When the Going Gets Tough, the Tough Restrict Their Movement – The Effect of Fluctuating Resources on the Daily Movements of African Elephants

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“A thesis submitted in partial fulfillment of the requirement for the degree of Master of Science and the Diploma of Imperial College London”
DECLARATION OF OWN WORK

I declare that this thesis “When the going gets tough, the tough restrict their movement – the effect of fluctuating resources on the daily movements of African elephants” is entirely my own work and that where material could be construed as the work of others, it is fully cited and referenced, and/or with appropriate acknowledgement given.

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<tr>
<td>AIC</td>
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<tr>
<td>CC</td>
<td>Concordance Criteria</td>
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<tr>
<td>GIS</td>
<td>Geographical Information System</td>
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<td>HFA</td>
<td>High Forage Availability</td>
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Abstract

Human population growth and increased resource consumption are the drivers of land use change and habitat modification, both of which are a major threat to wide ranging species. A simultaneous threat is climate change, which has already begun to cause ecological changes. Wide ranging species require large areas to meet their energy requirements and they often take their movement cues from nature in order to benefit from peaks in resource availability in spatiotemporally heterogeneous landscapes.

This study considers the daily movement of African elephants (*Loxodonta africana*) in the context of these threats. The study area is the Samburu region of Kenya, which has been and continues to be impacted by the aforementioned threats. The protected areas at the centre of this study site are small and consequently individuals must travel beyond their boundaries in order to meet their energy requirements. Additionally the bi-annual wet seasons are variable in their timing duration and intensity, meaning that individuals must be able to adapt to varying levels of forage availability.

Recent developments in GPS technology have increased the amount of high resolution, long term data sets available for understanding fine scale animal movements. Additionally, freely available remote sensing data allows the quantification of forage availability at relatively high temporal resolution. This study combines these two sources of data to analyse the daily movements of six female African elephants investigating their response to varying forage availability and protected area coverage.

The net squared displacement movement metric is used in combination with non-linear mixed effects models to firstly categorise the movement data into pre-defined movement categories; and latterly to identify differences in movement characteristics across forage availability categories and levels of protected area coverage.

The results showed that there is a positive relationship between forage availability and the magnitude of elephant movement and that elephant movement tends to be greater outside of protected areas. The findings of this study are concordant with previous findings in the literature, validating the use of this method as a way of researching animal movement and comparing this movement across both spatial and temporal variables.
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I would also like to extend my thanks to Team Desk for providing much appreciated advice, entertainment and copious amounts of tea. In particular, thanks to my remote field assistant, Billy and the friendly neighbourhood statistical guru, William.

Finally, I would like to thank my family for putting up with me and putting me up.
1. Introduction

1.1 Habitat Fragmentation and Climate Change

Landscape modification, habitat fragmentation and climate change are some of the key drivers of biodiversity loss (Fischer & Lindenmayer 2007; Fahrig 2003). One of the underlying causes of these issues is increasing human population and associated levels of consumption, a trend which is likely to continue (Ehrlich 1988; Lutz & K C 2010; Brooks et al. 2002). Additionally, recent climate change has already caused ecological changes to biodiversity (Parmesan 2006), such as the asynchrony between some species and their food source (Visser & Both 2005). These threats have severe impacts on wide ranging species, because of their innate requirement for large areas of habitat, which are increasingly rare (Shuter et al. 2011; Wilcove & Wikelski 2008; Fischer & Lindenmayer 2007). Impacts include the decline in abundance of migratory species and the loss of mass migratory behaviour in some species (Harris et al. 2009). These impacts necessitate a fuller understanding of how species respond to these changes in order to best inform conservation management.

As the combined threats of habitat loss and climate change persist they will continue to influence the spatio-temporal aspects of resource availability. With an increased understanding of spatial variation of resources and their fluctuations we are able to better predict how animal space use will be impacted by these threats allowing a more informed decision making process (Fryxell et al. 2005).

The movement of an individual is nature’s best adaptation to fluctuations in resource distribution and abundance, allowing animals to benefit from resource peaks in spatiotemporally variable landscapes (van Moorter et al. 2013; Dingle & Drake 2007). Fluctuations in both the distribution and abundance of resource availability are key drivers of movement, with the timing and distance of animal movements changing as a response (Birkett et al. 2012). An in depth understanding of how individuals move and respond to these spatiotemporal changes is necessary in order to conserve these species (Fryxell et al. 2005).

Using Thompson’s gazelle as a study subject Fryxell et al. (2005) found that in a spatiotemporally heterogeneous landscape, large areas of unrestricted access were needed in order for this species to survive; this was found to be especially so when there is spatial...
autocorrelation of resource abundance, meaning that there are restricted clusters of resource distributed unevenly across the landscape and the abundance of these vary through time – characteristic of African savannah.

1.2 Habitat Fragmentation and African Elephants

The International Union for Conservation of Nature (IUCN) assessment of the African elephant (*Loxodonta africana*) states that the main threat to this species is habitat fragmentation across its wide distribution (Blanc et al. 2008). The population of Kenya is approximately 44 million with a growth rate of 2.27%, the 39th highest in the world (CIA 2013), with such growth rates land use change is inevitable. This habitat fragmentation leads to increased inter-species competition for resources, particularly in the dry season, often leading to increased human-wildlife conflict (Wittemyer 2008).

Approximately only 30% of the species distribution is covered by small and isolated protected areas, although it is stated that most of the large remaining populations are centred in protected areas (Blanc et al. 2008). This coverage is insufficient for the long-term conservation of a species which is adapted to moving over long distances, with recorded home ranges in the study region varying between 102 – 5527 km² (Graham 2009; Thouless 1996). The remaining ~70% of the distribution is unprotected, therefore vulnerable to land use change, potentially reducing the future distribution of this species further, exacerbating the fragmentation of populations.

1.3 Climate Change and Kenya

The long rains in central Kenya (March – May) have decreased by 100mm since the mid-1970s with this trend expected to continue; additionally an expected warming of >1°C will act to cause drier conditions (Funk et al. 2010). The combined effects of both habitat loss and climate change would drive greatest biodiversity loss in areas with high maximum temperatures and where average precipitation has decreased over the last 100 years (Mantyka-Pringle et al. 2012) showing that current climate and climate change are key factors in determining habitat loss. Central Kenya, the region where this study is based, has both high temperatures and has experienced a decrease in average precipitation (Funk et al. 2010), indicating that on a global scale it is likely to be heavily impacted by habitat loss.
1.4 Movement and Heterogeneous Landscapes

Movement is a consequence of behavioural decisions and environmental factors, the latter of which are spatiotemporally heterogeneous and are investigated in this study. The spatiotemporal variation of both resources and threats is key to forming movement pathways of individuals which in turn can have further ecological and evolutionary consequences, such as the distribution and dynamics of populations and ecosystems (Nathan & Getz 2008). The understanding of movement and its drivers is crucial in addressing the crux issues in conservation, such as habitat fragmentation, climate change, invasive species and the spread of pests and diseases (Nathan 2008).

Long term data sets of fine scale movement data are increasingly available due to technological advances and increased affordability of GPS technology. These data sets allow a better understanding of fine scale movements, which have not previously been studied extensively due to the paucity of data, and can give greater insight into how individuals respond to landscape heterogeneity. The data used in this project is from Save The Elephants, who have been using GPS collars to track elephants since 1995, using the data to aid elephant management and conservation through the establishment of protected corridors and working towards minimising human-elephant conflict with local communities (Save The Elephants 2013).

This study will investigate how the daily movement behaviour of individuals changes in response to resource fluctuations. Do individuals increase their movement in order to increase the likelihood of locating forage, or is their movement restricted in an effort to conserve energy by maintaining proximity to areas of known forage? This study will also investigate how protected areas influence the movement characteristics of African elephants. Will movement be faster and greater in response to human activity, or will it be restricted to patches of resource availability?

