GIS and Remote Sensing Applications for Modelling the Distribution of Elephants and their Interaction with Vegetation

By

Henry Ndaimani (R0019417)

Thesis submitted to the Department of Geography and Environmental Science in fulfilment of the requirements for the award of Doctor of Philosophy degree in Science (Spatial Ecology)

November 2018

Dedication

To my wife Pertunia, and daughters Michelle Natalie and Brielle Yaretzi

Declaration 1: Originality

I hereby declare that this thesis submitted for the Doctor of Philosophy degree at the University of Zimbabwe is my original work and has not been previously submitted to any other institution of higher education. I further declare that all sources cited or quoted are indicated by means of a comprehensive list of references.

Henry Ndaimani

Copyright@University of Zimbabwe, 2018

Declaration 2: Publications

Details that form part and/or include research presented in this thesis include published manuscripts, manuscripts under review and give details of the contributions of each author to the research work and writing of each publication.

Publication 1: [1]Ndaimani, H., [2]Murwira, A., [3]Masocha, M., [4]Gara, T.W. and [5]Zengeya, F.M., 2017. Evaluating performance of aerial survey data in elephant habitat modelling. Published in the *African Journal of Ecology*, **55** (3), pp.270-281.

This work was done by the first author under the guidance and supervision of the second and third authors. The fourth and fifth authors helped in the conceptualisation and final editing of the manuscript.

[1-4] University of Zimbabwe, Department of Geography and Environmental Science, P. O. Box MP 167, Mount Pleasant, Harare, Zimbabwe

Publication 2: [1]Ndaimani, H., [2]Murwira, A. and [3]Masocha, M., 2018. A new method for correcting locational error from aerial surveys improves habitat model performance. Published in the *African Journal of Ecology*, **56** (4), pp.928-937.

This work was done by the first author under the guidance and supervision of the second and third authors.

[1-3] University of Zimbabwe, Department of Geography and Environmental Science, P. O. Box MP 167, Mount Pleasant, Harare, Zimbabwe

Publication 3: [1]Ndaimani, H., [2]Murwira, A., [3]Masocha, M. and [4]Zengeya, F.M., 2017. Elephant (*Loxodonta africana*) GPS collar data show multiple peaks of

occurrence farther from water sources. Published in *Cogent Environmental Science*, **3** (1), p.1-11.

This work was done by the first author under the guidance and supervision of the second and third authors. The fourth author commented on the manuscript.

[1-4] University of Zimbabwe, Department of Geography and Environmental Science, P. O. Box MP 167, Mount Pleasant, Harare, Zimbabwe.

Publication 4: [1]Ndaimani, H., [2]Murwira, A., [3]Masocha, M., [4]Gara, T. W. (Submitted to *PlosOne*), GPS-collar data confirm the selective use of a protected patchy African savannah landscape by elephants (*Loxodonta africana*)**.**

This work was done by the first author under the guidance and supervision of the second and third authors. The fourth author commented on the manuscript.

[1-3] Department of Geography and Environmental Science, University of Zimbabwe, P O Box MP 167, Mount Pleasant, Harare, Zimbabwe

[4]Faculty of Geo-Information Science and Earth Observation (ITC), University of Twente, Hengelosestraat 99, P O Box 6, 7500 AA, Enschede, The Netherlands

Publication 5: [1]Ndaimani, H., [2]Murwira, A., [3]Masocha, M. (Submitted to *Geocarto International*), Elephant (*Loxodonta africana*) movement is correlated with change in vegetation structure in a patchy savannah landscape**.**

This work was done by the first author under the guidance and supervision of the second and third authors.

[1-3] Department of Geography and Environmental Science, University of Zimbabwe, P O Box MP 167, Mount Pleasant, Harare, Zimbabwe

Certification by supervisors:

Prof. A. Murwira: ……...

Prof. M. Masocha: ……..

Acknowledgements

I would like to thank Professors Amon Murwira and Mhosisi Masocha who sacrificed many hours to guide and supervise my work. Additional thanks go to Dr Fadzai Michelle Zengeya and Mr Tawanda Winmore Gara for commenting on my manuscripts.

Part of this work was funded by the University of Zimbabwe Research Board Grant #91048. The University of Zimbabwe, Zimbabwe Defence Forces, Frankfurt Zoological Society, and Malilangwe Conservation Trust also funded collaring of elephants.

Table of Contents

Dedication i
Declaration 1: Originality ii
Declaration 2: Publications iii
Acknowledgements vi
Table of Contents vii
List of Figures x
List of Tables xiii
List of Abbreviations xiv
Abstract xvi
Chapter 1 1
1. General introduction 2
1.1 The impact of elephants on vegetation structure 2
1.2 Traditional methods for understanding the impact of elephants on vegetation structure 3
1.3 GIS, GPS and remote sensing use in understanding elephant impact on vegetation structure 4
1.4 Problem statement 8
1.5 Thesis objectives 8
1.6 Study area 9
1.7 Outline of the thesis 11
References 13
Chapter 2 25
2. Evaluating the performance of aerial survey data in elephant habitat modelling 26
2.1 Introduction 27
2.2 Materials and methods 30
2.3 Results 35
2.4 Discussion 39
2.5 Conclusion 41
References 43
Chapter 3 48
3. A new method for correcting locational error from aerial surveys improves habitat model performance 49
3.1 Introduction 50
3.2 Materials and methods 52
3.3 Results 63

3.4 Discussion ... 68
3.5 Conclusion ... 70
References ... 71
Chapter 4 ... 74
4. Elephant (*Loxodonta africana*) GPS collar data show multiple peaks of occurrence farther from water sources ... 75
4.1 Introduction ... 76
4.2 Materials and methods ... 79
4.3 Results ... 84
4.4 Discussion ... 88
4.5 Conclusion ... 90
References ... 92
Chapter 5 ... 96
5. GPS-collar data confirm the selective use of a protected patchy African savannah landscape by elephants (*Loxodonta africana*) ... 97
5.1 Introduction ... 98
5.2 Materials and methods ... 101
5.3 Results ... 109
5.4 Discussion ... 115
5.5 Conclusion ... 117
References ... 119
Chapter 6 ... 124
6. GPS-collar data show a correlation between elephant movement (*Loxodonta africana*) and tree cover change in a protected patchy African savannah landscape ... 125
6.1 Introduction ... 126
6.2 Materials and methods ... 129
6.3 Results ... 135
6.4 Discussion ... 141
6.5 Conclusion ... 143
References ... 144
Chapter 7 ... 149
7. Introduction ... 150
7.1 How do elephant distribution models built from GPS collar data compare to those built from aerial survey data? ... 151
7.2 A new method for correcting the locational error in aerial survey data ... 153
7.3 Does elephant presence peak farther from water? ... 155

7.4 Additional evidence for selective use of a heterogeneous savannah landscape by elephants 157
7.5 Different rates of vegetation change in vegetation/cover types 158
7.6 Contributions of this thesis to knowledge 159
7.7 Recommendations for future research 160
References 162

List of Figures

Figure 1-1: Location of the three study sites in Zimbabwe: (a) Mana Pools, (b) Gonarezhou, and (c) Hwange national park. Elephant presence data were collected during aerial surveys in 2014. 10
Figure 2-1: Conceptual framework illustrating the locational error associated with aerial survey presence data in relation to a typical habitat predictor. Note that at the NDVI spatial resolution of 30 m, the GPS point falls in a different pixel from the elephant location (a) but increasing the spatial resolution to say 250 metres, the GPS point, and the elephant lie within the same pixel (b). 28
Figure 2-2: Location of the study site in south-eastern Zimbabwe. Elephant presence data are overlaid to show the spatial distribution of data sets used in this study. 31
Figure 2-3: ROC curves for elephant distribution models built using presence data from aerial surveys and GPS collars as the response variable and NDVI and distance from water point data at 30, 250, 500 and 1000 metres spatial resolution as the predictors. 36
Figure 2-4: Mean area under the curve (± 95% confidence interval) for elephant habitat models built using aerial survey data and GPS collar data. The differences are shown for different spatial resolutions of the predictor variables (a) 30 m, (b) 250 m, (c) 500 m, and (d) 1,000 m. 37
Figure 2-5: Probability curves for elephant habitat models built using aerial survey and GPS collar data plotted against NDVI and distance from water points at different spatial resolutions: (a) 30 m, (b) 250 m, (c) 500 m, and (d) 1,000 m. 38
Figure 2-6: Elephant habitat predicted using aerial survey and GPS collar data against NDVI and distance from water points at spatial resolutions of 30 m, 250 m, 500 m and 1,000 m. 39
Figure 3-1: Location of (a) Mana Pools, (b) Gonarezhou, and (c) Hwange National Parks in Zimbabwe. Maps also show elephant sightings data from aerial surveys as well as rainfall from Bioclim data 52
Figure 3-2: The correction factor (D) = estimated distance between the line of flight (marked by the windsock) and the centre of the average strip width for the right and left observers. C = distance between outer markers for both observers; x_r = average strip width for the right observer; x_l = average strip width for the left observer; and Y is the width of the invisible area underneath the aircraft and between the inner markers of both observers 55
Figure 3-3: Location of selected uncorrected and corrected elephant presence points in (a) Gonarezhou; (b) Hwange; and (c) Mana Pools. Note that the transect bearing in (a) = 0°; (b) = 128°; and (c) = 90° 63
Figure 3-4: Comparison of estimated correction factors for Gonarezhou, Hwange and Mana Pools 64
Figure 3-5: Comparison of models built using corrected and uncorrected data. Results illustrate; no significant difference in performance of both data sets in Gonarezhou based on (a) TSS and (b) ROC; significant difference in the models based on (c) TSS and (d) ROC in Hwange; and significant difference in the models based on (c) TSS and (d) ROC in Mana Pools 65
Figure 3-6: Probability of elephant presence predicted using corrected and uncorrected location data in Gonarezhou, Hwange and Mana Pools 67

Figure 4-1: Hypothetical framework: the predicted response of elephants to water in (a) an imaginary homogeneous landscape characterised by uniform forage quantity and (b) a more realistic heterogeneous landscape characterised by non-uniform forage quantity 78
Figure 4-2: Elephant location data (from Global Positioning System (GPS) collars) collected from the eight elephants during 13 selected months between July 2009 and November 2011 in northern Gonarezhou National Park, south-east Zimbabwe.. 80
Figure 4-3: Probability of elephant occurrence (P (E)) plotted against distance from water sources and NDVI from July 2009 to November 2011. Elephant occurrence generally peaked at least twice with distance from water sources. The continuous horizontal line represents the logistic threshold value of equal training sensitivity and specificity (values above the line represent elephant habitat while those below represent non-habitat). 86
Figure 4-4: Probability of elephant occurrence (P (E)) – dotted line, and NDVI – continuous line plotted against distance from water sources, from July 2009 to November 2011. 88
Figure 5-1: Conceptual framework indicating habitat selection by elephants if they (a) uniformly; and (b) selectively utilise the landscape. 99
Figure 5-2: Location of (a) position fixes for 15 elephants fitted with GPS collars and; (b) Gonarezhou in Zimbabwe. 103
Figure 5-3: Major vegetation/cover types in the Gonarezhou National Park (adapted from Cuniliffe et al (2012)) 108
Figure 5-4: Selective use of vegetation /cover type by elephants in the Gonarezhou National Park, Zimbabwe. Cover type: 1=*Guibortia*; 2=*Brachystegia-Julbernadia*; 3=*Spyrostachys*; 4=Mopane; 5=mixed *Brachystegia*; 6=mixed woodland on clay; 7=*Combretum apiculatum*; 8=*Androstachys*; 9=mixed woodland on alluvium; 10-mixed *Galpinia-Lannea*; 11=*Terminalia-Strychnos*; 12=riverbed; 13=dam; 14=cultivation. 111
Figure 6-1: Conceptual diagram showing: (a) elephant selective use of a heterogeneous landscape; and (b) differential rates of change in vegetation structure 127
Figure 6-2: Study area: (a) location of the Gonarezhou National Park in Zimbabwe, and (b) location data for collared elephants (GNP = Gonarezhou National Park) 129
Figure 6-3: Vegetation/cover types in the Gonarezhou National Park, Zimbabwe (adapted from Cunliffe (2012)) 130
Figure 6-4: Results of pixel-based regression for tree cover change estimated from MOD44B data in the Gonarezhou national park (2000-2016): (a) Slope of the regression, (b) p-value, and (c) pixels where change is significant. 136
Figure 6-5: Tree cover change in major vegetation/cover types of Gonarezhou National Park: (a) area change per vegetation/cover type, and (b) proportion of the vegetation/cover type changed. 137
Figure 6-6: Mean slope of tree cover change in 14 vegetation/cover types in the Gonarezhou National Parks: (a) mean change and 95% confidence interval; and (b) histogram of the slope of change in pixels where change is significant (red dotted line separates negative and positive change). Change is based on MOD44B data (2000-2016). 138

Figure 6-7: Change in MOD13Q1-derived NDVI per vegetation/cover type plotted together with: (a) KDE; (b) LTD; and (c) speed of collared elephants in the Gonarezhou national park. 140

