EFFECT OF WATER AVAILABILITY, LANDSCAPE FRAGMENTATION AND FORAGE ABUNDANCE ON THE MOVEMENT AND HABITAT UTILIZATION OF ELEPHANTS

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FEBRUARY, 2014

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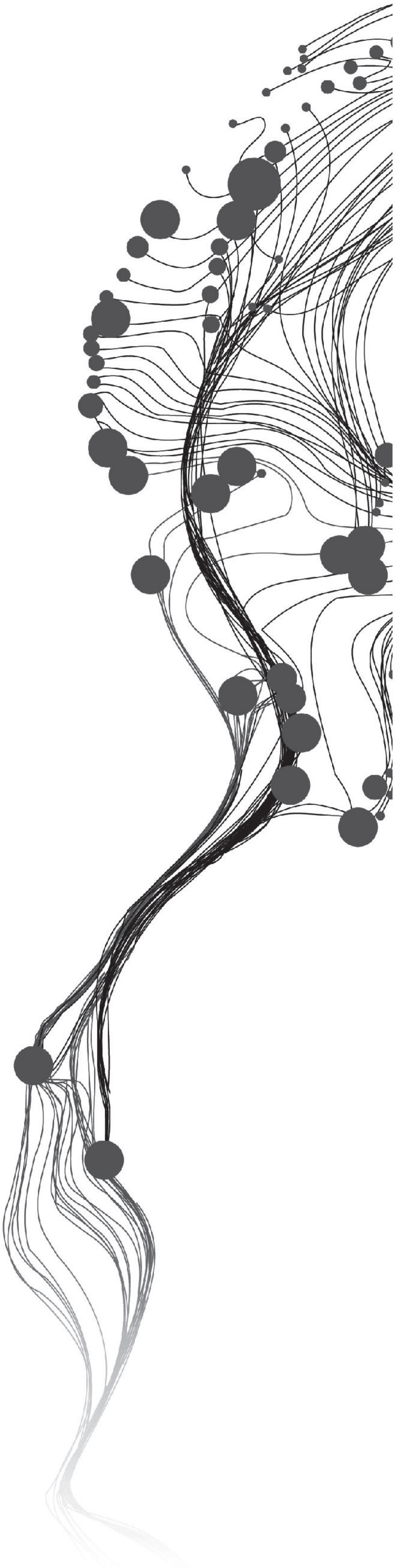

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TAWANDA WINMORE GARA
Enschede, The Netherlands, February, 2014

Thesis submitted to the Faculty of Geo-Information Science and Earth Observation of the University of Twente in partial fulfilment of the requirements for the degree of Master of Science in Geo-information Science and Earth Observation.
Specialization: Natural Resources Management

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ABSTRACT

Understanding the effect of water availability, landscape fragmentation and forage abundance on elephant behaviour is important for conservation and restoration of ecosystems in which these mega-herbivores populate. However, the current understanding of how these metrics modify wildlife behaviour in environments where wildlife and humans co-exist is poorly understood. Previous studies were mainly based of conventional methods of determining elephants presence such as dung, spoors and sightings. Although conventional methods have provided insights on elephants habitat selection, their major setback is the lack of temporal structure. The advancement of GPS telemetry have provided landscape ecologists an opportunity to explicitly understand elephant response to different ecological metrics. The aim of this study was to examine the effect of water availability, landscape fragmentation, and forage abundance on elephant movements and habitat utilization in the Amboseli ecosystem, Kenya. Specifically, the study seek to understand whether water availability, landscape fragmentation and forage abundance explain speed of movement and habitat utilization in the wet, transition and dry season. The study also aim to understand the landscape fragmentation level of elephant migration corridors. Speed of elephant movement and habitat utilization were derived from GPS collars fitted on five elephants of different groups. Habitat utilization was estimated using the novel "time density" algorithm. Water availability was quantified based on distance to waterholes and rivers. An effective mesh size landscape metric (m_{eff}) was used to quantify landscape fragmentation, while forage abundance was estimated using remotely sensed dry matter productivity (DMP) data. Elephant migration corridors were determined using a Brownian Bridge Movement Model (BBMM). The distance to water source map was categorized into three classes that is, close, intermediate and far distance to water sources. Speed of elephant movement and habitat utilization in each distance to water class was compared using *Kruskal Wallis test*. Regression analysis was used to test whether landscape fragmentation and forage abundance significantly explain speed of movement and habitat utilization. Fragmentation of the elephant migration corridors and their immediate surroundings were compared using *Wilcoxon* sum rank test. Results demonstrate that elephants move faster in the close and intermediate distance to water sources class compared to when they are far away from water (*Kruskal Wallis* $p < 0.05$). However, there was no significant difference (Kruskal Wallis test: $p > 0.05$) in habitat utilization in each of the distance to water classes. Elephants were observed to increase their speed of movement and spend less time in highly fragmented landscapes throughout the three seasons. Results demonstrated also that immediate landscapes surrounding corridors are more fragmented compared to landscapes used by elephants as corridors. Hence, elephants select less fragmented landscape as corridors to connect their fragmented habitats. Results also revealed that forage amounts significantly ($p < 0.05$) explained speed of movement and habitat utilization. Speed of elephants movement increase with decreasing forage amounts. A significant ($p < 0.05$) unimodal relationship between forage abundance and habitat utilization was also observed implying elephants spend much of their time in the intermediate forage amounts landscapes with less time being spent in the very low and very high forage amounts landscapes. The interaction effect of landscape fragmentation and forage abundance demonstrated that elephants move faster and spend less time in highly fragmented landscapes characterized by low forage amounts. Findings of this study are important for management of wildlife habitats especially migration corridors outside the protection area. Results of this study also feed into waterholes management across the landscapes in which elephants roam.

Keywords: Amboseli ecosystem, time density, effective mesh size, fragmentation geometries, dry matter productivity (DMP), migration corridors

ACKNOWLEDGEMENTS

I extend my heartfelt gratitude to Dr. Tiejun Wang, who patiently and tirelessly supervised this study to completion. Tiejun, thank you for your inspiration and hard work. You challenged me with robust scientific questions ad suggestions. I enjoyed working with you for the entire research period. My gratefulness also goes to my second supervisor, Prof. Dr A K. Skidmore for the critical comments and development of the research concept especially in the early stages of the study.

My appreciation and thankfulness goes to Kenya Wildlife Services (KWS) for granting me permission to carry out this study in the Amboseli ecosystem. I would like to express my acknowledgement to Dr. Shadrack Ngene and KWS for the elephant GPS tracking data, fragmentation geometry data, vehicle and assistance during my fieldwork in Amboseli. I also thank Africa Wildlife Foundation (AWF) for providing part of fragmentation geometry data. I also thank Joseph 'Joe' Mukeka (KWS) for the fieldwork assistance. I also acknowledge the International Fund for Animal Welfare (IFAW), for providing financial support to procure and deploy the collars to elephants. I acknowledge the School for Field Studies (SFS) at Kimana and The Amboseli Trust for Elephants (ATE) for their support with staff during the elephant collaring operation.

I really enjoyed my first visit to East Africa. Thank you so much my African brothers for the hospitality in Kenya. I hope to invite you to Zimbabwe in the near future.

I would also want to thank ITC for granting me an opportunity to enrol in their versatile MSc programme. It has been my wish over years to improve my GIS and remote sensing skills. ITC came to my rescue and provided me an opportunity sharpen my GIS skills. I also thank NUFFIC for funding my MSc programme. I hope to "stay in touch with the Dutch".

Willem Nieuwenhuis and Mitra Shariati Najafabadi, my sincere appreciation for the respective assistance you rendered in MODIS NDVI pre-processing. Am very grateful to Jake Wall for informal emails on the Movement Ecology Tools for ArcGIS (ArcMET). I also thank Jochen Jaeger for discussions via emails on the effective mesh size landscape metric. Your thoughts and recommendations made this study feasible.

To the SADC community at ITC, I thank you for the light moments we shared. It was challenging but possible. Thanks goes to Garikai Membele (Zambia), Bruce Siyambango (Namibia) and Volkwin Hilifaali Nekondo (Namibia). Special thanks also goes to Joseph Tuyishimire (Rwanda) and Shahriar Rahman (Bangladesh). Finally we made it guys.

I am also greatly indebted to my parents and all family members for their moral and other forms of support. I love you guys. Most importantly, special thanks also go to Chipo Hatendi for moral support. You had challenging time when I left Zimbabwe for further studies in the Netherlands. I had little time for you Chipo but you understood and encouraged me to work tirelessly.

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1. INTRODUCTION

1.1. Background

Mega-herbivores such as the African elephant *(Loxodonta africana* herein after elephant) transverse a mosaic of heterogeneous landscapes in search of resources namely forage, water and potential mates. The distribution of these resources in African landscapes especially savannas is spatially and temporally heterogeneous (de Beer and van Aarde, 2008). Thus, elephants objectively roam the landscape guided by their own instincts in order to maximize on forage intake and water availability as well as minimize human contact (Harris *et al.*, 2008).

In the savanna plains water availability poses a major constraint on elephants movement and their habitat utilization in the dry season (Chamaillé-Jammes *et al.*, 2007). Elephants are water-dependent ungulates requiring frequent and volumes of water for thermoregulation (Dunkin *et al.*, 2013). In a typical nature reserve where human influence is minimal elephants are known to spend considerable amount of time close to water sources during the dry season (Chamaillé-Jammes *et al.*, 2013; Chamaillé-Jammes *et al.*, 2007). This results in overgrazing and degradation of landscapes in close proximity to water sources (Epaphras *et al.*, 2008; Thrash, 1998). Elephants are bulk-feeders, consuming a daily average of approximately 7% of their body weight (Ruggiero, 1992). Hence elephants need to balance the trade-off between foraging in landscapes far from water sources where forage quality and quantity are reasonably high and travelling long distances to meet their water requirements. In environments such as the Amboseli ecosystem where pastoralists and elephants co-exist, competition for water is rife especially during the dry season. This results in increased human-elephants conflict around water sources. Therefore, understanding elephants behaviour and habitat utilization in landscapes where livestock and wildlife compete for water is critical for water management and minimizing human-wildlife conflict at water sources.

Competition for water between elephants and livestock is not the only problem that elephants face in environments where human and wildlife co-exist. The existence of human infrastructure (herein after fragmentation geometries) such as roads, human settlements, fences and agriculture fields within elephant ranges do not only impede wildlife movement but also excise and fragment prime elephants habitats (BurnSilver *et al.*, 2008). For example, roads are known to act as barriers to wildlife movement, sources of mortality especially for small to medium size wild animals and also results in behaviour modifications even for large herbivores like elephants (Blake *et al.*, 2008). Understanding the effect of landscape fragmentation on elephant's habitat utilization and movement patterns especially in the face impending climate change and mounting poaching levels is critical for conservation and mitigating human-elephant conflicts in Africa. In most savanna ecosystem across Africa landscape fragmentation is understood to be a major threat to wildlife distribution (Groom and Western, 2013). In Kenya, most national parks, national reserves and sanctuaries aimed at *in-situ* conservation of different forms of wildlife are surrounded by human settlements (Graham *et al.*, 2009). The Amboseli National Park itself is surrounded by six community ranches that are used by the Maasai pastoralists for livestock grazing and subsistence crop production (Hobbs *et al.*, 2008). These community ranches in close proximity to the Amboseli National Park act as dispersal sinks and migratory corridors for elephants as they attempt to connect isolated habitats (BurnSilver *et al.*, 2008). However, these community ranches have experienced increased landscape fragmentation as a result of sedentarization of the Maasai, intensification of different landuse types and changing land tenure system (Ogutu *et al.*, 2009). Landscape fragmentation as a result of sedentarization in these community ranches has resulted in the increase of human-elephant conflict. Human-elephant conflicts in Amboseli are exacerbated by the fact that wild animals spends over 63% of their time outside the Amboseli national park (Okello and D'Amour, 2008).

A shift from extensive nomadic pastoralism and transhumance to intensive sedentary agro-pastoralism by the Maasai tribesman have increased the rate of landscape fragmentation in the last decades in Amboseli (Western *et al.*, 2009). Landscape fragmentation has occurred at three levels. Firstly, reduction (in size) as more land is cleared to create space for crop farming leading to isolation of habitats such as wetlands and woodlands. Secondly, the development of human infrastructure especially permanent settlements, towns and roads has resulted in habitat loss and excision of elephant habitat. Some of these human infrastructures were constructed within known elephant corridors thus increasing human-elephant conflict and affecting elephants ability to connect isolated habitats. Finally, sub-division of the community ranches as a result of new land tenure system (Thornton *et al.*, 2006). The sub-division of land has resulted in a mosaic of small individually owned parcels of land. These forms of landscape fragmentation have affected habitat utilization and movement patterns of elephants in Amboseli by restricting elephant mobility and access to landscape heterogeneous resources (Western *et al.*, 2009). Understanding the effect of anthropogenic activities on elephant habitat is critical for conservation and ecosystem restoration.

Studies that have attempted to quantify the effect of landscape fragmentation on elephants have mainly related fragmentation geometries such as roads (Barnes *et al.*, 1991; Blake *et al.*, 2008), crop fields (Graham *et al.*, 2009; Hoare, 1999), settlements (Harris *et al.*, 2008) to elephant distribution in isolation. Although this approach provided an insight on elephant response to each of the fragmentation geometries, it is important to understand the holistic effect of these infrastructures on elephant movement rather than understanding the effect of each fragmentation geometries in isolation. It is worthwhile to note that fragmentation geometries (roads, settlements, fields and fences) collectively contribute in dissecting elephant ranges into a mosaic of smaller and isolated habitats. In this regard, it is imperative to test the effect of all fragmentation geometries. An effective mesh size landscape metric provides an opportunity to integrate all fragmentation geometries and assess their combined effect on elephant movement. The application of the effective mesh size landscape metric in quantifying landscape fragmentation in African savannas is still rudimentary.

Forage abundance is an important ecological metric that govern use of space by elephants. However, quantification of forage abundance over space and time has been a challenge for landscape ecologists. A number of studies (Loarie. Scott *et al.*, 2009; Matawa *et al.*, 2012; Murwira and Skidmore, 2005; Pittiglio *et al.*, 2013; Wall *et al.*, 2013) used vegetation indices such as Normalised Difference Vegetation Index (NDVI) and Enhanced Vegetation Index (EVI) as a surrogate for forage abundance for elephants. Although vegetation indices are correlated to primary productivity and thus forage abundance, the exclusion of meteorological parameters such as temperature and solar radiation to estimate forage abundance result in an average to poor relationship between vegetation indices and forage abundance (Xu *et al.*, 2012). Moreover, vegetation indices computed from a single-date satellite imagery only provides a snapshot of vegetation vigour for that particular day. Consequently, single date vegetation indices do not provide explicit temporal variations in vegetation condition which is important to quantify the amount of forage available to wildlife. The advancement of remote sensing techniques have provided an opportunity to combined satellite data with meteorological parameters such as temperature and solar radiation to estimate net primary production with minimum error. The Flemish Institute for Technological Research developed a dry matter productivity (DMP) index (Copernicus, 2013) by combining satellite data with meteorological data (solar radiation and temperature) following the classical Monteith approach (Monteith, 1972). The fusion of different data sources has resulted in DMP data being highly correlated to forage abundance compared to vegetation indices (Copernicus, 2013). However, the application of DMP data to wildlife studies has received limited to no attention despite its ability to characterize forage abundance with minimal error. Understanding the link between DMP and elephants movement patterns and habitat utilization of wildlife is important for conservation ecology especially in African savanna where seasonality influences the amount of forage available to wildlife.

Prior to the application of DMP data in wildlife studies, it is important for landscape ecologists to understand theories and processes that govern wildlife foraging habits. The forage maturation hypothesis (FMH) provides ecologists an opportunity to understand forage development and its implication on elephants movement patterns and habitat utilization. FMH postulates that habitat selection and utilization by herbivores is governed by forage quality. Forage quality declines with plant maturation, while forage digestibility weaken as plant biomass matures (Figure 1) because of the changes in cell-wall composition over time (Fryxell, 1991; Gross *et al.*, 1993). In light of this background, forage intake by herbivores is minimal in landscape of very high biomass amounts (Hebblewhite *et al.*, 2008). Moreover, areas with very high standing biomass are characterized by closed woodlands that hinder elephants penetration (de Boer *et al.*, 2013). Therefore, elephant habitat utilization is expected to be low in areas with very high biomass habitats. Elephants are mix feeders whose feeding patterns are governed by the trade-off between forage quantity (Codron *et al.*, 2006), thus elephants do not prefer foraging in low forage amounts because of the low net energy intake that are associated with these landscapes. Elephants are thus expected to utilize landscapes of intermediate to high forage amounts to maximize energy intake. In light of this knowledge, a unimodal relationship is expected between DMP and habitat utilization i.e. elephants are expected to spend less time in very high and very low forage amounts landscapes, with more time being spent in the intermediate to high DMP landscapes.