1.5 Aims and Objectives

Aim: To use novel spatial ecology modelling techniques to further understand the impacts of fluctuating resource availability and extent of protected areas on the daily movement patterns of African elephants (*Loxodonta africana*).
Objectives:

1. To identify how temporal changes in resource availability impacts the movement of African elephants.
2. To identify how protected areas influence the movement characteristics of African elephants.
2. Background

2.1 African Elephants

The African savannah elephant is listed as vulnerable on the IUCN Red List and as such is a species of conservation concern. The main threats are listed as; poaching for ivory and meat; habitat loss and fragmentation due to an expanding human population (Blanc, 2008). Poaching of African elephant for ivory and meat is a major cause of population declines for this species, especially due to its long generation length, increasing its vulnerability to over-exploitation (Mace & Reynolds 2001).

This species is the largest extant living terrestrial mammal, with fully mature bulls averaging over 3m and 5000kg and cows 2.5m and 3000kg. Their diet varies seasonally, focussing on grasses and herbs during the wet season and moving onto woody plants during the dry season, although their diet is broader than most other herbivores. The inclusion of trees in their diet means that the impact of elephants on their ecosystem is particularly large (Estes 1991); hence their presence both within and outside of protected areas is crucial to the maintenance of the African savannah (Graham et al. 2009).

Historically the family *Elephantidae* first occurred in Africa between 11.6 and 5.3 Ma. The former range of African elephant was expansive covering most of sub-Saharan Africa, wherever sufficient water and forage were available (Estes 1991). However with growing human populations and encroaching development this distribution has consequently shrunk, with the current distribution shown in Figure 2.1. Alongside this a >1300% increase in the price of ivory during the 1970s resulted in a great rise in poaching causing a population decline of approximately 80% in eastern Africa; from which populations have not recovered (Douglas-Hamilton 1987; Blanc et al. 2008).
2.2 Telemetry

This study will focus on telemetry data, gathered by Save The Elephants, from GPS tagged elephants in the Samburu region of Kenya. Satellite tags are particularly useful for tracking animals which have large home ranges and inhabit areas that are remote or inaccessible (Venkataraman & Saandeep 2005). GPS data provides a huge wealth of fine scale spatial and temporal movement data which can be used to explore how tagged individuals interact with the ecosystems they inhabit (Cagnacci et al. 2010; Hebblewhite & Haydon 2010). Through studying the movement of individuals their spatiotemporal space use can be better understood therefore informing conservation planning.

Relatively recent technological developments have increased the efficiency and longevity of GPS units, enabling the study of animal movement at a finer scale over multi-year time periods. Alongside technological developments, these data are increasingly becoming freely available through initiatives such as Movebank (Kranstauber et al. 2011) and Env-DATA (Dodge et al. 2013). Together these advances have led to a surge of publications within movement ecology and the development of methods with which to analyse this new
abundance of data. This change in movement ecology has been characterised as a step away from the Eulerian approach, which focuses on how a population uses a given space; and a move towards the Lagrangian approach which focuses on individual animals and their movement (Nathan & Getz 2008). There are also a number of studies which work towards scaling up this individual level information in order to further understand population level dynamics (Morales et al. 2010; Singh et al. 2012; Hebblewhite et al. 2008). These improvements alongside increases in computational capacity mean that analysis of such high resolution data is now possible using standard desktop computers.

A disadvantage of using GPS collars which is often overlooked is the frequent collar failure, either through malfunction or lack of signal, which can result in reduced sample sizes and systematic bias in the data (Hebblewhite & Haydon 2010; Hurford 2009). This study overcomes this issue by cleaning the data using the method described in Bjørneraas et al. (2010), which is described fully in the Methods; and looking at a short time-frame (daily rather than seasonal). This increases the sample size markedly and provides enough data to allow for discarding sparsely recorded days, i.e. days with less than 20 GPS fixes.

2.3 Seasonal Change and Movement

The movement of large herbivores is a result of the internal and external factors influencing an individual, such as hunger, topography, presence and distribution of forage and water and the proximity of competitors or predators (Morales et al. 2005). The African Savannah is characteristically spatiotemporally heterogeneous in terms of resource availability (Du Toit 2003); with the bi-annual wet season driving fluctuations in resource availability. African elephants are adapted to this in their ability to cover great distances and hence are able to respond to fluctuations in resource availability and the presence of a threat or competition by changing their movement (Wittemyer 2008).

Loarie et al. (2009) states that elephant movement is complex and varies seasonally as do the environmental factors influencing movement; such as forage availability which becomes limited in the dry season. This restricts the area available for the population to utilise, leading to repeated movement to and greater competition within these patches. This is supported in a study by Wittemyer (2008) which found that autocorrelation of elephant movement is greatest during the dry season, when resources are heterogeneously
distributed. It was also found that longer (multiday) movements were more common during the dry season, in order to move between locations with resources/protected areas.

Thomas et al. (2012) found that during the dry season African elephants occupied smaller home ranges than in the wet season and Birkett et al. (2012) found that during the dry season female elephants in Kruger National Park travelled shorter, less variable distances, due to the limited amount of forage available. This was also found when looking at daily movements, with lower levels of movement found when resources were less available, reflecting an energy conservation strategy (Polansky et al. in prep.).

However, during the dry season, when resources are heterogeneously distributed, the area required by an individual to meet its energy requirements increases, and it may be forced to make long distance movements between patches (Fryxell et al. 2005; O’Neill et al. 1988). Loarie et al. (2009) found that elephants move more during the dry season because of the “necessity to stay close to water is compromised by their search for scarce vegetation”. This study will aim to investigate how daily movements are influenced by resource availability and if there is evidence for restricted movement during the dry season, or long distance movements between sparsely distributed patches of resources.

2.4 Protected Areas and Movement

Studies such as Graham (2009), Wall et al. (2013) and Douglas-Hamilton et al. (2005), have explicitly considered African elephants response to risk, with risk being defined as interspecific and intraspecific competition and human presence; who are the main predators of this species (Wittemyer et al. 2007). These studies found that in areas of higher risk, such as outside of protected areas or near human settlement, individuals are more active at night, move further and with increased speed.

The Samburu and Buffalo Springs National Reserves receive a high density of elephant use, relative to the study region, with 54.8% of all of the GPS fixes from this study being located within either of the two protected areas, despite their relatively small size. As a result of this high elephant density there is intraspecific competition. This causes some elephants to move out of the protected areas, in order to find resources; particularly during the dry season (Wittemyer et al. 2007).
Interspecific competition is also more prevalent during the dry season, particularly with other wild ungulates and livestock, outside of the protected areas (Odadi et al. 2011). This may increase potential for human-wildlife conflict due to greater competition for limited resources (Cerling et al. 2009). The presence of pastoralists and their livestock causes elephants to spend more time at permanent water during the night in order to avoid livestock which occupy this space during the day (Wittemyer et al. 2007).

2.5 Net Squared Displacement

Net Squared Displacement (NSD) is the squared distance between a GPS location fix and the point of origin on an individual’s movement path (Turchin 1998), with the distance being squared in order to remove the effect of direction. For this study, which considers daily movement patterns, the point of origin will be the location of the individual at 00:00 hrs each day and the NSD will be calculated for each hourly GPS fix after this (assuming no missing location). This daily movement will be referred to as a trip throughout this project.

Net Squared Displacement (NSD) is a way of utilising GPS data to quantify and model the movement of individuals. Movement data are made up of three dimensions – latitude, longitude and time. NSD combines the latitude and longitude dimensions so that the data becomes two dimensional and easier to analyse with standard statistical techniques. An additionally benefit of using NSD is that the models are able to account for variation between individuals and there are no arbitrary cut off points for the timing, duration and magnitude of movements (Bunnefeld et al. 2011).