List of Tables

Table 3-1: Details of the strata, sightings, transects and the dates on which data were collected in Gonarezhou, Hwange and Mana Pools National Parks (Adapted from Dunham et al.2014)..... 59
Table 3-2: Comparison of NDVI, distance to water and terrain ruggedness at corrected and uncorrected elephant presence sites 68
Table 4-1: Elephant occurrence points used in the prediction of elephant habitat and the dates on which the terra/MODIS NDVI image was acquired. 81
Table 4-2: Performance and variable contribution of the MaxEnt models predicting the geographical distribution of elephants in the GNP during the dry season months of 2009, 2010 and 2011 85
Table 4-3: Peaks of elephant occurrence away from water sources and minimum NDVI within elephant habitat (habitat = probability values > the logistic threshold of equal training sensitivity and specificity) 87
Table 5-1: Details of the collared elephants (♂ = male and ♀ = female) 104
Table 5-2: Results of compositional analysis showing more use of open water (13) and riverbed (12) by elephants in the Gonarezhou National Park. A "+" is used when the vegetation type in the row is used more than the type in a column, and "-" otherwise. When the difference is significant, the sign is tripled. 110
Table 5-3: Pairwise comparisons of elephant speed in the vegetation types (values represent mean difference while * shows significant difference at the 0.05 alpha level) ... 112
Table 5-4: Ranked median speed of elephant movement, range, and number of samples in different vegetation types 113
Table 5-5: Pairwise comparisons for LTD among vegetation types (values represent mean difference while * shows significant difference) 114
Table 5-6: Ranked median LTD of elephant, range, and number of samples in different vegetation types..... 114
Table 6-1: Details of the collared elephants (♂ = male, ♀ = female)..... 131

List of Abbreviations

ANOVA	Analysis of Variance
AUC	Area Under Curve
DEM	Digital Elevation Model
DN	Digital Number value
GCP	Ground Control Point
GIS	Geographical Information Systems
GLTFCA	Great Limpopo Transfrontier Conservation Area
GNP	Gonarezhou National Park
GPS	Global Positioning System
IDH	Intermediate Disturbance Hypothesis
KDE	Kernel Density Estimator
LTD	Linear Time Density
MAXENT	Maximum Entropy Species Distribution Modelling
MCP	Minimum Convex Polygon
MNDWI	Modified Normalised Difference Water Index
MODIS	Moderate Resolution Imaging Spectroradiometer
NDVI	Normalised Difference Vegetation Index
NIR	Near Infrared
R	Red
ROC	Receiver Operating Characteristic
SDM	Species Distribution Modelling
SIN	Sinusoidal
TM	Thematic Mapper
TOA	Top of Atmosphere

TRI	Terrain Ruggedness Index
TSS	True Skill Statistic
UTM	Universal Transverse Mercator

Abstract

Knowledge of elephant (*Loxodonta africana*) interaction with vegetation is critical for conservation of the mega-herbivore and of other wildlife species found in the ecosystem. Although the impact of elephants on vegetation structure has been investigated before, location and time specific knowledge on changes in the landscape has remained largely inconclusive. This is because most of the early studies largely depended on plot-based observations that are limited in scope both spatially and temporally. This thesis develops and applies GIS and remote sensing methods aimed at understanding the spatial pattern of elephant-vegetation interaction in a predominantly savannah landscape. Specific objectives of the study were to: (1) understand the predictive ability of elephant distribution models developed using presence data collected from GPS collars and compare them to those developed from aerial survey data; (2) develop and test new methods for correcting locational error in aerial survey data for improving models of elephant distribution; (3) test whether elephant presence peaks farther from water points in addition to the known peak near water; (4) investigate whether elephants selectively utilise a heterogeneous landscape; and (5) test whether and how the rate of change in vegetation structure differs across a heterogeneous landscape. Firstly, results of the study show that elephant presence models built from GPS collar data outperformed those built from aerial survey data. Secondly, a new method suggested for correcting error in aerial survey data shifted location by 143 to 177m from the line of flight. In addition, the models of elephant presence built from the corrected dataset had better predictive ability than those built from uncorrected data. Thirdly, elephant presence peaked at places located farther from water sources in addition to the known peak near water. The peaks occurred in areas of high vegetation cover. Fourthly, elephant speed of movement and utilisation of the landscape (i.e., speed, Linear Time Density and the Kernel Density Estimator) differed by vegetation/cover type. Finally, the rate of tree cover change differed by vegetation/cover type. The change was also observed to be correlated with elephant movement and utilisation of the landscape. Results of the thesis thus suggest that GIS and Remote sensing-based methods improve our understanding of elephant-vegetation dynamics in space and time. These findings underscore the utility of GIS and remote sensing in studies that investigate the spatial pattern of elephant interaction with vegetation. Knowledge of those patterns could be applied in the formulation of strategies aimed at conserving the African elephant as well as other wildlife species that co-occur with the megaherbivore.

Chapter 1

General Introduction

1. General introduction

1.1 The impact of elephants on vegetation structure

Understanding whether and how African elephants (*Loxodonta africana*) potentially drive change in vegetation structure, especially in protected wildlife areas, is important for conservation. Existing knowledge underscores the role of the megaherbivore as a driver of change in ecosystem structure and function (Kalwij et al., 2010, Asner and Levick, 2012). This is largely because elephants are known to typically push, uproot and ring bark trees when foraging (Guy, 1976, Kohi et al., 2011, O'Connor et al., 2007). It is for this reason that elephants have been described as ecosystem engineers (Nasseri et al., 2011). Thus, elephant-dominated landscapes tend to be slowly transformed in terms of vegetation structure (Vanak et al., 2012, Tafangenyasha, 1997).

Studies that test the impact of elephants on vegetation structure provide evidence that the mega-herbivore is largely selective when foraging (Holdo, 2003, Codron et al., 2006). As a result, it could be predicted that due to overutilization the targeted species may slowly disappear from the ecosystem; together with other life forms that depend on it for survival (Jacobs and Biggs, 2002, Swanepoel, 1993). Thus, it is logical to postulate that transformation of vegetation structure by elephants may have far-reaching implications on ecosystem structure and function. In fact, the transformation of vegetation by elephants is not only a threat to the mega-herbivore itself but could be a threat to its own habitat, as well as other species that depend on the habitat for survival. Transformation of vegetation as a result of elephant foraging likely occurs in landscapes that are either fenced up or where the mega-herbivore occurs at high densities.

Although we have known for some time that protected wildlife areas are established to maintain biological diversity (Scott et al., 2001, Shafer, 1999), it has become apparent from existing

studies that several ecosystem disturbances affect the dynamically stable state (Thom and Seidl, 2016, Seidl et al., 2016). Previous studies have consistently shown that these disturbances include, among others, climate extremes (Midgley and Bond, 2015, Scheiter and Savadogo, 2016), veld fires (Staver et al., 2017, Luvuno et al., 2016) and foraging by mega-herbivores like the African elephant (Bakker et al., 2016, Asner et al., 2016). For instance, ecologists generally agree that elephants change their own habitats as well as that of other animal species when foraging (Pringle et al., 2015, Herremans, 1995). Thus, change in vegetation structure driven by elephant foraging is a key topic in ecological disturbance theory.

1.2 Traditional methods for understanding the impact of elephants on vegetation structure

In the absence of Geographical Information Science (GIS), Global Positioning System (GPS) tracking and remote sensing, studies that seek to investigate the impacts of elephants on vegetation largely rely on fieldwork. For instance, observations made in the field suggest that elephants drive the highest rates of change in vegetation structure especially near water points (Mukwashi et al., 2012, Franz et al., 2010). This change is largely attributable to the mega-herbivore which intensively forages in areas around water points since it is water-dependent. This phenomenon is in line with the piosphere effect which was first described by Lange (1969) and later by several other authors (e.g., Graetz and Ludwig, 1976, Andrew, 1988, Heshmatti et al., 2002, Egeru et al., 2015). Most descriptions of vegetation structure in the piosphere base their conclusions on data collected in plots located at increasing distances from water sources (e.g., Valeix et al., 2011, Mukwashi et al., 2012, Thrash et al., 1991). While these plot-based observations offered useful insights into elephant-vegetation dynamics in localised areas where fieldwork was conducted, they remained largely limited in spatial and temporal scope.

This means that early knowledge on the foraging behaviour of elephants was largely based on following them in the field and recording what they eat including other activities (Guy, 1976, Adams and Berg, 1980, Barnes, 1982). This data collection method lies at the centre of modern understanding of elephant foraging ecology although it could be reasoned that its accuracy possibly depends on how close the observer can be to the target animals. For instance, when observing dangerous animals like elephants, observations could be made from long distances to minimise the risk of attack (Guy, 1976). Thus, the accuracy of such observations remains largely limited. Even in cases where the animals followed are not dangerous and data are collected at the shortest distances to the animal, the window of observation is limited to particular times of the day. This is because it is practically difficult to follow an animal nonstop for 24hrs in the field. For instance, night-time observations are mostly limited by reduced visibility unless specialised equipment is used. Thus, studies that are based on field-based observations of target animals are limited in scope both spatially and temporally.

1.3 GIS, GPS and remote sensing use in understanding elephant impact on vegetation structure

While earlier methods for understanding the impact of elephants on vegetation structure are limited both in temporal and spatial scope, GIS, GPS tracking and remote sensing enable a wider window of observation. For instance, increased use of radio telemetry to track the movement of target animals has enhanced knowledge on their day and night movement across entire home ranges (e.g., Lindeque and Lindeque, 1991, Galanti et al., 2000, Ngene et al., 2017). Radio tracking of wildlife enables researchers to determine the exact location of the target animal in the field and possibly infer what they are doing (Soltis et al., 2016, Hacker et al., 2015). In addition, wildlife tracking enables estimation of the size of an animal's home range (Ngene et al., 2017, Venter et al., 2015), as well as the habitat types preferred (De Boer et al., 2005, Harris et al., 2008). To date, some GPS collars are programmed to take position fixes

even at the 15 minutes interval thus widening the window of observation of the target animals (e.g., Clark et al., 2006). Moreover, the tracking units measure location with minimal error thus making observation comparatively accurate in space (Hulbert and French, 2001, Moen et al., 1997). Based on these recent advances in animal tracking using GPS collars, it is therefore imperative that hypotheses that investigate the movement pattern of elephants be revisited to obtain enhanced insights on how they move in the landscape.

Knowledge of how elephants move in the landscape and the potential impact of that movement on the structure of vegetation depends to a large extent on the quality of location data used to understand their distribution. The main sources of location data used to model elephant distribution include GPS collars (Galanti et al., 2006, Graham et al., 2009) and aerial surveys (Matawa et al., 2012, Murwira and Skidmore, 2005). In most African countries, aerial survey data are collected in 150m wide strips located to the right and left of fixed-wing aircraft flying at ~90m above the ground and along predetermined systematic transects (Dirschl et al., 1981, Norton-Griffiths, 1978). Aerial surveys are primarily designed to collect data used to estimate the population sizes of elephants and other large animals that are visible from the air. A full description of the procedure for aerial surveys was made by Norton-Griffiths (1978).

Location data collected during aerial surveys have been used extensively to predict the distribution of animals in the landscape (Forbes and Theberge, 1993, Redfern et al., 2006, Zhang et al., 2018). However, these data come with their shortcomings. For instance, where distance sampling is not applied (Lerczak and Hobbs, 1998) or where the aircraft is not specially designed to offer full view of the area underneath (e.g., Whitt et al., 2013, Laake et al., 1997), the location of the sighting is recorded along the line of flight of the aeroplane when in actual fact it is located several metres away from the line of flight (Thomas et al., 2010). In fact, modelling from such data could introduce error since the location point used is different from

the actual position of the sighting. A number of studies acknowledged that aerial survey data are associated with locational error (Murwira and Skidmore, 2005, Cumming and Lynam, 1995) but, to the best of our knowledge, no attempt has ever been made to correct it. Thus, it is critical to test whether the locational error associated with aerial survey data could influence the predictive ability of elephant distribution models to enhance conservation effort.

In most protected areas of Africa, limited availability of animal presence data either from GPS collars or aerial surveys has made it difficult to undertake studies to investigate the distribution of elephants. This is largely due to the costs associated with data collection. The costs of GPS collars (Creel et al., 2013, Girard et al., 2002) and aerial surveys (Whittaker et al., 2003, Watts et al., 2010) has been reported before in literature. Thus, even in landscapes where only aerial survey data are available, it is better to correct locational error than disregard the data in elephant modelling effort. To the best of our knowledge, limited effort has been made to correct the locational error associated with aerial survey data for better modelling results.