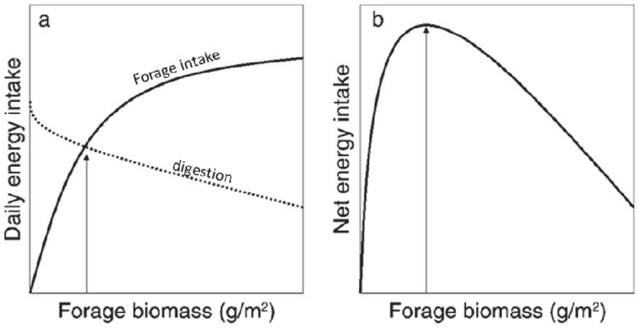


Figure 1: Hypothetical illustration of the forage maturation hypothesis a) relationship between forage intake and digestion b) maximum energy intake at intermediate forage biomass. Adapted from Fryxell (1991)

Most studies that have linked and forage abundance (de Boer *et al.*, 2013; Harris *et al.*, 2008) and fragmentation geometries (Barnes *et al.*, 1991; Eltringham, 1990; Hoare, 1999) to elephants distribution were based on conventional methods of determining elephant presence. The methods aim at determining evidence of presence of the elephant based on fresh elephant dung, pulled down tree branches, spoors and elephant sightings. Although these methods have to some extent provided answers in determining the elephant distribution in relation to fragmentation geometries, they are associated with a number of limitations. Firstly, conventional methods are not feasible in bad weather and rugged terrain. Secondly, these methods are difficult to determine explicit nocturnal movement patterns of wildlife Thirdly, it is difficult to determine true absence based on field observation. Finally, the conventional methods are time consuming, too costly and lack a temporal structure. In the mid 70s there was an increased application of radio tracking telemetry to trace the movement of wildlife within their habitats (Douglas-Hamilton, 1973). Radio tracking telemetry requires stalking the collared animal on foot, vehicle or aircraft. Although this was an improvement to conventional methods, it is associated with problems of system malfunction and geometric errors (Whyte, 1996). In this regard, lack of explicit spatio-temporal information on wildlife movements and habitat utilization has affected conservation of wildlife and ecosystems in which wild animals inhabit.

The advent of GPS telemetry has provided high spatio-temporal data which is important for monitoring wildlife movement and habitat utilization in all weather conditions, unfeasible environments and during the night in real-time. Real time wildlife movement is important for habitat modelling, conservation of wildlife and mitigating human wildlife conflict. A number of studies have used GPS telemetry to determine elephant feeding habits, home ranges, habitat selection and speed of movements between gender (Christ *et al.*, 2008; Douglas-Hamilton *et al.*, 2005; Graham *et al.*, 2009; Grainger *et al.*, 2005; Ngene *et al.*, 2010). However, little is known about the effect of landscape fragmentation on speed of elephant movement and habitat utilization derived from GPS telemetry. This information is vital for decision making that is aimed at sound conservation of this vulnerable specie. In this study, the African elephant was selected for three reasons. Firstly, the International Union for Conservation of Nature (IUCN) list the African elephant as a vulnerable species (IUCN, 2013) that should be given maximum conservation priority especially in East Africa were elephant populations are significantly low (Shannon *et al.*, 2006). Secondly, the elephant is an "ecosystem engineer" (Jones *et al.*, 1994) and a keystone species in the African savanna playing a key role in ecological dynamics such as converting woodlands into shrubland. Lastly, elephants travel long distances, transversing human dominated landscapes to meet their nutritional requirements.

1.2. Elephants in Amboseli ecosystem

Elephants in Amboseli are the most studied ungulates in Amboseli (Moss, 2001). These studies include elephant demography (Moss, 2001), elephant migratory corridors (Graham *et al.*, 2009), elephant distribution (Kioko *et al.*, 2006), human-elephant conflict (Kioko *et al.*, 2008). Moreover, the Amboseli Elephant Research Project has individually identified and monitored all elephant in the ecosystem since 1972. Between 1972 and 1978 elephant population decreased to a population of less than 500 due to droughts and poaching. However since 1979 elephant populations in Amboseli have grown steadily with an estimated population of 1 087 in 1999 comprising of 52 families (Moss, 2001). The current population is estimated at about 1 400 individuals (Chiyo *et al.*, 2011). Elephants in Amboseli used to roam an extensive landscape. Historical evidence show that elephants used to range and mix with elephants from as far as the Nairobi National Park-which is over 200 km from Amboseli National Park (Moss, 2001). However, since the 1960s elephants ranging landscape has been reduced to a mere 3 000 km^2. The reduction in ranging landscape has mainly been a result of increases in human population that have led to agricultural area expansion. Area under cultivation in Kajiado District which encompass the Amboseli ecosystem increased from 40 000 ha to 90 000 ha between 1989 and 1994 (Chiyo *et al.*, 2011). Currently, Amboseli elephants mix and breed with elephant populations in Tsavo-West and the Chyulu Hills NP. Elephant density is known to be high outside the Amboseli National Park especially in the wet season when water does not constrain elephant movement over the Amboseli landscape. In the wet season forage abundance and water availability do not constrain elephant movement (BurnSilver *et al.*, 2008). However, in the dry season most elephant forage close to the national park because of water availability in the swamps. As a result of increasing human population and agriculture expansion human-wildlife conflicts have increased. Human-wildlife conflict involving crop raiding by elephants especially bulls are common in Amboseli ecosystem (Chiyo *et al.*, 2011).

Figure 2: A herd of elephants in Amboseli National Park (courtesy of Amboseli Trust for Elephants)

1.3. Wildlife tracking, GIS and remote sensing

In the mid 60s there was an increased application of very high frequency (VHF) radio tracking to monitor the movement of wildlife within their habitats (Hebblewhite and Haydon, 2010). VHF radio tracking telemetry requires stalking the animal fitted with a transmitter to acquire the signal. Although this was an improvement to conventional method of physical observing the animal within their habitat, it was associated with problems of system malfunction, geometric errors and topographic errors (Whyte, 1996). Moreover, radio tracking is not feasible in bad weather and rugged terrain as well as determining nocturnal movements of wildlife. These drawbacks necessitated the development of the satellite tracking system. Satellite tracking involves the use of Platform Transmitter Terminals (PPT) that are attached (externally) or implanted on an animal (Perras and Nebel, 2012). The PPT sends radio signals to a satellite system. The Argos system is the widely used satellite system in satellite tracking of wildlife (Ngene, 2010). During a satellite overpass the location of the PPT is fixed. The location and time data of the PPT is then sent by the satellite system to the scientist via email (Miller *et al.*, 2005). However, the satellite tracking collars fitted on elephants experienced problems associated with elevation, transmitter instability and orbit errors (Ngene, 2010). Moreover, the Argos satellite system do not have a constant return period, thus it may not be possible to collect sufficient location data to accurately monitor spatio-temporal animal movement (Wall *et al.*, 2006). These complications motivated the development of Geographical Positioning System (GPS) tracking. GPS collar fitted on an animal receives signals from satellite and logs the location and the time data on the device. GPS tracking system gives continuous positioning system because of the constant availability of satellites in space (Wilson *et al.*, 2002). The GPS tracking data is then remotely downloaded to a computer. This development resulted in wildlife biologist to collect large volumes of animal location data thus providing an opportunity to continuously monitor the animal in greater detail (Frair *et al.*, 2010). A number of studies have used to GPS tracking data to characterize elephant migratory corridors (Douglas-Hamilton *et al.*, 2005) home ranges (Grainger *et al.*, 2005) and habitat selection (Loarie *et al.*, 2009).

Advancement in GIS and remote sensing has aided an understanding and management of wildlife movement. The development of GIS and remote sensing products such as hyper-temporal vegetation indices i.e. NDVI, EVI, Dry Matter Productivity (DMP) and Tropical Rainfall Monitoring Mission (TRMM) and digital elevation model (DEM) have provided ecologists and wildlife managers an opportunity to link GPS tracking data to the products for improved wildlife management. Hyper-temporal NDVI and DMP can be used as surrogate for forage abundance, while TRMM data can be used to assess water availability (Loarie. Scott *et al.*, 2009). DEM derived slope and hillshade has also been used to characterize wildlife habitat. For example de Knegt *et al*, (2011) used elevation and slope to characterize elephant habitat in Kruger National Park, South Africa. Understanding the link between products derived from GIS and remote sensing, anthropogenic data such as landscape fragmentation and wildlife movement data derived from GPS telemetry is critical for wildlife conservation, habitat management and restoration. However, the application of DMP in elephant movements patterns is yet to be tested.

1.4. Problem statement

Human dominated landscapes surrounding wildlife conservation areas are historically known to act as wildlife dispersal sinks and migratory routes (BurnSilver *et al.*, 2008). Shifts from extensive pastoralism and transhumance to intensive agro-pastoralism and sedentarization of the Maasai tribesman have resulted in landscape fragmentation and habitat loss in landscapes surrounding wildlife conservation areas (Groom and Western, 2013). Subdivision of wildlife habitats into small, discontinuous and disjoint patches has threatened the sustainability of ecosystems outside wildlife conservation areas to optimally support wildlife. In this context, a few studies attempted to link landscape fragmentation and elephant home ranges especially in southern Africa savanna (Graham *et al.*, 2009; Hoare, 1999). However, knowledge on the effect of landscape fragmentation due to fragmentation geometries on the speed of movement and habitat utilization of elephant is rudimentary especially in East Africa where landscape fragmentation is high due to sedentarization and population increase.

Although evidence of elephant movements outside the wildlife parks are well documented (de Leeuw *et al.*, 2001; Graham *et al.*, 2009; Western *et al.*, 2009), knowledge on fragmentation levels of elephants migratory corridors outside the park is scanty. Studies that have been done mainly compared speed of movement of elephants in these corridors and their usual habitats (Douglas-Hamilton *et al.*, 2005; Ngene *et al.*, 2010). Considering that human dominated landscapes outside the park are used by elephants for dispersal and as migratory corridor, it is therefore important to understand fragmentation levels of migratory corridors used by elephants in these landscapes. This information is important for land use planning that is compatible with wildlife management and conservation.

Studies that have quantified habitat utilization of different forms of wildlife predominantly use habitat preference index as a proxy for habitat selection (Ntumi *et al.*, 2005; Shannon *et al.*, 2006). The habitat preference index expresses the percentage of GPS locations or evidence of presence per land cover class, i.e., the proportion of number of GPS locations in a particular land cover type (Graham *et al.*, 2009). Although this method has received widespread attention and has been widely used by ecologists, it has one major setback. It does not consider the temporal structure i.e. total amount of time that an animal spend per unit area of landscape or land cover class. To this end, this study proposes for the first time, the application of time density function in quantifying habitat utilization in the savanna landscapes of

Southern Kenya. This study also proposes to examine the effect of landscape fragmentation on habitat utilization of elephants derived from the time density algorithm.

The application of DMP data as a proxy for forage abundance in wildlife studies especially elephants movement patterns and habitat utilization has received limited or no attention. Most studies used vegetation indices such as NDVI and EVI as an estimate for forage abundance (de Boer *et al.*, 2013; Murwira and Skidmore, 2005). NDVI is known to saturate in high forage amounts, and thus has a high chance of failing to adequately quantify forage abundance especially in dense woodlands (de Boer *et al.*, 2013). Contrary, DMP is linearly correlated with vegetation growth and thus a better predictor of forage availability compared to NDVI. In light of this background, this study hypothesize that DMP is an important parameter in explaining speed of movement and habitat utilization of elephants in savanna ecosystems of East Africa. To the best of our knowledge no study have attempted to explain elephant movement speed and habitat utilization using DMP data.

1.5. Research objectives

The main objective of the study is to examine the effects of water availability, landscape fragmentation, and forage abundance on elephant movements and habitat utilization in the Amboseli ecosystem. The specific objectives are:

- To examine the effect of distance to water source on speed of movement and habitat utilization of elephants in the dry season
- To examine the speed of movement and habitat utilization of elephants by season (i.e. dry, transitional and wet season) in landscapes of different levels of fragmentation
- To examine relations between elephant migration routes and levels of landscape fragmentation
- To examine relations between forage abundance, speed of movement and habitat utilization of elephants per season
- To examine the interaction effect of landscape fragmentation and forage abundance on the speed of movement and habitat utilization per season

1.6. Research hypothesis

Hypothesis 1

- **H_1**: Elephants move faster close to water sources compared to further away from water sources during the dry season

Hypothesis 2

- **H_1**: Elephants spend more time close to water sources than further away during the dry season

Hypothesis 3

- **H_1**: The speed of movement of elephants increase with increasing level of landscape fragmentation in all seasons

Hypothesis 4

- **H_1**: Habitat utilization decrease as landscape fragmentation level increase in all seasons

Hypothesis 5

- **H_1**: Landscape fragmentation is lower in elephant migration corridors compared to the immediate surrounding landscapes

Hypothesis 6

- **H_1**: The speed of movement of elephants decrease with increasing forage amounts in all seasons

Hypothesis 7

- **H_1**: A unimodal relationship exists between elephant habitat utilization and forage amounts

Hypothesis 8

- **H_1**: The interaction of landscape fragmentation and forage abundance explain speed of elephant movement and habitat utilization better (with a high R^2) compared to their individual contribution

2. MATERIALS AND METHODS

2.1. Study area

The Amboseli ecosystem (Figure 3) is located in Kajiado District, Rift Valley Province and covers an area of approximately 8 500 km^2 (BurnSilver *et al.*, 2008). The area falls in agro-ecological zone *VI* and *V* hence classified as arid to semi-arid savanna. Rainfall is spatially and temporally heterogeneous. Annual rainfall ranges from 500-600 mm in the north to 250-300 mm in Amboseli National Park. Rain falls in two seasons ('short rains' from Nov to Dec and 'long rains' from March to May) interspersed by two dry periods and two transition seasons (Altmann *et al.*, 2002) (Figure 4). Surface water is scarce save for permanent water in swamps and artificial waterholes in the southeast (BurnSilver *et al.*, 2008). Temperature ranges between 20-30^{o}C. Elevation ranges between 850-1350 m above sea level. Dominant vegetation types are the broad leaf, dry tropical forests and woodlands on the Kilimanjaro and Chyulu slopes, open grassland, riverine forest, halophytic grass and scrubland in the Amboseli Basin, scattered *Commiphora* and *Acacia* woodlands (Howe *et al.*, 2013; Western, 2007).

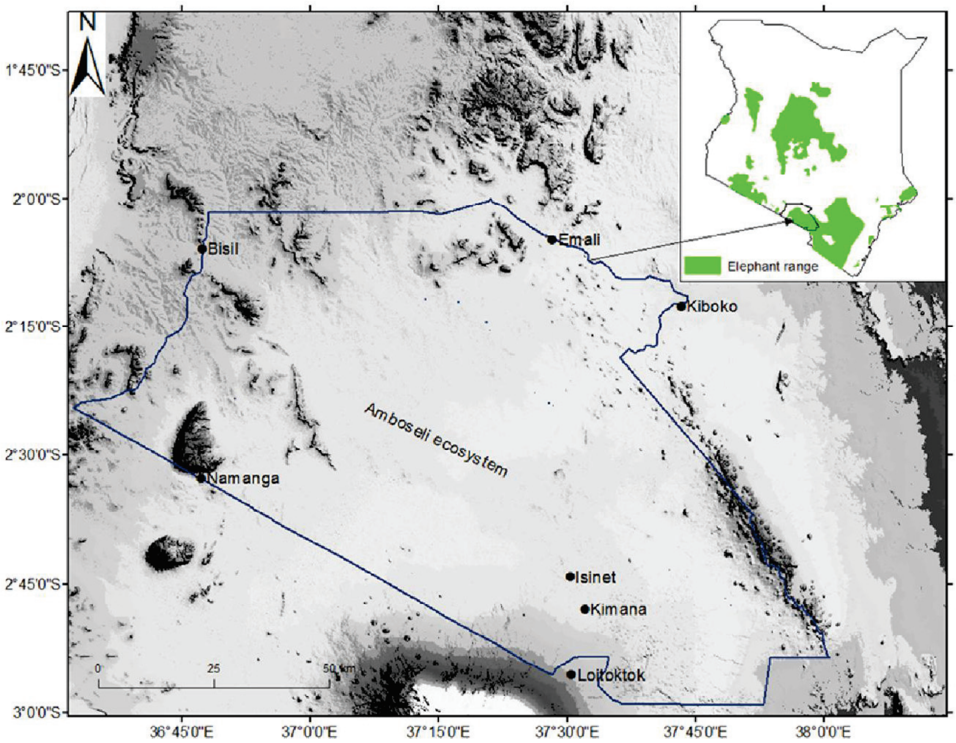


Figure 3: The location of the study area and elephant range in Kenya (Insert)

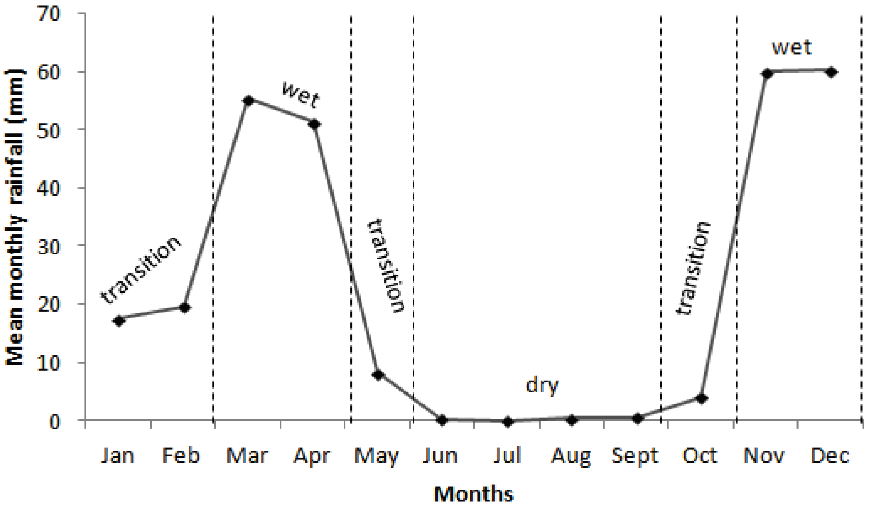


Figure 4: Mean monthly rainfall variations in Amboseli National Park (2006-2011) (rain gauge measurements)

2.2. Elephant GPS tracking data

Between 18th of February and 15th of March 2013, Kenya Wildlife Service (KWS) and International Fund for Animal Welfare (IFAW) darted and fitted four male and two female elephants with GPS collars in Amboseli ecosystem. The elephants belonged to different families. However, one of the collared elephant (female) moved to Tsavo West National Park during the entire tracking period and was thus eliminated from the analysis for this study. All the elephants were collared outside the Amboseli National park, with the idea of observing and monitoring movement patterns of elephants outside the park. Table 1 detail the characteristics of the collared elephants that were considered for analysis.

