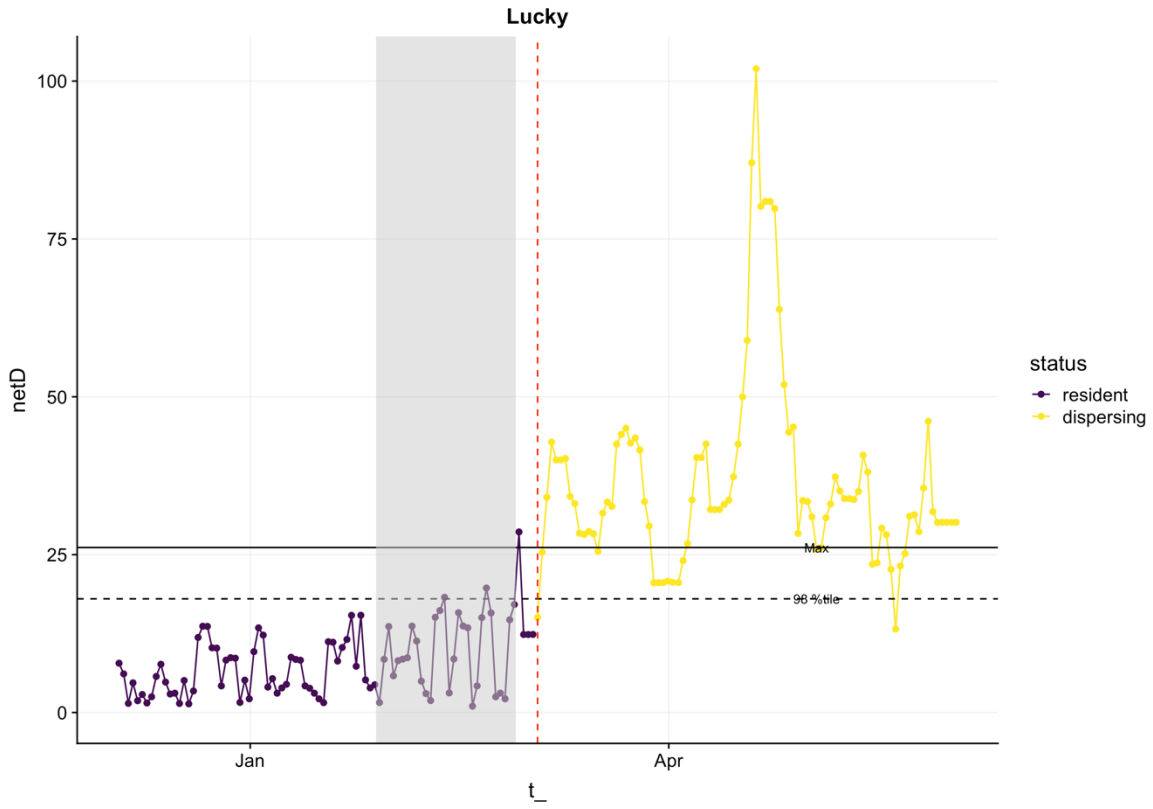
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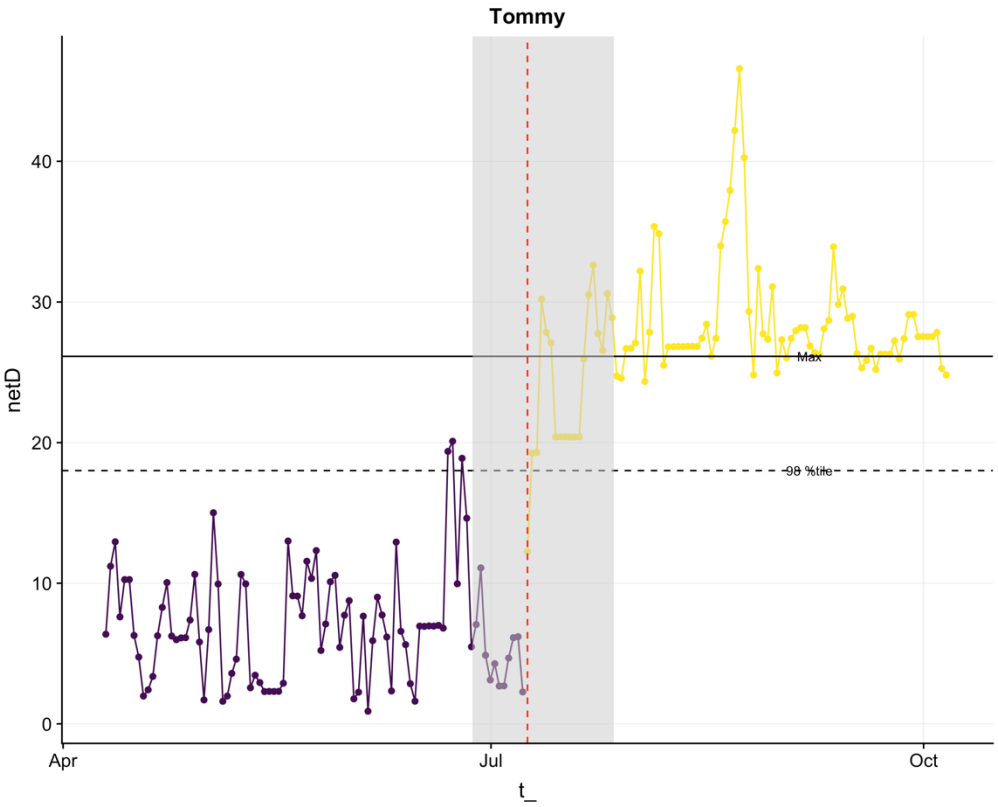
Supplementary results from distance-threshold approach for identifying periods of dispersal

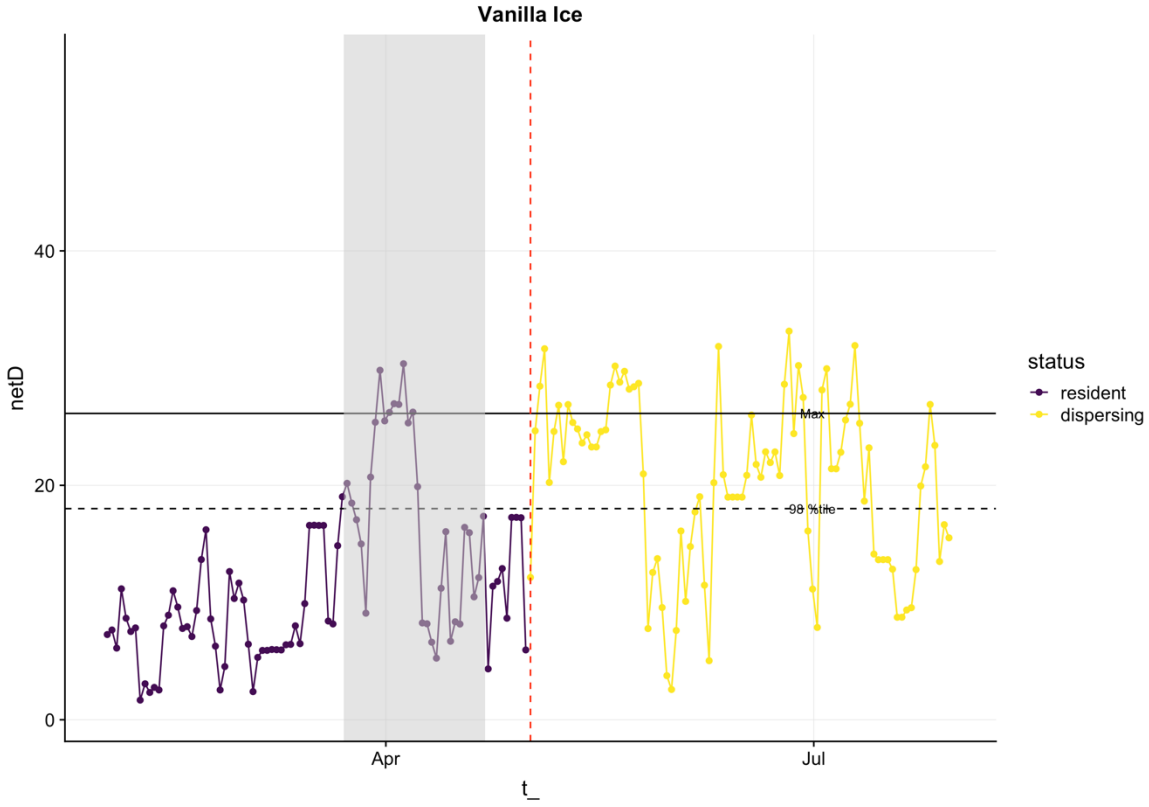
The following figures show net squared displacement from the centroid of the first three months of GPS points for each of our five subadult male lions with labelled dispersal data. The grey shaded boxes represent the 30-day window where dispersal was estimated to occur based on field observation of the last time subadults were seen with their natal prides (Elliot, Cushman, Loveridge, *et al.*, 2014; Elliot, Cushman, Macdonald, *et al.*, 2014; Elliot, Valeix, Macdonald, *et al.*, 2014). The red dashed lines indicate the point of dispersal estimated from movement data alone. In two cases (Lucky and Vanilla Ice), the movement point of dispersal fell outside of the observation-derived window by a margin of days (5 and 10 days, respectively), showing overall high agreement between the two approaches.