Recent advances in remote sensing make it possible to test hypotheses at large spatial extents which include the global scale (e.g., Mayaux et al., 2004, Prince and Goward, 1995, Asner et al., 2003). Thus, remote sensing provides landscape-scale data that enables investigation of elephant movement patterns at large spatial extents (Chamaillé-Jammes et al., 2009, Asner et al., 2009). This is opposed to plot-based observations, whose window of observation remains limited to the areas visited. Remote sensing also enables the collection of data in inaccessible areas while plot-based observations can only be conducted in areas that are accessible. In addition, continued availability of freely available remotely sensed products also makes it a cheaper data collection option than fieldwork (Jha et al., 2008, Mumby et al., 1999). Thus remote sensing can be regarded as a cost-effective approach that enables rapid investigation of elephant movement patterns, including their impact on ecosystems.

More so, remote sensing enables repetitive observation of the same area thus making it possible to investigate large-scale changes in landscape characteristics over time (Petropoulos et al., 2009, Kumari, 2017, Hegazy and Kaloop, 2015). For instance, it is possible to investigate daily changes in vegetation condition from MODIS-based images which are acquired daily. Previous studies have consistently shown that remotely sensed data can be used to account for fine temporal-scale changes in landscape structure (Arnett et al., 2015, McDowell et al., 2015). Thus, it is now possible to investigate changes in forage and water distribution based on remotely sensed data (Ehrlén and Morris, 2015, Imai et al., 2017, Seager et al., 2013). Evidence from existing studies shows that these factors drive the movement pattern of elephants and thus affect the way they utilise the landscape (Marshal et al., 2011, Bhola et al., 2012, Ogutu et al., 2014). It is therefore imperative that in the face of ever-increasing availability of remotely sensed data, hypotheses that test how elephants move in the landscape and their potential impact on vegetation need to be revisited.

Remote sensing devices collect data without contact with the ground hence they minimise the impact on target ecosystems (Azmy et al., 2012). On the other hand, field-based observations of elephant-driven vegetation change are often intrusive since they require presence in the field. Thus, field workers potentially disturb the animals and plants found in the areas where they collect data (Tejedo et al., 2012, Monz et al., 2010). Another advantage of remote sensing when pitted against field work is its ability to provide reflectance data at various wavelengths including those found outside the visible range of the electromagnetic spectrum (Adam et al., 2010, Estes et al., 2010). Existing studies have underscored the utility of the near infrared and red edge bands in monitoring vegetation change (Clevers and Gitelson, 2013, Mutanga et al., 2012). Thus in this thesis, we use remotely sensed data to investigate elephant-driven vegetation change in the study areas. Nevertheless, it has to be noted that despite the discussed usefulness of remotely sensed data, they cannot replace fieldwork but should ideally complement it.

1.4 Problem statement

Although ecologists generally agree that elephant foraging leads to opening up or densification of vegetation (e.g., Mapaure and Moe, 2009, Kalwij et al., 2010), knowledge on the pattern of that change at the landscape scale remains largely underdeveloped. That knowledge has largely been limited by field-work based approaches that are limited both in spatial and temporal scope. While plot-based observations provide critical insights into elephant-vegetation dynamics, they remain limited to the areas where data collection was undertaken. As a result, knowledge generated by this method on the changes to vegetation structure occurring at long distances from the water points remained largely elusive. The few studies that shifted attention to other areas not linked to the piosphere largely remained limited to plot-based observations targeting vegetation types of interest (e.g., Holdo, 2006, Ben-Shahar, 1996). However, recent developments in GIS, GPS tracking and remote sensing technologies provide an opportunity to revisit hypotheses investigating the impact of elephant foraging on vegetation structure at the landscape scale. An attempt to adequately model changes in vegetation structure driven by elephants, especially at the landscape scale, provides knowledge on possible changes in ecosystem structure and function which in turn can be used to better manage protected wildlife areas.

1.5 Thesis objectives

In this thesis, the main objective was to develop, test and apply Geographical Information Systems (GIS) and remote sensing methods to understand whether and how elephant foraging drives change in vegetation structure across a largely heterogeneous savannah landscape.

The specific objectives of the thesis were to:

1) develop elephant distribution models from presence data collected using GPS collars and compare their predictive ability to those developed from aerial survey data;

2) propose a new method for correcting locational error in aerial survey data and to test whether the correction improves elephant distribution modelling results;
3) determine whether elephant presence peaks farther from water points in addition to the known peak near water;
4) validate selective utilisation of a heterogeneous landscape by elephants; and
5) investigate whether and how the rate of change in vegetation structure differs across a heterogeneous landscape.

1.6 Study area

The majority of the hypotheses were tested in the Gonarezhou national park (longitude 31.32ºE – 32.41ºE and latitude 21.11ºS -22.22ºS) located to the south-east of Zimbabwe (Figure 1-1). Additional hypotheses were tested in the Hwange (longitude 25.79ºE – 27.46ºE and latitude 18.50ºS – 19.88ºS) and Mana Pools (longitude 29.15ºE – 29.74ºE and latitude 15.67ºS -16.29ºS) national parks located to the north-west and north of the country respectively. Hwange National Park is the largest national park while Mana Pools is third in size.

Elevation in the Gonarezhou national park ranges between 155m and 567m. Vegetation is typical dry deciduous savannah dominated by *Colophospermum mopane* on the clay and loam soils; and *Combretum spp* on the sandy soils. The climate in the national park is subtropical savannah characterised by summer rainfall received from November to April. Long-term annual rainfall is ~600mm. January is the hottest month with maximum temperatures averaging ~36°C while June is coldest with minimum temperatures averaging 9°C.

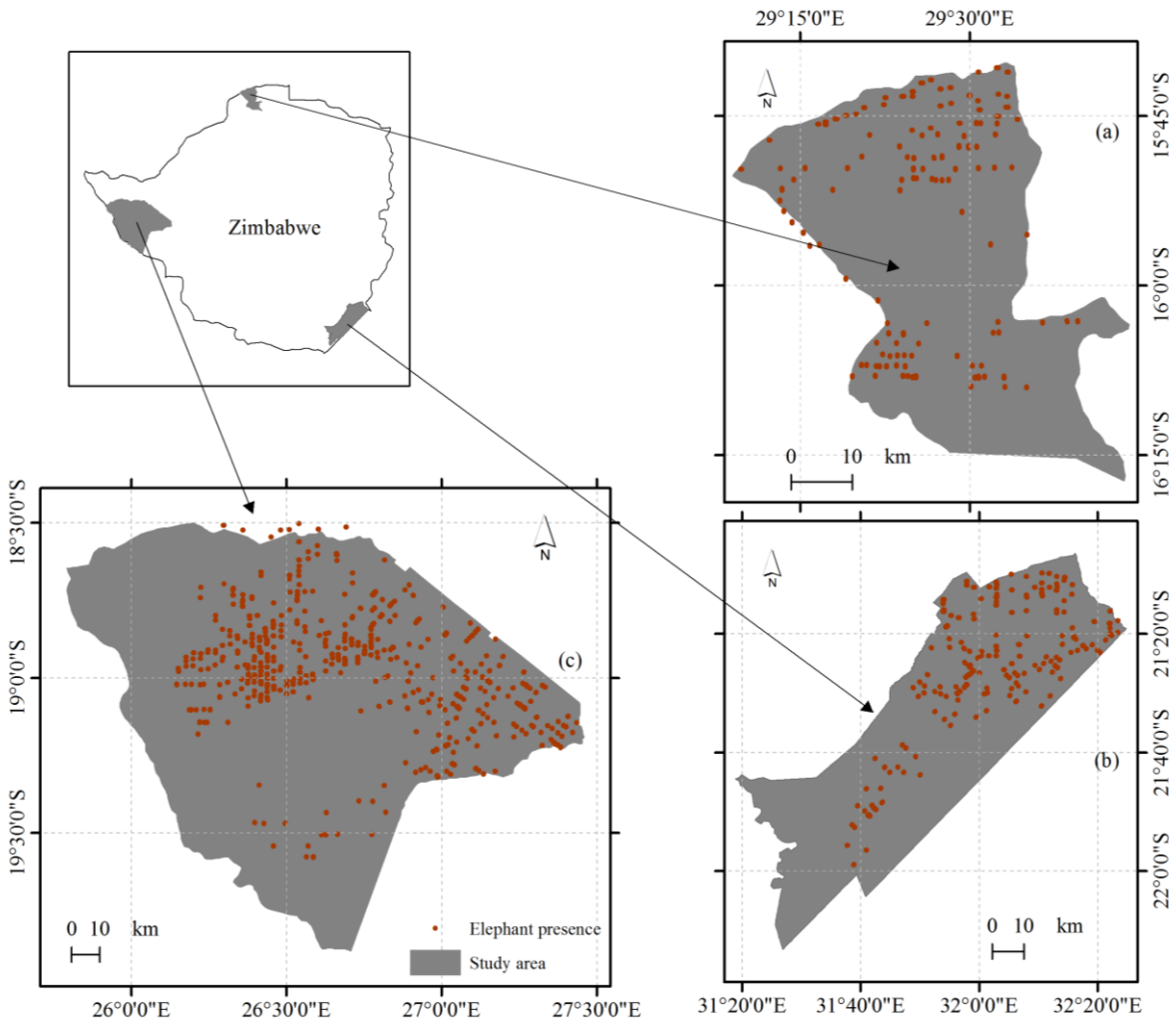

Figure 1-1: Location of the three study sites in Zimbabwe: (a) Mana Pools, (b) Gonarezhou, and (c) Hwange national park. Elephant presence data were collected during aerial surveys in 2014.

Gonarezhou is the second largest national park in the country after Hwange national park. It was gazetted as a game reserve in the 1930s and covers an area ~5000km^2 in size (Zisadza et al., 2010). The park supports ~11000 elephants making it the second largest meta-population in the country (Dunham, 2015). In fact, the park has one of the healthiest elephant populations in the country when compared to the rest of the range areas where populations were reported to be declining (Robson et al., 2017). A growing elephant population at densities >2 individuals/km^2 is of interest to ecologists since elephants have been known to drive change in vegetation structure where they occur at high densities.

Typical uses of the park include photographic safaris and camping. Surrounding areas are characterised by safari hunting and communal landuses. The study area falls in the Great Limpopo Transfrontier Conservation Area which combines wildlife areas found in Zimbabwe, Mozambique and South Africa (Andersson and de Garine-Wichatitsky, 2017).

1.7 Outline of the thesis

This thesis consists of seven chapters. Five of the chapters (Chapter 2-6) are manuscripts which have either been published or are under review and they address the five main objectives of the thesis. These five chapters are presented in the thesis as separate papers. Thus repetition of some sections was inevitable. Chapter 1 consists of a general introduction and background information on the impact of elephants on vegetation structure. The chapter also provides the basis of the research designs adopted in subsequent chapters. More so, the chapter highlights the objectives of the study. Chapter 2 develops elephant distribution models from GPS collar data and compares their predictive ability to those built from aerial survey data. The chapter aims to establish the best elephant presence datasets to use for reliable modelling results. Chapter 3 proposes a new method for correcting the locational error associated with elephant location data collected from aerial surveys. The chapter further investigates whether the correction method suggested improves model performance. Based on the evidence provided in the chapter, a decision is made on using GPS collar data for best modelling results. Chapter 4 utilises elephant presence data collected from GPS collar, together with distance from water points and NDVI, to determine whether there exist other peaks of elephant presence located far from water. The chapter seeks to enhance knowledge on how elephants utilise landscapes in areas not linked to the piosphere. Chapter 5 validates selective utilisation of a heterogeneous savannah landscape by elephants. Chapter 6 investigates whether percentage tree cover changed in the Gonarezhou national park from 2000 to 2017. The chapter further tests whether a change in percentage tree cover is correlated with elephant movement in particular vegetation/cover

types. Chapter 7 is a synthesis of the main results of the thesis. Contributions of the thesis to the current understanding of the spatial pattern of elephant impact on vegetation structure are discussed. The chapter further explores the possibilities for future research.

References

Adam, E., Mutanga, O. & Rugege, D. (2010) Multispectral and hyperspectral remote sensing for identification and mapping of wetland vegetation: a review. Wetlands Ecology and Management, 18, 281-296.

Adams, J. & Berg, J. K. (1980) Behavior of female African elephants (*Loxodonta africana*) in captivity. Applied Animal Ethology, 6, 257-276.

Andrew, M. (1988) Grazing impact in relation to livestock watering points. Trends in Ecology & Evolution, 3, 336-339.

Arnett, J. T., Coops, N. C., Daniels, L. D. & Falls, R. W. (2015) Detecting forest damage after a low-severity fire using remote sensing at multiple scales. International Journal of Applied Earth Observation and Geoinformation, 35, 239-246.

Asner, G. P. & Levick, S. R. (2012) Landscape-scale effects of herbivores on treefall in African savannas. Ecology Letters, 15, 1211-1217.

Asner, G. P., Levick, S. R., Kennedy-Bowdoin, T., Knapp, D. E., Emerson, R., Jacobson, J., Colgan, M. S. & Martin, R. E. (2009) Large-scale impacts of herbivores on the structural diversity of African savannas. Proceedings of the National Academy of Sciences, 106, 4947-4952.

Asner, G. P., Scurlock, J. M. & A. Hicke, J. (2003) Global synthesis of leaf area index observations: implications for ecological and remote sensing studies. Global Ecology and Biogeography, 12, 191-205.