Table 1: Demographic data of collared elephants and the collaring system used

Name	Sex	Collar number	Age (approx)	Date of collaring	GPS fixes used	% of GPS fixes missing
Kimana	Male	00580824VTI9E75	26	19 February	1021	3.2
Osewan	Male	00580819VTI0A5C	30	20 February	1004	4.2
Porini	Male	00580810VTI662F	33	20 February	981	5.4
Cuku	Female	00580813VTIF23E	26	15 March	892	7.0
Mbirikani	Male	00580812VTI6E39	22	15 March	974	6.6

The collared elephants were immobilized with *Etorphine hydrochloride* (18mg) administered via a dart gun and then revived with *diprenorphine* (54mg). The GPS collars were configured to acquire one GPS fix every four hours. The GPS collars provided a spatio-temporal dimension of elephant movement pattern i.e. coordinates (x, y) at an accuracy of 10m and the time (GMT +3). The GPS fixes were acquired in geographic coordinates (latitude/longitude) and were re-projected to Universal Transverse Mercator (UTM) WGS-84 reference system (Zone 37M) in ArcGIS 10.1 (ESRI, 2011). Before analysis the GPS fixes were checked for any positional irregularities i.e. whether GPS fixes were within acceptable locations within and around study area. The GPS collar dataset had GPS errors (missing coordinates) and these points were eliminated from the dataset before analysis. The errors are mainly a result of GPS collar temporal malfunction. The data available for analysis after data screening ranged between 93% and 96.8% per elephant group, which is within acceptable range to characterize wildlife movements patterns and make sound inference (Frair *et al.*, 2010). After GPS tracking data screening a total of 4 872 points were available for analysis (Figure 5).

Elephant GPS tracking data for each elephant was then classified into three seasons (wet, transition and dry season). Elephant GPS fixes were categorized into three seasons for two reasons. Firstly previous studies demonstrate that elephant behaviour is season dependent i.e. the speed of movement is known to vary from one season to another (Buij *et al.*, 2007; de Beer and van Aarde, 2008; Ngene *et al.*, 2010). Moreover, an ANCOVA test demonstrated that seasonality has a significant (ANCOVA: $p>0.05$) effect on the speed of movement and habitat utilization. Data on the speed of movements and habitat utilization of each elephant group were all derived from the GPS fixes. It is important to note that each elephant tracking data represent a family.

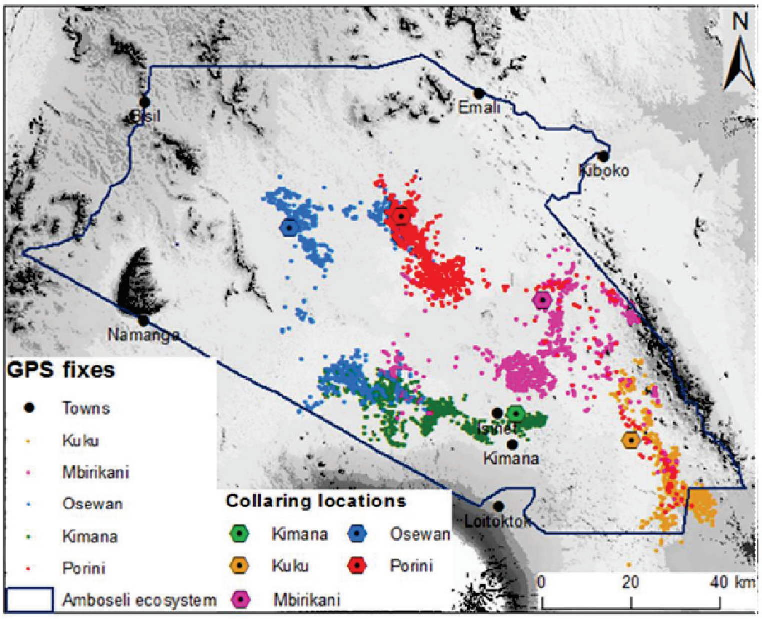


Figure 5: Spatial distribution of GPS fixes for each elephant group in the study area

2.3. Surface water availibility

In Amboseli, during the wet and part of transition season rain collects in pools and other seasonally flooding lowlands. Moreover, in the transition most ephemeral rivers will have substantial amount of water. However, in the dry season water availability is scarce thus exerting a constrain on space use and movement by elephants (Chamaillé-Jammes *et al.*, 2013). During the dry season surface water availability is limited mainly to waterholes where water is pumped from underground and a few permanent water pool along the major rivers. In this study it was assumed that artificial waterholes and dominant rivers are key drivers that determine elephant movement and habitat utilization in the dry season. GIS datasets provided by KWS showing the spatial distribution of artificial waterholes and rivers was used to quantify surface water availability for the dry season (Figure 6). Using these datasets a distance to water map was created, calculated as the Euclidean distance of the centre of a 3 km by 3 km grid to the nearest water source.

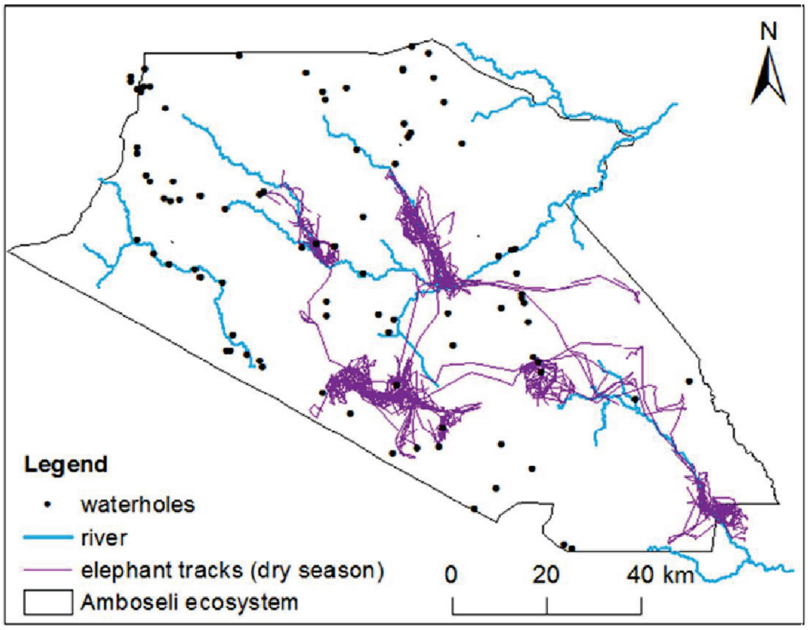


Figure 6: Distribution of waterholes and rivers system in Amboseli ecosystem

2.4. Forage abundance (Dry matter productivity)

Forage abundance was estimated from 10 day DMP composite (dekadal) 1km * 1km resolution dry matter productivity data (Copernicus, 2013) made available by Flemish Institute for Technological Research (VITO) (www.vito.be). DMP is derived from SPOT-VEGETATION sensor on board of SPOT-4/5 satellite. DMP is a proxy for dry matter biomass increase i.e. vegetation growth rate expressed in kilograms of dry matter per hectare per day (kg DM/ha/day) (Copernicus, 2013). It is directly proportional to net primary production (NPP) thus a measure of forage available for elephants. The dry matter productivity is derived by combining satellite data with meteorological data (solar radiation and temperature) following the classical Monteith approach (Monteith, 1972). The physical units of DMP was derived using the formulae:

physical units= (digital number*Sc)+off..(1)

where: Sc is the scaling factor and Off is the Offset parameter. The scaling factor and offset parameter were retrieved from the DMP metadata files.

Pre-processing of DMP data was executed in VGTExtract version 2.1.0. After pre-processing the raw DMP data, the mean DMP for each season was computed in ENVI IDL (Appendix 5). The mean DMP for each grid coinciding with elephant tracking data was extracted using the average of a 3*3 pixel (3*3km) window centred on the GPS location of centre of each grid. Areas with very high DMP are characterized by thick woodlands that can affect elephants penetration, thus elephant habitat utilization is expected to be low in very high DMP values (de Boer *et al.*, 2013). In this regard a unimodal relationship is expected between DMP and habitat utilization.

2.5. Defining elephant migration corridors

An elephant migration corridor is defined as a 'path of continuous movement of at least 10 km distance' (Douglas-Hamilton *et al.*, 2005). The width of the migratory corridor often range between 2-7 km (Ngene, 2010). The migration corridors were determined using the Brownian bridge movement model (BBMM). The BBMM is a continuous-time stochastic model of animal movement in which the probability of animal presence in a region or unit area of landscapes is a function of two successive locations, the distance between the locations, the time between the locations and animal speed of movement (Figure 7) (Horne *et al.*, 2007). The BBMM computes a probability of occurrence of the animal during the entire time of observation. The occurrence in the corridor (connecting two high habitat utilization distributions) are often low because elephant move faster than their normal travelling speed in migration corridor (Douglas-Hamilton *et al.*, 2005). Elephant migration corridors are often narrow compared to habitats that elephants spend much of their time mainly because of the speed of movement which is high in corridors. In this study, the GPS telemetry error of 10m was used (the spatial accuracy of the GPS receiver) because of the unavailability of independent estimate for each GPS fixes. Migration corridor were then digitized in ArcMap 10.1 (ESRI, 2011). A buffer of 7 km around the migration corridor was created to represent non-corridors that is the immediate landscape surrounding migration corridors. A width of 7 km was selected because that is the average width of elephant migration corridor observed in Marsabit National Park, Kenya (Ngene, 2010).

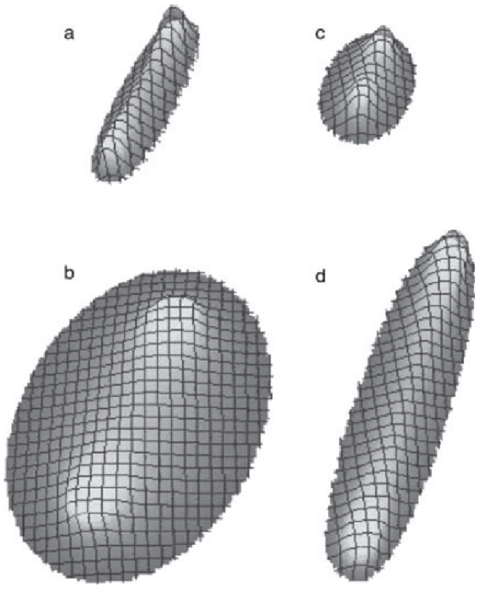


Figure 7: Illustration of probability densities computed using Brownian bridge movement model with GPS fixes separated by different time lapses and distances. Probability densities in **a**) and **b**) are computed from two fixes separated by the same distance but different time lapse **a**) short time of 20 minutes **b**) longer time of 240 minutes. For **c** and **d** the time is similar (40minutes), but distance is different with 275 m and 925m for **c** and **d** respectively. Probabilities for **a** and **d** typical represents corridors. Adapted from Horne *et al.*(2007)

2.6. Calculating the speed of movement of elephants

Assuming elephants move in a linear direction, the speed of movement was computed from the GPS fixes. Speed of movement was calculated in kilometres per hour (km hr^{-1}) by dividing the distance between two consecutive GPS fixes by time lapse between the fixes (Galanti *et al.*, 2006). After computing speed of movement of each elephant, the data was checked for consistency with known knowledge on elephant speed of movement. The maximum speed of movement of an African elephant is approximately 13 km/hr (Wall *et al.*, 2013), thus any speed of movement beyond the maximum threshold was be removed from the dataset before analysis. Only one track was removed from the data set. The abnormal speed of the track was a result of missing of consecutive fixes due to GPS malfunction. After computing the speed for each elephant, the speed data was merged and a velocity grid tool in Movement Ecology Tools for ArcGIS (ArcMET) (Wall, 2013) was used to summarize the mean speed of movement per 9 km^2 grid for each of the three seasons (Appendix 3). The velocity grid tool computes the mean speed of all tracks intersecting a user specified grid, in this case a 9 km^2 grid was used. A grid cell of 9 km^2 was selected because the minimum home range area required by a elephant is 10 km^2 (Douglas-Hamilton *et al.*, 2005).

2.7. Estimation of the habitat utilization of elephants

Habitat utilization for each elephant tracking data was calculated using a 'time density' algorithm (Wall *et al.*, 2013). The algorithm determines the amount of time (time occupancy) an elephant spent per unit area of a landscape (space use). Firstly, linear time density range (LTDR) quantifying the time (in seconds) between consecutive GPS fixes were computed for each elephant using the Movement Ecology Tools for ArcGIS (ArcMET) (Wall, 2013). Secondly, a spatial integrator tool was used to sum fractional linear path lengths (LTDR) between successive GPS locations intersecting a spatial grid cell. For example, a spatial grid cell G, the time density was determined using the formulae:

$$T_G = \sum_{k=1}^{N} \frac{d_k}{s_k} \qquad \text{....................(2)}$$

where d_k is the length of track segment that insects grid cell G, N is the total number of track segments in the animal's trajectory and s_k is the elephant speed over track segment k (Wall, 2013).

Time density was calculated separately for each of the three seasons (Appendix 4). Time density for all the elephant tracking data was computed per 9 km^2 grid cell. Table 2 shows the descriptive statistics for speed of movement and habitat utilization. The highest speed of elephants movement was observed in the dry season.

Table 2: Descriptive statistics of time density and speed of movement per season:

Season	Variable	Minimum	Maximum	Mean	Standard deviation
Wet	Time density	0.02	284.9	27.72	42.84
	Speed	0.004	1.95	0.59	0.33
Transition	Time density	0.01	114.5	13.37	18.73
	Speed	0.003	2.8	0.84	0.56
Dry	Time density	0.05	328	27.3	47.82
	Speed	0.12	2.94	0.94	0.63

Speed is in km/hr and time density is in hrs

Elephant tracks for speed of movement and time density were pooled together specifically for three reasons. Firstly there were no major differences in the behaviour of the collared elephants i.e. speed of movement and time densities between elephant groups in each season (Appendix 1 and Appendix 2).

Secondly most studies pool elephant data for statistical inference (de Beer and van Aarde, 2008; de Knegt *et al.*, 2011; Douglas-Hamilton *et al.*, 2005). Finally, wildlife response to changing environments is often assessed at the entire population level (Graham *et al.*, 2009; Grainger *et al.*, 2005; Loarie. Scott *et al.*, 2009).

2.8. Deriving agriculture fields from land use and landcover classification

The Amboseli landscape is characterized by rain-fed agriculture and small scale irrigation projects. These landuses contribute in fragmenting the landscape. Thus in this study it was important to characterize current agriculture fields because this dataset was not available. Agricultural fields were derived from a classified 16 day MODIS 250m NDVI (MOD13Q1 H21 V9) dataset. MODIS NDVI images from August 2010 to August 2013 were downloaded from US Geological Survey Global Visualization Viewer (GloVis) MODIS NDVI archive (http:/glovis.usgs.gov/). A total of 69 NDVI images were downloaded. The MODIS NDVI dataset was pre-processed using the Savitzky–Golay filter to reduce noise caused by remnants of clouds (Li and Liu, 2011). The NDVI data was converted from sinusoidal to Universal Transverse Mercator projection using the nearest neighbour operator. The dataset was then compressed to 23 NDVI images by computing the mean NDVI of each 16 day period over the three years in ENVI IDL (ITT Visual Information Solutions, 2009).

A maximum likelihood classification (MLC) algorithm was then used to classify the MODIS NDVI dataset in three landcover types i.e. agricultural fields, water and non-agriculture in Erdas Imagine 2013 (Figure 8). The overall classification accuracy using 42 ground control points was 85% (K = 0.68). The non-agriculture class composed of bare grounds, wooded grasslands, shrubland, woodland, riverine woodland. The agricultural fields were then extracted from the classification image and then converted to polygons. The polygons were used as input fragmentation geometry in landscape fragmentation computation.