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C

CTMM Error Calibration & Data Processing

C.1 DEVICE CALIBRATION & ERROR-MODEL SELECTION

Chapter 3 presents, in full the approach I have taken in accounting for locational error, diurnal changes in movement behaviour and autocorrelation in the telemetry datasets used throughout the thesis. This appendix is an account of the error calibration process and selection of a device-specific error model for use in continuous-time movement models (CTMMs).

The telemetry datasets come from a range of GPS collars over time, and vary in their sampling schedules, the collar models and manufacturers, and the level of detail available on location error. All of the above can contribute to error-induced biases, alongside movement characteristics and habitat structure [Fleming et al., 2020] – if error is ignored, it is quite possible that differential bias could confound biological inference. This is particularly true in the case of fine-scale tracking data where the magnitude of location error might be large in relation to the movement exhibited by the animal between fixes.

On the other hand, there are practical reasons why it might be reasonable to ignore error in some cases. For example if the scales of error are much smaller than the scale of the animal movement between fixes, then it might be safe to ignore error to reduce the computational demands of the analysis. By exploring the impact of location error on derived quantities of interest (e.g. speed estimation[1]) using a subset of the data with the highest level of error information (calibration data and collar derived quality indicator) I was able to make informed decisions based on the scale of movement, magnitude of error and potential bias introduced. This is particularly relevant to my thesis dataset, where some tracking data was only available without error information.

[1] see Chapter 3 Sources of bias in modelling movement and space use of African lions

In this appendix I apply error-model selection to estimate root-mean-square (RMS) user equivalent range error (UERE) using calibration data from two common collar brands for lions: Vectronic Aerospace GmbH and African Wildlife Tracking, hereafter simply Vectronic and AWT. By combining homoskedastic RMS UEREs with dilution of precision (DOP) values returned by devices, we can estimate heteroskedastic location error for each fix.

All analyses were carried out in the R package *ctmm* [R Core Team, 2020, Fleming and Calabrese, 2020] following the general framework presented in Fleming et al. [2020].

```
library(ctmm)
```

Calibration data collection and error-model selection

Calibration data

```
# load calibration datasets
load("./data/cal-10270-a.Rda")
load("./data/cal-10270-b.Rda")
load("./data/cal-19579-a.Rda")
load("./data/cal-19579-b.Rda")
load("./data/cal-19579-c.Rda")
load("./data/cal-19579-d.Rda")
load("./data/cal-11518.Rda")
load("./data/cal-39947-a.Rda")
load("./data/cal-39947-b.Rda")
load("./data/cal-39960-a.Rda")
load("./data/cal-39960-b.Rda")
load("./data/cal-11424.Rda")
load("./data/cal-16378.Rda")
load("./data/cal-16379.Rda")
load("./data/cal-2316-a.Rda")
load("./data/cal-2316-b.Rda")
load("./data/cal-2317-a.Rda")
load("./data/cal-2317-b.Rda")
load("./data/cal-2319.Rda")
# load some deployed collar data - for comparison of dop range etc
load("./data/max-11518.Rda")
load("./data/sem-10270.Rda")
load("./data/maip-19579.Rda")
load("./data/hit-11424.Rda")
load("./data/not-16379-a.Rda")
load("./data/aar-39947.Rda")
load("./data/pfi-16378.Rda")
load("./data/inc-2319.Rda")
load("./data/inn-2316.Rda")
load("./data/mex-2317.Rda")
```

Eight Vectronic collars (five GPS Plus and three Vertex Plus models) were left stationary in a research camp outside Khutse Game Reserve, Botswana to collect calibration datasets. All collars were set to record hourly fixes, to match the sampling rate of the majority of deployed collars.[2] We were also able to recover "opportunistic" calibration data from three AWT IR-SAT collars by retrieving data where the collars were in camp pre-deployment, or after the animal died. A

[2] as suggested in Fleming et al. [2020]

summary of these datasets is provided below in table 1.

Table 1: Summary table of calibration datasets for African Wildlife Tracking (AWT) and Vectronic Aerospace GmbH (Vectronic) collars. Some collars had multiple calibration datasets, denoted by the column *period*.

CollarID	Period	Manufacturer	Model	Duration	NumFix
11518	1	Vectronic	GPS Plus	27.28 days	649
10270	1	Vectronic	GPS Plus	1.88 days	56
10270	2	Vectronic	GPS Plus	1.96 days	48
11424	1	Vectronic	GPS Plus	6.58 days	169
16378	1	Vectronic	GPS Plus	6.58 days	171
16379	1	Vectronic	GPS Plus	6.29 days	162
19579	1	Vectronic	Vertex Plus	1.88 days	53
19579	2	Vectronic	Vertex Plus	1.96 days	48
19579	3	Vectronic	Vertex Plus	6.50 days	157
19579	4	Vectronic	Vertex Plus	6.58 days	159
39947	1	Vectronic	Vertex Plus	6.50 days	157
39947	2	Vectronic	Vertex Plus	6.58 days	159
39960	1	Vectronic	Vertex Plus	6.50 days	157
39960	2	Vectronic	Vertex Plus	6.58 days	159
2316	1	AWT	IR-SAT	0.42 days	11
2316	2	AWT	IR-SAT	0.46 days	12
2317	1	AWT	IR-SAT	1.39 days	28
2317	2	AWT	IR-SAT	1.90 days	38
2319	1	AWT	IR-SAT	0.34 days	9

Some of these periods were rather short, meaning there is a possibility that the full range of possible satellite coverage was not captured. Table 2 presents a summary of the range of error values obtained in the stationary periods compared to data from the same devices deployed on lions (except 33960 where no deployment data was available yet). We can see from this table that shorter deployments are less likely to capture a full range of dop values[3]. Unfortunately we did not have access to the AWT collars to collect further calibration data. Additionally, all of our Vertex Plus collars returned a single Fix Type of the highest quality. Given the consistency across the calibration sets, it seems unlikely that increasing the time would change this. Perhaps for this model, lower quality fixes are only obtained e.g. when an animal is moving.

[3] particularly for the AWT collars

Table 2: Summary table of error information from calibration datasets for African Wildlife Tracking (AWT) and Vectronic Aerospace GmbH (Vectronic) collars. The column *FixTypes* relates to the quality of fix returned by Vectronic colllars, where the possible range of values (from worst to best) are GPS-2D, GPS-3D, val. GPS-3D. Columns suffixed by *C* indicate calibration values, while *D* indicates values from deployed collars as a comparison.

CollarID	TotDuration	FixTypesC	FixTypesD	DOPminC	DOPmaxC	DOPminD	DO
11518	27.28 days	All	All	1.0	13.8	0	
10270	3.83 days	All	All	1.2	12.6	1	
11424	6.58 days	val. GPS-3D	All	1.2	6.6	1	
16378	6.58 days	GPS-3D & val. GPS-3D	All	1.2	7.4	1	
16379	6.29 days	GPS-2D & val. GPS-3D	All	1.2	11.8	0	
19579	16.92 days	val. GPS-3D	All	1.2	8.8	0	
39947	13.08 days	val. GPS-3D	GPS-3D & val. GPS-3D	1.2	7.6	0	
39960	13.08 days	val. GPS-3D	NA	1.2	7.4	NA	
2316	0.89 days	NA	NA	10.0	10.0	10	
2317	3.28 days	NA	NA	10.0	20.0	10	
2319	0.34 days	NA	NA	10.0	20.0	10	

```
# create telemetry objects from calibration data
tel.cal.11518 <- as.telemetry(cal.11518, timezone = "Africa/Gaborone", keep=TRUE)
tel.cal.10270.a <- as.telemetry(cal.10270.a, timezone = "Africa/Gaborone", keep=TRUE)
tel.cal.10270.b <- as.telemetry(cal.10270.b, timezone = "Africa/Gaborone", keep=TRUE)
tel.cal.11424 <- as.telemetry(cal.11424, timezone = "Africa/Gaborone", keep=TRUE)
tel.cal.16378 <- as.telemetry(cal.16378, timezone = "Africa/Gaborone", keep=TRUE)
tel.cal.16379 <- as.telemetry(cal.16379, timezone = "Africa/Gaborone", keep=TRUE)
tel.cal.19579.a <- as.telemetry(cal.19579.a, timezone = "Africa/Gaborone", keep=TRUE)
tel.cal.19579.b <- as.telemetry(cal.19579.b, timezone = "Africa/Gaborone", keep=TRUE)
tel.cal.19579.c <- as.telemetry(cal.19579.c, timezone = "Africa/Gaborone", keep=TRUE)
tel.cal.19579.d <- as.telemetry(cal.19579.d, timezone = "Africa/Gaborone", keep=TRUE)
tel.cal.39947.a <- as.telemetry(cal.39947.a, timezone = "Africa/Gaborone", keep=TRUE)
tel.cal.39947.b <- as.telemetry(cal.39947.b, timezone = "Africa/Gaborone", keep=TRUE)
tel.cal.39960.a <- as.telemetry(cal.39960.a, timezone = "Africa/Gaborone", keep=TRUE)
tel.cal.39960.b <- as.telemetry(cal.39960.b, timezone = "Africa/Gaborone", keep=TRUE)
tel.cal.2319 <- as.telemetry(cal.2319, timezone = "Africa/Gaborone", keep=TRUE)
tel.cal.2316.a <- as.telemetry(cal.2316.a, timezone = "Africa/Gaborone", keep=TRUE)
tel.cal.2316.b <- as.telemetry(cal.2316.b, timezone = "Africa/Gaborone", keep=TRUE)
tel.cal.2317.a <- as.telemetry(cal.2317.a, timezone = "Africa/Gaborone", keep=TRUE)
tel.cal.2317.b <- as.telemetry(cal.2317.b, timezone = "Africa/Gaborone", keep=TRUE)
```

Error models

The next step is to use the *uere.fit* function from the *cttm* package to estimate RMS UERE parameters from the calibration data and perform model selection. Model selection can be used to determine what error information will be the most predictive by importing data with different error information and selecting among the candidate models. You can also compare joint UERE models[4] to individual UERE objects. Model selection is completed using AICc and reduced Z squared statistics[5]. For more details on the goodness-of-fit criteria, see Fleming et al. [2020].