Asner, G. P., Vaughn, N., Smit, I. P. & Levick, S. (2016) Ecosystem-scale effects of megafauna in African savannas. Ecography, 39, 240-252.

Azmy, S. N., Sah, S. A. M., Shafie, N. J., Ariffin, A., Majid, Z., Ismail, M. N. A. & Shamsir, M. S. (2012) Counting in the dark: Non-intrusive laser scanning for population counting and identifying roosting bats. Scientific Reports, 2, 524

Bakker, E. S., Gill, J. L., Johnson, C. N., Vera, F. W., Sandom, C. J., Asner, G. P. & Svenning, J.-C. (2016) Combining paleo-data and modern exclosure experiments to assess the impact of megafauna extinctions on woody vegetation. Proceedings of the National Academy of Sciences, 113, 847-855.

Barnes, R. (1982) Elephant feeding behaviour in Ruaha National Park, Tanzania. African Journal of Ecology, 20, 123-136.

Ben-Shahar, R. (1996) Woodland dynamics under the influence of elephants and fire in northern Botswana. Vegetatio, 123, 153-163.

Bhola, N., Ogutu, J. O., Said, M. Y., Piepho, H. P. & Olff, H. (2012) The distribution of large herbivore hotspots in relation to environmental and anthropogenic correlates in the Mara region of Kenya. Journal of Animal Ecology, 81, 1268-1287.

Chamaillé-Jammes, S., Fritz, H. & Madzikanda, H. (2009) Piosphere contribution to landscape heterogeneity: a case study of remote-sensed woody cover in a high elephant density landscape. Ecography, 32, 871-880.

Clark, P. E., Johnson, D. E., Kniep, M. A., Jermann, P., Huttash, B., Wood, A., Johnson, M., Mcgillivan, C. & Titus, K. (2006) An advanced, low-cost, GPS-based animal tracking system. Rangeland Ecology & Management, 59, 334-340.

Clevers, J. G. & Gitelson, A. A. (2013) Remote estimation of crop and grass chlorophyll and nitrogen content using red-edge bands on Sentinel-2 and-3. International Journal of Applied Earth Observation and Geoinformation, 23, 344-351.

Codron, J., Lee-Thorp, J. A., Sponheimer, M., Codron, D., Grant, R. C. & De Ruiter, D. J. (2006) Elephant (*Loxodonta africana*) diets in Kruger National Park, South Africa: spatial and landscape differences. Journal of Mammalogy, 87, 27-34.

Creel, S., Winnie Jr, J. A. & Christianson, D. (2013) Underestimating the frequency, strength, and cost of antipredator responses with data from GPS collars: an example with wolves and elk. Ecology and Evolution, 3, 5189-5200.

Cumming, D. & Lynam, T. (1997) Landuse Changes, Wildlife Conservation and Utilisation, and the Sustainability of Agro-ecosystems in the Zambezi Valley: Final Technical Report, WWF, Harare, Zimbabwe.

De Boer, W. F., Fairall, N., Van Aarde, R. J. & Ntumi, C. P. (2005) Use of space and habitat by elephants (*Loxodonta africana*) in the Maputo Elephant Reserve, Mozambique. South African Journal of Wildlife Research-24-month delayed open access, 35, 139-146.

Dirschl, H. J., Norton-Griffiths, M. & Wetmore, S. P. (1981) Training observers for aerial surveys of herbivores. Wildlife Society Bulletin, 9, 108-115.

Egeru, A., Wasonga, O., Macopiyo, L., Mburu, J., Tabuti, J. R. & Majaliwa, M. G. (2015) Piospheric influence on forage species composition and abundance in semi-arid Karamoja sub-region, Uganda. Pastoralism, 5, 1-17.

Ehrlén, J. & Morris, W. F. (2015) Predicting changes in the distribution and abundance of species under environmental change. Ecology Letters, 18, 303-314.

Estes, L., Reillo, P., Mwangi, A., Okin, G. & Shugart, H. (2010) Remote sensing of structural complexity indices for habitat and species distribution modeling. Remote Sensing of Environment, 114, 792-804.

Forbes, G. J. & Theberge, J. B. (1993) Multiple landscape scales and winter distribution of moose (*Alces alces*) in a forest ecotone, Can. Field-Nat. 107: 201-207.

Franz, M., Kramer-Schadt, S., Kilian, W., Wissel, C. & Groeneveld, J. (2010) Understanding the effects of rainfall on elephant–vegetation interactions around waterholes. Ecological Modelling, 221, 2909-2917.

Galanti, V., Preatoni, D., Martinoli, A., Wauters, L. & Tosi, G. (2006) Space and habitat use of the African elephant in the Tarangire–Manyara ecosystem, Tanzania: Implications for conservation. Mammalian Biology-Zeitschrift für Säugetierkunde, 71, 99-114.

Galanti, V., Tosi, G., Rossi, R. & Foley, C. (2000) The use of GPS radio-collars to track elephants (*Loxodonta africana*) in the Tarangire National Park (Tanzania). Hystrix, 11. 27-37

Girard, I., Ouellet, J.-P., Courtois, R., Dussault, C. & Breton, L. (2002) Effects of sampling effort based on GPS telemetry on home-range size estimations. The Journal of Wildlife Management, 66, 1290-1300.

Graetz, R. & Ludwig, J. (1976) A method for the analysis of piosphere data applicable to range assessment. The Rangeland Journal, 1, 126-136.

Graham, M. D., Douglas-Hamilton, I., Adams, W. M. & Lee, P. C. (2009) The movement of African elephants in a human-dominated land-use mosaic. Animal Conservation, 12, 445-455.

Guy, P. (1976) The feeding behaviour of elephant (*Loxodonta africana*) in the Sengwa area Rhodesia. South African Journal of Wildlife Research-24-month delayed open access, 6, 55-63.

Hacker, C. E., Horback, K. M. & Miller, L. J. (2015) GPS technology as a proxy tool for determining relationships in social animals: An example with African elephants. Applied Animal Behaviour Science, 163, 175-182.

Harris, G. M., Russell, G. J., Van Aarde, R. I. & Pimm, S. L. (2008) Rules of habitat use by elephants *Loxodonta africana* in southern Africa: insights for regional management. Oryx, 42, 66-75.

Hegazy, I. R. & Kaloop, M. R. (2015) Monitoring urban growth and land use change detection with GIS and remote sensing techniques in Daqahlia governorate Egypt. International Journal of Sustainable Built Environment, 4, 117-124.

Herremans, M. (1995) Effects of woodland modification by African elephant *Loxodonta africana* on bird diversity in northern Botswana. Ecography, 18, 440-454.

Heshmatti, G., Facelli, J. & Conran, J. (2002) The piosphere revisited: plant species patterns close to waterpoints in small, fenced paddocks in chenopod shrublands of South Australia. Journal of Arid Environments, 51, 547-560.

Holdo, R. M. (2003) Woody plant damage by African elephants in relation to leaf nutrients in western Zimbabwe. Journal of Tropical Ecology, 19, 189-196.

Holdo, R. M. (2006) Elephant herbivory, frost damage and topkill in Kalahari sand woodland savanna trees. Journal of Vegetation Science, 17, 509-518.

Hulbert, I. A. & French, J. (2001) The accuracy of GPS for wildlife telemetry and habitat mapping. Journal of Applied Ecology, 38, 869-878.

Imai, S., Ito, T., Kinugasa, T., Shinoda, M., Tsunekawa, A. & Lhagvasuren, B. (2017) Effects of spatiotemporal heterogeneity of forage availability on annual range size of Mongolian gazelles. Journal of Zoology, 301, 133-140.

Jacobs, O. & Biggs, R. (2002) The impact of the African elephant on marula trees in the Kruger National Park. South African Journal of Wildlife Research-24-month delayed open access, 32, 13-22.

Jha, M. N., Levy, J. & Gao, Y. (2008) Advances in remote sensing for oil spill disaster management: state-of-the-art sensors technology for oil spill surveillance. Sensors, 8, 236-255.

Kalwij, J., De Boer, W., Mucina, L., Prins, H., Skarpe, C. & Winterbach, C. (2010) Tree cover and biomass increase in a southern African savanna despite growing elephant population. Ecological Applications, 20, 222-233.

Kohi, E. M., De Boer, W. F., Peel, M. J., Slotow, R., Van Der Waal, C., Heitkönig, I. M., Skidmore, A. & Prins, H. H. (2011) African elephants *Loxodonta africana* amplify browse heterogeneity in African savanna. Biotropica, 43, 711-721.

Kumari, N. V. (2017) Application of Remote Sensing Techniques for Mapping Shifting Cultivation. International Journal of Engineering Research and Applications, 7, 10-14.

Laake, J. L., Calambokidis, J., Osmek, S. D. & Rugh, D. J. (1997) Probability of detecting harbor porpoise from aerial surveys: estimating g (0). The Journal of Wildlife Management, 61, 63-75.

Lange, R. T. (1969) The piosphere: sheep track and dung patterns. Journal of Range Management, 22, 396-400.

Lerczak, J. A. & Hobbs, R. C. (1998) Calculating sighting distances from angular readings during shipboard, aerial, and shore-based marine mammal surveys. Marine Mammal Science, 14, 590-598.

Lindeque, M. & Lindeque, P. (1991) Satellite tracking of elephants in northwestern Namibia. African Journal of Ecology, 29, 196-206.

Luvuno, L., Kotze, D. & Kirkman, K. (2016) Long-term landscape changes in vegetation structure: fire management in the wetlands of KwaMbonambi, South Africa. African Journal of Aquatic Science, 41, 279-288.

Mapaure, I. & Moe, S. R. (2009) Changes in the structure and composition of miombo woodlands mediated by elephants (*Loxodonta africana*) and fire over a 26-year period in north-western Zimbabwe. African Journal of Ecology, 47, 175-183.

Marshal, J. P., Rajah, A., Parrini, F., Henley, M., Henley, S. R. & Erasmus, B. F. (2011) Scale-dependent selection of greenness by African elephants in the Kruger-private reserve transboundary region, South Africa. European Journal of Wildlife Research, 57, 537-548.

Matawa, F., Murwira, A. & Schmidt, K. S. (2012) Explaining elephant (*Loxodonta africana*) and buffalo (*Syncerus caffer*) spatial distribution in the Zambezi Valley using maximum entropy modelling. Ecological Modelling, 242, 189-197.

Mayaux, P., Bartholomé, E., Fritz, S. & Belward, A. (2004) A new land cover map of Africa for the year 2000. Journal of Biogeography, 31, 861-877.

Mcdowell, N. G., Coops, N. C., Beck, P. S., Chambers, J. Q., Gangodagamage, C., Hicke, J. A., Huang, C.-Y., Kennedy, R., Krofcheck, D. J. & Litvak, M. (2015) Global satellite monitoring of climate-induced vegetation disturbances. Trends in Plant Science, 20, 114-123.

Midgley, G. F. & Bond, W. J. (2015) Future of African terrestrial biodiversity and ecosystems under anthropogenic climate change. Nature Climate Change, 5, 823-829.

Moen, R., Pastor, J. & Cohen, Y. (1997) Accuracy of GPS telemetry collar locations with differential correction. The Journal of Wildlife Management, 61, 530-539.

Monz, C. A., Marion, J. L., Goonan, K. A., Manning, R. E., Wimpey, J. & Carr, C. (2010) Assessment and monitoring of recreation impacts and resource conditions on mountain summits: Examples from the Northern Forest, USA. Mountain Research and Development, 30, 332-343.

Mukwashi, K., Gandiwa, E. & Kativu, S. (2012) Impact of African elephants on *Baikiaea plurijuga* woodland around natural and artificial watering points in northern Hwange National Park, Zimbabwe. International Journal of Environmental Sciences, 2, 1355-1368.

Mumby, P., Green, E., Edwards, A. & Clark, C. (1999) The cost-effectiveness of remote sensing for tropical coastal resources assessment and management. Journal of Environmental Management, 55, 157-166.

Murwira, A. & Skidmore, A. K. (2005) The response of elephants to the spatial heterogeneity of vegetation in a Southern African agricultural landscape. Landscape Ecology, 20, 217-234.

Nasseri, N. A., Mcbrayer, L. D. & Schulte, B. A. (2011) The impact of tree modification by African elephant (Loxodonta africana) on herpetofaunal species richness in northern Tanzania. African Journal of Ecology, 49, 133-140.

Mutanga, O., Adam, E. & Cho, M. A. (2012) High density biomass estimation for wetland vegetation using WorldView-2 imagery and random forest regression algorithm. International Journal of Applied Earth Observation and Geoinformation, 18, 399-406.

Ngene, S., Okello, M. M., Mukeka, J., Muya, S., Njumbi, S. & Isiche, J. (2017) Home range sizes and space use of African elephants (*Loxodonta africana*) in the Southern Kenya

and Northern Tanzania borderland landscape. International Journal of Biodiversity and Conservation, 9, 9-26.

Norton-Griffiths, M. (1978) Counting animals, Serengeti Ecological Monitoring Programme, African Wildlife Leadership Foundation. Nairobi, Kenya.