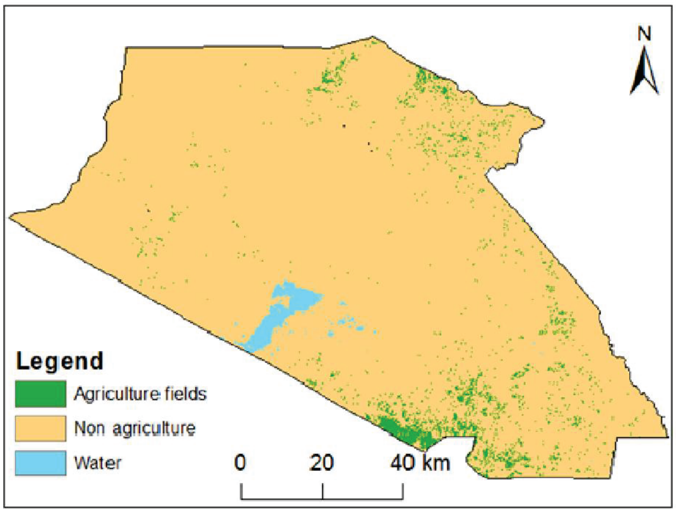


Figure 8 : Distribution of agriculture fields in Amboseli ecosystem

2.9. Quantifying landscape fragmentation

Landscape fragmentation is herein defined as the subdivision and isolation of elephants ranges as a result of any human infrastructure that impedes the accessibility of a habitat to an elephant (Girvetz *et al.*, 2008; Jaeger, 2000). Fragmentation geometries responsible for landscape fragmentation in Amboseli ecosystem are mainly caused by roads, agricultural fields, towns and human settlements. These fragmentation geometries affects elephant movement and habitat utilization. Effective mesh size landscape metric (m_{eff})

was used to quantify landscape fragmentation in this study. Effective mesh size landscape metric expresses the probability that any two locations in a landscape are connected (not separated by barriers such as roads, urban areas, agriculture fields and human settlements) (Girvetz *et al.*, 2008). The probability that the two locations are connected is then converted into size of an area called the effective mesh size. The more barriers to movement and habitat utilization the less the chance that habitats are connected (Jaeger, 2000). The effective mesh size can also be interpreted as the average area accessible to an animal placed randomly in an area without crossing any barrier. In this regard, landscape fragmentation reduces the likelihood of two locations being connected (Moser *et al.*, 2007). Increasing levels of fragmentation as a result of fragmentation geometry results in low effective mesh size. The effective mesh size landscape metric is defined as

$$m_{eff} = \frac{1}{A_t}\sum_{i=1}^{n} A_i^{2} \qquad \dots\dots(3)$$

where n = the number of remaining patches (excluding human infrastructural development), A_i = size of patch i, and At = the total area of the landscape under consideration which has been fragmented. A m_{eff} quantifies landscape fragmentation based on the patch area and number of patches within a planning unit (3 km by 3 km grids).

In this study, human settlements, roads, town, roads (Figure 9) and agricultural fields (Figure 8) were used to quantify landscape fragmentation. Human settlements (individual homesteads, schools) were derived from a March 2010 aerial count dataset conducted by Kenyan Wildlife Services (KWS). The settlements were also overlaid on Google Earth for verification and digitization of missing settlements. KWS also provided a dataset on major roads within the study area.

Fragmentation geometries influence elephants behaviour within a certain distance. Areas close to landscapes dominated and used by human being is excised for elephants utilization and thus affect elephant behaviour. In this study, a buffer of 500m was created for roads (Blake *et al.*, 2008) as well as settlements (Harris *et al.*, 2008), while for towns a buffer of 4 km from the town centre was created (Harris *et al.*, 2008). Landscape fragmentation analysis was performed per 3 x 3 km grid cell to harmonize the dataset with speed of elephant movement and habitat utilization datasets. Computation of the effective mesh size was executed in ArcGIS 10.1 (ESRI, 2011), using the add-in effective mesh size tool (Girvetz *et al.*, 2007).

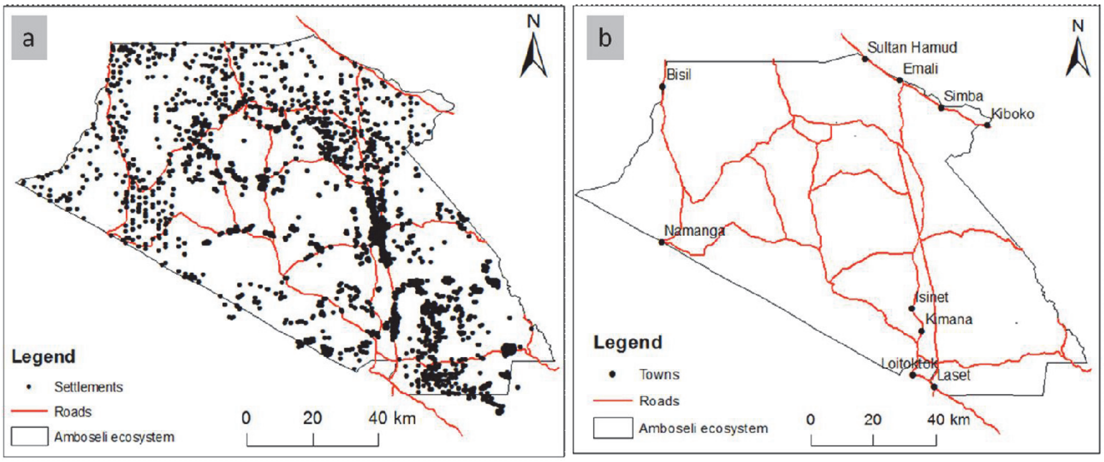


Figure 9: Fragmentation geometries used in the study a) settlements b)roads and towns

2.10. Statistical analysis

2.10.1. Time density, speed of movement and distance from water

A scatter plot of distance to water against time density or speed of movement was random and did not show any particular pattern. The distance to water was then categorized into three distance classes following Sitters *et al* (2009) work conducted in the Amboseli ecosystem. The classes are 1) close water (> 5km), 2) intermediate distance to water 5-10 and 3) far from water <10 km). The speed of movement and habitat utilization of elephants in each distance class was compared using a non parametric *Kruskal Wallis* test statistic (R Development Core Team, 2012). This test statistic was used because both speed of movement and habitat utilization did not follow a normal distribution (*Shapiro Wilk test:* $p<0.05$) even after trying out a number of transformation methods. Pairwise comparison were computed using *Wilcoxon* rank sum test when a significant difference between at least one pair was detected using the *Kruskal Wallis* test (R Development Core Team, 2012).

2.10.2. Relating elephant speed, time density with DMP and landscape fragmentation level

Regression analysis was used to examine relations between speed of movement, time density with landscape fragmentation level and DMP. Prior to regression analysis time density and speed of movement were tested for spatial auto-correlation per season using the *Moran I* to test for conformity with the least squares regression assumption of randomness (Tiefelsdorf, 2002). In all seasons, the speed of movement and time density were significantly spatially auto-correlated. The data was then randomly selected at increasing distance interval until spatial auto-correlation was at its minimal. It was important to balance the trade-off between spatial-auto-correlation and the number of points available for analysis (sample size). An optimal minimum distance between grids centers was achieved at 6 km. In all regression analysis speed of movement and time density were dependent variable, while DMP and landscape fragmentation level were the independent variable. Initially, univariate regression analysis were performed to determine how DMP and landscape fragmentation level individually explained speed of movement or time density. After univariate regression analysis, multiple regression was performed to test whether DMP and landscape fragmentation level collectively improves the explained variance in speed of movement or time density explanations.

Multi-collinearity tests

Prior to regression analysis existence of multi-collinearity among covariates (input explanatory variable in the multiple regression) were tested using variance inflation factor (VIF) statistic (Dormann *et al.*, 2013; O'brien, 2007). Multi-collinearity inflates standard deviations of the regression coefficients resulting in small *t-values* and consequently failure to reject the null hypothesis that the coefficients are significantly different from zero (Brauner and Shacham, 1998). Thus, multi-collinearity can result in insignificant coefficients even when the R^2 is high. Moreover, when multi-collinearity exists, the coefficients became highly unstable reducing the confidence in the estimations. In all cases the VIF between DMP and effective mesh size for also seasons was less than 10 (Table 3) meaning collinearity did not exist between the explanatory variables.

Table 3: Variance inflation factor for the covariates (DMP and effective mesh size)

	R^2	VIF
Wet	0.038	1.03
Transition	0.0031	1.003
Dry	0.099	1.11

Model validation

A *k-fold* cross validation was used to check the performance of the regression models. The *k-fold* value of 10 was used in all cross validation analysis. The operation splits the dataset into 10 equal partitions. At each iteration one partition was used for validation while the other nine segments (*k-1*) were used for model calibration. This process was repeat iteratively until all the partitions were used for model validation as well for model calibration. The operation was computed in R software using the Data Analysis And Graphics (DAAG) package (R Development Core Team, 2012). The *k-fold* validation output (overall mean square) was then used to calculate the root mean square error (RMSE).

2.10.3. Comparison of fragmentation of corridors and non-corridors

Landscape fragmentation levels between corridors and non corridors were compared using a *Wilcoxon* rank sum test with continuity correction (R Development Core Team, 2012). Prior to comparison the fragmentation level data for corridors and non-corridors were tested for normality using the *Shapiro Wilk* test. Landscape fragmentation data did not follow a normal distribution ($p>0.05$) even after trying out a number of transformation methods. Thus, a non-parametric *Wilcoxon* rank sum test was used to compare level of fragmentation between the corridors and non corridors. The operation was executed in R software (R Development Core Team, 2012).

3. RESULTS

3.1. Effect of water availability on speed of movement and habitat utilization

There was no significant difference in the time elephants spent in each distance to water source class (*Kruskal Wallis* chi squared = 1.09, p = 0.59) (Figure 10a). However, significant differences in the speed of elephant movement were observed among the three distance to water source classes (*Kruskal Wallis* chi squared= 7.84, p = 0.02) (Figure 10b). A pairwise comparison showed that there was no significant difference in the speed of movement between the close and intermediate distance to water sources classes (*Wilcoxon* rank sum test: W= 255, p = 0.06). A significant difference in speed of movement was however observed between the close and far (*Wilcoxon* rank sum test: W= 145, p = 0.01) and the intermediate and far (*Wilcoxon* rank sum test: W= 38, p = 0.00) distance to water source classes.

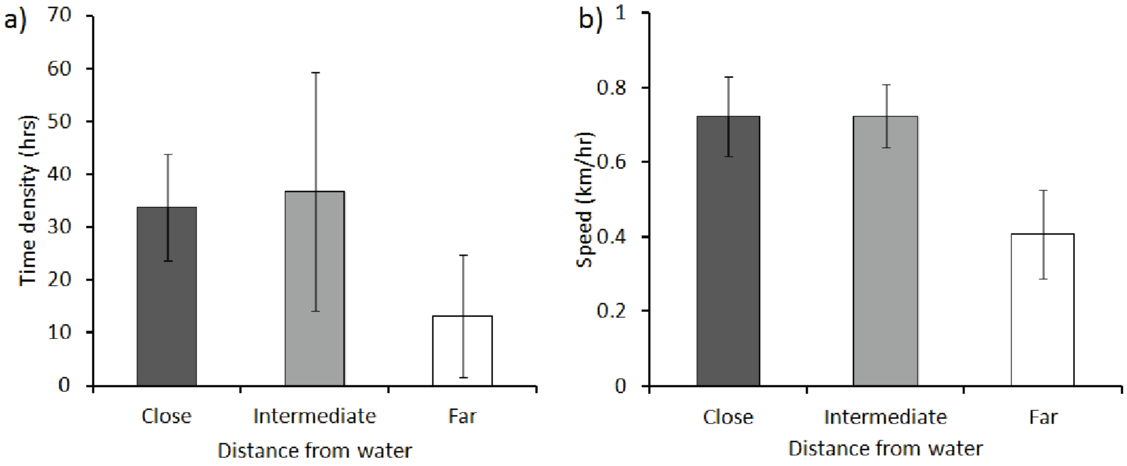


Figure 10: Comparison of a) time density b) speed of movement amongst distance to water classes

3.2. Effect of landscape fragmentation on speed of movement and habitat utilization

The nature and strength of relationship between landscape fragmentation and speed of movement varied from one season to another (Figure 12). All regression equations are significant ($p<0.05$). Landscape fragmentation explained 31% (RMSE = 0.16), 34% (RMSE = 0.18), 22% (RMSE = 0.34), variance in speed of movement in the wet, transition and dry season respectively. In addition, the relationship between landscape fragmentation and speed of movement for all the three seasons are best described by non-linear regression models. An increase in level of landscape fragmentation results in an increase in speed. This implies that elephants move faster in more fragmented landscapes and generally reduce speed in less fragmented landscapes.

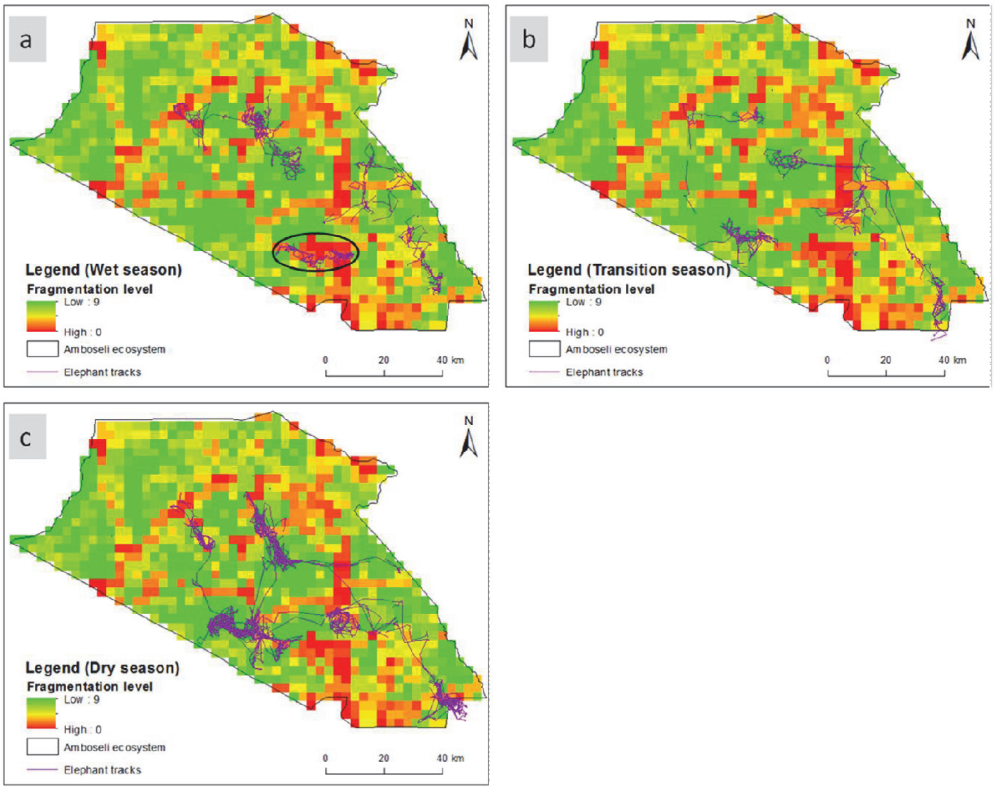


Figure 11: Elephants tracks overlaid for the three season overlaid on the landscape fragmentation maps (encircled ring demonstrated elephant occupancy in fragmented area in the wet season)

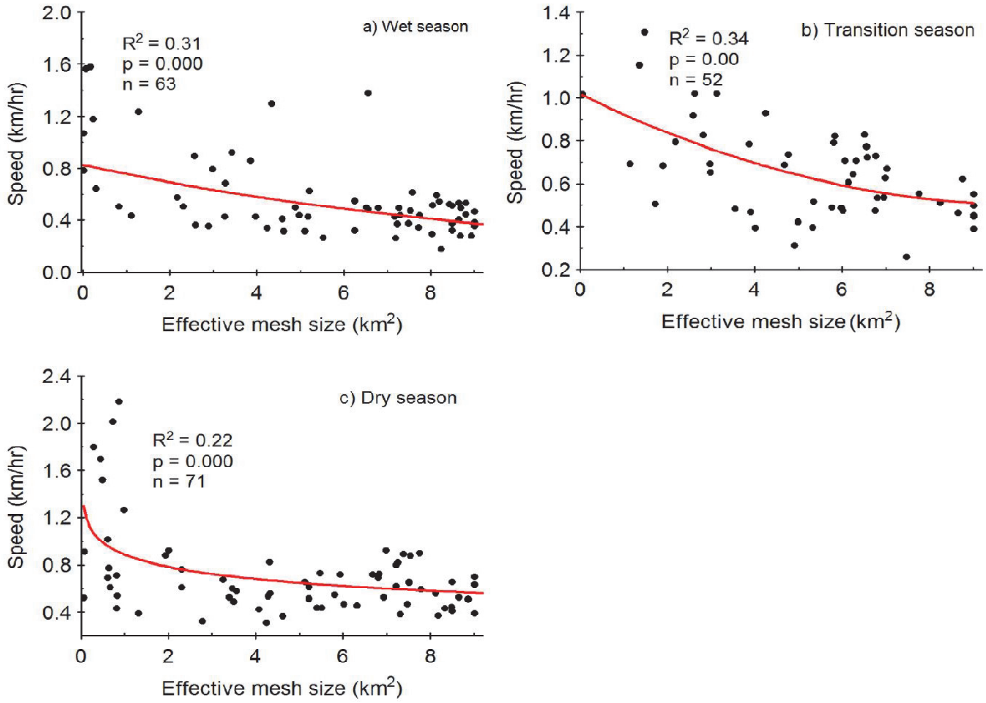


Figure 12: Relationships between speed of movement and landscape fragmentation for a) wet season b) transition season c) dry season

Elephants generally respond to landscape fragmentation in the same way throughout the year. The relationship between landscape fragmentation and time density is significant ($p>0.05$) through the three seasons. Time density decreased with increasing level of landscape fragmentation (Figure 13). This implies that elephants spent less time in highly fragmented landscapes where human activities are high. However, the explained variance are generally low (<0.5) and vary from one season to another. Explained variance of 48% (RMSE = 1.06) was observed for the transition season while 44% (RMSE = 5.78) and 31% (RMSE = 1.19) variance in time density was explained in the dry and wet season respectively. The root mean square error for the dry season is relatively high compared to the transition and wet season demonstrating that time density predictions are relatively poor in the dry season. It is important to note that in the wet season elephant GPS tracks were observed in the highly fragmented landscapes (encircled ring) (Figure 11).