Where a given collar had more than one section of calibration data over time, we always ran these as joint error models as we did not expect device performance to vary substantially over time. For AWT collars, the only error information is ambiguous DOP values, whereas Vectronic collars return DOP alongside information on the fix type, and for the GPS Plus models an estimation of "3D error" in metres.

Vectronic Collars

For the Vectronic Vertex Plus model, all the fixes returned were of the fix type val. GPS-3D, therefore we can only explore whether or not the DOP values are informative.

[4] a joint UERE model assumes there are no substantial differences between collars of the same make/model.

[5] Goodness-of-fit statistic, akin to reduced chi squared

```
# create list of the sections of vertex plus calibration data
list <- list()
list[[1]] <- tel.cal.19579.a
list[[2]] <- tel.cal.19579.b
list[[3]] <- tel.cal.19579.c
list[[4]] <- tel.cal.19579.d
list[[5]] <- tel.cal.39947.a
list[[6]] <- tel.cal.39947.b
list[[7]] <- tel.cal.39960.a
list[[8]] <- tel.cal.39960.b

# remove class (fix type) info
list <- lapply(list, function(t){t$class <- NULL; t })
# fit joint UERE model
UERE.vertex <- uere.fit(list)
# remove dop values to fit error under the assumption on homoskedastic errors
# class already removed
list.nothing <- lapply(list, function(t){t$HDOP <- NULL; t })
UERE.vertex.nothing <- uere.fit(list.nothing)
# apply model selection ot the UERE models fits by summarizing them in a list
summary(list(HDOP=UERE.vertex, homoskedastic=UERE.vertex.nothing))

##                  ΔAICc  Z[red]²
```

```
## HDOP            0.0000 2.515199
## homoskedastic 836.0876 3.202930
```

Although horizontal and vertical error can be assessed, we focus on the horizontal error as vertical movement is not expected to play a role in lion movement in this landscape. Here we can see that the HDOP model outperforms the assumption of homoskedastic errors in both model criteria. It is worth nothing that, we initially ran this analysis with only a single, shorter time series[6] from 19547 where the error model with DOP values did not outperform the assumption of homoskedastic errors. Moving forward with a homoskedastic model would make the assumption that all calibration data and tracking data are collected in the same kind of environment, with respect to satellite reception[7] which is unlikely to be true for the Kalahari environment. This highlights the importance of a sufficient sample size for error calibration.

[6] two periods of two days each

[7] C. Fleming 2020, pers. comms, 7 September

We can then test if there are substantial differences between devices of this make/model by making a list of individual UERE objects to compare to the joint UERE model.

```
# test for differences between devices.
UERES.vertex <- list()
UERES.vertex[[1]] <- uere.fit(list[1:4]) # individual model for 19547
UERES.vertex[[2]] <- uere.fit(list[5:6]) # individual model for 39947
UERES.vertex[[3]] <- uere.fit(list[7:8]) # individual model for 39960
summary(list(joint=UERE.vertex,individual=UERES.vertex))
```

```
##               ΔAICc  Z[red]²
## individual  0.00000 2.490305
## joint      19.93956 2.515199
```

There is some difference between Vertex Plus devices, however this difference is small[8].In an ideal world you would use individual calibration data for each device, however given that we do not have calibration data for every collar deployed, moving forward with the joint model as seems reasonable.

[8] ~0.02 in reduced Z squared

```
data.frame(UERE = c("joint","19547","39947","39960"),
           UERE.est = c(summary(UERE.vertex)[2],summary(UERES.vertex[[1]])[2],
                        summary(UERES.vertex[[2]])[2],summary(UERES.vertex[[3]])[2]))
```

```
##    UERE UERE.est
## 1 joint 1.997354
## 2 19547 2.116092
## 3 39947 2.053207
## 4 39960 1.766568
```

We can see here that the UERE estimate for the devices ranges from 1.77 - 2.12. Given the median DOP seen on deployed collars (around 2.2), this represents a difference of median locational error of 3.90 - 4.62 metres. Testing more devices in the future would shed light on the full extent of device-device error differences.

For the GPS Plus collars, we can test combinations of HDOP and fix type, as well as the collar-derived 3D error estimates. 3 collars did not produce all categories of fix type, therefore we exclude them from this stage of the comparison.

```
list <- list()
list[[1]] <- tel.cal.10270.a
list[[2]] <- tel.cal.10270.b
list[[3]] <- tel.cal.11518
UERE.gpsPlus <- uere.fit(list)
# replace HDOP values with 3D error, remove class info
list.error <- lapply(list, function(t){t$HDOP <- t$X3D_Error; t$class <- NULL; t })
# remove class info
list.noClass <- lapply(list, function(t){t$class <- NULL; t })
# remove HDOP info
list.noHDOP <- lapply(list, function(t){t$HDOP <- NULL; t })
# homoskedastic errors
list.nothing <- lapply(list, function(t){t$HDOP <- NULL; t$class <- NULL; t })
UERE.gpsPlus.error <- uere.fit(list.error)
UERE.gpsPlus.noClass <- uere.fit(list.noClass)
UERE.gpsPlus.noHDOP <- uere.fit(list.noHDOP)
UERE.gpsPlus.nothing <- uere.fit(list.nothing)
summary(list(HDOP.class=UERE.gpsPlus,
             class=UERE.gpsPlus.noHDOP,
             HDOP=UERE.gpsPlus.noClass,
             homoskedastic=UERE.gpsPlus.nothing,
             error = UERE.gpsPlus.error))
```

```
##                  ΔAICc  Z[red]²
## error           0.0000 1.943876
## HDOP.class    235.2614 2.153085
## HDOP          252.8251 2.146653
## class         430.7702 2.251189
## homoskedastic 440.4786 2.202306
```

Here the model based on 3D error is clearly the most informative, both in terms of AICc statistic and reduced Z squared statistic. There is quite a big jump in AICc between error and the other models. The next model down, HDOP.class outperforms HDOP alone based on AICc, but not by reduced Z squared. Where the information is available, the 3D error model is a good candidate for accounting for error.

However, having examined data from deployed lions, 3D error is not always returned for all fixes, meaning this criteria would risk throwing out valid data points. In contrast, all time points with a locational fix returned a DOP value, making this on balance a preferable option. At this stage we can test for differences between these two collars based on a "3D error" model.

```
# test for differences between devices.
UERES.gpsPlus <- list()
UERES.gpsPlus[[1]] <- uere.fit(list.error[1:2]) # individual model for 10270
UERES.gpsPlus[[2]] <- uere.fit(list.error[3]) # individual model for 11518
summary(list(joint=UERE.gpsPlus.error,individual=UERES.gpsPlus))
```

```
##              ΔAICc  Z[red]²
## individual 0.00000 1.948289
## joint      3.68882 1.943876
```

Here the values for individual and joint models are very close for both AICc and reduced Z squared criteria, indicating that differences between devices are small. We can repeat the same thing on all GPS Plus collars for the 3D error models and HDOP only model.

```
list <- list()
list[[1]] <- tel.cal.10270.a
list[[2]] <- tel.cal.10270.b
list[[3]] <- tel.cal.11518
list[[4]] <- tel.cal.11424
list[[5]] <- tel.cal.16378
list[[6]] <- tel.cal.16379
# replace HDOP values with 3D error, remove class info
list.error <- lapply(list, function(t){t$HDOP <- t$X3D_Error; t$class <- NULL; t })
# remove class info
list.noClass <- lapply(list, function(t){t$class <- NULL; t })
# homoskedastic errors
list.nothing <- lapply(list, function(t){t$HDOP <- NULL; t$class <- NULL; t })
UERE.gpsPlus.error <- uere.fit(list.error)
UERE.gpsPlus.noClass <- uere.fit(list.noClass)
UERE.gpsPlus.nothing <- uere.fit(list.nothing)
summary(list(HDOP=UERE.gpsPlus.noClass,
             homoskedastic=UERE.gpsPlus.nothing,
             error = UERE.gpsPlus.error))
```

```
##                    ΔAICc  Z[red]²
## error              0.0000 1.803279
## HDOP             391.5497 2.111434
## homoskedastic 1034.2423 2.332554
```