Previously NSD has mostly been used to look at long-term movements, such as the seasonal migration patterns of moose (*Alces alces*) (Bunnefeld et al. 2011; Singh et al. 2012). It was used to identify the proportion of migratory individuals within moose populations, with the aim of predicting migratory movements; providing a key tool in the management and conservation of a migratory species.

However as the axes are scale independent it is possible to use this measure for much finer temporal resolutions; Fryxell et al. (2008) studied the movement patterns of elk (*Cervus elaphus*) at several time scales, from minutes to years. NSD has also been used to investigate the daily movement characteristics of different livelihood groups in humans (Papworth et al. 2012).
There is a full spectrum of movement types, from the nomadic random walk to migration (Jonzen et al. 2011). Bunnefeld et al. (2011) used NSD to create movement models describing five different movement types along this spectrum, which can be seen in Figure 2.2.

![Figure 2.2 – The movement models that will be used to categorise the daily movement trips in this study, from Bunnefeld et al. (2011).]

For the purposes of this study the movement models will describe the following daily movements as classified in Bunnefeld et al. (2011):

**Migratory:**

\[
NSD = \frac{\delta}{1 + \exp\left(\frac{t_a - t}{\varphi_a}\right)} + \frac{-\delta}{1 + \exp\left(\frac{t_b - t}{\varphi_b}\right)} \quad \text{Eqn1}
\]

Eqn1 describes the movement where the individual sets out from a resting place, travels to a foraging location where it stays for a length of time, and then returns to its original resting place, characteristic of a central place forager. The flat sections of this curve describe the resting and foraging times; with the steep curves showing movement, through changes in net squared displacement.

**Mixed migratory:**
\[ \text{NSD} = \frac{\delta_a}{1 + \exp\left(\frac{\theta_a - t}{\varphi_a}\right)} + \frac{-\delta_b}{1 + \exp\left(\frac{\theta_b - t}{\varphi_b}\right)} \]  

Eqn2

This movement is similar to the migratory model; apart from the final resting location is not the same as the place of origin, so the individual does not return the full distance, requiring two asymptotes in the model.

Dispersal:

\[ \text{NSD} = \frac{\delta}{1 + \exp\left(\frac{\theta - t}{\varphi}\right)} \]  

Eqn3

Eqn3 is the first half of the migratory model (Eqn1), describing just the outward journey. This would describe an outward movement away from the place of origin on to a new location, where the individual rests; with no return movement.

Nomadic:

\[ \text{NSD} = c + t \]  

Eqn4

This describes a random walk scenario, where the individual moves at a constant rate throughout the day, away from the point of origin, resulting in a steady increase in NSD.

Home range:

\[ \text{NSD} = c \]  

Eqn5

This movement type describes the individual staying near to the point of origin throughout the day, showing no significant change in NSD.

\( \delta_a \) and \( \delta_b \) are the asymptotes of the models. \( \delta_a \) is the distance from the point of origin at which the individual rests. \( \delta_b \) is only in the mixed migratory model and describes the distance of the return journey, between \( \delta_a \) and the second rest.

\( \theta_a \) and \( \theta_b \) are the xmid values, the point in time at which the individual reaches half of the asymptotic height, an objective way of comparing movement timing; with smaller values corresponding to earlier movement. \( \theta_a \) refers to the outward journey and \( \theta_b \) refers to the return journey; \( \theta_b \) only occurs in the migratory and mixed migratory models.
$\phi_a$ and $\phi_b$ are the scale values, the time between an individual reaching $\frac{1}{2}$ and $\frac{3}{4}$ of the asymptotic height, and can be used to estimate the speed of the individual. $\phi_a$ refers to the outward scale and $\phi_b$ refers to the return scale, with $\phi_b$ only occurring in migratory and mixed migratory models.

c is a constant and reflects restricted movement with the individual remaining in the same area throughout the day.

t is the number of minutes since the daily trip has started, in this study the number of minutes after midnight.

Biologically relevant information can be obtained from the parameters of these models, such as the asymptote will reflect the distance travelled; the scale parameter can be used to estimate the speed of movement. For the movement patterns identified it is the differences in the parameters which will be compared in order to identify differences in movement characteristics between forage availability groups and between protected areas and non-protected areas.

2.6 Normalised Difference Vegetation Index

The Normalised Difference Vegetation Index (NDVI) is an index calculated using remote sensing data and is a ratio between red and near infra-red reflectance, which is used to measure the ‘greenness’ of an area and it is a spatiotemporal measure of productivity (Rasmussen et al. 2006). NDVI has been used extensively in movement ecology, as the temporal changes can be linked with movement data in order to investigate movement behaviour as resources vary through time (Pettorelli et al. 2011). NDVI has been used to study African elephant movement, with findings showing that seasonal home range size is correlated with NDVI productivity (Young et al. 2009) and that movements are more directed in the dry season and more random in the wet season (Wittemyer et al. 2009).

For this study NDVI is used as a way of capturing the temporal fluctuations in resource availability. The benefit of using NDVI is the global availability of this data and the temporal regularity with which it is available. The NDVI scenes available come in 16 day time frames meaning that the resolution for categorising forage availability categories will also be this
length, restricting the temporal resolution. Despite this issue, NDVI is still the best option when working at fine spatiotemporal scales (Duffy & Pettorelli 2012).

2.7 Study Site

This study uses data gathered from elephants tagged within the Samburu and Buffalo Springs Nature Reserves, Kenya, which is situated within the greater Laikipia-Samburu region. The study location and GPS data can be seen in Figure 2.3 and Figure 2.4. The two national reserves are separated by the Ewaso Ngiro River, the main water source in the area and therefore a key habitat feature for wildlife (Wittemyer 2001). The climate of this region is typically hot, dry and variable with 360 ± 170mm (SD) of precipitation per year, largely during the bi-annual rains, with the long rains occurring in March-May and short rains occurring in October-December, although the timing and intensity of these vary inter-annually (Wittemyer 2001).

Figure 2.3 Map of eastern Africa showing the location of the study site, which is shown in detail below, in Figure 2.4. (Jarvis et al. 2008; Lehner & Doll 2004; GADM 2012)
The elephants within the Samburu and Buffalo Springs Nature Reserves are a sub-population of the greater Laikipia-Samburu region (Thouless 1996). This region is home to the second largest population of African elephants in Kenya, with the largest population of free ranging elephants (Wittemyer 2001). The fact that the elephants are free ranging is significant when considering movement behaviour, as it means that there are no ‘hard’ barriers to movement, such as fences which can heavily impact on movement patterns (Loarie et al. 2009).

A 2012 aerial count observed 6,365 elephants in Laikipia-Samburu ecosystem (Ngene et al. 2013), down from a 2008 estimate of 7,415 (Litoroh et al. 2010), which had previously increased from 5,447 in 2002 (Omondi et al. 2002). The population decline since 2008 is thought to be due to an increased level of poaching and severe drought in 2009, markedly increasing the number natural deaths in that year (Ngene et al. 2013; Zwaagstra et al. 2010). The trend during these years show an annual growth rate of -0.04%, which if extrapolated indicates a population extinction by 2037 (Ngene et al. 2013).