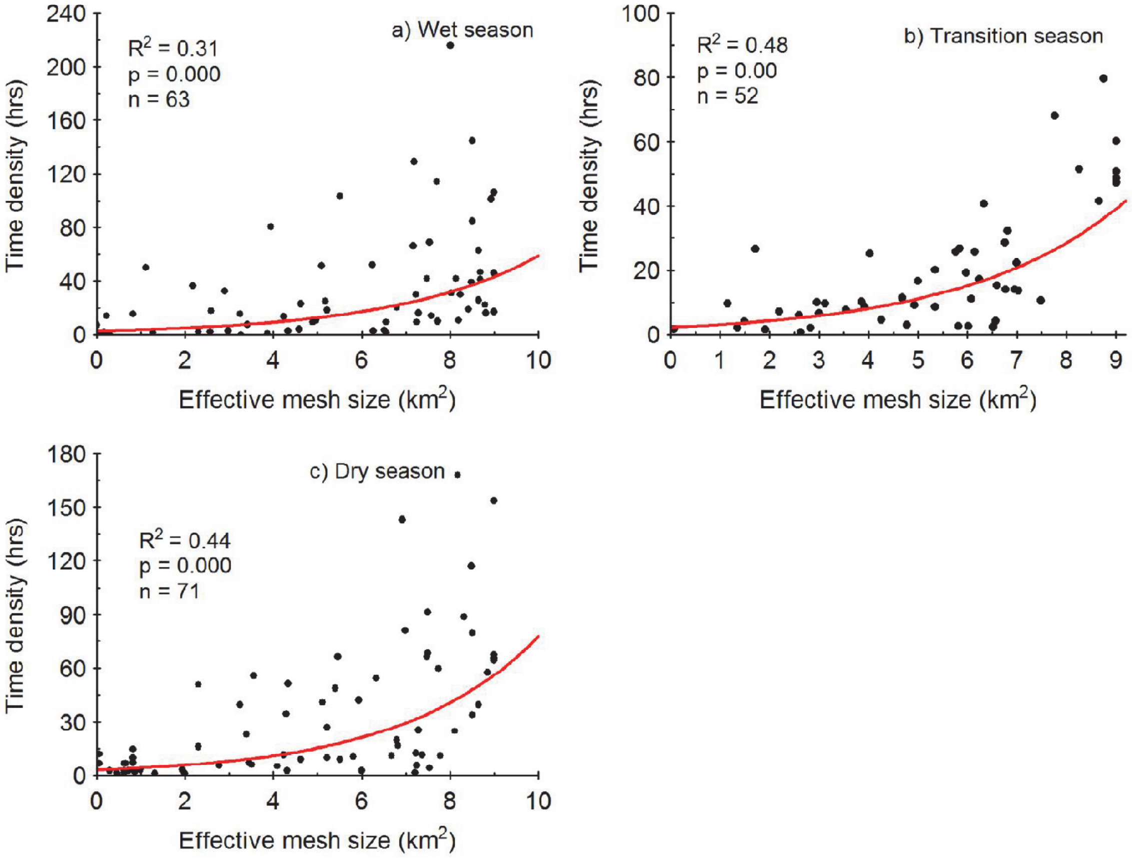


Figure 13: Relationships between landscape fragmentation level and time density for a) wet season b) transition season c) dry season

3.2.1. Landscape fragmentation and migration corridors

Figure 14 shows the probability of occurrence of elephants as estimated by a BBMM. Intensively utilised areas (red regions) can be observed during the entire track period of the elephants. Corridors connecting intensively used habitats can be observed. Corridors are narrow and also characterized by a low probability of occurrence. Surrounding the migration routes are non-corridors which elephants tend to avoid (**Figure 15**).

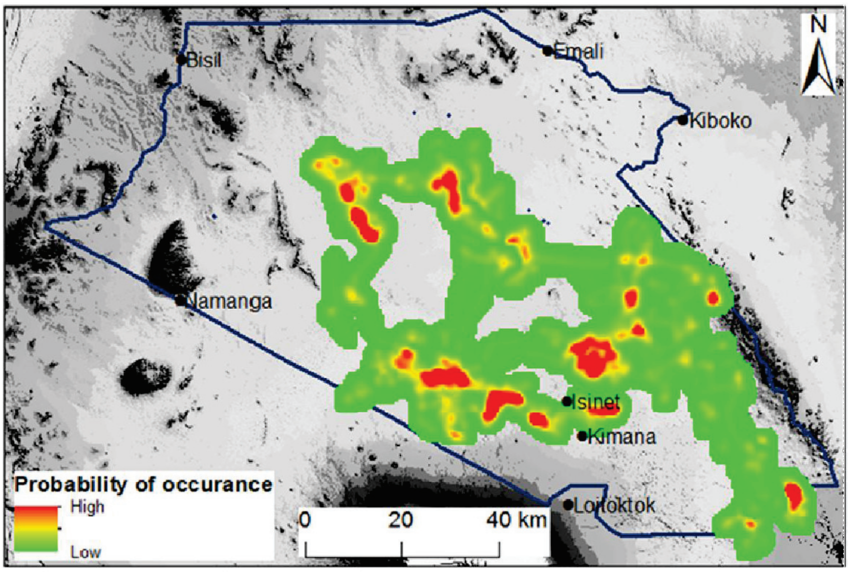


Figure 14: Estimated probability of occurrence of elephants as estimated from the BBMM b) delineation of the corridors and surrounding (non corridor)

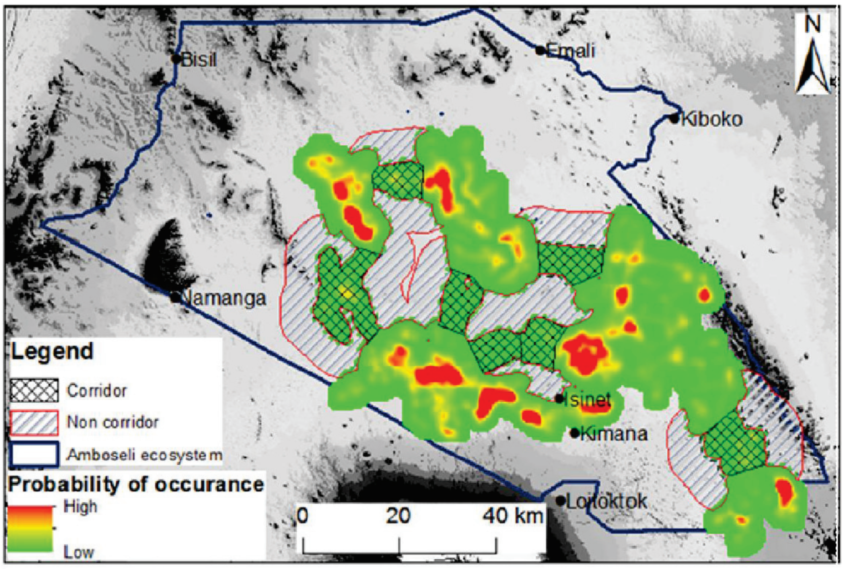


Figure 15: Delineation of migration corridors and surroundings (non corridor)

The fragmentation level of the corridor was significantly lower (*Wilcoxon* sum rank test: W= 6121.5, $p<0.05$) than that of their immediate surrounding (non corridor) (Figure 16). It is important to note that the higher the effective mesh size value the lower the level of landscape fragmentation. Fragmentation geometries also exist in landscapes currently used by elephants as migration corridors.

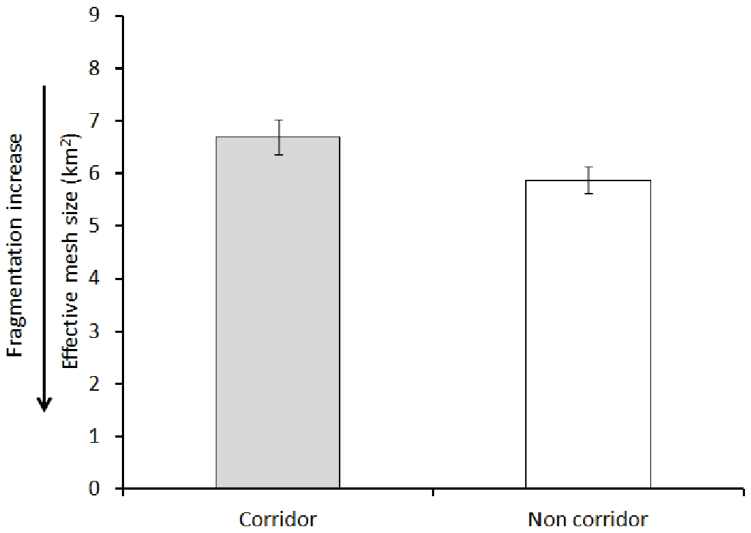


Figure 16: Comparison of the landscape fragmentation level between the corridor and the non corridor

3.3. Effect of forage abundance on speed of movement and habitat utilization

A significant ($p < 0.05$) negative relationship was observed between forage amounts and speed of movement throughout the three seasons (Figure 17). Elephants moved faster where there was low forage amounts. Elephants are known to move very slowly when foraging (Owen-Smith *et al.*, 2010) thus in low forage amounts foraging activities are limited. In the wet season the explained variance was 39% (RMSE = 0.25) , while 16% (RMSE = 0.21) and 26% (RMSE = 0.32) explained variance was explained in the transition and dry season respectively.

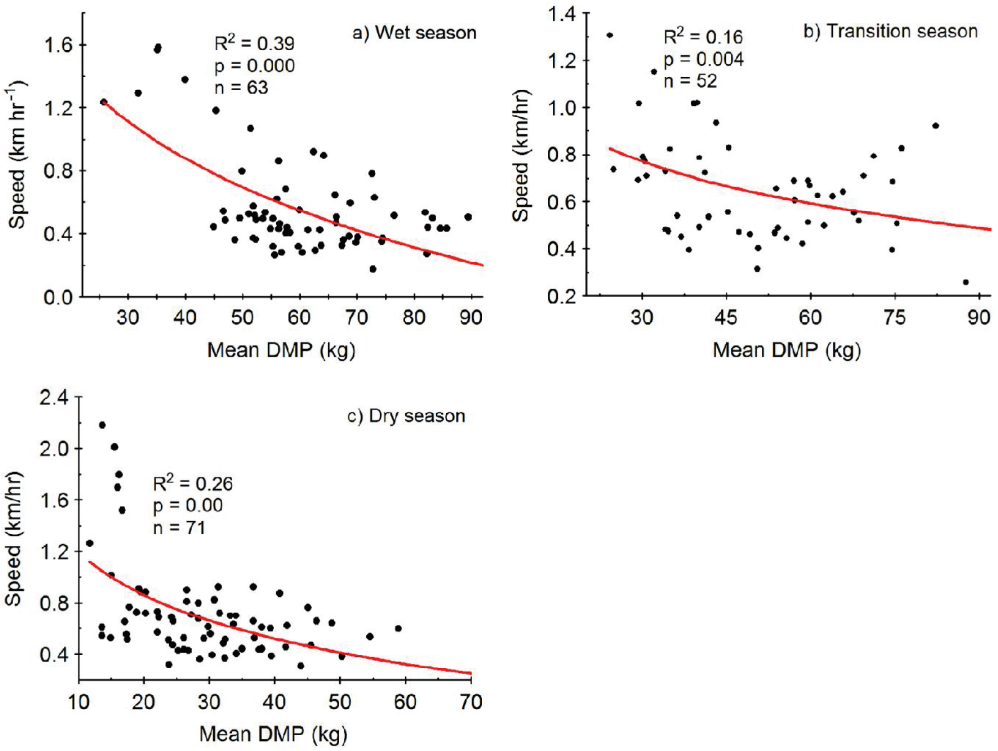


Figure 17: Relationships between forage abundance and speed of movement a) wet season b) transition season c) dry season

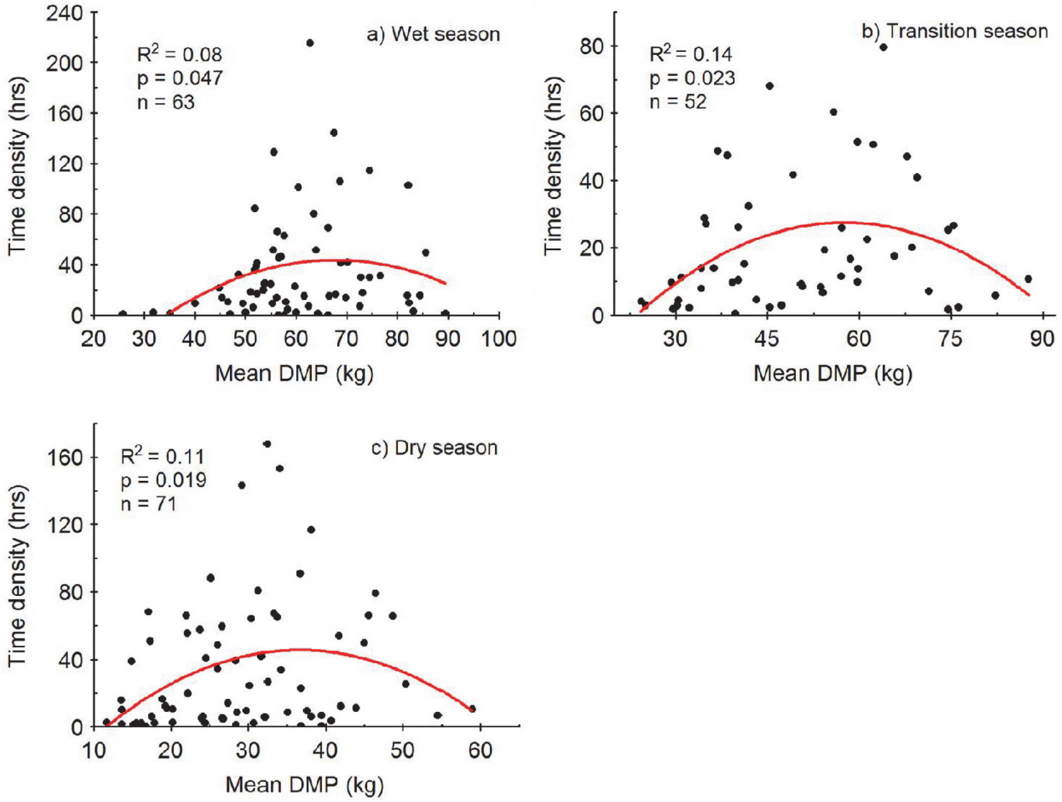


Figure 18: Relationships between forage abundance and time density a) wet season b) transition season c) dry season

A unimodal relationship between time density and DMP throughout the three seasons was observed (Figure 18). Elephants spent much of their time in the intermediate DMP landscapes while less of their time was spent in very high and very low DMP landscapes. All the models are significant ($p<0.05$) and the explained variance are generally low with DMP explaining 8% (RMSE =40.1 hrs), 14% (RMSE =18.3 hrs) and 11% (RMSE =36.5 hrs) variance in time density in the wet, transition and dry season respectively. The root mean square error are very high throughout the three seasons. The relationship between DMP and time density is well pronounced in the transition and dry season when forage amounts pose a constraint on elephants habitat utilisation.