Error is still the top selected model, followed by HDOP, with both outperforming homoskedastic errors.

```
# test for differences between devices (using 3D error model)
UERES.gpsPlus <- list()
UERES.gpsPlus[[1]] <- uere.fit(list.error[1:2]) # individual model for 10270
UERES.gpsPlus[[2]] <- uere.fit(list.error[3]) # individual model for 11518
UERES.gpsPlus[[3]] <- uere.fit(list.error[4]) # individual model for 11424
UERES.gpsPlus[[4]] <- uere.fit(list.error[5]) # individual model for 16378
UERES.gpsPlus[[5]] <- uere.fit(list.error[6]) # individual model for 16379

summary(list(joint=UERE.gpsPlus.error,individual=UERES.gpsPlus))
```

```
##                ΔAICc  Z[red]²
## individual  0.00000 1.773470
## joint      34.00054 1.803279
```

The difference between joint and individual models with more collars is larger (as might be expected). We can also test the same thing for the HDOP model.

```
# test for differences between devices (using HDOP model)
UERES.gpsPlus <- list()
UERES.gpsPlus[[1]] <- uere.fit(list.noClass[1:2]) # individual model for 10270
UERES.gpsPlus[[2]] <- uere.fit(list.noClass[3]) # individual model for 11518
UERES.gpsPlus[[3]] <- uere.fit(list.noClass[4]) # individual model for 11424
UERES.gpsPlus[[4]] <- uere.fit(list.noClass[5]) # individual model for 16378
UERES.gpsPlus[[5]] <- uere.fit(list.noClass[6]) # individual model for 16379

summary(list(joint=UERE.gpsPlus.noClass,individual=UERES.gpsPlus))
```

```
##                ΔAICc  Z[red]²
## individual   0.0000 1.917494
## joint      169.1021 2.111434
```

The difference here is noticeably larger (~0.03 to ~ 0.19) than the "3D error" – perhaps because 3D error encompasses all error information, rather than just DOP value. Given a balance of trade off between discarding data and increase in error precision, the decision might lie in your evaluation of the relative merits of each. Given the locational error these represent and the relatively large movement of lions at an hourly scale, I opt to move forward with the HDOP model[9]. Again as with the Vertex Collars, it would be worth testing further collars to determine the extent of between device variation, and perhaps a greater variation in the habitat where collars are placed to try to emulate a greater range of fix Types for all collars.

[9] which still significantly outperforms an assumption of homoskedastic errors.

AWT IR-SAT collars

```
list <- list()
list[[1]] <- tel.cal.2316.a
list[[2]] <- tel.cal.2316.b
list[[3]] <- tel.cal.2317.a
list[[4]] <- tel.cal.2317.b
list[[5]] <- tel.cal.2319
# fit joint UERE model
UERE.awt <- uere.fit(list)
# remove dop values to fit error under the assumption on homoskedastic errors
# also remove class (fix type) info as all one class
list.nothing <- lapply(list, function(t){t$HDOP <- NULL; t$class <- NULL; t })
UERE.awt.nothing <- uere.fit(list.nothing)
# apply model selection ot the UERE models fits by summarizing them in a list
summary(list(HDOP=UERE.awt, homoskedastic=UERE.awt.nothing))
```

```
##                   ΔAICc  Z[red]²
## homoskedastic  0.00000 1.476847
## HDOP          10.38727 1.603216
```

Here a homoskedastic error model was selected across both criteria. Given the previous Vertex Plus test, it is posssible that this is because the AWT collars had less input calibration data than Vectronic devices. This apparent lack of informative DOP values could be explained by the narrow range of DOP values obtained during the calibration periods. A venture such as a shared, open database of calibration data for each device would make error calibration more easily accessible in future studies and avoid this issue.

```
# Joint vs individual for HDOP model
UERES.awt <- list()
UERES.awt[[1]] <- uere.fit(list[1:2]) # individual model for 2316
UERES.awt[[2]] <- uere.fit(list[3:4]) # individual model for 2317
UERES.awt[[3]] <- uere.fit(list[5]) # individual model for 2319
summary(list(joint=UERE.awt,individual=UERES.awt))
```

```
##                ΔAICc  Z[red]²
## individual  0.00000 1.571629
## joint      12.32348 1.603216
```

Again here, the individual model is preferred, suggesting there may be between device differences. However, given the benefits in terms of increased sample size[10], I opted for the joint error model.

A summary of the selected error models and the horizontal RMS UERE parameters is presented in table 3.

[10] given each individual dataset is rather short

Table 3: Horizontal error models for selected models, with corresponding goodness-of-fit statistics (ZsqRed) and root-mean-square location error (RMSE). Reduced Z squared (ZsqRed) statistics are given for both the joint and inividualised error model. When these two statistics are similar, error calibration can be assumed to be transferable among devices of these types. Low, high, and point estimates of the RMSE UERE values are given for the joint models. Note that for the AWT IR-Sat devices the HDOP was not significantly better than the null HDOP model of homoskedastic errors.

Manufacturer	Model	Error.Info	RMSE.low	RMSE.est	RMSE.high	ZsqRed.Joint	ZsqRed.Individual
Vectronic	Vertex Plus	HDOP	1.94	2.00	2.06	2.52	2.49
Vectronic	GPS Plus	3D Error	1.54	1.58	1.63	2.11	1.92
AWT	IR-SAT	HDOP	1.98	2.20	2.42	1.60	1.57

```
# save UERE objects for use in subsequent analyses
save(UERE.awt, file = "./data/UERE-awt.Rda")
save(UERE.awt.nothing, file = "./data/UERE-awt-nothing.Rda")
save(UERE.vertex, file = "./data/UERE-vertex.Rda")
save(UERE.vertex.nothing, file = "./data/UERE-vertex-nothing.Rda")
save(UERE.gpsPlus.noClass, file = "./data/UERE-gpsPlus.Rda")
save(UERE.gpsPlus.nothing, file = "./data/UERE-gpsPlus-nothing.Rda")
```

References

C. H. Fleming, J. Drescher-Lehman, M. J. Noonan, T. S. B. Akre, D. J. Brown, M. M. Cochrane, N. Dejid, V. DeNicola, C. S. DePerno, J. N. Dunlop, N. P. Gould, J. Hollins, H. Ishii, Y. Kaneko, R. Kays, S. S. Killen, B. Koeck, S. A. Lambertucci, S. D. LaPoint, E. P. Medici, B.-U. Meyburg, T. A. Miller, R. A. Moen, T. Mueller, T. Pfeiffer, K. N. Pike, A. Roulin, K. Safi, R. Séchaud, A. K. Scharf, J. M. Shephard, J. A. Stabach, K. Stein, C. M. Tonra, K. Yamazaki, W. F. Fagan, and J. M. Calabrese. A comprehensive framework for handling location error in animal tracking data*. *bioRxiv*, page 2020.06.12.130195, jun 2020. DOI: 10.1101/2020.06.12.130195. URL `https://doi.org/10.1101/2020.06.12.130195`.

Christen H. Fleming and Justin M. Calabrese. *ctmm: Continuous-Time Movement Modeling*, 2020. https://github.com/ctmm-initiative/ctmm, http://biology.umd.edu/movement.html.

R Core Team. *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna, Austria, 2020. URL `https://www.R-project.org/`.

C.2 AN EXAMPLE OF ERROR-INFORMED OUTLIER DETECTION

Outlier detection in telemetry data broadly involves filtering for fixes that are deemed to be irreflective of the true animal's movement. A common approach is to filter based on a threshold of dilution of precision (DOP) values (insert citation next time I come across it). This is easy to implement, but is reliant on collars producing informative DOP values, and additionally DOP is not comparable across different device types. I.e. it is a relative value, that should be interpreted in combination with the minimum UERE RMS of the device (cite recent error paper). An alternative approach is to screen for outliers in impossible or improbable spikes of speed (cite Bjornxxx). Outlier detection in the *ctmm* package builds on this by using error information to estimate straight-line speeds between sampled times and core deviation[1]. This information can then be plotted in various ways to identify 'suspicious' relocations based on speed and proximity to the bulk of the data (given the expected error around the location).

In total we removed fewer than ten relocations our raw datasets, and a worked example is given below for the animal Semariri.