O'connor, T. G., Goodman, P. S. & Clegg, B. (2007) A functional hypothesis of the threat of local extirpation of woody plant species by elephant in Africa. Biological Conservation, 136, 329-345.

Ogutu, J. O., Reid, R. S., Piepho, H.-P., Hobbs, N. T., Rainy, M. E., Kruska, R. L., Worden, J. S. & Nyabenge, M. (2014) Large herbivore responses to surface water and land use in an East African savanna: implications for conservation and human-wildlife conflicts. Biodiversity and Conservation, 23, 573-596.

Petropoulos, G., Carlson, T., Wooster, M. & Islam, S. (2009) A review of Ts/VI remote sensing based methods for the retrieval of land surface energy fluxes and soil surface moisture. Progress in Physical Geography, 33, 224-250.

Prince, S. D. & Goward, S. N. (1995) Global primary production: a remote sensing approach. Journal of Biogeography, 22, 815-835.

Pringle, R. M., Kimuyu, D. M., Sensenig, R. L., Palmer, T. M., Riginos, C., Veblen, K. E. & Young, T. P. (2015) Synergistic effects of fire and elephants on arboreal animals in an African savanna. Journal of Animal Ecology, 84, 1637-1645.

Redfern, J., Ferguson, M., Becker, E., Hyrenbach, K., Good, C., Barlow, J., Kaschner, K., Baumgartner, M. F., Forney, K. & Ballance, L. (2006) Techniques for cetacean–habitat modeling. Marine Ecology Progress Series, 310, 271-295.

Scheiter, S. & Savadogo, P. (2016) Ecosystem management can mitigate vegetation shifts induced by climate change in West Africa. Ecological Modelling, 332, 19-27.

Scott, J. M., Davis, F. W., Mcghie, R. G., Wright, R. G., Groves, C. & Estes, J. (2001) Nature reserves: Do they capture the full range of America's biological diversity? Ecological Applications, 11, 999-1007.

Seager, R., Ting, M., Li, C., Naik, N., Cook, B., Nakamura, J. & Liu, H. (2013) Projections of declining surface-water availability for the southwestern United States. Nature Climate Change, 3, 482-486.

Seidl, R., Spies, T. A., Peterson, D. L., Stephens, S. L. & Hicke, J. A. (2016) Searching for resilience: addressing the impacts of changing disturbance regimes on forest ecosystem services. Journal of Applied Ecology, 53, 120-129.

Shafer, C. L. (1999) National park and reserve planning to protect biological diversity: some basic elements. Landscape and Urban Planning, 44, 123-153.

Soltis, J., King, L., Vollrath, F. & Douglas-Hamilton, I. (2016) Accelerometers and simple algorithms identify activity budgets and body orientation in African elephants *Loxodonta africana*. Endangered Species Research, 31, 1-12.

Staver, A. C., Botha, J. & Hedin, L. (2017) Soils and fire jointly determine vegetation structure in an African savanna. New Phytologist, 216, 1151-1160.

Swanepoel, C. (1993) Baobab damage in Mana Pools National Park, Zimbabwe. African Journal of Ecology, 31, 220-225.

Tafangenyasha, C. (1997) Tree loss in the Gonarezhou National Park (Zimbabwe) between 1970 and 1983. Journal of Environmental Management, 49, 355-366.

Tejedo, P., Pertierra, L. R., Benayas, J., Convey, P., Justel, A. & Quesada, A. (2012) Trampling on maritime Antarctica: can soil ecosystems be effectively protected through existing codes of conduct? Polar Research, 31, 10888.

Thom, D. & Seidl, R. (2016) Natural disturbance impacts on ecosystem services and biodiversity in temperate and boreal forests. Biological Reviews, 91, 760-781.

Thomas, L., Buckland, S. T., Rexstad, E. A., Laake, J. L., Strindberg, S., Hedley, S. L., Bishop, J. R., Marques, T. A. & Burnham, K. P. (2010) Distance software: design and analysis of distance sampling surveys for estimating population size. Journal of Applied Ecology, 47, 5-14.

Thrash, I., Nel, P., Theron, G. & Bothma, J. D. P. (1991) The impact of the provision of water for game on the woody vegetation around a dam in the Kruger National Park. Koedoe, 34, 131-148.

Valeix, M., Fritz, H., Sabatier, R., Murindagomo, F., Cumming, D. & Duncan, P. (2011) Elephant-induced structural changes in the vegetation and habitat selection by large herbivores in an African savanna. Biological Conservation, 144, 902-912.

Vanak, A. T., Shannon, G., Thaker, M., Page, B., Grant, R. & Slotow, R. (2012) Biocomplexity in large tree mortality: interactions between elephant, fire and landscape in an African savanna. Ecography, 35, 315-321.

Venter, J. A., Prins, H. H., Mashanova, A., De Boer, W. F. & Slotow, R. (2015) Intrinsic and extrinsic factors influencing large African herbivore movements. Ecological Informatics, 30, 257-262.

Watts, A. C., Perry, J. H., Smith, S. E., Burgess, M. A., Wilkinson, B. E., Szantoi, Z., Ifju, P. G. & Percival, H. F. (2010) Small unmanned aircraft systems for low-altitude aerial surveys. The Journal of Wildlife Management, 74, 1614-1619.

Whitt, A. D., Dudzinski, K. & Laliberté, J. R. (2013) North Atlantic right whale distribution and seasonal occurrence in nearshore waters off New Jersey, USA, and implications for management. Endangered Species Research, 20, 59-69.

Whittaker, D. G., Van Dyke, W. A. & Love, S. L. (2003) Evaluation of aerial line transect for estimating pronghorn antelope abundance in low-density populations. Wildlife Society Bulletin, 31, 443-453.

Zhang, G., Zhu, A.-X., Windels, S. K. & Qin, C.-Z. (2018) Modelling species habitat suitability from presence-only data using kernel density estimation. Ecological Indicators, 93, 387-396.

Chapter 2

Evaluating the performance of aerial survey data in elephant habitat modelling

This chapter is based on:

Ndaimani, H., Murwira, A., Masocha, M., Gara, T.W. and Zengeya, F.M., 2017. Evaluating the performance of aerial survey data in elephant habitat modelling. *African Journal of Ecology* **55** (3), pp.270-281.

2. Evaluating the performance of aerial survey data in elephant habitat modelling

Abstract

Aerial survey data are widely used to model the distribution of wildlife. However, their performance in habitat modelling remains largely untested. We used aerial survey and satellite-linked Global Positioning System (GPS) collar data for elephants, to test: (1) whether there is an optimal spatial resolution of predictor variables at which habitat models based on aerial survey data that are uncorrected for locational error can accurately predict elephant habitat and, (2) whether habitat models based on these data sets can accurately predict the presence of elephants in closed woodland habitats. We applied maximum entropy modelling (MaxEnt) to these datasets and used the Normalised Difference Vegetation Index (NDVI) as well as distance from water points as the habitat predictors to answer these questions. Our results demonstrate the better ability of aerial survey data to predict elephant presence at the coarser spatial resolution of 1000 m of both predictor variables. Habitat models derived from aerial survey data under predicted elephant presence in more closed woodland habitats than those derived from GPS collar data. This result implies that elephants located under dense tree canopies are likely missed during an aerial survey. Our study is one of the first to empirically test and report results on the poor performance of aerial survey data in habitat modelling, especially in dense woodlands.

2.1 Introduction

Understanding the spatial distribution of wildlife species in a landscape is critical for their management and biodiversity conservation. In recent years, the possibility of determining the spatial distribution of wildlife species has been enhanced by advances in remote sensing technology as well as the introduction of novel species distribution modelling techniques that use satellite data (Elith et al., 2006, Nagendra et al., 2013, Ross and Howell, 2013). Accurate prediction of habitat for target species is important as it helps strengthen efforts to prevent further habitat loss (Bean et al., 2014). This is particularly important for African elephants (*Loxodonta africana*) because they are known to transform habitats (Lagendijk et al., 2011, Valeix et al., 2011, Van Langevelde et al., 2003). Failure to accurately predict elephant driven habitat changes in a timely manner may also threaten the existence of other wildlife species that use the affected habitats (Head et al., 2012, Young et al., 2005). This is mainly because elephants are keystone species and protection of their habitat is beneficial to other species in the ecosystem (Laws, 1970). Thus, sustainable management of wildlife areas benefits directly from accurate prediction of wildlife habitats especially elephant habitat.

However, the ability of habitat models to accurately predict the presence of wildlife species is influenced by the spatial characteristics of the response and predictor variables, especially spatial resolution and locational error. In landscapes where ground-based surveys are time-consuming and costly, aerial survey data have extensively been used in modelling habitats for wildlife species (Scheidat et al., 2012, Kiffner et al., 2013, Pittiglio et al., 2013). However, the utility of aerial survey data uncorrected for locational error in wildlife habitat modelling work remains largely untested. Given the extensive spatial coverage of aerial surveys, one would expect these data to produce better habitat models since a wide variety of habitats are sampled. Ideally, the presence data used in modelling should represent the full range of values of the predictor variable in the study area so as to ensure good modelling results (Vaughan and

Ormerod, 2003). Location data that are collected from aerial surveys and have not been corrected for locational error generally lack spatial accuracy as depicted in Figure 2-1 (Murwira and Skidmore, 2005).

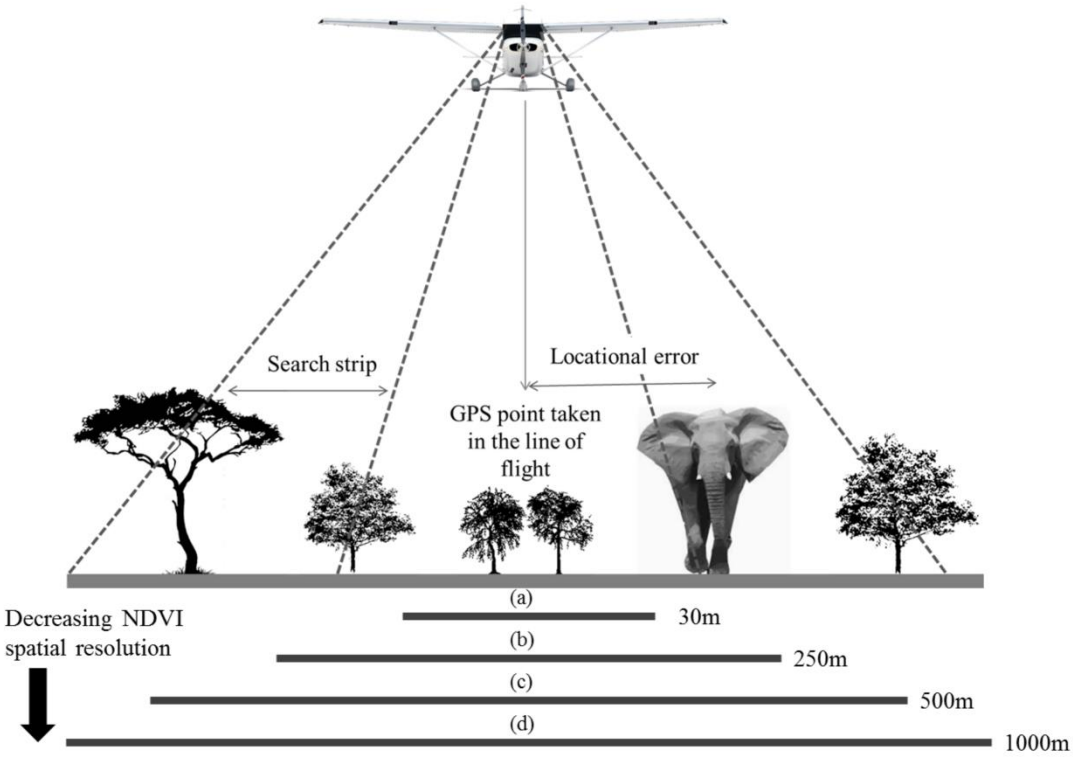

Figure 2-1: Conceptual framework illustrating the locational error associated with aerial survey presence data in relation to a typical habitat predictor. Note that at the NDVI spatial resolution of 30 m, the GPS point falls in a different pixel from the elephant location (a) but increasing the spatial resolution to say 250 metres, the GPS point, and the elephant lie within the same pixel (b).

The locational error is often unavoidable in aerial surveys (Figure 2-1) except where distance sampling methods are used to get more accurate measurements of location (Witting and Pike, 2009). When aerial surveys are conducted, the area below the aircraft is usually not visible to observers except in a few specialised surveys where a double window aircraft offering a full view underneath the aircraft is used (Whitt et al., 2013). From Figure 2-1, we can also deduce that if the predictor variable used in elephant habitat modelling is available at a spatial

resolution smaller than the locational error inherent in aerial survey data, poor model performance is likely to occur; but this needs to be subjected to a rigorous empirical test before any conclusions can be drawn.