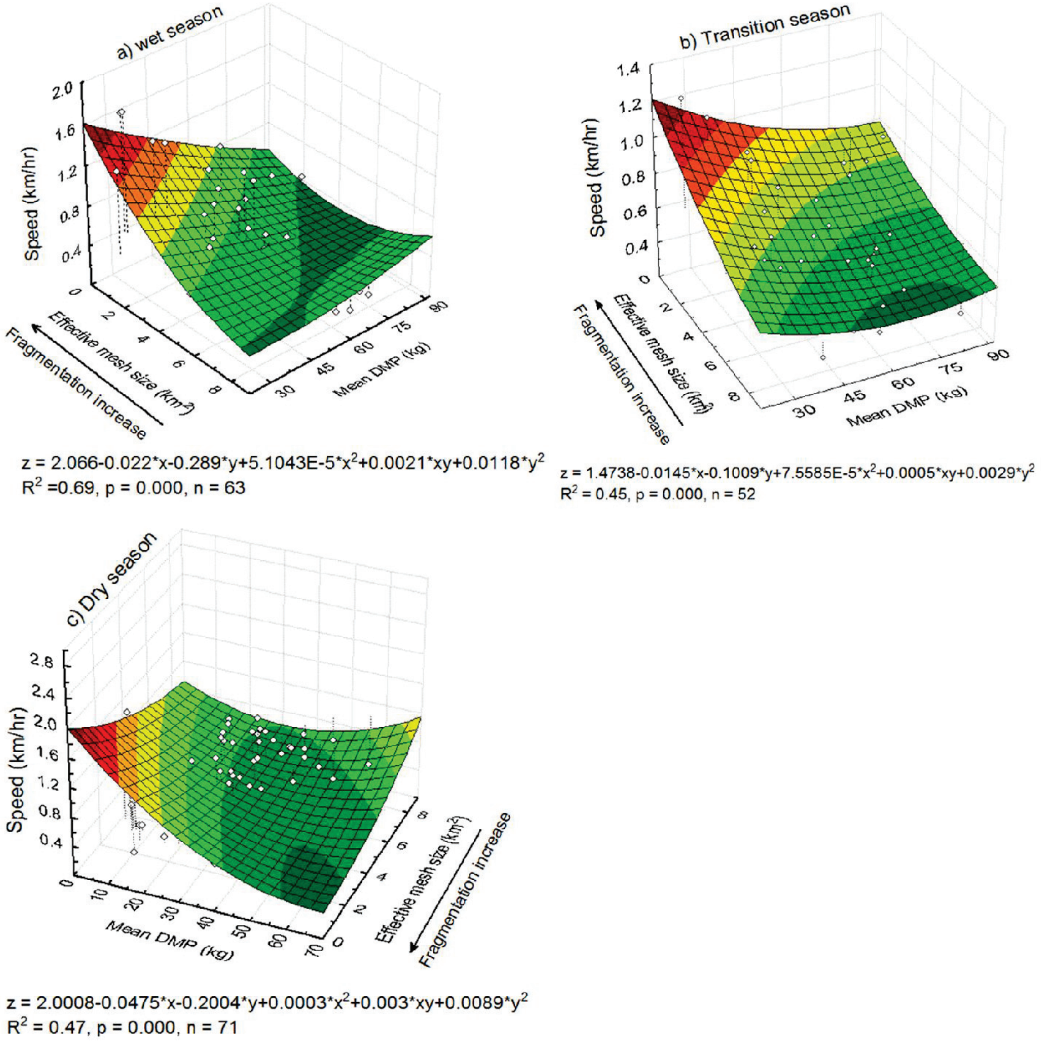
Table 4: Summary of regression models

Season	Dependent	Independent 1	Independent 2	Model	F	AIC	RMSE
Wet	Speed	DMP		$3.883-1.876*\log10(x)$	$F_{1,63}= 40.9$	5.56	0.25
		M_{eff}		$0.826*\exp(-0.088*x)$	$F_{1.63}= 28.2$	-45.5	0.16
	Time	DMP		$-135.23+5.29*x-0.039*x^2$	$F_{2,63}= 3.23$	669	40.1
		M_{eff}		$2.769*\exp(0.305*x)$	$F_{1,63}= 27.7$	118	1.19
	Speed	DMP	M_{eff}	$2.066-0.022*x-0.289 *y + 5.104E5+0.0021*xy +0.0118*y^2$	$F_{5.59}= 25.8$	-27.6	0.2
	Time	DMP	M_{eff}	$-91.32-5.38*x+3.59*y+0.707*x^2 +0.062*xy-0.0028*y^2$	$F_{5,59}= 3.48$	666	39.1
Transition	Speed	DMP		$1.6494-0.5994*\log10(x)$	$F_{1,50}= 9.3$	-15.1	0.21
		M_{eff}		$1.019-0.099*x+0.0048*x^2$	$F_{2,49}= 12.6$	-25.4	0.18
	Time	DMP		$-51.048+2.728*x-0.023*x^2$	$F_{2,49}= 4.03$	454	18.3
		M_{eff}		$2.326*\exp(0.314*x)$	$F_{1,50}= 46.6$	40	1.06
	Speed	DMP	M_{eff}	$1.473-0.014*x-0.1009*y+7.55E-x^2+0.0005*xy+ 0.0029*y^2$	$F_{5,46}= 7.6$	406	0.19
	Time	DMP	M_{eff}	$-24.762+1.631*x-8.35*y-0.013*x^2-0.0158*xy+ 1.406*y^2$	$F_{5,46}= 22$	-27.5	12.2
Dry	Speed	DMP		$2.323-1.124*\log10(x)$	$F_{1,69}= 24$	43.3	0.32
		M_{eff}		$0.887-0.34*\log10(x)$	$F_{1,69}= 19.1$	47.2	0.34
	Time	DMP		$-51.59+5.312*x-0.072*x^2$	$F_{2,68}= 4.18$	718	36.5
		M_{eff}		$3.08*\exp(0.323*x)$	$F_{1,69}= 55$	99	5.78
	Speed	DMP	M_{eff}	$2-0.0475*x-0.2*y+0.0003*x^2 +0.003*xy+ 0.0089*y^2$	$F_{5,65}= 11.5$	29.1	0.29
	Time	DMP	M_{eff}	$-34.344+3.487*x-5.348*y-0.056*x^2+0.00445*xy + 1.2*y^2$	$F_{5,65}= 9.28$	695	31.5

RMSE values for speed are in km/hr and time density in hrs

3.4. Interaction effect of landscape fragmentation levels and forage abundance on speed of movement and habitat utilization

Elephants move faster in landscapes that are highly fragmented and contain very low forage for the three Amboseli seasons (Figure 19). The explained variance was 69% (RMSE = 0.2 km/hr) in the wet season with 45% (RMSE = 0.19 km/hr) and 47% (RMSE = 0.28 km/hr) variance in speed of movement explained in the transition and dry season respectively. Interestingly, the lowest speed of elephants movement per season (dark green region on graphs) were characterized in different landscapes. In the wet season, the lowest speed of movement spreads across all DMP values and in fragmented landscapes of greater than 2 km^2. In the transition season, the lowest speed of elephants movement can be observed in less fragmented landscapes of greater than 7 km^2 and DMP values of between 50 and 80 kg. In the dry season, the model predicted a low speed of elephant movements in highly fragmented landscapes (less than 4 km^2) that have high forage amounts of more than 50 kg. It worthwhile to note that the interaction effect landscape fragmentation and DMP on speed of elephant movement improved explained variance in all seasons (Table 4).



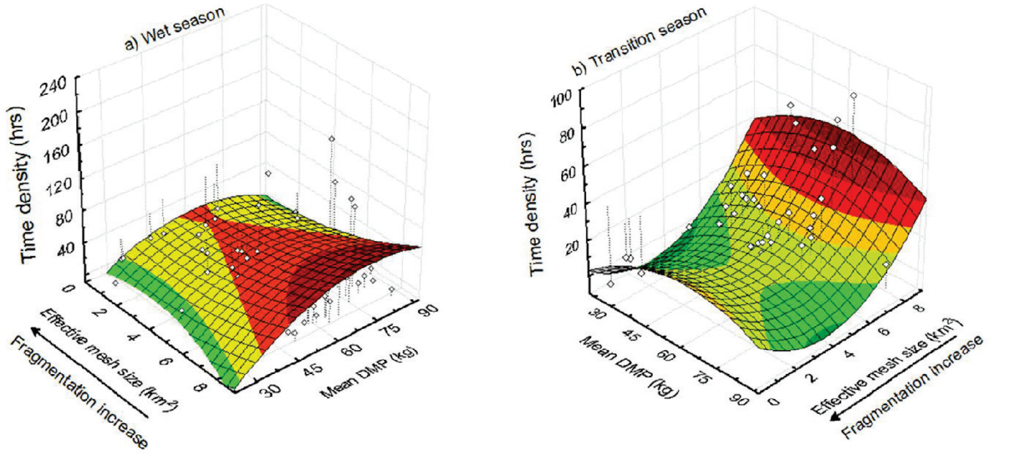
$z = 2.066-0.022*x-0.289*y+5.1043E-5*x^2+0.0021*xy+0.0118*y^2$
$R^2 = 0.69$, $p = 0.000$, $n = 63$

$z = 1.4738-0.0145*x-0.1009*y+7.5585E-5*x^2+0.0005*xy+0.0029*y^2$
$R^2 = 0.45$, $p = 0.000$, $n = 52$

$z = 2.0008-0.0475*x-0.2004*y+0.0003*x^2+0.003*xy+0.0089*y^2$
$R^2 = 0.47$, $p = 0.000$, $n = 71$

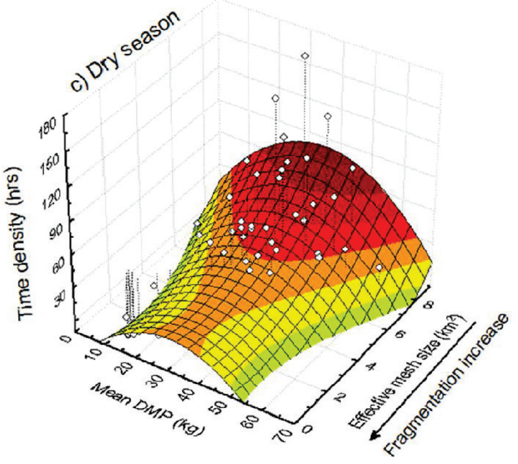
Figure 19: Relationships between landscape fragmentation level, forage abundance and speed of movement. Speed increase from dark green (low speed) to dark red (high speed). White dots represent points used to compute the model.

Throughout the three seasons elephants spent much of their time in non-fragmented (intact) landscape and intermediate forage amounts (dark red regions on all the graphs) (Figure 20). This implies that elephants prefer landscapes were human activity is low and forage quality and quantity are high. Elephants do not favour highly fragmented landscapes with low forage amounts as well as less fragmented landscapes of low forage amounts. Throughout the three season the unimodal relationship (hump shaped) is clearly observable. The explained variance varied from one season to another with 29% (RMSE = 39.1 hrs), 70% (RMSE=12.2 hrs) and 42% (RMSE=31.5 hrs) variation in time density explained in the wet, transition and dry season respectively. All multiple regressions models are significant ($p<0.05$). It important to note that in all seasons the explained variance improved and the RMSE dropped when landscape fragmentation and DMP were used simultaneously as explanatory variables (Table 4).



$z = -91.3207+3.5934*x-5.3756*y-0.0287*x^2+0.0617*xy+0.7072*y^2$
$R^2 = 0.29$, $n = 63$

$z = -24.762+1.631*x-8.3516*y-0.013*x^2-0.0158*xy+1.406*y^2$
$R^2 = 0.7$, $p = 0.000$, $n = 52$



$z = -34.344+3.487*x-5.348*y-0.056*x^2+0.0445*xy+1.2*y^2$
$R^2 = 0.42$, $p = 0.000$, $n = 71$

Figure 20: Relationships between landscape fragmentation level, forage abundance and time density. Time density increase from dark green (low speed) to dark red (high speed). White dots represent points used to compute the model

4. DISCUSSION

4.1. Effect of distance to water on speed of movement and habitat utilization

The speed of movement of elephants were observed to be influenced by distance from water sources. Results of this study demonstrated that elephants significantly ($p< 0.05$) move faster within the close and intermediate distance to water source classes compared to when they are far away from water sources. There was a near significant ($p = 0.06$) difference in the speed of movement between close and intermediate distance to water class. However, the speed of movement of elephants within the far to water source distance class was significantly lower compared to that of close and intermediate distance to water source class. This observation can be attributed to the fact that when elephants visit water sources they often travel continuously without making many stopovers on their way (Chamaille-Jammes *et al.*, 2007). Elephants forage in faraway places from water sources where forage resources are relatively high (Roever *et al.*, 2013). In Amboseli, Sitters *et al.*(2009) observed that grass greenness (a measure of forage quantity and quality) was significantly higher in landscapes further away from the water points compared to those close to water points. Hence elephants move slowly in landscapes far away from water sources to maximise on improved forage resources by reducing speed and concentrate on forage intake. Ultimately, elephants may incur travelling long distance at higher speeds from prime habitats far away from water sources. The landscape between the far areas where elephants forage and water source are therefore used as transit landscapes in which elephants move faster to link prime forage habitats and water sources. This notion will then result in elephant speed of movement being higher and almost similar within transit landscape i.e. close and intermediate distance to water classes whilst low in the far distance to water class.

An unexpected result of this study was failure to reject the hypothesis that there is no significant difference in the time elephants spent in different distance to water source classes. Most studies demonstrate high elephant densities in landscapes close to water sources (de Boer *et al.*, 2013; Roever *et al.*, 2013). The unexpected result of our study could be explained by the presence of livestock around water source during the day. In a study conducted in northern Kenya, de Leeuw *et al.* (2001) observed that livestock were significantly clustered around water sources while high wildlife densities were observed far away from the waterholes. High livestock densities around water sources drive away wildlife especially during the day. As elephants can to endure long periods (24 - 48 hrs) without visiting water sources (Chamaillé-Jammes *et al.*, 2013) they are likely to prefer to drinking water when livestock numbers around water sources subside possibly at sunset, night or during early hours of the day. In this regard, elephants balance the trade-off between foraging in landscapes far away from water sources by drinking once in a day or two. However, this assumption remains unknown and untested, hence further research is required to validate this trade-off. It is important to note that although previous studies demonstrated high elephant densities in close proximity to water sources to best of our knowledge no study has quantified the explicit time elephants spends in different distance to water classes.

Previous studies conducted in Amboseli demonstrated that forage quality and quantity is poor around water sources due to overgrazing (Sitters *et al.*, 2009). Moreover, landscape around waterholes endure intensive utilization mainly by livestock resulting in loosening of the soil. This result in soils around water sources susceptible to erosion consequently affecting establishment of high quality and quantity forage. In light of this background, elephants are likely to spend significant amount of time foraging in landscapes of intermediate and far distance to water sources classes where forage quality and quantity are considerable high. Elephants are likely to visit waterholes and spent some time when livestock presence subside. These two scenarios are likely to balance the time elephants spend in all distance to water source classes. Sitters *et al,* (2009) observed that wildlife densities were high further away from the water sources in the dry season. In relation to this, ecologists also believe that elephants do not necessarily drink at waterholes close to their foraging locations but however prefer certain waterholes mainly because of water quality. However, this assertion remains untested in the Amboseli ecosystem.

4.2. The role of landscape fragmentation on speed of movement and habitat utilization

Results of this study demonstrated that landscape fragmentation significantly ($p<0.05$) explained the speed of movement and habitat utilization of elephants in Amboseli ecosystem. The results are consistent with the initial hypothesis that elephants move faster and spend less time in highly fragmented landscapes. In Amboseli, fragmented landscapes are characterized by increasing human presence and intensive landuse such as rain-fed or small scale irrigation agriculture and pastoralism. Human presence pose a high risk to elephants as they roam the Amboseli landscape in search of forage and water. Within human dominated landscapes elephants move faster than their average speed. There has been increased incidents of human-elephant conflict in Amboseli ecosystem as a result of sedentarization and encroachment of agricultural fields into elephant ranges especially wetlands, (Kioko and Seno, 2011). The Amboseli population depends on livestock production and subsistence agriculture for their livelihoods (Okello and D'Amour, 2008). Locals or even wildlife authorities injure or even kill elephants and other animals that invade crop fields or attack humans and livestock. "Look out" structures used to deter elephants and other wild animals from raiding crops in the wet season were observed during the field visit. Chiyo *et al,* (2011) observed spear cuts on elephants that regularly invaded crop fields in Amboseli. Moreover, in the Maasai culture, young men are expected to express their virility by killing elephants with spears (Bates *et al.*, 2007). However, this perception is changing with increased environmental education (Moss, 2001) and in addition provision of wildlife related incentives (Maingi *et al.*, 2012). In this regard, elephants perceive human related risk and thus prefer areas where human activities are low.

Landscape fragmentation explained less than 50% variation in time density throughout all seasons. The explained variance in the wet season was the lowest (31%), while 48% and 44% variance in time density was explained in the dry and transition season respectively. Two reasons can be attributed to the low explained variance for the wet season. Firstly, elephants especially males are known to raid agriculture fields towards the end of the wet season when crops are mature and ripe (Chiyo *et al.*, 2011). At maturity level crops are nutritious and highly palatable compared to natural forage plants, thus elephants risk foraging in agriculture fields in the wet season. Considering that GPS tracking data used in this study consists of four male elephants (Table 1), chances of crop raids among collared elephant groups are high. Consequently, crop raids by elephants weaken the relationship between landscape fragmentation and habitat utilization. Secondly, during the wet season visibility is low because of vegetation vigour and regrowth, thus elephants can get close to settlements or roads. The improved explained variance in the dry and transition season might be due to the fact that agriculture fields are fallow and visibility is high. In this regard, elephants do not forage in agriculture fields or closer to settlements and towns during the dry season because the landscape is mainly bare and forage resources are poor. Buij *et al,* (2007) also observed that elephants significantly avoided settlements and roads in the dry season in Gabon.