[1] distance from the median lon/lat i.e., the bulk of the data

```
load("../ctmm-lion-data/calibration-data/sem.Rda") # load in tracking data
load("../ctmm-lion-data/calibration-data/UERE-gpsPlus-error.Rda") # load in UERE object for GPS Plus Co
tel.sem <- as.telemetry(sem, timezone = "Africa/Gaborone", keep=TRUE) # create telemtry object
```

```
## HDOP values not found. Using ambiguous DOP.
```

```
## Minimum sampling interval of 12 seconds in 10270
```

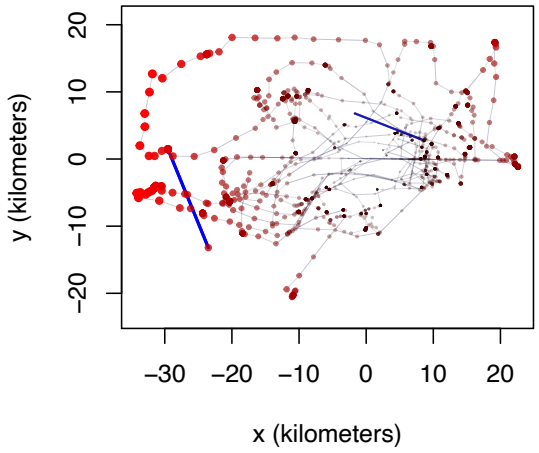
The next step is to 'calibrate' the telemetry object using the UEREs estimated in Appendix 3.1. For the collar Semariri was fitted with (Vectronic GPS Plus), the most supported error model was using the 3D Error values. To ensure *ctmm* recognises these as the error information to use during calibration, we replace the HDOP values with these. We also remove the information stored as "class" as the error model did not include this[2]. We can then use the function *uere()* to calibrate the telemetry object, based on the RMS UERE values.

[2] otherwise error columns will all get "Inf"

```
tel.sem$HDOP <- tel.sem$X3D_Error
tel.sem$class <- NULL
uere(tel.sem) <- UERE.gpsPlus.error
```

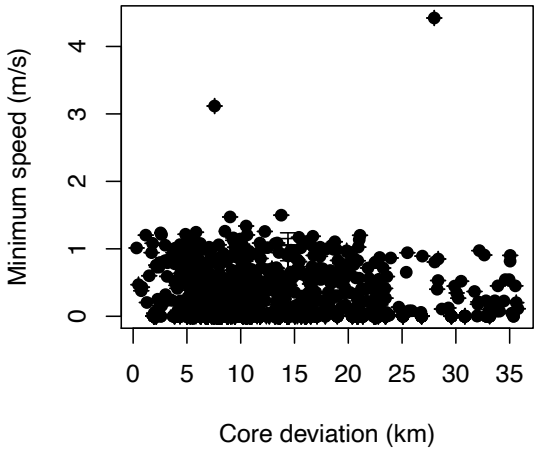
We can then use the function *outlie()* to carry out the outlier detection process.

```
outlie(tel.sem) -> OUT
```



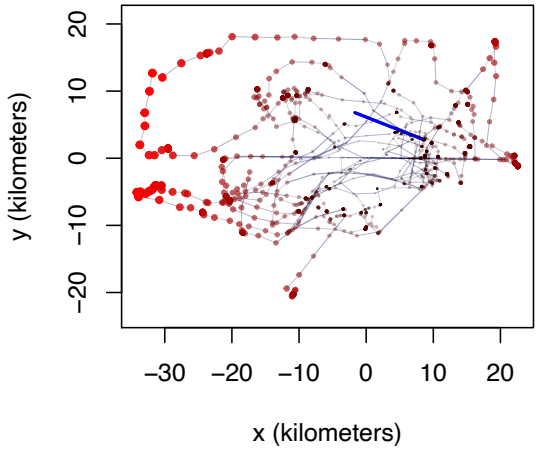
The function generates a dataframe of speeds and core deviation at each timestep, it also generates the above plot as a default. Here, high values for core deviation are shown in red, and high speeds in blue. From this, there are two spikes in blue that look unlikely to represent true animal movement. We can also visualise these in the following way.

```
plot(OUT)
```

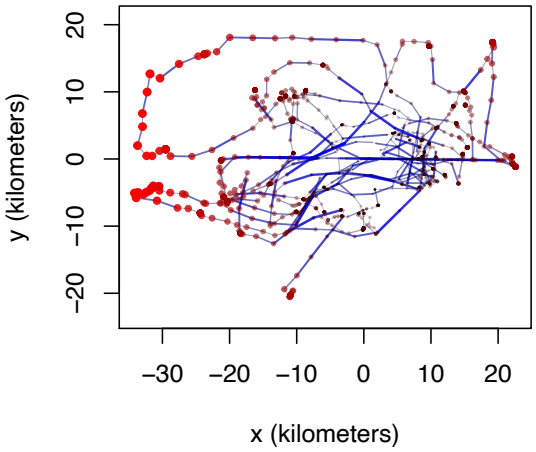


Here we can see that given the apparent error information, there are two clear outliers in terms of speed (corresponding to the blue lines in the first plot). The speed shown here is the minimum speed needed to explain the displacement between points. These values represent a sustained speed of ~ 10-15 km/h which is biologically improbable. We can therefore remove these points and reexamine the remaining data.

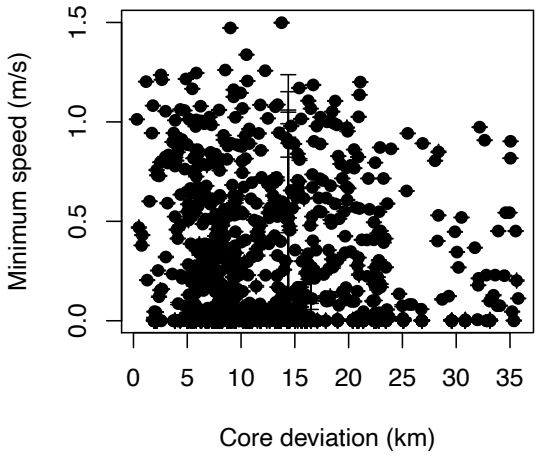
```
BAD <- which.max(OUT$speed)
tel.sem<- tel.sem[-BAD,] # remove first outlier
outlie(tel.sem) -> OUT
```




```
BAD <- which.max(OUT$speed)
tel.sem<- tel.sem[-BAD,] # remove second outlier
outlie(tel.sem) -> OUT
```




```
plot(OUT)
```



This looks much more convincing.

You can find more detail on this process in the *ctmm* error vignette.

C.3 SUPPLEMENTARY RESULTS FOR CHAPTER 4

C.3.1 Likelihood Ratio Tests for beta regression models describing cross-validation outcomes

Effective sample size, dispersion models

KDE_{95}:

```
Models:
m1: perc95.kde ~ dof.area, zi=~0, disp=~1
m2: perc95.kde ~ dof.area, zi=~0, disp=~dof.area
   Df     AIC     BIC logLik deviance  Chisq Chi Df Pr(>Chisq)
m1  3 -53.623 -48.710 29.811  -59.623
m2  4 -57.439 -50.889 32.720  -65.439 5.8163      1    0.01588 *
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1
```

KDE50:

```
Models:
m3: perc50.kde ~ dof.area, zi=~0, disp=~1
m4: perc50.kde ~ dof.area, zi=~0, disp=~dof.area
   Df     AIC     BIC logLik deviance Chisq Chi Df Pr(>Chisq)
m3  3 -34.822 -29.909 20.411  -40.822
m4  4 -41.775 -35.225 24.887  -49.775 8.953      1    0.00277
**
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’
1
```

AKDE95:

```
Models:
m5: perc95.akde.s ~ dof.area, zi=~0, disp=~1
m6: perc95.akde.s ~ dof.area, zi=~0, disp=~dof.area
   Df     AIC     BIC logLik deviance  Chisq Chi Df
Pr(>Chisq)
m5  3 -116.49 -111.58 61.246  -122.49
m6  4 -122.10 -115.55 65.051  -130.10 7.6103      1
0.005804 **
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’
1
```

AKDE50:

```
Models:
```

```
m8: perc50.akde ~ dof.area, zi=~0, disp=~1
m9: perc50.akde ~ dof.area, zi=~0, disp=~dof.area
   Df     AIC     BIC logLik deviance  Chisq Chi Df Pr(>Chisq)
m8  3 -16.152 -11.239 11.076  -22.152
m9  4 -22.766 -16.216 15.383  -30.766 8.6141      1   0.003336 **
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1
```

Effective sample size, conditional models

KDE95:

```
Single term deletions

Model:
perc95.kde ~ dof.area
         Df     AIC    LRT Pr(>Chi)
<none>      -53.623
dof.area  1 -47.515 8.1076 0.004408 **
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’
1
```

KDE50:

```
Single term deletions

Model:
perc50.kde ~ dof.area
         Df     AIC    LRT  Pr(>Chi)
<none>      -41.775
dof.area  1 -31.812 11.963 0.0005425 ***
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’
1
```

AKDE95:

```
Single term deletions

Model:
perc95.akde.s ~ dof.area
         Df     AIC    LRT Pr(>Chi)
<none>      -122.10
dof.area  1 -121.81 2.2931   0.1299
```

AKDE50:

```
Single term deletions

Model:
perc50.akde ~ dof.area
         Df     AIC     LRT Pr(>Chi)
<none>      -22.766
dof.area  1 -24.444 0.32156   0.5707
```

C.3.2 Models describing relationship between home range area, AKDE and KDE methods, and effective sample size

To extract the mean 95% home-range sizes per method, we fit a linear mixed model (implemented in R package *lme4*) describing home-range area estimate as a function of kernel density estimation methods with a random intercept for individual. Summary model output is listed below:

```
Linear mixed model fit by REML ['lmerMod']
Formula: est ~ method + (1 | name)
   Data: hrs.df

REML criterion at convergence: 2339.7

Scaled residuals:
    Min      1Q  Median      3Q     Max
-2.0178 -0.5592 -0.1220  0.4381  4.0476

Random effects:
 Groups   Name        Variance Std.Dev.
 name     (Intercept)  654056   808.7
 Residual             1030090  1014.9
Number of obs: 140, groups:  name, 21

Fixed effects:
            Estimate Std. Error t value
(Intercept)   2057.5      223.6   9.200
methodkde     -706.9      171.6  -4.121
```

The AKDE method is used as reference level in these models. Conditional and marginal R squared values (obtained using *R.squaredGLMM()* from the R package *MuMIn*) were 0.07 an 0.43, indicating high levels of individual variation in mean home-range area.