In this paper, we claim that the performance of aerial survey data uncorrected for locational error in species habitat models may be established by comparing candidate models to those derived from superior datasets such as GPS collar data. The use of GPS collar data has shown that higher accuracy can be achieved in species distribution modelling (Loe et al., 2012, Wells et al., 2014). Previous studies consistently established that GPS collars exhibit locational error that does not exceed 100 m (Stache et al., 2012, Adams et al., 2013), which is considerably smaller than the locational error of up to 500 m reported for aerial survey data (Murwira and Skidmore, 2005). In essence, the locational errors of aerial survey data is a function of the strip width used in the survey and could also vary between surveys. Although under ideal circumstances many animals covering a large area would be collared, it is frequently the case that limited resources permit collaring of only a small number of animals covering a much smaller spatial extent. In effect, aerial surveys could offer a limited representation of habitat assuming, for example, a single flight and a fairly sparse population, where one would get a snapshot of a subset of individuals in just one of the habitats they likely use. Overall, testing how aerial survey data perform in species habitat modelling against GPS collar data may provide empirical evidence of the relative performance of these sampling methods.

In this study, we aimed to establish the utility of aerial survey data that are not corrected for locational error in elephant habitat modelling. We specifically asked whether there is an optimal spatial resolution of the predictor variable at which aerial survey data produce more reliable elephant habitat models. We also asked whether habitat models based on aerial survey data are able to accurately predict the occurrence of elephants in dense woodland habitats. To answer

these questions, we applied MaxEnt to aerial survey and GPS collar data for elephants obtained from Gonarezhou National Park of Zimbabwe. For each dataset, we used NDVI and distance from the nearest water point available at different spatial resolutions as the habitat predictors.

2.2 Materials and methods

2.2.1 Study site

This study was conducted in northern Gonarezhou national park (GNP) located in south-eastern Zimbabwe (Figure 2-2). The site is ideal for testing our hypotheses because: (1) data on elephant presence from aerial surveys and GPS collars were collected during the same month of September 2009, thus making the datasets comparable and, (2) GNP has an estimated elephant population of 10,000 (Dunham et al., 2013) which is amongst the largest in the country. This makes the study site important for elephant conservation in the country.

Elephant presence data were collected in an area approximately 2,733 km2 in size, between latitudes 21.10° and 21.76° South and longitudes 31.75° and 32.41° East. Altitude ranges from 155 m to 567 m above sea level. Typical vegetation in the study area is dry deciduous savannah dominated by *Colophospermum mopane* and *Combretum apiculatum*. Tree density in the mopane woodlands ranges from 98 to 543 trees/ha (Gandiwa and Kativu, 2009b). Mean annual rainfall is 466 mm per annum and is received from December to March (Gandiwa and Kativu, 2009a).

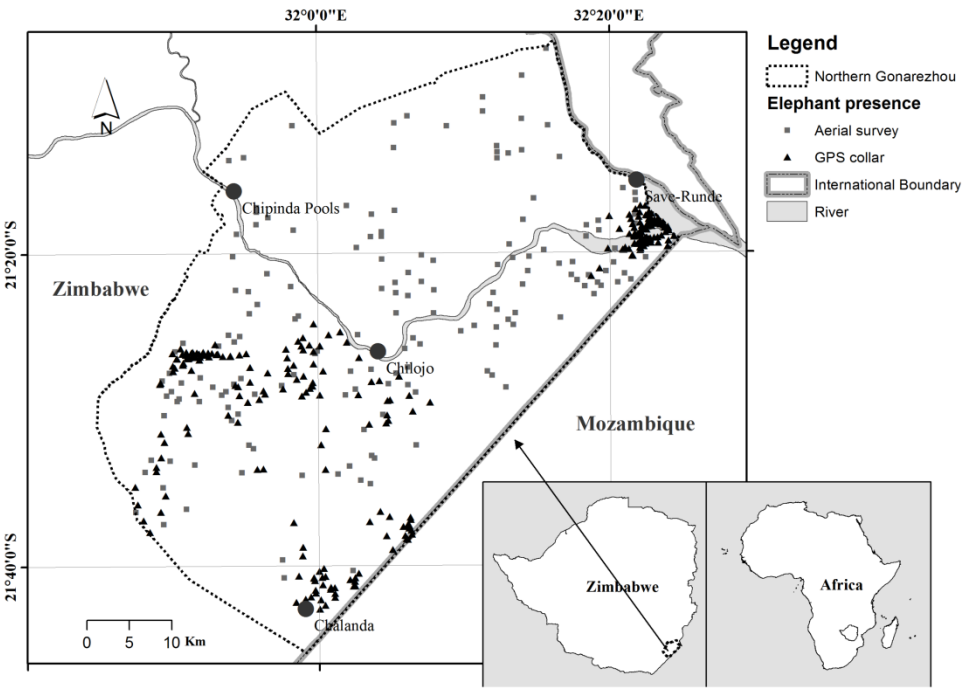

Figure 2-2: Location of the study site in south-eastern Zimbabwe. Elephant presence data are overlaid to show the spatial distribution of data sets used in this study.

2.2.2 Elephant presence data

Data on elephant presence were collected from a sample aerial survey and satellite-linked GPS collars fitted on 8 elephants (5 cows and 3 bulls). The aerial survey was conducted over the period from 4 to 9 September 2009 and the sampling effort ranged from 12.2 % to 21.1 % in the different survey strata (Dunham et al., 2010). Elephants were sighted by two observers scanning both sides of systematic line transects spaced by 2.5 km and covered from the air by a Cessna 185 fixed wing aircraft. The line transects were selected based on stratified random sampling where the starting point was randomly selected and subsequent ones had an equal separation distance to enhance representativeness. The average ground speed of the aircraft was 160 km/hr whilst the flying height was about 300 ft (91.44 m) above the ground measured using a radar altimeter. The ground speed of the aircraft was slightly higher than the speed of between 130 and 150 km/hr recommended by Norton-Griffiths (1978). Each time an elephant was sighted, the GPS location of the aircraft at the time of sighting the animals was recorded. A

detailed description of the methods used in that survey is available in Norton-Griffiths (1978) and Dunham (2012). We used a total of 222 elephant locations from the aerial survey in our analyses. Data from GPS collars were collected from 1 to 24 September 2009. These dates coincided with the period when aerial survey data were collected, that is from 4 to 9 September 2009. Lack of perfect overlap in the data collection dates for the two datasets possibly had minimum effect on model performance since we expected a non-significant change in vegetation biomass (estimated by NDVI) over the entire data collection period. GPS collar data used in our analyses (collected in September 2009) had a fix success rate of 100%. These data were collected from eight satellite collars supplied by Africa Wildlife Tracking (South Africa), fitted on eight elephants and programmed to take three fixes per day (two during the day and one during the night). The elephants fitted with the collars were selected during random flights in the national park and considerable separation distance between individual animals was maintained to ensure more complete coverage of representative habitats. Only the GPS collar fixes taken during the day were used in our analyses to ensure comparability with aerial survey data which were also collected during the day. We based our analyses on location fixes located inside the study site and left out those outside. To ensure equal sample size to the aerial survey dataset, we used 222 points randomly selected from a total of 284 elephant locations obtained from the GPS collars in our analyses. We used the random point selection tool implemented in a GIS to select the 222 points from GPS collar data.

2.2.3 NDVI data

We used NDVI as one of the habitat predictors because it correlates positively with vegetation biomass (Tucker, 1979). In addition, vegetation has been shown to be a key predictor of elephant habitat (Murwira and Skidmore, 2005). NDVI was calculated from cloud-free Landsat TM and Moderate Resolution Imaging Spectroradiometer (MODIS) images acquired in September 2009 to coincide with elephant presence data. Landsat and MODIS data were

downloaded from www.usgs.gov. Landsat bands used to compute NDVI (red and near-infrared bands) had a spatial resolution of 30 m whilst MODIS bands were available at 250 m, 500 m and 1,000 m spatial resolutions. Landsat data were acquired on 16 September 2009 while MODIS data at 250 m spatial resolution were acquired on 6 September 2009 and the data at 500 m and 1000 m were both acquired on 17 September 2009. Prior to computing NDVI, Landsat data were converted from digital numbers (DN values) to top of the atmosphere reflectance (TOA) following the method described by Chander et al. (2009). Landsat data were geometrically corrected to less than a 30 m by 30 m pixel (Root Mean Square Error (RMSE) of 0.87) based on 20 Ground Control Points (GCPs) collected in the field using a GPS at a positional error of ±5 m. Twenty GCPs are generally considered adequate for the 2nd order (12 terms) polynomial transformation used in this study (Toutin, 2004). MODIS data were re-projected from the geographic coordinate system to Universal Transverse Mercator (UTM) Zone 36 South in ENVI 5.1 (Exelis Visual Information Solutions, Boulder, Colorado) to be compatible with elephant presence data.

2.2.4 Distance from water points

We also used the distance from the nearest water point as a predictor variable in the model. The location of water points at the time of sampling was established using the Modified Normalised Difference Water Index (MNDWI) described in detail by Han-qiu (2005). The index was calculated using Landsat data described in detail in the previous section. All pixels with MNDWI values greater than 0 were classified as water points as suggested by Han-qiu (2005). Later, the Euclidian distance calculation algorithm was used to compute the distance of individual pixels from the nearest water points. In order to get data at the spatial resolutions of 250 m, 500 m, and 1000 m, the data on distance from water which were computed at the 30 m Landsat resolution were later resampled to the desired resolutions.

2.2.5 Elephant distribution modelling

In this study, MaxEnt was used to predict the distribution of elephants in northern Gonarezhou. MaxEnt was selected based on its ability to reliably predict species distribution from presence-only data. The algorithm is described in greater detail in Phillips and Dudik (2008). To generate elephant habitat models, elephant presence data from the aerial survey and GPS collars were used as the response variable separately whilst NDVI and distance from water points data calculated at four spatial resolutions of 30 m, 250 m, 500 m, and 1,000 m were the predictor variables. We used 70% of the elephant locations to calibrate the model whilst 30% of the data were set aside to validate the predictions as recommended in the literature (Araujo and Guisan, 2006). In total, eight habitat models were built (that is, four from each elephant presence dataset), at the NDVI and distance from water point spatial resolutions described earlier.

2.2.6 Model evaluation

For each elephant distribution model, the Area Under Curve (AUC) of the Receiver Operating Characteristic (ROC) curve was generated to assess the model's ability to predict elephant presence based on 30% of the dataset set aside for model validation. The sensitivity and specificity of the model predictions were assessed using the increasing probability of presence (logistic output) thresholds. ROC curves were generated using the method described in Sing et al. (2005). Elephant absence locations used in the computation of the ROC curves were obtained from the background pixels randomly created in MaxEnt. The AUCs were based on 500 bootstraps thus allowing calculation of confidence intervals. Differences in the AUCs of the habitat models based on aerial survey and GPS collar data at each spatial resolution of NDVI and distance from water points were inferred when their confidence intervals did not overlap. Confidence intervals were computed at the 95% confidence level. The spatial similarity between the predicted elephant habitats from both data sets was tested using the Jaccard Similarity Index. The index tests for similarity between two sample sets and is the ratio of the

size of the intersection to the size of the union of the same set. More detail on the index is described in Magurran (2004). In this study, bigger values of the index represented similarity in the predicted elephant habitats whereas lower values represented dissimilarity.

2.3 Results

2.3.1 Predictive ability of habitat models derived from aerial survey data

The AUCs for the models relating elephant presence data from aerial surveys to both predictors at spatial resolutions of 30 m, 250 m, 500 m, and 1000 m were significantly lower than those predicted based on GPS collar data (Figure 2-3 and 2-4). In particular, the AUC for the model relating aerial survey and GPS collar data to NDVI and distance from water points at the 30 m spatial resolution was 0.592 (95% CI [0.511, 0.669]) and 0.767 (95% CI [0.713, 0.820]) respectively. At the spatial resolution of 250 m for NDVI and distance from water point, the model based on aerial survey data had an AUC of 0. 603 (95% CI [0.526, 0.684]) whilst that for GPS collar data was 0.708 (95% CI [0.641, 0.773]). Similarly, the AUCs for models based on aerial survey and GPS collar data were 0.607 (95% CI [0.526, 0.692]) and 0.719 (95% CI [0.650, 0.789]) respectively at the NDVI and distance from water points spatial resolution of 500 m. Finally, at the spatial resolution of 1000 m for both predictors, the AUC for models based on aerial survey and GPS collar data were 0.590 (95% CI [0.516, 0.663]) and 0.678 (95% CI [0.589, 0.764]) respectively.