A shift from extensive nomadic pastoralism and transhumance to intensive sedentary agro-pastoralism has resulted in limited mobility of pastoral herds and establishment of permanent settlements in Amboseli ecosystem. The transition from nomadic pastoralism to sedentarization presented a twofold challenge to elephants. Firstly, excision of prime habitats due to an increase in permanent settlements and expanding agriculture. Worden (2007) observed low wildlife densities in Eselenkei (part of Amboseli ecosystem) where permanent settlements and high livestock concentration are known to exist in the dry season. Secondly, sedentarization also is known to affect landscape net productivity especially in grasslands and shrublands (Groom and Western, 2013). Sedentarization has resulted in landscapes around settlements being intensively used for grazing and agriculture hence making these landscapes susceptible to overgrazing and degradation. In the past, nomadic pastoralism gave pastures a reasonable time to recover from overgrazing and pasture degradation as livestock would seasonally move from one area to another. Studies have proved that rotational and moderate grazing can improve pasture conditions and thus improve forage quality and quantity (Western *et al.*, 2009). For instance, the intermediate disturbance hypothesis help to illustrate the effect of overgrazing as a form of disturbance on forage quality and quantity. The intermediate disturbance hypothesis states that plant species richness is high at intermediate levels of disturbance, while species richness is low in frequently and intensively disturbed landscapes as well as lowly disturbed landscapes. On one hand, overgrazing results in dominance of unpalatable grass which is resistant to cattle grazing. On the other hand, less disturbed landscapes are characterized by thick woodlands that are difficult for elephants to penetrate. This result in elephants avoiding foraging both in these two landscapes of low species richness i.e. highly disturbed or fragmented landscapes and less disturbed landscape with thick woodlands. It is worthwhile to note that, grass and shrub species richness are positively correlated to forage quality (Wang *et al.*, 2010). Thus, depletion in forage quality and quality within settlements vicinity due to overgrazing explain low utilization of these fragmented landscapes by elephants. A study conducted by Groom and Western (2013) in part of the Amboseli ecosystem demonstrated that pasture productivity decreased with increasing livestock numbers due to increased grazing intensity resulting in low densities of wildlife population in overgrazed areas.

The speed of elephants movement generally increased with increasing level of landscape fragmentation throughout the three seasons that is elephants moved faster in high fragmented landscapes. This change in behaviour is mainly a result of fear that human presence induces to elephants. The increase in speed of movement demonstrates that elephants are threatened in the human dominated landscapes hence elephants tend to quickly move out of these landscapes. In a related study carried out in Laikipia, central Kenya, Graham *et al.* (2009) observed that elephants moved at different speeds in different landuse types. Elephants were observed to move faster in pastoral and smallholder landuse types where human presence and activities are high compared to forests and large scale ranches landuse where human presence and activities are low. Elephants are known to increase their speed of movement when for example crossing roads. Blake *et al*, (2008) found out that elephants increase their average daily speed 14 folds when crossing roads in the Congo Basin. He also observed that the mean speed of elephant per day increased to 3.5 km when crossing roads compared to an average of 1 km/day in landscapes that have few roads. A number of studies have demonstrated that poaching is correlated with distance from roads (Barnes *et al.*, 1991; Blake *et al.*, 2008). Maingi *et al*,(2012) also demonstrated that the intensity of poaching decrease with increasing distance from the road in a study conducted in Tsavo West National which is adjacent to the Amboseli ecosystem. Poachers often operate in areas of good road network to evade wildlife rangers. Thus elephants forage away from roads for fear of being killed (Blake *et al.*, 2007). These studies support the notion that landscape fragmentation trigger behaviour change in elephants by either moving faster or spending less time in human dominated landscape.

It is worthwhile to note that previous studies have linked elephant movement and habitat utilization with fragmentation geometries such as agriculture fields (Hoare, 1999), roads (Barnes *et al.*, 1991; Blake *et al.*, 2008) and humans settlements in isolation. It is imperative to assess the combined effect of these fragmentation geometries on elephant movement and habitat utilization. The effective mesh size landscape metric provides an opportunity to integrate fragmentation geometries and quantify landscape fragmentation that can be linked to wildlife ecology. Such kind of an approach helps wildlife managers and landuse planners to make informed and compatible decisions that balance wildlife conservation and human need for space. Girvetz *et al*,(2008) demonstrate that landscape fragmentation derived using effective mesh size algorithm can aid in explaining wildlife abundance as well as probability of traffic mortality. However, to the best of knowledge landscape fragmentation derived from integration of all possible fragmentation geometries (agriculture fields, roads, town, and human settlement) has not being linked to a mega-herbivore such as African elephant. Assessing the effect of landscape fragmentation on wildlife especially elephants is important for conservation and restoration of elephant habitats especially in East Africa where sedentarization of the nomadic Maasai people is taking centre stage. Moreover, considering the low elephant populations in East Africa and the imminent encroachment of agriculture fields into the wildlife habitats it is important to understand the link between elephant movement and landscape fragmentation.

4.3. Fragmentation and migration corridors

Using a BBMM, elephant migration corridors were clearly observed and delineated. Elephants monitored in this study demonstrated that they selected less fragmented landscapes as corridors when they connect isolated habitats within their ranging landscape throughout the year. Elephants avoid selecting landscapes heavily dominated by agriculture fields, settlements and towns as corridors. Elephants are often killed or wounded as they transverse corridors. Kioko and Seno (2011) observed expansion of agriculture fields and establishment of human settlements in elephant migration corridors in Amboseli ecosystem. In a related study conducted in Tanzania, Caro *et al*, (2009) reported constriction of corridors due to rapid expansion of agriculture and settlements into wildlife migration corridors. The encroachment of human land uses into elephants migration corridors has resulted in increased human-elephant conflict in Amboseli. It is important to note that, although corridors were significantly less fragmented compared to non-corridors, the presence of fragmentation geometries in wildlife corridors is a cause of concern for wildlife managers. In the near future fragmentation geometries are likely to block the migration corridors. In this regard wildlife managers are challenged to ensure that elephant migration corridors are free of human presence and human dominated landuse. There is need to incorporate wildlife management in landuse planning, so that fragmentation geometries are eliminated within wildlife migration corridors. Such kind of integrated landuse planning approach would help to minimise human-elephant conflicts along corridors. It is also important for landuse planners to create landuse zones that are compatible with wildlife conservation.

4.4. The role of forage abundance on speed of movement and habitat selection

The speed of movement and habitat utilization of elephants monitored in this study demonstrated to be influenced by forage amounts. Results of this study demonstrate that elephants spent much of their time in landscapes of intermediate forage amounts throughout all seasons. This observation was consistent with the initial hypothesis that habitat utilization is lower in landscapes of very low and extremely high forage amounts. A unimodal relationship between elephant time density and DMP was observed. Elephants are bulk feeders consuming large amounts of forage because of their immense size. Scientists have proven that there is a relationship between an organism metabolic rate and body size (Healy *et al.*, 2013), explaining high forage intake by mega-herbivores such as elephants compared to small to medium sized ruminants (Owen-Smith and Chafota, 2012). A study conducted in Chobe National Park, Botswana demonstrated that elephants prefer woody vegetation of height between 5-7m (shrubs to small trees) (Owen-Smith and Chafota, 2012). This finding help to explain the unimodal relationship between elephants time density and DMP. Woody vegetation of between 5-7m fall within the intermediate DMP value range with grass or saplings and dense woodlands occupying the lower and upper extremes of DMP values respectively. de Boer *et al*, (2013) also observed a unimodal relationship between NDVI and elephant densities using regression analysis. Their study was based on elephant density at continent scale. However, the relationship between NDVI and elephants density in their study was not significant and the R^2 was very low (0.01). One of the reasons that could have influenced the poor performance of that relationship was the use of NDVI itself. NDVI is not linearly correlated with biomass and is known to saturate with increasing high biomass. Therefore, NDVI is a poor predictor of forage abundance in high biomass landscapes (Gu *et al.*, 2013). In this study, DMP data which is more related to forage amounts was used, resulting in an improvement in the explained variance to 14%. In another study carried out covering seven Southern African countries (Namibia, Zambia, Zimbabwe, Botswana, Malawi, South Africa and Mozambique, Loarie, *et al,* (2009) also observed that elephants avoided dense woodlands throughout the year. However, forage abundance was quantified using NDVI. It is important to accentuate that the unimodal relationship demonstrated in this study underlies the applicability and relevance of the forage maturation hypothesis in understanding habitat utilization of the vulnerable African elephant. This study demonstrated for the first time the existence of unimodal relationship between GPS derive habitat utilization and dry matter productivity.

Although there is no distinct difference in coefficient of determination among seasons, it important to highlight that DMP explained 8%, 14% and 11% variance in time density in wet, transition and dry season respectively. The slight difference in explained variance can be attributed to variations in forage amounts across the landscapes in each season. An analysis of forage amounts demonstrated that there is a lot of variation in forage amounts in the transition season compared to the wet and dry season (Figure 21). Wide variation in forage amounts across the landscapes in the transition season can be explained by the response of vegetation to diminishing soil moisture. In Amboseli, a distinct variation in vegetation greenness between riverine or floodplains vegetation and other vegetation in areas away from rivers has been observed in the transition to dry season (Western, 2007). In light of this background, it is expected that elephants show selective forage in the transition and dry season as they try to maximise on the limited and spatially distinct variation in forage amounts. Contrary, in the wet season forage is abundantly available and elephant do not show particular preference. It is has been observed that in the wet season elephants resort to mainly grazing and also spending considerable amount of time in the grassland (Ngene, 2010). This assertion could explain the low coefficient of determination obtained in the wet season.

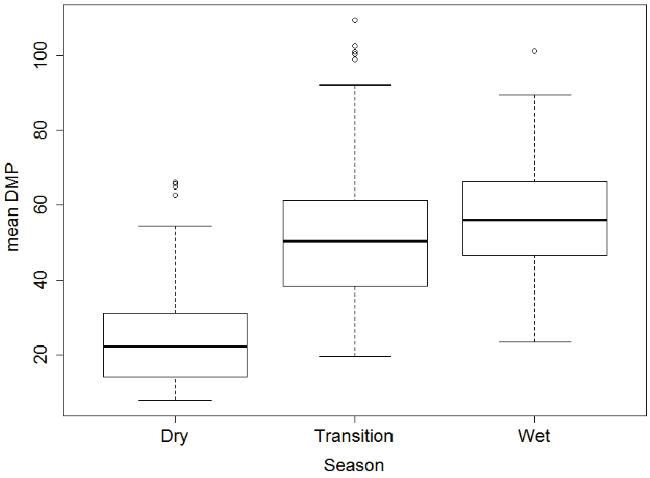


Figure 21: Variation in forage amounts within seasons

Results of this study also demonstrated that elephants speed of movement decreased with increasing forage abundance. Considering the fact that elephant move slowly when foraging (Owen-Smith *et al.*, 2010), it is expected therefore that the speed of movement will be low in high forage amounts landscapes. In landscapes of low forage amounts elephants move faster as they aim to reach high forage landscapes. DMP explained 39% variance in speed of movement in the wet season compared to 16% and 26% in the transition and dry season respectively. One reason that could explain the variation in the coefficient of determination derived is that elephant general move faster in the dry and transition season (Appendix 6) thus affecting the establishment of a good relation between speed of movement and DMP. However this finding need to be tested further by increasing the number of collared elephants as well as reducing the time lapse between the GPS fixes.

4.5. Interaction effect of landscape fragmentation and forage abundance on speed of movement and habitat selection

Using landscape fragmentation level and DMP simultaneously as explanatory variables improved the explained variance to a maximum of 70% and 69% for habitat utilization and speed of movement respectively. Landscape fragmentation only explained a maximum of 48% and 34% for habitat utilization and speed of movement respectively, while DMP when used a sole explanatory variable explained a maximum of 14% and 39% variance in habitat utilization and speed of movement respectively. In African savannas, it is common for a unfragmented landscapes to be characterized by low forage amounts. For example, unfragmented open grasslands are entirely bare during the dry season. Extensive grassland cover a substantial area in Amboseli (Western, 2007). Thus elephants are likely to move faster and spend less time in these landscapes since there will nothing to feed on unless a saltlick exists (Weir, 1969). On the contrary, there is also a possibility of having a fragmented landscape characterized by high forage amounts such as a fenced plantation or dense woodlands in close proximity to settlements or towns. Elephants are likely to spend less time in highly fragmented landscapes in spite of such landscape having abundant forage resources because of human associated risk. Using landscape fragmentation level and DMP simultaneously provided an opportunity to test whether elephants apply a cost-benefit kind of approach in habitat selection and utilization. Results of this study also demonstrate that elephants avoid landscapes where human risk is high despite the area having high forage amounts. Chase and Griffin (2011) observed that during the civil war in Angola elephant avoided Luiana Reserve preferring Caprivi strip, Namibia and Northern Botswana where forage quality and quantity is relatively low. Thousands of elephants were killed during the civil war in Angola. Nonetheless, elephant distribution and numbers in the Luiana Reserve have significantly improved following the end of the civil war in 2002,. Although, Chase and Griffin's (2011) study provided insights on how elephants avoid fragmented landscapes were risk of interacting is high despite the landscapes having high forage amounts, the study did not quantify forage amounts.

The response of elephants in terms of speed of movement to landscape fragmentation and forage abundance was almost similar throughout the three seasons. High speed of elephants' movement were observed in high fragmented landscapes of low forage amounts throughout the three seasons. However, low speed of movement was observed in landscapes of different forage and landscape fragmentation values across the three seasons. In the wet season, very low speed of elephant movement were observed in fragmented landscapes of greater than 2 km^2 and spread across all DMP values. In the dry season, very low speed of movement was observed in highly fragmented landscapes (less than 4 km^2) and high forage amounts. In the transition season, the lowest speed of elephants movement was observed in less fragmented landscapes of greater than 7 km^2 and DMP values of between 50 and 80 kg. A number of reasons can help to explain this observation. In the wet season forage is abundantly available (Western and Lindsay, 1984) and pose a minimal effect on the speed of movement hence fragmentation seem to be the major influence affecting elephant behaviour. In the transition season, elephants are highly selective moving at less speed in less fragmented landscapes of high forage landscape. However, in the dry season elephants risk foraging in high fragmented landscapes of high forage amounts because of dwindling forage resources across the whole landscape (Kioko and Seno, 2011). Results of this study demonstrate that the interaction effect DMP and landscape fragmentation improve the explanation of speed of movement and habitat utilization of African elephant.

5. CONCLUSIONS AND RECOMMENDATIONS

The main objective of this study was to test whether water availability, landscape fragmentation and forage amounts explain speed of movement and habitat utilization of African elephants in Amboseli. Furthermore, this study assessed the landscape fragmentation level of migration corridors. Results of this study demonstrated that elephants significantly ($p<0.05$) moved faster in the close and intermediate distance to water sources classes. This is likely to be explained by the poor forage resources in close proximity to water sources. The intermediate to close distance to water sources landscapes are used as transit landscapes linking the water sources and landscapes far from water sources where forage quality and quantity are high. Outcome of this study also demonstrated that there was no significant difference ($p>0.05$) in the time elephants spends in different distance to water classes. Competition for water between pastoralists and wildlife are likely to influence the relationship between wildlife and distance to water.

Results of this study also demonstrated that landscape fragmentation and forage amounts significantly ($p<0.05$) explain elephant speed of movement and habitat utilization of elephants. Elephants move faster in highly fragmented landscapes that are characterised low forage amounts throughout the whole year. Elephants spends much of their time in less fragmented landscapes. A unimodal relationship between elephants time density and forage amounts was observed. This implies that elephants prefer spending much of their time in landscapes of intermediate forage amounts. The study provides a first attempt to link landscape fragmentation derived from the effective mesh size landscape metric to elephants behaviour in African savanna. The study also tested for the first time the applicability of dry matter productivity (DMP) data in explaining speed of elephant movement and habitat utilization. The study demonstrated that the effective mesh size metric provides an easy-to-use tool for quantifying landscape fragmentation that can be integrated in landuse planning and wildlife management.

Outcome of this study also demonstrated that migration corridors used by elephants are significantly ($p<0.05$) less fragmented compared to their immediate surroundings. This observation suggests that elephants select less fragmented landscape as migration corridors as they seek to minimize human contact. However, the presence of fragmentation geometries in the corridors is a cause of concern for wildlife managers. There is evidence to demonstrate that migration corridors will eventually be blocked in the near future if no action is undertaken. Corridors are known to facilitate dispersal and movement of elephants and other forms of wildlife between meta-populations resulting in gene-flow between these populations(Caro *et al.*, 2009).

5.1. Recommendations for future management

Landscape fragmentation currently poses the greatest threat to elephants and other forms of wildlife in Amboseli ecosystem. It is important to devise sound regulations that reduce human pressure on ecosystems in which wildlife forms populate. Wildlife authorities with the aid of their governments need to establish nature conservative policies that integrate and benefit the local people. These policies if implemented are likely to transform the hostile perception that the local people have towards elephants. Sustainable wildlife conservation efforts requires landuse planning which balances the need for space for human activities and wildlife conservation.