Four (W2.2, W1.2, W1.3, W2.3) of the top six non-linear functions (shown below in Fig A5.4.1) describing the ratio $AKDE_{95}$:KDE_{95} as a function of effective sample size for

area (N_{Eff}) were from the Weibull function, the other two (LL.2, LL.3) belonged to variants of the log-logistic function.

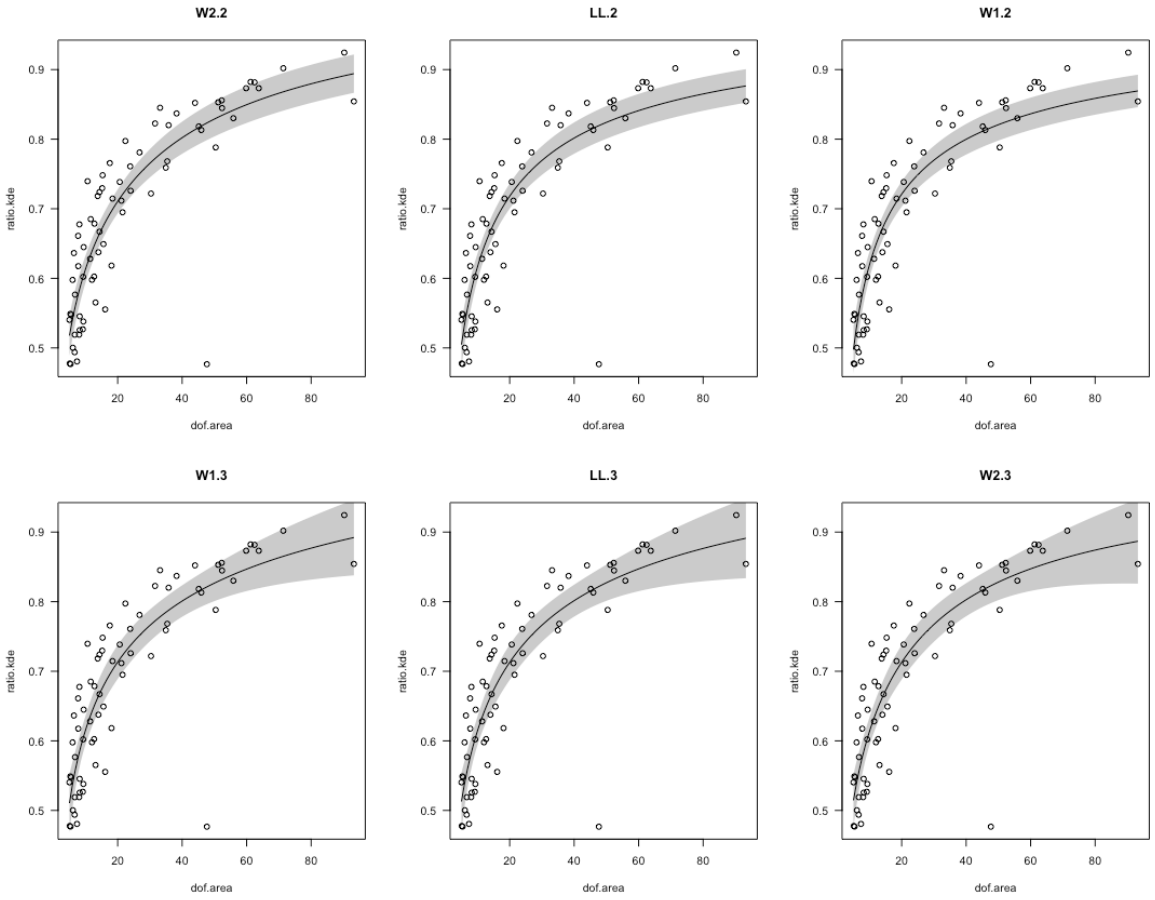


Figure C.3.1 scatterplots of ratio $AKDE_{95}$:KDE_{95} as a function of N_{Eff} for the top 6 best performing non-linear model fits, as determined by AIC.

All top performing models give qualitatively similar results, which is reassuring when difference in AIC is small. The full list of AIC comparisons (as given by the function *mselect* from *drc* package) for candidate models is given below — models are named according to the function call within *drm* model specification, and details of each one can be found in the *drc* help files:

```
         logLik        IC Lack of fit     Res var
W2.2  92.14550 -178.2910          NA 0.004332467
```

```
LL.2  92.06783 -178.1357          NA 0.004342093
W1.2  91.73609 -177.4722          NA 0.004383444
W1.3  92.23609 -176.4722          NA 0.004385764
LL.3  92.22603 -176.4521          NA 0.004387025
W2.3  92.18286 -176.3657          NA 0.004392440
MM.3  92.11753 -176.2351          NA 0.004400646
EXD.3 91.35930 -174.7186          NA 0.004497020
AR.3  91.35930 -174.7186          NA 0.004497020
LL.4  92.23023 -174.4605          NA 0.004452961
W1.4  92.22867 -174.4573          NA 0.004453159
W2.4  92.21651 -174.4330          NA 0.004454707
MM.2  90.13077 -174.2615          NA 0.004589178
G.3   91.05596 -174.1119          NA 0.004536166
L.3   90.75190 -173.5038          NA 0.004575744
G.4   91.19236 -172.3847          NA 0.004586984
L.4   91.16238 -172.3248          NA 0.004590915
G.2   86.44595 -166.8919          NA 0.005098679
L.2   85.33942 -164.6788          NA 0.005262449
AR.2  80.15691 -154.3138          NA 0.006102316
```

The summary output for the top model is printed below:

```
Model fitted: Weibull (type 2) with lower limit at 0 and upper
limit at 1 (2 parms)

Parameter estimates:

               Estimate Std. Error t-value   p-value
b:(Intercept)  0.385697   0.030018  12.849 < 2.2e-16 ***
e:(Intercept) 11.451831   0.738287  15.511 < 2.2e-16 ***
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

Residual standard error:

 0.06582148 (68 degrees of freedom)
```

For our non-linear models describing how the width of the confidence intervals decreases in relation to the point estimate as N_{Eff} increases the top models again included the Weibull and log-logistic functions (Fig C.3.2). While the relationship was well supported for the AKDE method (see model output summary below), there was no convincing relationship for KDE.

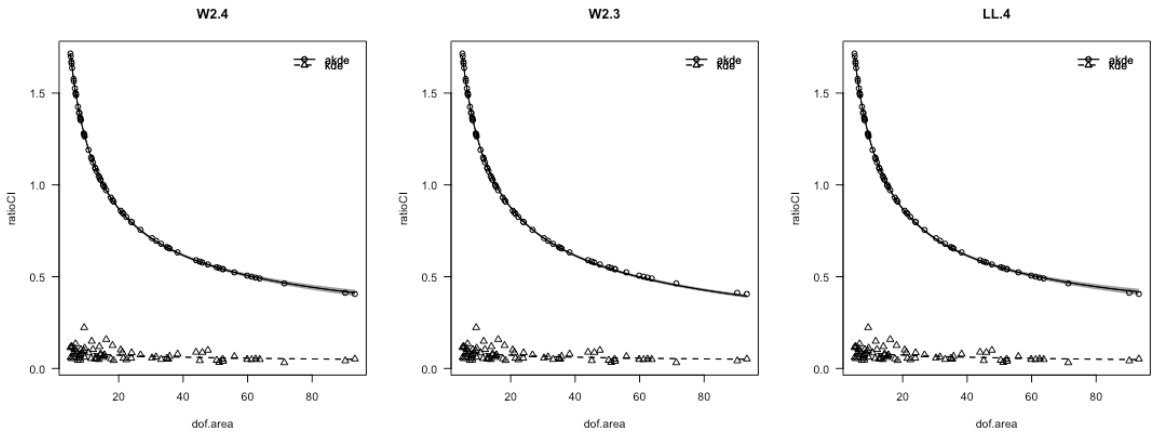


Figure C.3.2 scatterplots of ratio confidence interval width: area estimate as a function of N_{Eff} and method for the top 3 best performing non-linear model fits, as determined by AIC.