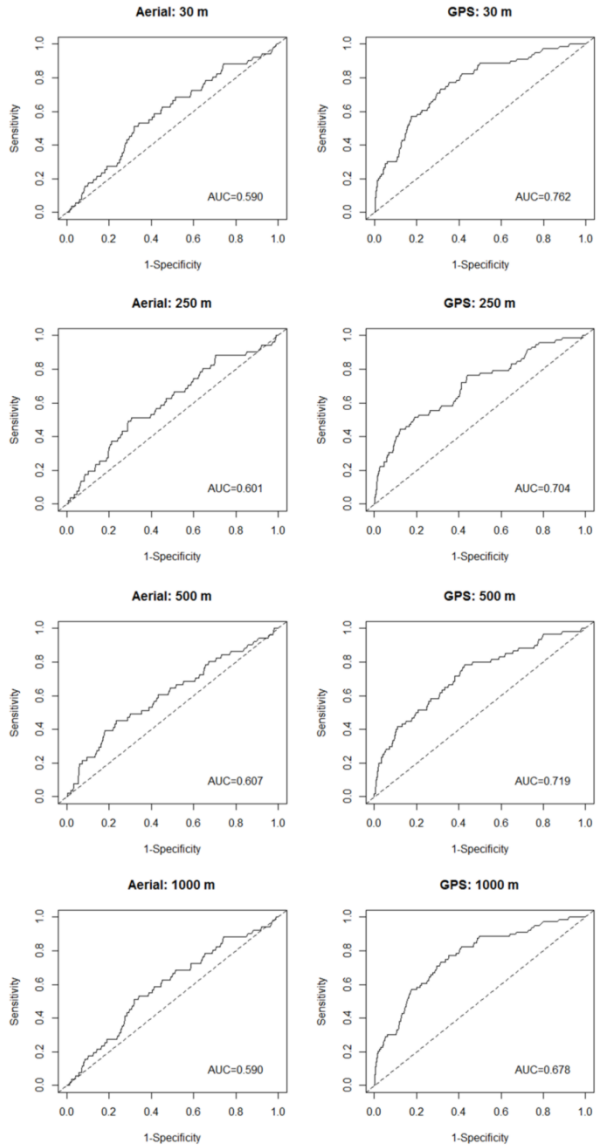

Figure 2-3: ROC curves for elephant distribution models built using presence data from aerial surveys and GPS collars as the response variable and NDVI and distance from water point data at 30, 250, 500 and 1000 metres spatial resolution as the predictors.

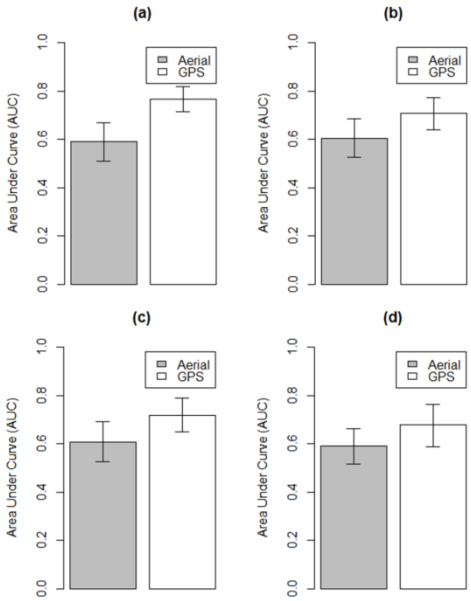

Figure 2-4: Mean area under the curve (± 95% confidence interval) for elephant habitat models built using aerial survey data and GPS collar data. The differences are shown for different spatial resolutions of the predictor variables (a) 30 m, (b) 250 m, (c) 500 m, and (d) 1,000 m.

2.3.2 Performance of aerial survey data in relation to vegetation density

Figure 2-5 illustrates the performance of elephant models built using aerial survey data and GPS collar data at different values of the predictor (NDVI). We observe that elephant distribution models built using aerial survey data achieved higher probabilities of elephant presence (logistic output) at lower NDVI values compared to those based on GPS collar data. In contrast, at higher NDVI values, habitat models based on aerial survey data showed lower probabilities of elephant presence when compared to those based on GPS collar data.

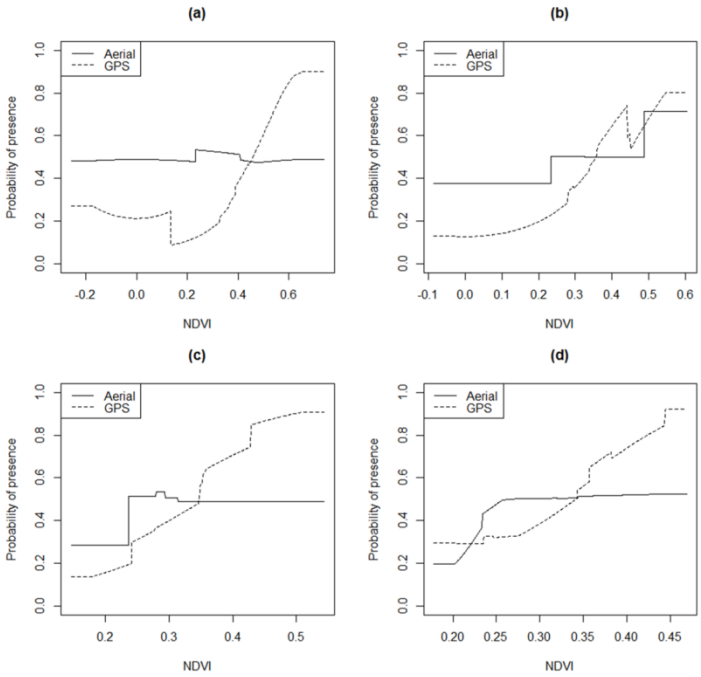

Figure 2-5: Probability curves for elephant habitat models built using aerial survey and GPS collar data plotted against NDVI and distance from water points at different spatial resolutions: (a) 30 m, (b) 250 m, (c) 500 m, and (d) 1,000 m.

2.3.3 Spatial similarity between the predicted elephant habitats

The spatial resolution of the predictor variable had a significant effect on the similarity and dissimilarity of habitat predicted using aerial survey and GPS collar data. We observed low similarity (J = 0.197) between elephant habitats predicted using aerial survey and GPS collar data when both predictors had a fine spatial resolution (30 m). Likewise, low similarity was detected when comparing habitats predicted using the two data sets at the 250 m and 500 m spatial resolutions (J = 0.245 and 0.178, respectively). The highest similarity was observed at the 1,000 m spatial resolution (J = 0.265). Figure 2-6 shows the maps of the predicted elephant habitats that were used in the calculation of the Jaccard's coefficient of similarity.

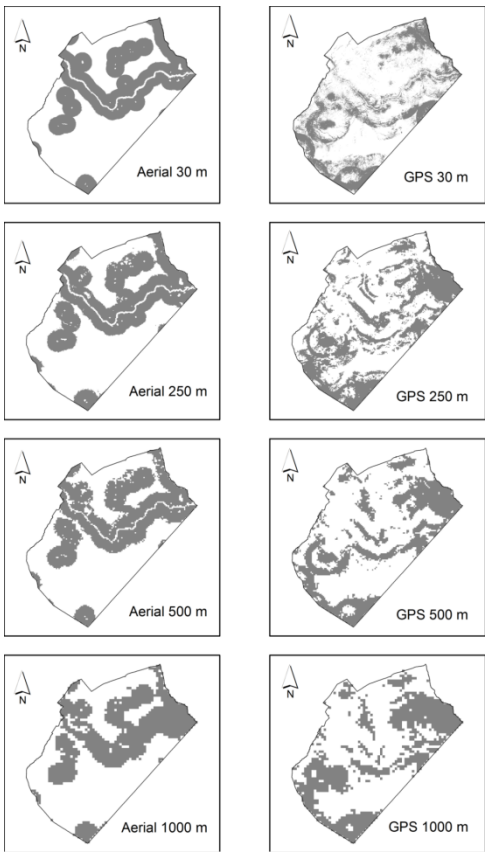

Figure 2-6: Elephant habitat predicted using aerial survey and GPS collar data against NDVI and distance from water points at spatial resolutions of 30 m, 250 m, 500 m and 1,000 m.

2.4 Discussion

We found that high spatial similarity between elephant habitats predicted using aerial survey and GPS collar datasets exist largely at the 1,000 m spatial resolution of the predictor variables and not at finer spatial resolutions. This key result indicates the poor performance of aerial survey data in elephant distribution modelling at finer scales of the predictor variables. Scale dependence in the performance of aerial survey data was previously suggested in the literature but until now empirical evidence confirming its effect had not been provided in a spatial modelling framework. In a previous study, locational error of up to 500 m associated with aerial survey data was reported in north-western Zimbabwe (Murwira and Skidmore, 2005). Unlike, aerial survey data, the locational error inherent in GPS collar data rarely exceeds 100 m (Rempel et al., 1995, Moen et al., 1996). From this result, we deduce that at most aerial survey data

uncorrected for this locational error can be used to provide reliable estimates of elephant distribution at a coarse spatial resolution of 1,000 m.

Another important aspect of the results of this study is the lower probability of elephant presence (logistic output) obtained from habitat models based on aerial survey data in high NDVI areas compared to those from GPS collar data. High NDVI values have been observed to be associated with high tree canopy area (Ndaimani et al., 2014). It, however, has to be emphasised that the logistic output of the MaxEnt model is not exactly the same as the probability of presence (Yackulic et al., 2013). This key result suggests that elephants under dense tree canopies are potentially missed during aerial surveys whilst those occurring in open areas with fewer trees have a better chance of being detected. The failure by aerial surveys to accurately detect animals under tree canopies has been documented (Jachmann, 2002, Pollock and Kendall, 1987) and this result simply confirms it. The finding that aerial surveys possibly miss elephants under dense tree canopies has far-reaching implications on habitat models predicted using aerial survey data and raises the question: if an aerial survey fails to spot the largest land mammals on Earth in a savannah then what hope do we have for spotting smaller mammals such as antelopes? On the other hand, the fact that habitat models based on GPS collar data succeeded in predicting higher probabilities of elephant presence in areas of high tree cover is also an important finding. The main reason for the superiority of GPS collar data is that whilst it is restricted in spatial extent since only a few individuals can be collared due to high costs, it has high locational accuracy. In addition, GPS data provide a more accurate representation for all the habitats (including the closed habitats) than aerial survey data. Nevertheless, elephant presence data from aerial surveys are collected over large spatial extents, thus enabling the sampling of a wide variety of habitats.

Overall, our study is amongst the first to test the advantage of using species presence data from aerial surveys in habitat modelling in an African savannah. Based on the evidence gathered in this study, we recommend that species distribution models built from aerial survey data uncorrected for locational error should, therefore, be treated with caution. Although the results reported here are robust given that two different presence datasets were used, our modelling framework is not perfect. First, NDVI and distance from the water points were the only predictors used to predict elephant presence yet other variables such as human-induced disturbance are known to play a major role in elephant distribution. This could have contributed to the poor performance of aerial survey data and hence the inclusion of other covariates warrants further investigation. Another potential limitation is that we used only one species distribution modelling technique (MaxEnt) but could have used other methods such as boosted regression trees (Elith et al., 2006). The choice of MaxEnt is justifiable since previous research has demonstrated its superiority over competing methods. In addition, our aim was not to build predictive models per se but to test the effect of the locational error on the performance of aerial survey data.

2.5 Conclusion

We conclude that presence data from aerial surveys, which are not corrected for locational error, perform poorly in species habitat modelling and should be used with care. Overall, our study also demonstrated the superiority of GPS collar data at different spatial resolutions of the predictor variable but given the limited spatial extent of the data, better results are likely to be obtained when it is used to complement aerial survey data which tend to have a large spatial coverage but low locational accuracy. However, it has to be noted that we are not suggesting the complete replacement of aerial survey data with GPS collar data. These two datasets a suited for different purposes. For instance, due to the survey design, aerial survey data still remain an important method for estimating animal populations whilst GPS collar data cannot be used for

that purpose since only a few individual animals can be collared at any given time. Future studies could test whether models that combine both data sets perform better since the combined data possibly samples a wider representation of habitats existing in the landscape. Further work could involve a comparison of models based on points collected in open and closed habitats in order to tease apart the effects of locational errors from those caused by changes in detectability.

References

Adams, A. L., Dickinson, K. J., Robertson, B. C. & Van Heezik, Y. (2013) An evaluation of the accuracy and performance of lightweight GPS collars in a suburban environment. PloS one, 8, e68496.

Araujo, M. B. & Guisan, A. (2006) Five (or so) challenges for species distribution modelling. Journal of Biogeography, 33, 1677-1688.

Bean, W., Prugh, L., Stafford, R., Butterfield, H., Westphal, M. & Brashares, J. (2014) Species distribution models of an endangered rodent offer conflicting measures of habitat quality at multiple scales. Journal of Applied Ecology, 51, 1116-1125.

Chander, G., Markham, B. L. & Helder, D. L. (2009) Summary of current radiometric calibration coefficients for Landsat MSS, TM, ETM+, and EO-1 ALI sensors. Remote Sensing of Environment, 113, 893-903.

Condit, R., Ashton, P. S., Baker, P., Bunyavejchewin, S., Gunatilleke, S., Gunatilleke, N., Hubbell, S. P., Foster, R. B., Itoh, A. & Lafrankie, J. V. (2000) Spatial patterns in the distribution of tropical tree species. Science, 288, 1414-1418.