There is need for Kenya Wildlife Services to extend management of elephant habitats to migration corridors outside protected area. Increase in fragmentation geometries in the migration corridors will eventually block the corridors and results in an increase in human-elephant conflict in Amboseli ecosystem. In most African countries wildlife authorities concentrate their management efforts on protected areas such as national parks with little or no effort addressed on management of elephant corridors outside conservation areas. Understanding bottle-necks affecting elephants movement outside the park is critical for elephant conservation and ecosystem restoration. Land-use zoning is proposed as a measure to protect migration corridors.

Although conclusions on the effect of landscape fragmentation and forage amounts were derived based on 4 hour interval GPS fixes. There is need for future studies to test whether high temporal resolution GPS fixes of probably 1 hour or less can improve results demonstrated in this study. Moreover, there is also need to fit GPS collars on more elephants of both sexes. GPS collaring on both males and female elephants will provide an opportunity to test the effect of landscape fragmentation and forage abundance at sex level.

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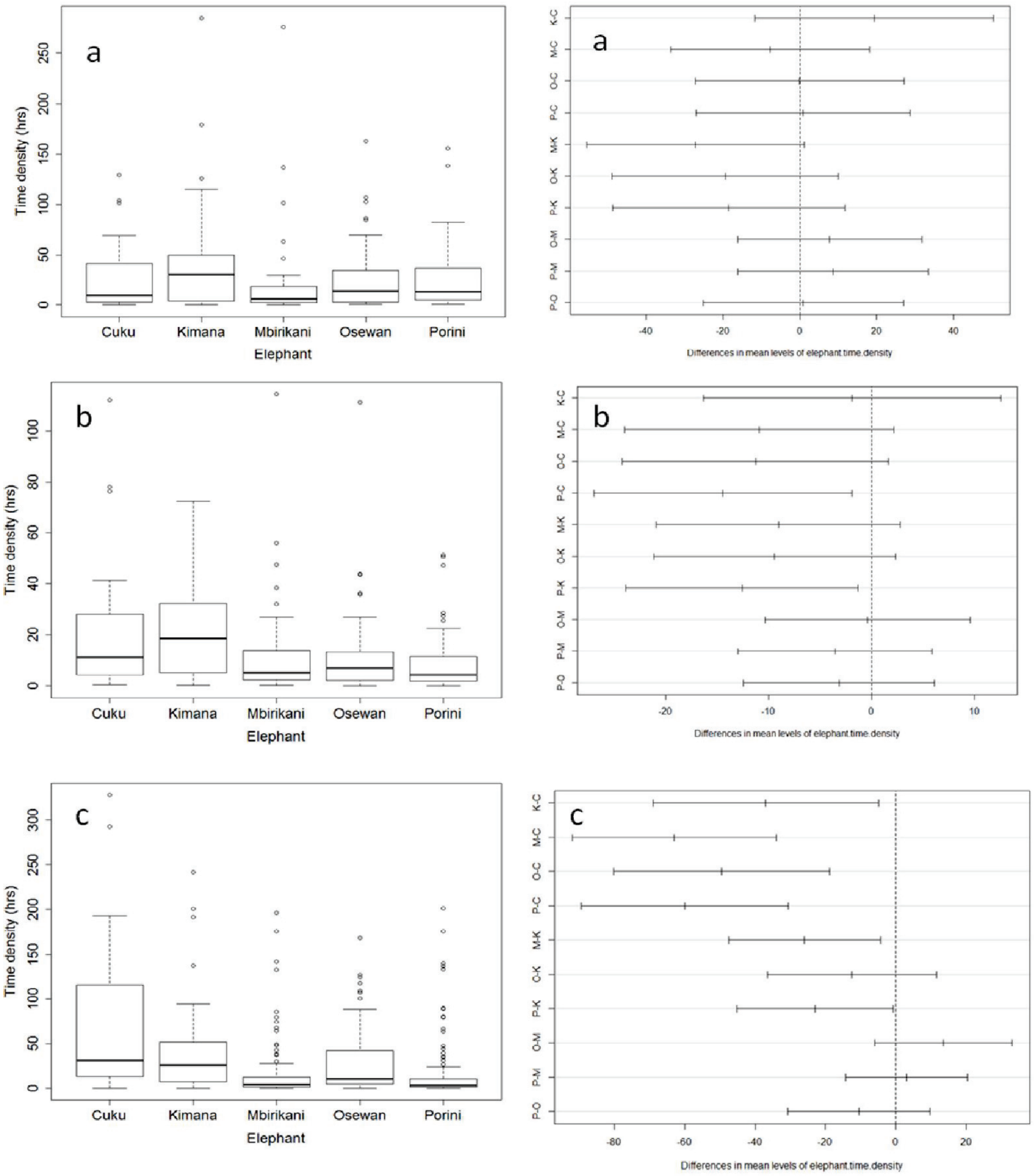
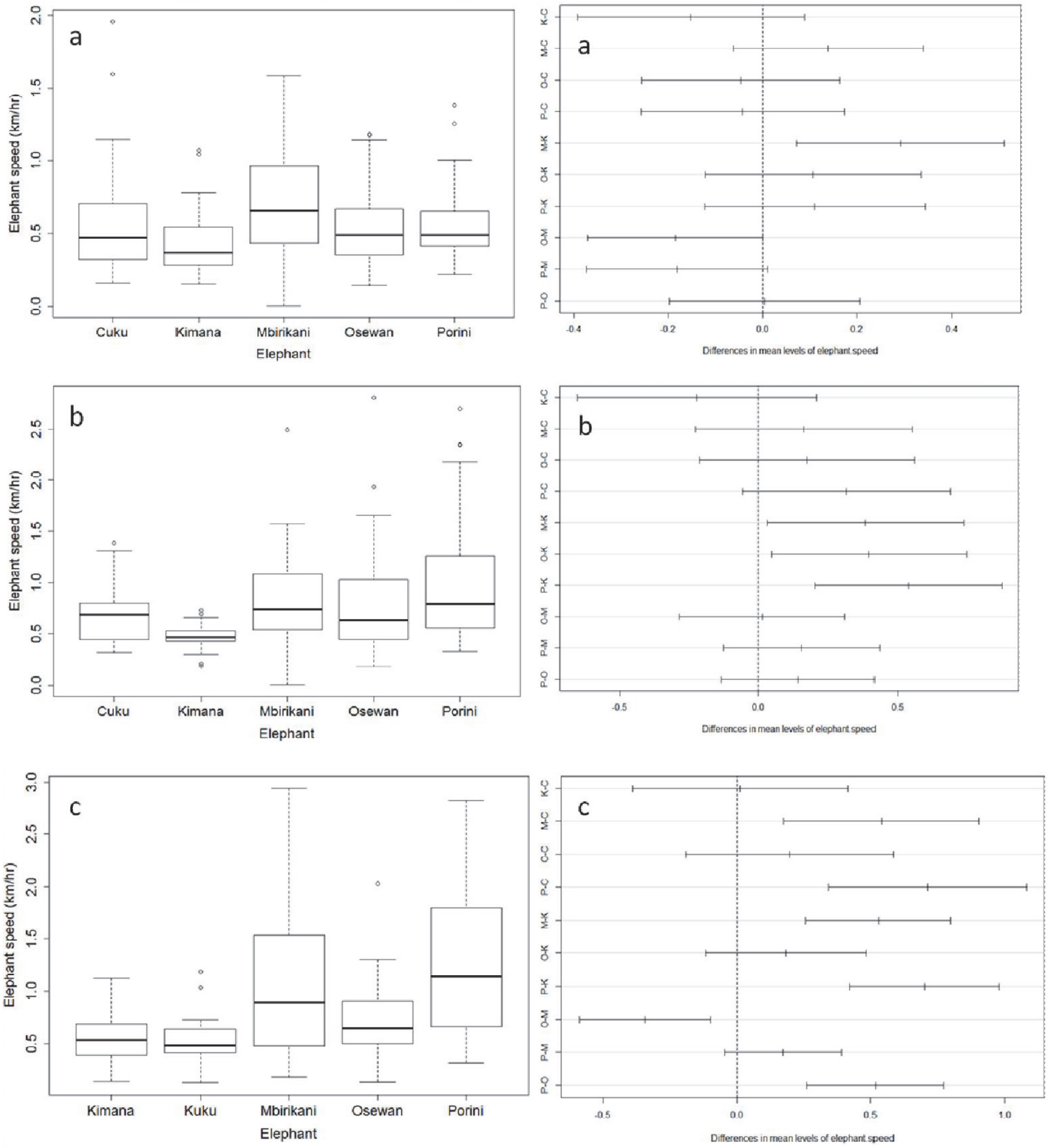
APPENDICES

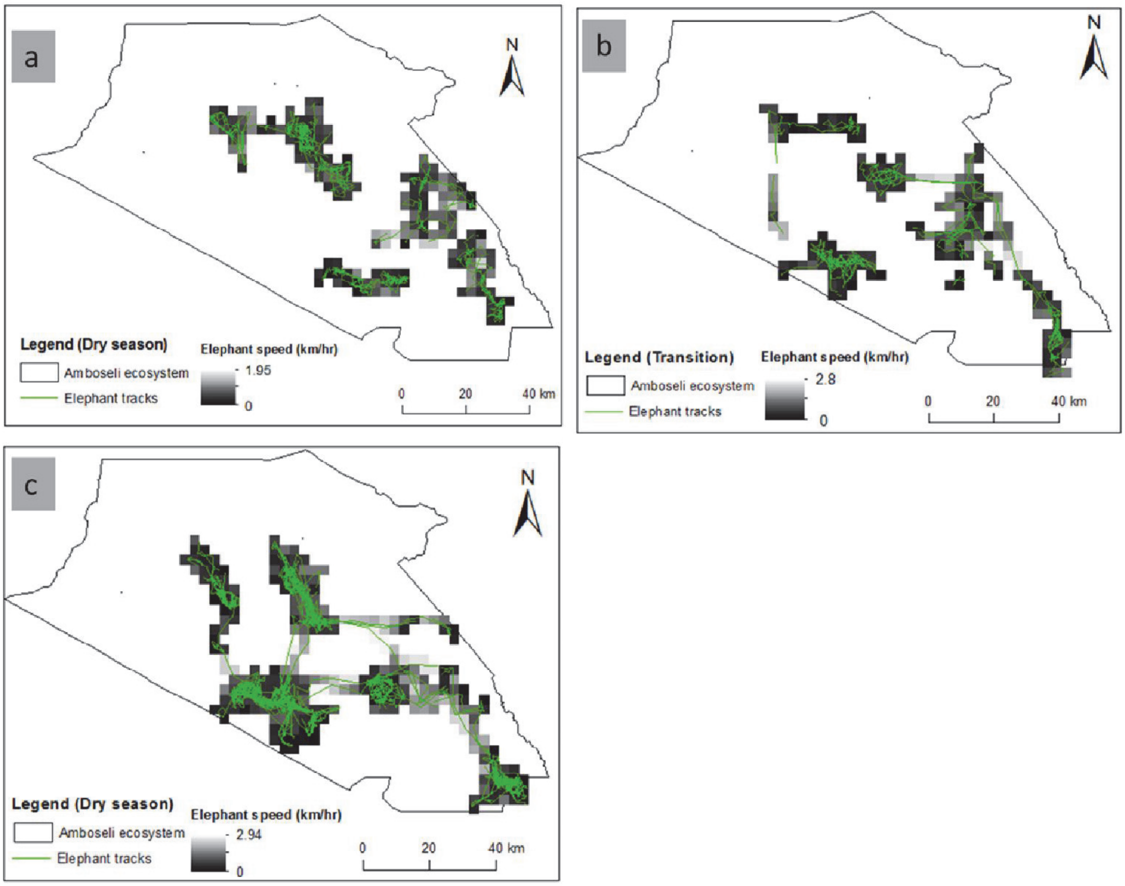
Appendix 1: Variation in time density for the collared elephants for a) wet season b) transition and c) dry season



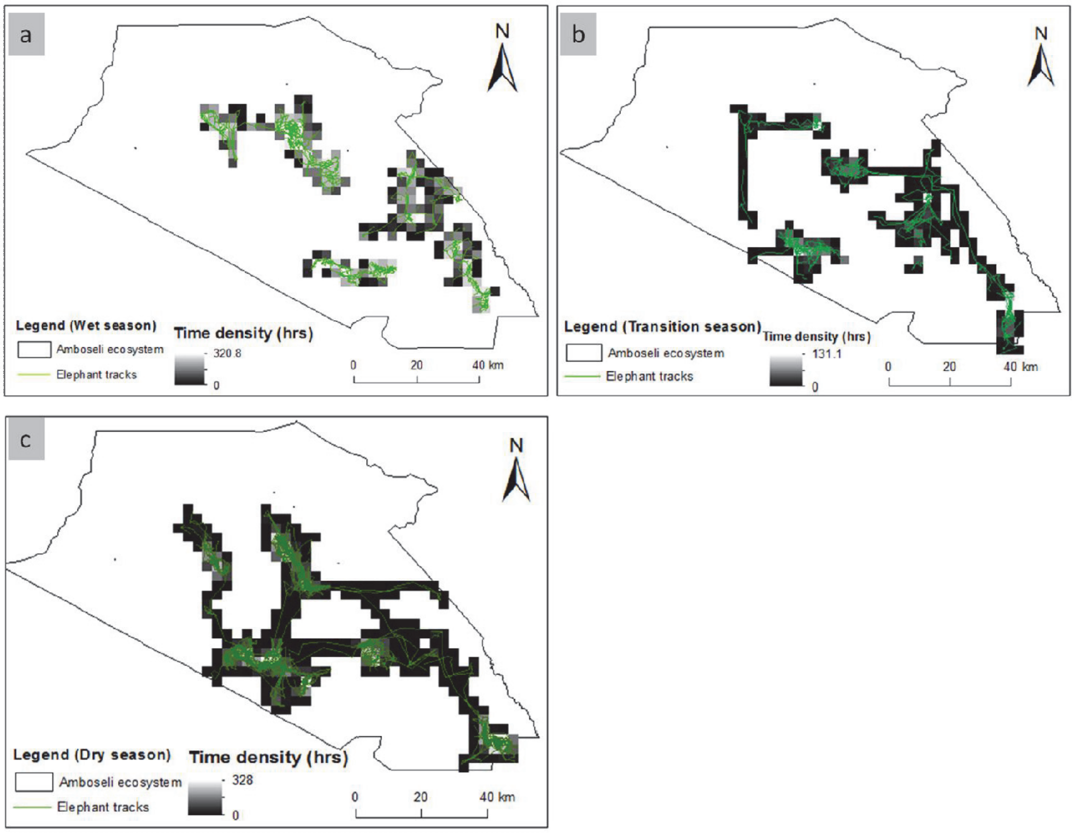
Appendix 2: Variation in speed of elephant movement for the collared elephants for a) wet season b) transition and c) dry season



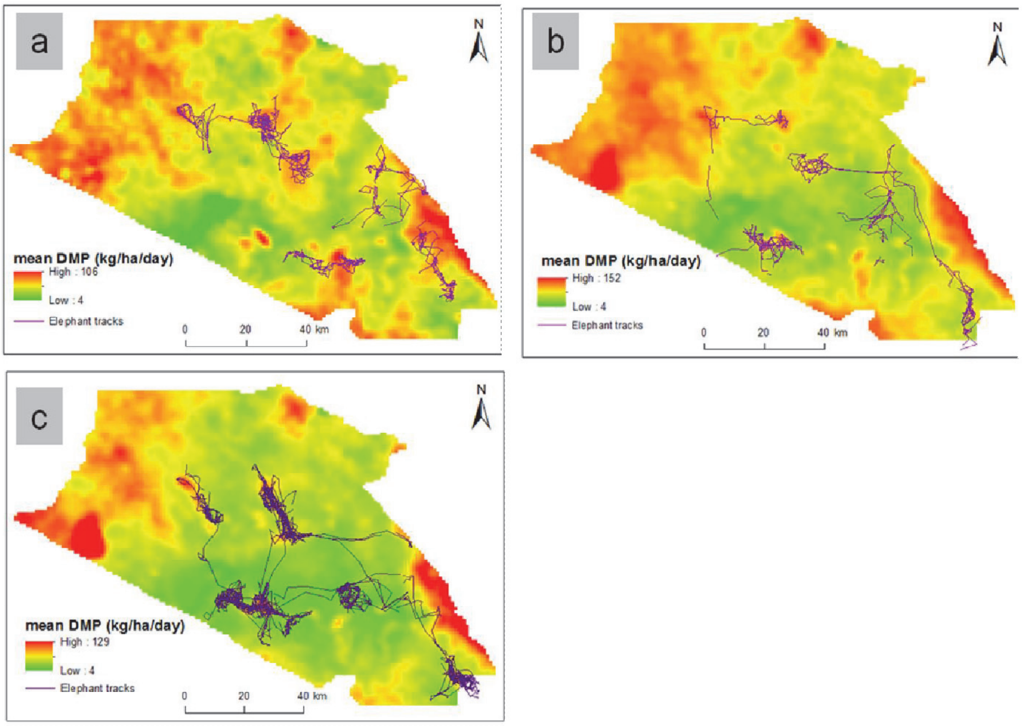
Appendix 3: Elephants speed of movement across the landscape for the a) wet b) transition and c)dry season



Appendix 4: Elephants time density across the landscape for the a) wet b) transition and c)dry season



Appendix 5: Variations in forage amounts for each season for the a) wet b) transition and c)dry season



Appendix 5: Variations in speed of movement between seasons