Summary output from top model:

```
Model fitted: Weibull (type 2) (4 parms)

Parameter estimates:

         Estimate Std. Error  t-value   p-value
b:akde -0.6334893  0.0531537 -11.9181 < 2.2e-16 ***
b:kde  -0.2634738  0.3543858  -0.7435   0.45852
c:akde  0.1054124  0.0458288   2.3001   0.02301 *
c:kde  -0.0083834  0.0875362  -0.0958   0.92385
d:akde  4.3037886  1.0669368   4.0338 9.237e-05 ***
d:kde   0.1906802  0.3435246   0.5551   0.57979
e:akde  1.5925559  0.9134720   1.7434   0.08359 .
e:kde   1.6694755 16.2693432   0.1026   0.91842
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

Residual standard error:

 0.02210002 (132 degrees of freedom)
```

D

Supplementary materials for Chapter 5

D.1 ADDITIONAL CLIMATOLOGY FIGURES

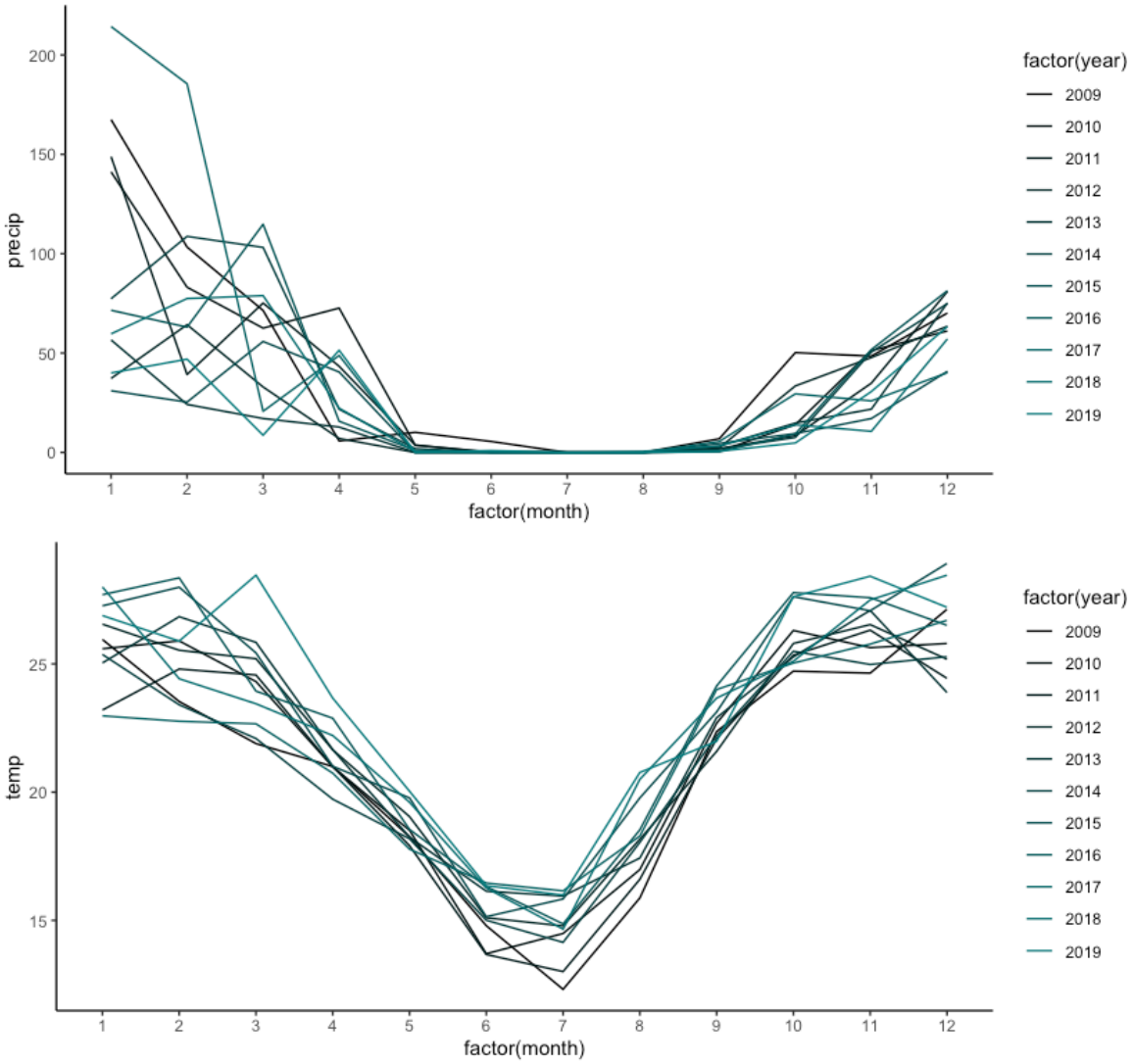


Figure D.1 Monthly precipitation (mm/month) and mean temperature (degrees C) over the study period.

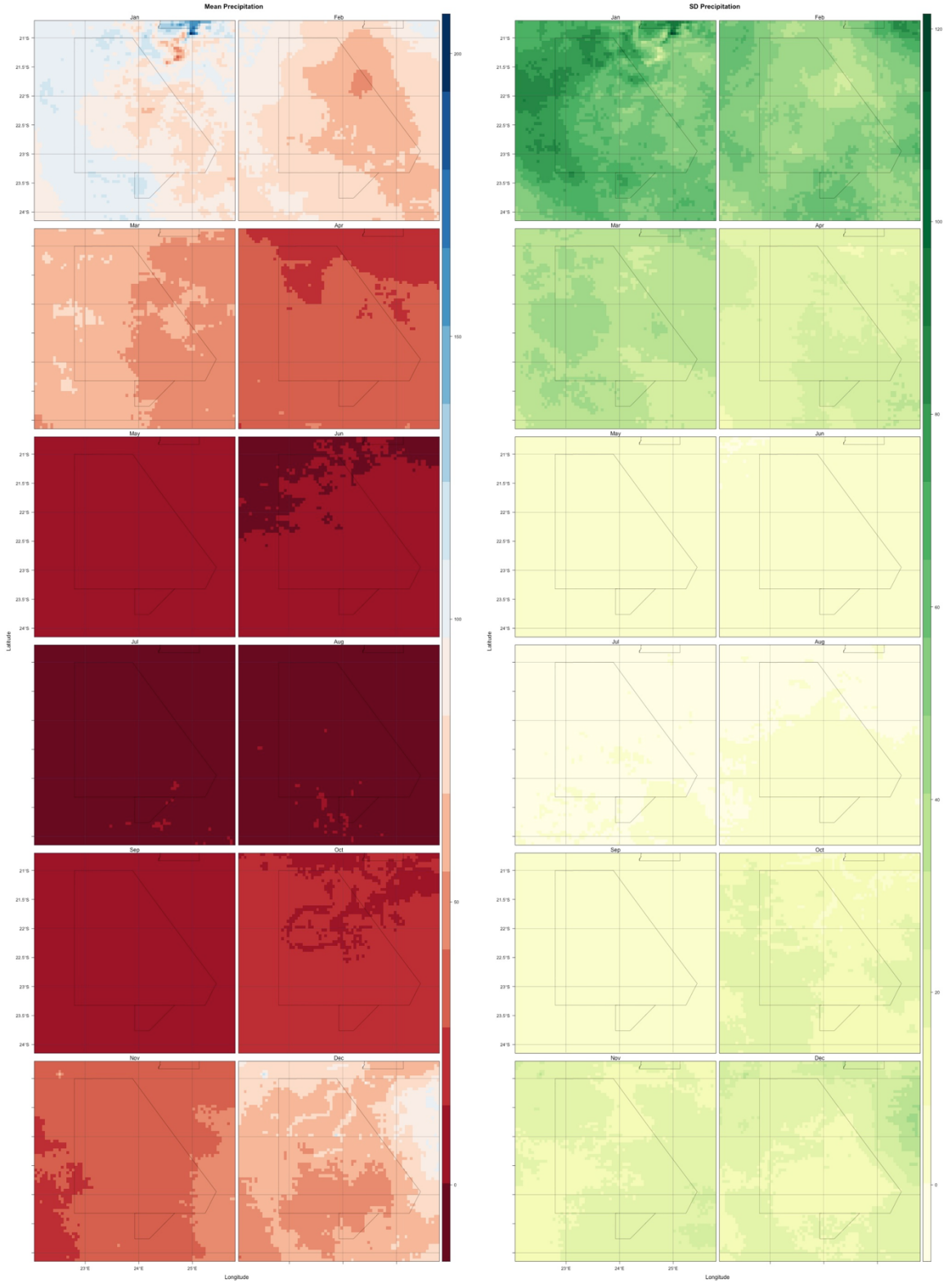


Figure D.2 Monthly precipitation values (mm/month) averaged over each month across the years 2009 – 2019 across the study area.