The Samburu and Buffalo Springs National Reserves cover 330 km² (4.5%) (Wittemyer et al. 2009) of the minimum convex polygon (7304.1 km²) of the GPS data. Despite the low area
coverage of the protected area, 66,104 (54.8%) of all the GPS fixes are found within the Samburu and Buffalo Springs Nature Reserves, indicating a high density of GPS points and therefore elephant activity within these protected areas, in comparison to the surrounding areas. This supports the notion that the ‘core zones’ of elephant movement are typically found within protected areas, whilst corridors of movement tend to be outside protected areas (Douglas-Hamilton et al. 2005a).
3. Methods

3.1 Outline

This study analyses GPS location fixes of six female African elephants across a three year period; investigating their response to resource fluctuations in terms of movement characteristics. The elephant movement patterns will be analysed and categorised using the approach outlined in Bunnefeld et al. (2011), which is detailed further on. The start time for each trip was set to midnight towards the beginning of the nightly rest period. Daily peak the bi-modal activity peaks occurred at 06:00-10:00 hrs and 18:00 – 20:00 hrs, dawn and dusk.

This method uses GPS location data collected at hourly intervals to model the daily movement patterns of African elephants and categorise these patterns by comparing the fit of the NSD data to five curves, which describe different movement types. The resulting models will provide information on the distance, timing and duration of movements and rest periods. This information will be used to explore how movement characteristics vary with resource availability and location with respect to protected areas.

3.1 Data collection

The expected number of GPS points over the three year study period was 157,824, however only 120,694 were received, a success rate of 76.5%. The difference between the expected and received data points is largely down malfunctioning collars with some gaps in the data being up to several months long. There were also missing data points from failed location attempts, with occasional hourly points missing. These omissions may be due to a lack of signal, reduced satellite coverage, habitat features, or time of year.

3.2 Data Cleaning

The data were cleaned using the method outlined in Bjørneraas et al. (2010) and using the R code supplied by the same paper. Location error is considered likely if either of the following two criteria is true:
1- Points are more than a set distance apart, indicating a biologically unlikely speed and therefore likely to be an erroneous fix. In this case 13km was used the threshold distance, as suggested in (Graham 2009).

2 – A turning angle of approximately 180 degrees, characterised by ‘spiky’ movement data where it appears the animal has travelled to a location and almost immediately turned back on itself.

This method detected 2,226 (1.84%) location errors which were subsequently removed from the dataset. Additionally, days with less than 20 GPS location fixes were removed from the data set, as recommended in Polansky et al. (in prep), removing a further 10,494 (8.69%); so that 107,974 (89.46%) GPS points were used in the analysis.

3.3 Forage Availability

The NDVI data are from the Moderate Resolution Imaging Spectroradiometer (MODIS) sensor on board of the Terra satellite. The MOD13Q1 data were used for this project, these were chosen as they provide the best compromise between spatial and temporal resolution. There is an NDVI scene every 16 days with a 250 m resolution. The NDVI data were downloaded from the University of Natural Resources and Life Sciences’ website (Vuolo et al. 2012). These NDVI data were pre-filtered using the method described in Atkinson et al. (2012), which filters out clouds remaining after the compositing process, reducing noise in the data. The resulting filtered data shows a notable improvement in quality.

There were no appropriate rainfall data available for the study site therefore NDVI data were used as the sole proxy for forage availability. The NDVI scenes were used to categorise the three year study period into 16 day periods of high, medium or low forage availability (henceforth HFA, MFA and LFA respectively). This was done by clipping the NDVI scenes to the rectangular extent of the study site, in order to make the definition of seasons as spatially relevant as possible, then calculating the mean NDVI value for each 16 day scene, using the ‘raster’ (Hijmans, 2003) and ‘rgdal’ (Keitt, 2013) packages in R.

The range of the scene level average NDVI values over the three year period was calculated and split into three equal bins, which were then used to categorise each of the NDVI scenes as being either HFA, MFA or LFA, as in (Polansky et al. in prep.); the results of which can be
seen in Table 3.1. The daily trips were also grouped into these categories, depending on which 16 day period they fell within. The coarse temporal resolution of the NDVI data is a limitation and is the main reason why this method was used rather than the more binary approach of attempting to identify wet and dry seasons from the same NDVI data. The medium forage availability category provides an intermediate between the extremes of forage availability, which the seasonal division would not.

Table 3.1 – NDVI range of each forage availability category and the number of scenes within each of them.

<table>
<thead>
<tr>
<th>Forage Availability</th>
<th>NDVI Range</th>
<th>Number of scenes</th>
</tr>
</thead>
<tbody>
<tr>
<td>High (HFA)</td>
<td>0.47878 - 0.59042</td>
<td>14</td>
</tr>
<tr>
<td>Medium (MFA)</td>
<td>0.36714 - 0.47877</td>
<td>20</td>
</tr>
<tr>
<td>Low (LFA)</td>
<td>0.25548 - 0.36713</td>
<td>35</td>
</tr>
</tbody>
</table>

3.4 Protected Area

In order to compare the movement characteristics of trips inside and outside protected areas on movement, the GPS points were spatially joined to a shapefile of the Buffalo Springs and Samburu Nature Reserves (IUCN & UNEP 2013), using the ‘Point Sampling Tool’ in QGIS (QGIS Development Team 2013). This tool identified whether or not the GPS points were inside the protected area. This information was then used to categorise the daily trips as being either inside or outside the protected areas, with trips that crossed the protected area boundary being discarded, in order to make a distinct comparison.

3.5 Net Squared Displacement

The trip length in this study will be daily, in order to take advantage of the long-term and high resolution data set (4,700 trips). This study will model the net squared displacement of elephants with the aim of building upon previous studies of elephant movement, particularly with reference to forage availability and protected areas. This technique has not previously been applied to a study where the environmental resource varies through time, providing a novel aspect to this project.
The movement trajectories and net squared displacement were calculated in R, using the ‘adehabitat’ package (Calenge 2006). The trips were categorised into movement types using the ‘nlme’ package (Pinheiro & Bates 2013).

Non-linear mixed effects models were preferred to linear models as they are more parsimonious with the parameters having biological meaning (Pinheiro and Bates, 2000). The fit of each of the models was assessed using Concordance Criteria (CC) (Huang et al. 2009), which returns a value between -1 and 1, with values closer to 1 indicating better model fit. Each of the daily trips were then categorised as a movement type based on which model they fitted best according to CC. Only trips which had a CC value of 0.90 or above were retained, so that only models with a ‘good’ fit were used in the rest of the analysis.

3.6 Concordance criteria

CC was used rather than AIC (Akaike Information Criterion) as it was developed for use with nonlinear models and focusses directly on the fit between the observed values and fitted values; whereas AIC is a measure of relative model ‘goodness’ rather than absolute, with AIC values only showing how well models fit in relation to each other (Börger & Fryxell 2012; Huang et al. 2009).

\[
CC_i = 1 - \frac{\sum_{j=1}^{n_i} (y_{ij} - \hat{y}_{ij})^2}{\sum_{j=1}^{n_i} (y_{ij} - \bar{y})^2 + \sum_{j=1}^{n_i} (\hat{y}_{ij} - \bar{y})^2 + n_i (\bar{y} - \bar{y})^2}
\]

Figure 3.1 – The calculation of Concordance Criteria. Taken from Huang et al. (2009)

\(y\) = observed NSD at each point
\(\bar{y}\) = mean observed NSD at each point
\(\hat{y}\) = fitted NSD at each point
\(\bar{y}\) = mean fitted NSD at each point
\(n\) = number of observations per trip
A limitation of using CC is that if two models are similar, such as mixed migratory and dispersal, a trip may fit well to both movement types; resulting in both receiving similar CC scores. This issue would also arise with AIC, however CC is able to show if none of the models fit well, which AIC cannot. In this study the trips have been categorised based on whichever model gave the highest CC score for, because it is the characteristics derived from the model that are important rather than the categorisation itself, particularly when models are similar such as the dispersal and mixed-migratory categories.