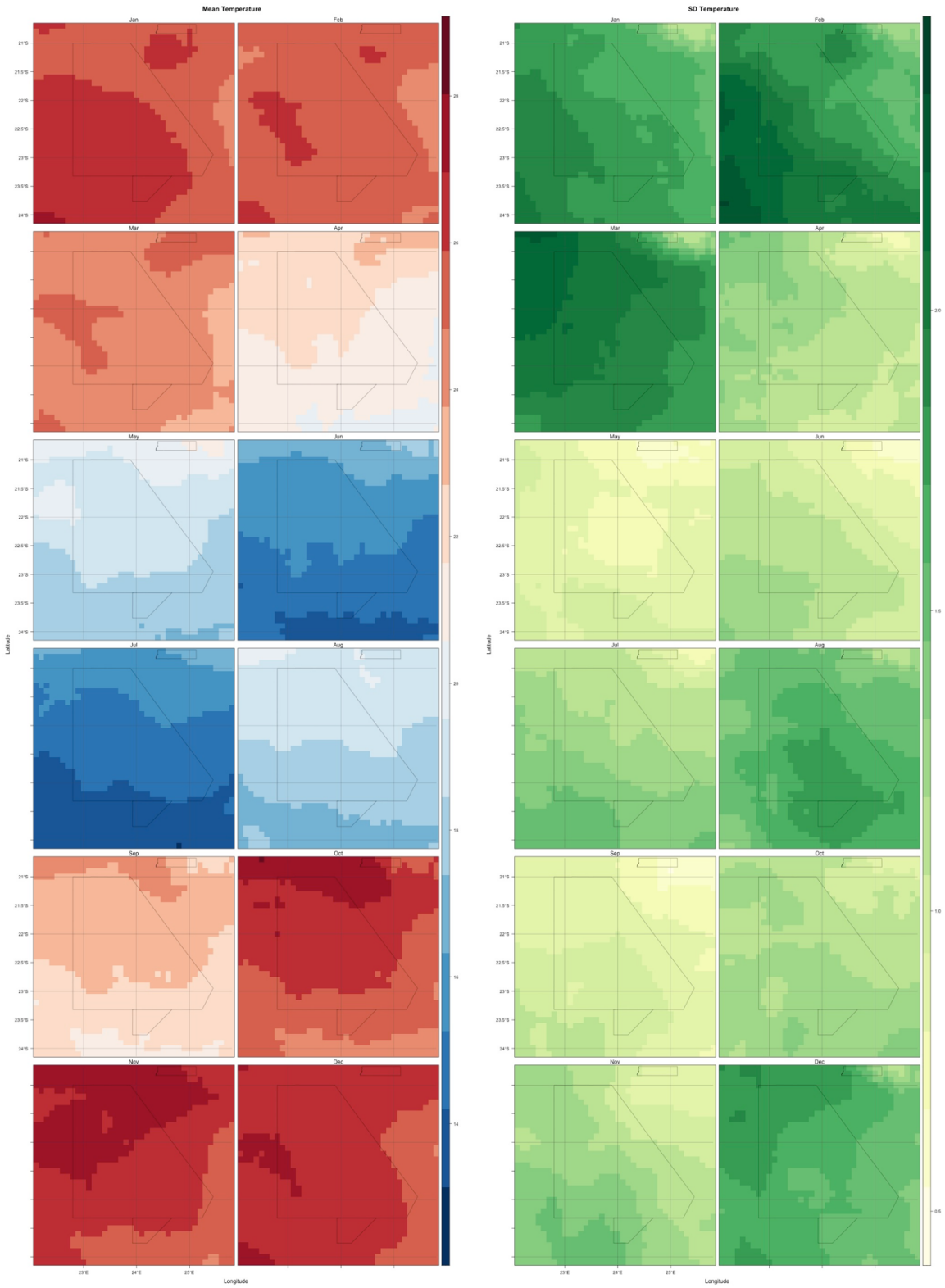


Figure D.3 Monthly temperature values (degrees C) averaged over each month across the years 2009 – 2019 across the study area.

D.2 THERMAL PERFORMANCE CURVE MODEL SELECTION

There are 24 model formulations available in the package rTPC for fitting a thermal performance curve (TPC). The models differ in their parameters, their assumptions about the values rates can take, and their data requirements (more parameters require more data). We fit a candidate subset of the six model formulations that directly estimate the parameter optimum temperature (topt), and take strictly positive rate values, to each of our four datasets (Female/Dry; Female/Rainy; Male/Dry; Male/Rainy; Figure C.4). For each dataset we selected the model formulation with the lowest AICc value (Table C.1) to estimate traits associated with movement performance across a range of thermal conditions (as described in main text).

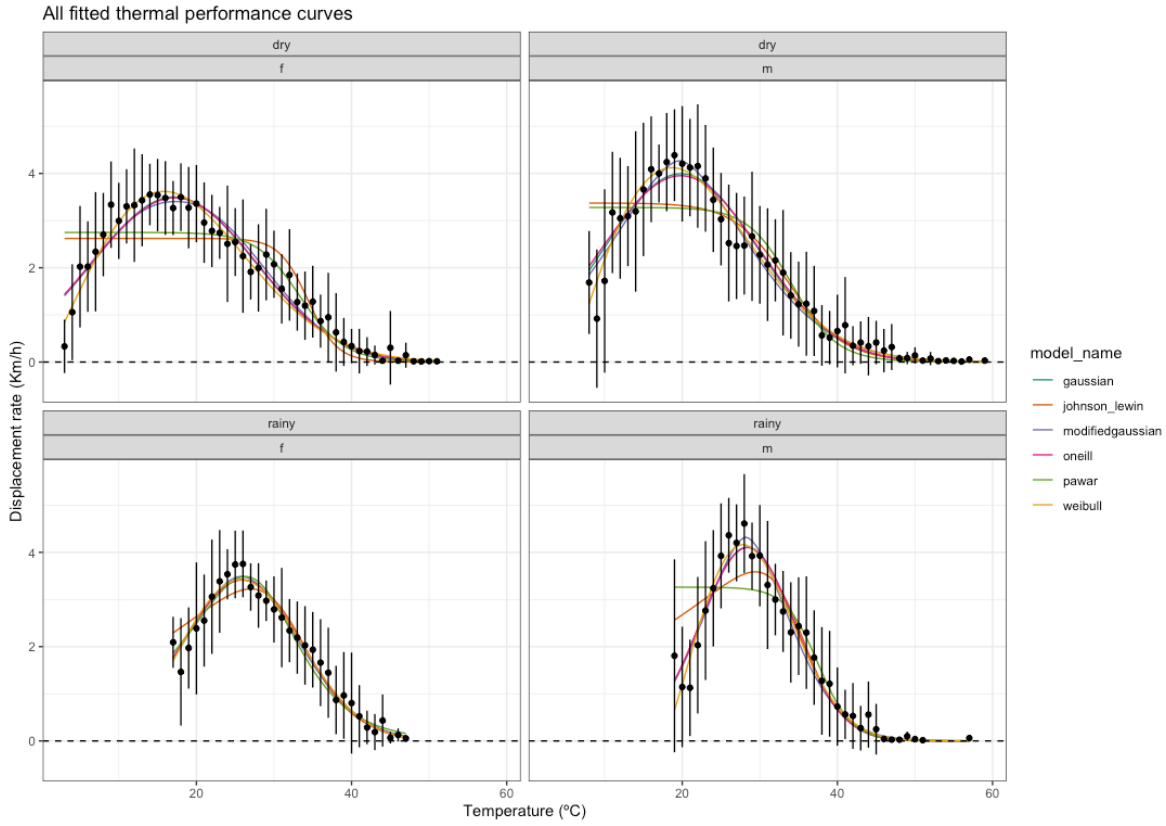


Figure D.4 Predictions of movement performance as a function of temperature from non-linear least squares

regressions using the six candidate TPC model formulations. Equations for each model formulation can be found in the rTPC package documentation.

Table C.1 AICc based model comparisons

season	sex	model_name	TPC params	dAICc
dry	**f**	**modifiedgaussian**	**rmax, topt**	**0.00**
dry	f	oneill	rmax, ctmax, topt, q10	12.41
dry	f	gaussian	rmax, topt	16.66
dry	f	pawar	e, eh, topt	39.22
dry	f	johnson_lewin	e, eh, topt	65.28
dry	f	weibull	topt	67.24
rainy	**f**	**gaussian**	**rmax, topt**	**0.00**
rainy	f	oneill	rmax, ctmax, topt, q10	2.14
rainy	f	weibull	topt	3.10
rainy	f	modifiedgaussian	rmax, topt	7.52
rainy	f	johnson_lewin	e, eh, topt	21.95
rainy	f	pawar	e, eh, topt	29.80
dry	**m**	**oneill**	**rmax, ctmax, topt, q10**	**0.00**
dry	m	gaussian	rmax, topt	4.46
dry	m	johnson_lewin	e, eh, topt	28.15
dry	m	weibull	topt	48.01
dry	m	pawar	e, eh, topt	66.61
dry	m	modifiedgaussian	rmax, topt	72.78
rainy	**m**	**gaussian**	**rmax, topt**	**0.00**
rainy	m	oneill	rmax, ctmax, topt, q10	3.30
rainy	m	weibull	topt	6.73
rainy	m	modifiedgaussian	rmax, topt	13.13
rainy	m	johnson_lewin	e, eh, topt	23.53
rainy	m	pawar	e, eh, topt	29.25