3.7 Modelling

For the models used to compare movement across forage availability and protected area categories, the trip was nested within individual as a random effect and these varied with the asymptote, or both asymptotes in the case of mixed migratory. This was done to account for differences between individual trips and multiple trips undertaken by the same individual. The benefit of using a non-linear mixed effects model over a non-linear least squares model is that it is possible to incorporate individual and trip variation into the model as random effects, rather than these differences being absorbed into standard error, as is the case with non-linear least squares models.

The non-linear mixed effects models were run using the prevalent movement types with each of the models below was run once with per movement type.

The models were run in order to compare the following aspects of the data.

1. To compare the movement characteristics of the trips within each of the three forage availability categories.

2. To compare the movement characteristics of trips within the protected area to those outside the protected area.

3.

   a. To compare the movement characteristics of the trips within each of the forage availability categories when inside the protected area.

   b. To compare the movement characteristics of the trips within each of the forage availability categories when outside the protected area.
4. Results

4.1 Forage Availability

The fluctuations in these forage availability categories are shown alongside the regional mean NDVI throughout the study period in Figure 4.1. The bi-annual wet seasons and associated ‘greening up’ can be identified by the peaks in both of these metrics. Figure 4.1 also shows that 2005 was a relatively dry year, with no HFA scenes. The GPS data was also split into the forage availability categories, as shown in Figure 4.2.

![Figure 4.1](image_url)

Figure 4.1 – The mean regional NDVI changing through time over the three year study period. The figure also shows the categorisation of the NDVI scenes into high, medium or low forage availability.
Figure 4.2 - The study site showing the GPS points for each forage availability category
Figure 4.3 shows how hourly movement rates vary throughout the day, with clear peaks at dawn and dusk. Figure 4.2 also shows that at a daily scale there is greater movement during times of HFA, shown with greater movement rates during the day time hours (06:00 – 19:00), but with similar rates of movements during the night 19:00-06:00.

4.2 Model Results

Table 4.1 shows the number of trips within each movement type that have been fitted and had a CC score of >= 0.9. The predominant movement types are dispersal and mixed migratory which together make up 70.2% of the total. It is because of this that these two movement types that will be used in further analysis. The other movement types are not included as the data will be split into sub-categories causing the sample size within each sub-category to decrease.
Table 4.1 – NSD data fitted to the movement models and the percentage retained when only the trips with a CC value >= 0.9 were kept for further analysis.

<table>
<thead>
<tr>
<th>Movement Pattern</th>
<th>No. Trips</th>
<th>Fitted</th>
<th>Trips &gt;= 0.90 CC</th>
<th>%</th>
</tr>
</thead>
<tbody>
<tr>
<td>Dispersal</td>
<td>1594</td>
<td>1126</td>
<td>33.1</td>
<td></td>
</tr>
<tr>
<td>Mixed Migratory</td>
<td>1269</td>
<td>1261</td>
<td>37.1</td>
<td></td>
</tr>
<tr>
<td>Migratory</td>
<td>785</td>
<td>745</td>
<td>21.9</td>
<td></td>
</tr>
<tr>
<td>Nomadic</td>
<td>1038</td>
<td>266</td>
<td>7.8</td>
<td></td>
</tr>
<tr>
<td>Home Range</td>
<td>14</td>
<td>0</td>
<td>0</td>
<td></td>
</tr>
<tr>
<td>Total</td>
<td>4700</td>
<td>3398</td>
<td>100</td>
<td></td>
</tr>
</tbody>
</table>

Table 4.2 shows that the mixed migratory movement type is more prevalent within protected areas than outside; with this becoming more evident as forage availability increases. There is a fairly even split of the dispersal movement type both inside and outside of the protected area.

Table 4.2 – The proportion of each movement type inside and outside of the protected areas, in each of the forage availability categories

<table>
<thead>
<tr>
<th>Forage Availability</th>
<th>Trips Inside PA %</th>
<th>Trips Outside PA %</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Dispersal</td>
<td>Mixed Migratory</td>
</tr>
<tr>
<td>HFA</td>
<td>54.7</td>
<td>45.3</td>
</tr>
<tr>
<td>MFA</td>
<td>47.2</td>
<td>52.8</td>
</tr>
<tr>
<td>LFA</td>
<td>52.2</td>
<td>47.8</td>
</tr>
</tbody>
</table>

In the following tables the values in the brackets are ± one standard error and the asterisk’s refer to the p values as: 0 = ***, 0.005 >= **, 0.05 >= *
4.2.1 Dispersal – Forage Availability

Figure 4.4 – The output of a non-linear mixed effects model, comparing the daily trip movement characteristics of the dispersal movement type across the three forage availability categories.

Table 4.3 – Comparing movement characteristic predictions of the dispersal movement type from a non-linear mixed effects model across the three forage availability categories.

<table>
<thead>
<tr>
<th>Dispersal</th>
<th>HFA</th>
<th>MFA</th>
<th>LFA</th>
</tr>
</thead>
<tbody>
<tr>
<td>Asymptote δ (km²)</td>
<td>40.3 (36.3-44.3)**</td>
<td>30.5 (26.8-34.2)*</td>
<td>18.8 (15.4-22.2)***</td>
</tr>
<tr>
<td>Xmid θ (mins)</td>
<td>964.5 (951.9-977.1)**</td>
<td>607.6 (594.4-620.8)***</td>
<td>434.1 (421.0-447.2)***</td>
</tr>
<tr>
<td>Scale φ (mins)</td>
<td>229.8 (223.4-236.2)**</td>
<td>187.3 (180.2-194.4)***</td>
<td>175.8 (168.8-182.8)***</td>
</tr>
<tr>
<td>Movement Speed (kmh⁻¹)</td>
<td>0.42</td>
<td>0.44</td>
<td>0.37</td>
</tr>
<tr>
<td>Individuals</td>
<td>6</td>
<td>6</td>
<td>6</td>
</tr>
<tr>
<td>Trips</td>
<td>230</td>
<td>320</td>
<td>576</td>
</tr>
<tr>
<td>Points</td>
<td>5331</td>
<td>7418</td>
<td>13359</td>
</tr>
</tbody>
</table>

As shown in Table 4.3 the asymptote parameter for the dispersal movement category is significantly different across all forage availability levels, decreasing in value as forage availability decreases. The xmid value is significantly different for all levels, with individuals moving earlier in the trip as forage availability decreases.
The estimated speed, calculated using the scale parameter, is similar across all groups, but is lowest in LFA, at 0.37 kmh$^{-1}$. 
4.2.2 Mixed Migratory – Forage Availability

Figure 4.5 and Table 4.4 show the results of the mixed migratory models compared across forage availability levels. Asymptote A shows a similar pattern to the dispersal movement.
type, with a progressively smaller asymptote as the forage availability levels decrease. However the xmid A and xmid B values are similar across all levels, meaning a similar timing of movement across all the forage availability groups. Movement speed A decreases with forage availability, but movement speed B increases. This may be due to the negligible value for Asymptote B in HFA, resulting in a lower estimated movement speed B for this category.
4.2.3 Protected Area – Dispersal

Figure 4.6 – The output of a non-linear mixed effects model, comparing the daily trip movement characteristics of the dispersal movement type inside and outside the protected areas.

Table 4.5 – Comparing movement characteristic predictions of the dispersal movement type from a non-linear mixed effects model inside and outside the protected areas.

<table>
<thead>
<tr>
<th>Dispersal</th>
<th>Inside PA</th>
<th>Outside PA</th>
</tr>
</thead>
<tbody>
<tr>
<td>Asymptote (km²)</td>
<td>21.6 (18.3 – 24.9)***</td>
<td>23.2 (20.9 – 25.5)</td>
</tr>
<tr>
<td>Xmid (mins)</td>
<td>668.1 (659.6 – 676.6)***</td>
<td>494.4 (484.9 – 503.9)***</td>
</tr>
<tr>
<td>Scale (mins)</td>
<td>239.5 (233.5 – 245.5)***</td>
<td>202.6 (195.6 – 209.6)***</td>
</tr>
<tr>
<td>Movement Speed (kmh⁻¹)</td>
<td>0.29</td>
<td>0.35</td>
</tr>
<tr>
<td>Individuals</td>
<td>6</td>
<td>6</td>
</tr>
<tr>
<td>Trips</td>
<td>446</td>
<td>426</td>
</tr>
<tr>
<td>Points</td>
<td>10390</td>
<td>9865</td>
</tr>
</tbody>
</table>

Figure 4.6 and Table 4.5 show the results of the dispersal model comparing the movement characteristics of trips inside and outside the protected areas. The asymptote is 1.6km² higher for trips outside of the protected areas, indicating that individuals are travelling slightly further outside of the protected area. The xmid value is 36.9 minutes lower outside
the protected areas, meaning that the trips area starting closer to midnight. The scale value is lower outside of the protected areas, corresponding to faster movement in these areas.
4.2.4 Protected Area- Mixed Migratory

Figure 4.7 – The output of a non-linear mixed effects model, comparing the daily trip movement characteristics of the mixed migratory movement type inside and outside the protected areas.

Table 4.6 – Comparing movement characteristic predictions of the mixed migratory movement type from a non-linear mixed effects model inside and outside the protected areas.

<table>
<thead>
<tr>
<th>Mixed Migratory</th>
<th>Inside PA</th>
<th>Outside PA</th>
</tr>
</thead>
<tbody>
<tr>
<td>Asymptote A $\delta_a$ (km$^2$)</td>
<td>16.3 (14.8 - 17.8)**</td>
<td>25.2 (23.4-27.0)**</td>
</tr>
<tr>
<td>Xmid A $\theta_a$ (mins)</td>
<td>508.8 (507.3 – 510.3)***</td>
<td>646.2 (622.9 - 669.5)***</td>
</tr>
<tr>
<td>Scale A $\varphi_a$ (mins)</td>
<td>53.8 (52.6 - 55.0)***</td>
<td>418.1 (410.1 – 426.1)***</td>
</tr>
<tr>
<td>Movement Speed A (kmh$^{-1}$)</td>
<td>1.13</td>
<td>0.18</td>
</tr>
<tr>
<td>Asymptote B $\delta_b$ (km$^2$)</td>
<td>4.5 (3.6 – 5.4)***</td>
<td>4.2 (2.6-5.8)</td>
</tr>
<tr>
<td>Xmid B $\theta_b$ (mins)</td>
<td>1058.8 (1056.6 - 1061.0)***</td>
<td>1168.7 (1165.1 – 1172.3)***</td>
</tr>
<tr>
<td>Scale B $\varphi_b$ (mins)</td>
<td>73.7 (71.7 – 75.7)***</td>
<td>-29.7 (-32.8 - -26.6)***</td>
</tr>
<tr>
<td>Movement Speed B (kmh$^{-1}$)</td>
<td>0.43</td>
<td>1.04</td>
</tr>
<tr>
<td>Individuals</td>
<td>6</td>
<td>6</td>
</tr>
<tr>
<td>Trips</td>
<td>589</td>
<td>297</td>
</tr>
<tr>
<td>Points</td>
<td>13616</td>
<td>6831</td>
</tr>
</tbody>
</table>

Table 4.6 shows that asymptote A is 8.9km$^2$ higher outside of the protected area. However unlike the dispersal model, both the xmid A and movement speed A are higher outside of
the PA, indicating a slower and later movement. The trips outside of the PA look more similar to a dispersal movement type, with no significant return to the point of origin. Inside the PA there is more of a return movement.
### 4.2.5 Inside Protected Area - Dispersal

Figure 4.8 – The output of a non-linear mixed effects model, comparing the daily trip movement characteristics of the dispersal movement type inside the protected areas, across the forage availability categories.

Table 4.7 – Comparing movement characteristic predictions of the dispersal movement type inside the protected areas from a non-linear mixed effects model, across the three forage availability categories.

<table>
<thead>
<tr>
<th>Dispersal - Inside Protected Area</th>
<th>HFA</th>
<th>MFA</th>
<th>LFA</th>
</tr>
</thead>
<tbody>
<tr>
<td>Asymptote δ (km$^2$)</td>
<td>34.6 (29.9 – 39.3)***</td>
<td>29.3 (25.6 – 33.0)</td>
<td>15.2 (11.8 – 18.6)***</td>
</tr>
<tr>
<td>Xmid θ (mins)</td>
<td>880.3 (866.3 – 894.3)***</td>
<td>637.9 (620.3 – 655.5)***</td>
<td>472.5 (456.7 – 488.3)***</td>
</tr>
<tr>
<td>Scale φ (mins)</td>
<td>230.5 (222.5 – 238.5)***</td>
<td>252.8 (241.8 – 263.8)*</td>
<td>155.7 (145.5 – 165.9)***</td>
</tr>
<tr>
<td>Movement Speed (kmh$^{-1}$)</td>
<td>0.38</td>
<td>0.32</td>
<td>0.38</td>
</tr>
<tr>
<td>Individuals</td>
<td>6</td>
<td>6</td>
<td>6</td>
</tr>
<tr>
<td>Trips</td>
<td>93</td>
<td>116</td>
<td>218</td>
</tr>
<tr>
<td>Points</td>
<td>2162</td>
<td>2713</td>
<td>5515</td>
</tr>
</tbody>
</table>

This dispersal movement model compares how fluctuations in forage availability influence the characteristics of the daily trips inside the protected area, with the results shown in Figure 4.8 and Table 4.7. These results show again that movement decreases with forage availability, with the asymptotic distance being 2.02 km (34%) lower in LFA than HFA. The
xmid value also decreases with forage availability, with movement in HFA reaching xmid at 14:40 hrs, 10:38 hrs in MFA and 07:53 hrs in LFA. This shows that movement is starting much earlier when forage availability is low, inside of protected areas.
4.2.6 Outside Protected Area – Dispersal

![Figure 4.9](image)

Figure 4.9 – The output of a non-linear mixed effects model, comparing the daily trip movement characteristics of the dispersal movement type outside the protected areas, across the forage availability categories.

Table 4.8 – Comparing movement characteristic predictions of the mixed migratory movement type inside the protected areas from a non-linear mixed effects model, across the three forage availability categories.

<table>
<thead>
<tr>
<th>Dispersal - Outside Protected Area</th>
<th>HFA</th>
<th>MFA</th>
<th>LFA</th>
</tr>
</thead>
<tbody>
<tr>
<td>Asymptote δ (km²)</td>
<td>36.0 (29.5 – 42.5)***</td>
<td>24.0 (18.5 – 29.5)*</td>
<td>22.4 (17.3 – 27.5)*</td>
</tr>
<tr>
<td>Xmid θ (mins)</td>
<td>973.5 (962.9 – 984.1)***</td>
<td>715.1 (696.0 – 734.2)***</td>
<td>367.5 (356.5 – 378.5)***</td>
</tr>
<tr>
<td>Scale ϕ (mins)</td>
<td>161.6 (155.0 – 168.2)***</td>
<td>232.0 (219.4 – 244.6)***</td>
<td>121.2 (114.1 – 128.3)***</td>
</tr>
<tr>
<td>Movement Speed (kmh⁻¹)</td>
<td>0.56</td>
<td>0.32</td>
<td>0.59</td>
</tr>
<tr>
<td>Individuals</td>
<td>6</td>
<td>6</td>
<td>6</td>
</tr>
<tr>
<td>Trips</td>
<td>77</td>
<td>131</td>
<td>218</td>
</tr>
<tr>
<td>Points</td>
<td>1792</td>
<td>3031</td>
<td>5042</td>
</tr>
</tbody>
</table>

This dispersal movement model compares the characteristics of movement outside the protected areas, across forage availability categories. There is less variation in the asymptote outside of the protected area, than inside, but still a noticeable decrease in movement as forage availability becomes limited. There is great variation in the xmid
parameter, with the time xmid is reached changing from 16:14 in HFA, 11:55 in MFA and 06:08 in LFA. The speed of movement is similar in LFA and HFA, but lowest in MFA.
4.2.7 Inside Protected Area – Mixed Migratory

Figure 4.10 – The output of a non-linear mixed effects model, comparing the daily trip movement characteristics of the mixed migratory movement type inside the protected areas, across the forage availability categories.

Table 4.9 – Comparing movement characteristic predictions of the dispersal movement type outside the protected areas from a non-linear mixed effects model, across the three forage availability categories.

<table>
<thead>
<tr>
<th>Movement Type</th>
<th>Inside Protected Area</th>
<th>Mixed Migratory</th>
<th>LFA</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Asymptote A δα (km²)</strong></td>
<td>20.4 (18.5 - 22.3)***</td>
<td>17.9 (16.0 – 19.8)</td>
<td>12.8 (11.0 – 14.6)***</td>
</tr>
<tr>
<td><strong>Xmid A θα (mins)</strong></td>
<td>502.9 (501.2 - 504.6)***</td>
<td>527.9 (525.4 - 530.4)***</td>
<td>494.1 (491.5 - 496.7)***</td>
</tr>
<tr>
<td><strong>Scale A φα (mins)</strong></td>
<td>48.4 (46.9 – 49.9)***</td>
<td>49.5 (47.4 – 51.6)</td>
<td>58.6 (56.4 – 60.8)***</td>
</tr>
<tr>
<td><strong>Movement Speed A (kmh⁻¹)</strong></td>
<td>1.40</td>
<td>1.28</td>
<td>0.92</td>
</tr>
<tr>
<td><strong>Asymptote B δβ (km²)</strong></td>
<td>2.6 (0.3 – 4.9)</td>
<td>6.6 (3.8 – 9.4)</td>
<td>4.7 (2.1 – 7.3)</td>
</tr>
<tr>
<td><strong>Xmid B θβ (mins)</strong></td>
<td>1057.8 (1055.2 – 1060.4)***</td>
<td>1064.8 (1060.3 – 1069.1)</td>
<td>1068.7 (1064.8 – 1072.7)*</td>
</tr>
<tr>
<td><strong>Scale B φβ (mins)</strong></td>
<td>89.5 (87.0 - 92)***</td>
<td>84.4 (80.3 – 88.5)</td>
<td>60.1 (56.5 – 63.7)***</td>
</tr>
<tr>
<td><strong>Movement Speed B (kmh⁻¹)</strong></td>
<td>0.27</td>
<td>0.46</td>
<td>0.54</td>
</tr>
<tr>
<td><strong>Individuals</strong></td>
<td>6</td>
<td>6</td>
<td>6</td>
</tr>
<tr>
<td><strong>Trips</strong></td>
<td>134</td>
<td>169</td>
<td>286</td>
</tr>
<tr>
<td><strong>Points</strong></td>
<td>3069</td>
<td>3925</td>
<td>6622</td>
</tr>
</tbody>
</table>
This mixed migratory movement model compares the movement characteristics of trips inside the protected area, across the forage availability levels. Compared to the dispersal movement strategy the asymptotic values are generally lower and the Xmid A values are generally earlier, but with much less variation than in the dispersal movement model.

The value for asymptote A decreases with forage availability; however this relationship is not replicated in any other of the parameters. There seems to be a greater return to the point of origin in MFA and LFA, whereas in HFA this movement is much less so. The timings of movement are similar across all of the categories, indicating dawn and dusk movement activity, but with little variation due to forage availability. Speed of movement decreases with forage availability on the outward journey, but increases with forage availability on the return journey.
4.2.8 Outside Protected Area – Mixed Migratory

Figure 4.11 – The output of a non-linear mixed effects model, comparing the daily trip movement characteristics of mixed migratory movement type outside the protected areas, across the forage availability categories.

Table 4.10 – Comparing movement characteristic predictions of the mixed migratory movement type outside the protected areas from a non-linear mixed effects model, across the three forage availability categories.

<table>
<thead>
<tr>
<th></th>
<th>Outside Protected Area - Mixed Migratory</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>HFA</td>
</tr>
<tr>
<td>Asymptote A ( \delta_a ) (km(^2))</td>
<td>14.4 (11.8 – 17.0)***</td>
</tr>
<tr>
<td>Xmid A ( \theta_a ) (mins)</td>
<td>553.4 (548.9 – 557.9)***</td>
</tr>
<tr>
<td>Scale A ( \varphi_a ) (mins)</td>
<td>75.8 (72.1 – 79.5)***</td>
</tr>
<tr>
<td>Movement Speed A (kmh(^{-1}))</td>
<td>0.75</td>
</tr>
<tr>
<td>Asymptote B ( \delta_b ) (km(^2))</td>
<td>-17.2 (-23.4 - -11.0)*</td>
</tr>
<tr>
<td>Xmid B ( \theta_b ) (mins)</td>
<td>1213.4 (1204.4 – 1222.4)***</td>
</tr>
<tr>
<td>Scale B ( \varphi_b ) (mins)</td>
<td>112.5 (106.8 – 118.2)***</td>
</tr>
<tr>
<td>Movement Speed B (kmh(^{-1}))</td>
<td>0.55</td>
</tr>
<tr>
<td>Individuals</td>
<td>6</td>
</tr>
<tr>
<td>Trips</td>
<td>52</td>
</tr>
<tr>
<td>Points</td>
<td>1200</td>
</tr>
</tbody>
</table>
Figure 4.11 and Table 4.10 show the results of the mixed migratory models comparing the movement characteristics of trips outside of protected areas, across forage availability levels.

This model shows an unusual mixed migratory shape, with a negative Asymptote B value, indicating rather than returning to the point of origin after resting; the individuals continue to move away from this point, especially in the case of HFA - travelling more than the distance of asymptote A, again.

The values for xmid A and xmid B are similar across the forage availability categories, showing similar timings of movement and estimated values for speed are similar across all forage categories.
5. Discussion

5.1 Overview

The main movement types found in the daily movement of African elephants are dispersal and mixed migratory, both of which reflect a rest period after an initial movement. However, the key difference is that dispersal indicates movement away from the point of origin, whereas mixed migratory movements typically have some return towards the point of origin; suggesting that the individuals are to some extent staying in the same area. This may be due to the presence of a required resource, for example water or forage, or perhaps the absence of competition or predators. As shown in Table 4.2 the mixed migratory movement is more prevalent inside of protected areas, particularly when there is higher forage availability, perhaps indicating it is the preferred movement strategy when there are few limitations to energy acquisition; such as uniform forage distribution and as a result little competition.

5.1.1 Key Findings

- The key findings of this study are summarised below:
- Movement decreases with declining forage availability.
- Movements were smaller within protected areas than outside.
- The mixed migratory movement is more prevalent within the protected area and this movement type showed smaller movements than dispersal.
- Within the dispersal movement, the timing of movement was influenced by forage availability, with movements starting earlier in the day as forage availability declines.
- The timing of movement in the mixed migratory model varies relatively little, with movement activity peaking at dawn and dusk.
- Resource availability seems to have larger impact on daily movement inside of the protected areas than outside – where perhaps there are other factors that are more influential on movement, at least at a daily scale.

These findings will be discussed in detail in the following sections.
5.2 Differences in Forage Availability Categories

The results of all the models comparing movement characteristics across forage availability levels support those of Birkett et al. (2012) who found that during the dry season, elephants travel less. Polansky et al. (in prep.), a study which also focussed on the daily movements of elephants also found that during times of LFA elephant movement is less than in times of HFA, reflecting an energy conservation strategy.

It has been stated that species tend to cover larger home ranges when resources are sparse, as a greater area is needed to meet energy requirements (O’Neill et al. 1988; Fryxell et al. 2005). The data from this study do seem to support this, as seen in Figure 4.2. It seems counter intuitive to the finding that they travel less on a daily basis during times of LFA. The larger home ranges may be due to occasional long distance movements between patches of resources (Wittemyer et al. 2007; Fryxell et al. 2005), which can be seen in the LFA and MFA panels of Figure 4.4.

There are some particularly large movements in the LFA panel, with the biggest being 707.12km² (26.6km) covered in a single day, well above the model asymptotic value of 18.8 km² (4.3km). These long distance movements tend to occur outside of the protected area in times of LFA as can be seen in Figure 4.9; supporting the theory that these movements are long distance movements between patches. It is possible that as they are common outside of the protected area, that they may be a response to a threat or inter-species competition.

5.3 Differences Inside and Outside Protected Areas

The results show that in both movement models, individuals move further outside of protected areas than inside, especially so in the mixed migratory, this finding is in concordance with the findings from Graham (2009). The dispersal model also shows that elephants move more quickly outside of protected areas as previously found in the literature (Wall et al. 2013; Graham 2009; Douglas-Hamilton et al. 2005b).

Figure 4.6, comparing dispersal movement inside and outside protected areas, displays a number of large movements, outside of the protected areas, with NSD increasing quickly.
directly after midnight. The xmid value outside of the protected area is 8:14AM, whereas it is almost three hours later inside the protected area, at 11:08AM. This means that elephant movement activity occurs much earlier outside of protected areas than inside, perhaps due to increased nocturnal activity. Wittemyer et al. (2007) suggested that a temporal shift in activity is part of a conflict avoidance strategy, due to the presence of pastoralists and their livestock occupying locations with access to water during the day.

The mixed migratory model shows quite different results to the dispersal model, with much slower movement and a later xmid value outside of the protected areas, indicating that perhaps this movement type does not exhibit night time activity. However, there is a very distinct difference between movement inside and outside the protected areas, with the movement inside showing a slight return to the point of origin in asymptote B; conversely outside the protected areas the second movement continues away from the point of origin. This may be due to the increased presence of risk outside of protected areas (Graham 2009), encouraging continued movement rather than returning someway to the point of origin as is normally expected from mixed migratory movements.

5.4 Differences in Forage Availability and Protected Area Coverage

There are similar movement patterns when comparing how availability impacts the dispersal model inside and outside protected areas forage. The asymptote decreases as forage availability decreases both inside and outside protected areas, but to a greater extent inside protected areas, decreasing by 19.4 km2 (4.4km) between HFA and LFA.

The xmid value is smallest in LFA outside of the protected areas, again perhaps reflecting a higher number of overnight activities, which would be expected at this time and in this location. The movement speed is faster outside of the protected areas, for LFA and HFA, but it remains the same for MFA.

The asymptotes for the mixed migratory model are lower than for dispersal, across all categories, there is also less variation between the forage categories in the mixed migratory model. This may indicate that mixed migratory movement is more typical when elephants
are near to forage, whereas dispersal movements may be more typical of when a journey is required to reach forage.

There is distinct difference in the shape of the mixed migratory model, when comparing between inside and outside protected areas. The models inside the protected area show a more ‘classic’ mixed migratory model, with a greater proportional return to the point of origin seen in MFA and LFA, showing a return of 36.8% and 36.7% of the asymptote A value, respectively, and HFA showing a return of only 12.7%.

The models outside of the protected area show a very different pattern, rather than a return there is an on-going movement towards a second asymptote further away from the point of origin. The reason for this shape could be a response to the risks that are more abundant outside of the protected areas, causing elephants to continually move through the landscape rather than returning towards a point of origin. This movement away is particularly evident in the HFA category and becomes less evident as forage availability decreases; perhaps due to movement being restricted where resources available and a greater need to conserve energy during times of LFA.

The xmid A and xmid B values vary very little throughout the mixed migratory models, with the range of xmid A times being 07:48 – 09:13 and the range of xmid B times being 17:38 – 20:13. These times show that there are movements dawn and dusk, with this factor showing little influence from either forage availability or location with respect to protected area. The dispersal models have much more varied x mid values, perhaps due to the influence of overnight movements which seem to be more prevalent in the dispersal movement type.

5.5 Limitations

This study does not consider the impacts of social status on movement, with previous studies finding that it is an important factor, particularly in the dry season when subordinate individuals are out-competed away from the optimal areas and as a result are forced to move out of the protected areas (Wittemyer et al. 2007; Wittemyer 2008; Polansky et al. in prep.). This factor was not explicitly addressed in this study due to the
small sample size (n=6) and the change in the social status of one of the individuals after the death of a matriarch, during the study period. However the variations between individuals were accounted for as a random effect in the non-linear mixed effects model.

The distinction between inside protected area and outside protected area is perhaps too stark, with all of the trips that crossed the boundary being omitted from this comparison. However it may have been better to include these trips as an intermediate category to compare their movement characteristics to those inside and outside the protected areas. There were no male elephants included in this study, which may limit the applicability of the results to the population. Male elephants may have different movement patterns, particularly due to periods of ‘musth’ causing increased movement speed and direction (Wall et al. 2013).

The temporal resolution of the NDVI data was 16 day scenes, and therefore the forage availability classes which were of the same length. This is significantly larger than the GPS data, which has an hourly resolution. There is currently no environmental data of comparably high resolution, limiting the extent to which behavioural inferences can be made on movement data (Hebblewhite & Haydon 2010).

5.6 Future Work

The water availability and distribution has been found to be a significant factor influencing elephant movement (de Beer & van Aarde 2008; Loarie et al. 2009), however it has not been included in this study as the presence of water in this system is ephemeral and difficult to quantify and map. Should this challenge be overcome water may prove to be a more important factor than forage in influencing animal movement.

The inclusion of a fourth forage availability category, ‘very low forage availability’ could be a valuable inclusion in future work. The LFA category was considerably larger than MFA and HFA and there was no distinction between LFA categories occurring directly after an MFA scene and an LFA scene that had been preceded by five LFA scenes and therefore probably has much less available forage. Would daily movements become increasingly restricted as
forage availability continues to decline or do large movements become more frequent in an effort to reach the very limited patches of forage?

5.7 Conclusion

The findings of this study suggest that forage availability is a key factor influencing the movement of elephants, with movement being restricted to the limited areas of forage as the resource availability and distribution declines. In the context of the threats of habitat fragmentation and climate change it is important that there is not only sufficient protected area coverage for this wide ranging species, but that this space provides patches of resource availability when forage availability is generally low; which is likely to become a more common occurrence annual precipitation may continue to decrease and there will be increased pressure and competition on the available land as human populations grow.

This study has provided insight into the daily movement patterns of African elephants and how these movements change both with forage availability and with protected area coverage. This methodological technique has not previously been applied in order to compare how movement varies with a temporally fluctuating factor, such as NDVI. Previous studies have compared the influence of latitude (Singh et al. 2012) and the activity of individuals (Papworth et al. 2012; Bunnefeld et al. 2011). This study supports the premise that this technique can be applied to a wide range of scenarios within movement ecology and provides an improved understanding of the movement characteristics of individuals.
6. References