Dunham, K., Van Der Westhuizen, E., Van Der Westhuizen, H. & Gandiwa, E. (2010) Aerial survey of elephants and other large herbivores in Gonarezhou National Park (Zimbabwe), Zinave National Park (Mozambique) and surrounds: 2009, Zimbabwe Parks and Wildlife Management Authority.

Dunham, K., Van Der Westhuizen, E., Van Der Westhuizen, H. & Ndaimani, H. (2013) Aerial survey of elephants and other large herbivores in Gonarezhou National Park (Zimbabwe), and surrounding areas: 2013, Zimbabwe Parks and Wildlife Management Authority.

Dunham, K. M. (2012) Trends in populations of elephant and other large herbivores in Gonarezhou National Park, Zimbabwe, as revealed by sample aerial surveys. African Journal of Ecology, 50, 476-488.

Elith, J., H. Graham, C., P. Anderson, R., Dudík, M., Ferrier, S., Guisan, A., J. Hijmans, R., Huettmann, F., R. Leathwick, J., Lehmann, A., Li, J., G. Lohmann, L., A. Loiselle, B., Manion, G., Moritz, C., Nakamura, M., Nakazawa, Y., Mcc. M. Overton, J., Townsend Peterson, A., J. Phillips, S., Richardson, K., Scachetti-Pereira, R., E. Schapire, R., Soberón, J., Williams, S., S. Wisz, M. & E. Zimmermann, N. (2006) Novel Methods Improve Prediction of Species' distributions from occurrence data. Ecography, 29, 129-151.

Gandiwa, E. & Kativu, S. (2009a) Influence of fire frequency on *Colophospermum mopane* and *Combretum apiculatum* woodland structure and composition in northern Gonarezhou National Park, Zimbabwe. Koedoe, 51, 1-13.

Han-Qiu, X. (2005) A Study on Information Extraction of Water Body with the Modified Normalized Difference Water Index (MNDWI). Journal of Remote Sensing, 5, 589-595.

Head, J. S., Robbins, M. M., Mundry, R., Makaga, L. & Boesch, C. (2012) Remote video-camera traps measure habitat use and competitive exclusion among sympatric chimpanzee, gorilla and elephant in Loango National Park, Gabon. Journal of Tropical Ecology, 28, 571-583.

Jachmann, H. (2002) Comparison of aerial counts with ground counts for large African herbivores. Journal of Applied Ecology, 39, 841-852.

Kiffner, C., Stoner, C. & Caro, T. (2013) Edge effects and large mammal distributions in a national park. Animal Conservation, 16, 97-107.

Lagendijk, D. G., Mackey, R. L., Page, B. R. & Slotow, R. (2011) The effects of herbivory by a mega-and mesoherbivore on tree recruitment in Sand Forest, South Africa. PloS one, 6, e17983.

Laws, R. M. (1970) Elephants as agents of habitat and landscape change in East Africa. Oikos, 21, 1-15.

Loe, L. E., Bonenfant, C., Meisingset, E. L. & Mysterud, A. (2012) Effects of spatial scale and sample size in GPS-based species distribution models: are the best models trivial for red deer management? European Journal of Wildlife Research, 58, 195-203.

Magurran, A. E. (2004) Measuring biological diversity. Blackwell Science Ltd, USA.

Moen, R., Pastor, J., Cohen, Y. & Schwartz, C. C. (1996) Effects of moose movement and habitat use on GPS collar performance. The Journal of Wildlife Management, 60, 659-668.

Murwira, A. & Skidmore, A. K. (2005) The response of elephants to the spatial heterogeneity of vegetation in a Southern African agricultural landscape. Landscape Ecology, 20, 217-234.

Nagendra, H., Lucas, R., Honrado, J. P., Jongman, R. H., Tarantino, C., Adamo, M. & Mairota, P. (2013) Remote sensing for conservation monitoring: Assessing protected areas, habitat extent, habitat condition, species diversity, and threats. Ecological Indicators, 33, 45-59.

Ndaimani, H., Murwira, A. & Kativu, S. (2014) Predicting the spatial distribution of hunted and non-hunted Sable antelope (*Hippotragus niger niger*) using remotely sensed woody cover in a Southern African savannah. Geocarto International, 29, 198-210.

Norton-Griffiths, M. (1978) Counting Animals, 2nd Edition, African Wildlife Leadership Foundation, Nairobi.

Perry, G. L., Miller, B. P. & Enright, N. J. (2006) A comparison of methods for the statistical analysis of spatial point patterns in plant ecology. Plant Ecology, 187, 59-82.

Phillips, S. J. & Dudík, M. (2008) Modeling of species distributions with Maxent: new extensions and a comprehensive evaluation. Ecography, 31, 161-175.

Pittiglio, C., Skidmore, A. K., Van Gils, H. A. & Prins, H. H. (2013) Elephant response to spatial heterogeneity in a savanna landscape of northern Tanzania. Ecography, 36, 819-831.

Pollock, K. H. & Kendall, W. L. (1987) Visibility Bias in Aerial Surveys: A Review of Estimation Procedures. The Journal of Wildlife Management, 51, 502-510.

Rempel, R. S., Rodgers, A. R. & Abraham, K. F. (1995) Performance of a GPS animal location system under boreal forest canopy. The Journal of Wildlife Management, 59, 543-551.

Ross, R. E. & Howell, K. L. (2013) Use of predictive habitat modelling to assess the distribution and extent of the current protection of 'listed'deep-sea habitats. Diversity and Distributions, 19, 433-445.

Scheidat, M., Verdaat, H. & Aarts, G. (2012) Using aerial surveys to estimate density and distribution of harbour porpoises in Dutch waters. Journal of Sea Research, 69, 1-7.

Sing, T., Sander, O., Beerenwinkel, N. & Lengauer, T. (2005) ROCR: visualizing classifier performance in R. Bioinformatics, 21, 3940-3941.

Stache, A., Löttker, P. & Heurich, M. (2012) Red deer telemetry: Dependency of the position acquisition rate and accuracy of GPS collars on the structure of a temperate forest dominated by European beech and Norway spruce. Silva Gabreta, 18, 35-48.

Toutin, T. (2004) Review article: Geometric processing of remote sensing images: models, algorithms and methods. International Journal of Remote Sensing, 25, 1893-1924.

Tucker, C. J. (1979) Red and photographic infrared linear combinations for monitoring vegetation. Remote Sensing of Environment, 8, 127-150.

Valeix, M., Fritz, H., Sabatier, R., Murindagomo, F., Cumming, D. & Duncan, P. (2011) Elephant-induced structural changes in the vegetation and habitat selection by large herbivores in an African savanna. Biological Conservation, 144, 902-912.

Van Langevelde, F., Van De Vijver, C. A., Kumar, L., Van De Koppel, J., De Ridder, N., Van Andel, J., Skidmore, A. K., Hearne, J. W., Stroosnijder, L. & Bond, W. J. (2003) Effects of fire and herbivory on the stability of savanna ecosystems. Ecology, 84, 337-350.

Vaughan, I. P. & Ormerod, S. J. (2003) Improving the Quality of Distribution Models for Conservation by Addressing Shortcomings in the Field Collection of Training Data. Conservation Biology, 17, 1601-1611.

Wells, A. G., Blair, C. C., Garton, E. O., Rice, C. G., Horne, J. S., Rachlow, J. L. & Wallin, D. O. (2014) The Brownian bridge synoptic model of habitat selection and space use for animals using GPS telemetry data. Ecological Modelling, 273, 242-250.

Whitlow, J. (1987) Vegetation in Zimbabwe. East and South-Eastern Zimbabwe. Papers from the 1987 study tour of the Geographical Association of Zimbabwe. Geographical Association of Zimbabwe, 11-15.

Whitt, A. D., Dudzinski, K. & Laliberté, J. R. (2013) North Atlantic right whale distribution and seasonal occurrence in nearshore waters off New Jersey, USA, and implications for management. Endangered Species Research, 20, 59-69.

Witting, L. & Pike, D. G. (2009) Distance estimation experiment for aerial minke whale surveys. NAMMCO Scientific Publications, 7, 111-116.

Yackulic, C. B., Chandler, R., Zipkin, E. F., Royle, J. A., Nichols, J. D., Campbell Grant, E. H. & Veran, S. (2013) Presence-only modelling using MAXENT: when can we trust the inferences? Methods in Ecology and Evolution, 4, 236-243.

Young, T. P., Palmer, T. M. & Gadd, M. E. (2005) Competition and compensation among cattle, zebras, and elephants in a semi-arid savanna in Laikipia, Kenya. Biological Conservation, 122, 351-359.

Chapter 3

A new method for correcting locational error from aerial surveys improves habitat model performance

This chapter is based on:

Ndaimani, H., Murwira, A. & Masocha, M. (2018) A new method for correcting locational error from aerial surveys improves habitat model performance. *African Journal of Ecology*, 56, 928-937.

3. A new method for correcting locational error from aerial surveys improves habitat model performance

Abstract

The utility of aerial survey data in modelling the distribution of wildlife has been questioned due to locational errors. Yet, little effort has been made to correct these errors. Here, a new method is proposed for correcting locational errors associated with aerial survey data. We further tested whether the correction improves model performance using elephant aerial survey data collected at three protected sites in Zimbabwe. Our correction method succeeded in shifting location by 143 to 177 m from the line of flight. Based on the true skill statistic, models built using corrected data in Hwange and Mana Pools national parks were significantly better than those from uncorrected data and only in Gonarezhou national park were no significant differences in model performance observed. These results underscore the benefit of applying the new correction method for modelling wildlife distribution. The other key result is that the correction seems to be more beneficial in heterogeneous landscapes than homogeneous ones for, in the former, a small shift in location results in the sampling of different habitats than where sightings were made. The proposed method opens new opportunities for improving the accuracy of aerial survey data in species distribution modelling.

3.1 Introduction

The development of models to predict the spatial distribution of wildlife in a landscape is important for conservation. For instance, models that accurately predict the distribution of target species in a landscape provide useful insights into the ecology of the species thereby enabling targeted allocation of resources for their protection. However, it is generally agreed that the accuracy of the wildlife distribution model predictions depends on, inter alia, the quality of wildlife location data (Wisz et al., 2008, Elith et al., 2006). Thus, the development of methods to improve the quality of wildlife location data is critical.

Several attempts have been made to improve the quality of wildlife data. However, the focus has mainly been on developing methods for improving the quality of predictor variable data such as vegetation cover and terrain, largely collected from remote sensing (Moisen et al., 2006). While the accuracy of wildlife presence data collected from radio telemetry has either been questioned or documented since the 1960s (Heezen and Tester, 1967) and several improvements have been suggested (e.g., Fedak et al., 2002, Frair et al., 2010), the locational accuracy of data from aerial surveys has remained untested especially when applied together with remotely sensed predictor variables. Thus, focusing attention on ascertaining and improving the accuracy of wildlife locational data from aerial surveys is critical.

Typical data collection using aerial surveys involves flying a fixed-wing plane along pre-selected transects and recording animals sighted within ~150 m wide search strips to the right and left of the flight path (see Figure 3-2). If distance sampling theory (Buckland et al., 2005) is not applied during the survey, the position of a particular animal sighting is recorded along the line of flight when in fact the true position of the sighting is a distance away. Therefore, use of aerial survey data, uncorrected for locational error, in modelling assumes that the sampled position is in the line of flight when, in fact, it should be somewhere inside the search strips. In

highly heterogeneous landscapes, points separated by several metres might represent different habitats. Thus, the use of uncorrected data in those landscapes for predicting the potential distribution of target species possibly compromises model performance. Previous studies that used aerial survey data for habitat modelling have had to use coarse scale environmental variables in order to avoid the pitfall of locational error. For instance, Murwira and Skidmore (2005) indicated that the magnitude of error for aerial survey data is less than 500 m and had to use coarse environmental variable data to avoid significantly influencing model performance.

To date, some studies that have used the uncorrected data in modelling have assumed that the error is so minimal that it has a negligible effect on model performance (e.g., Murwira and Skidmore, 2005). In addition, to the best of our knowledge, little attempt has been made to objectively test whether correction of the data would affect the performance of models that predict the potential distribution of species in the landscape. In fact, knowledge on whether correcting locational error inherent in data collected from aerial surveys would improve model performance remains largely rudimentary.

In this study, we tested the utility of a method for correcting the locational error in animal presence data collected from aerial surveys. We tested whether the correction factors estimated in different study sites were the same. We also asked whether the corrected presence data would improve the performance of models predicting the potential distribution of African elephants (*Loxodonta africana*) in three sites located in Zimbabwe. It was also deemed that if the correction method can work in multiple sites, it is likely to work in other savannah landscapes, thereby being generalizable.

3.2 Materials and methods

3.2.1 Study sites

The study was conducted in the Gonarezhou, Hwange and Mana Pools National Parks of Zimbabwe (Figure 3-1). These three sites are similar in that no hunting and other forms of consumptive use of wildlife are permitted. However, the three sites differ in size, rainfall, vegetation, soils and elephant density. We selected the study sites because they represent key elephant range areas in the country (Child, 2004) and have different environmental gradients.

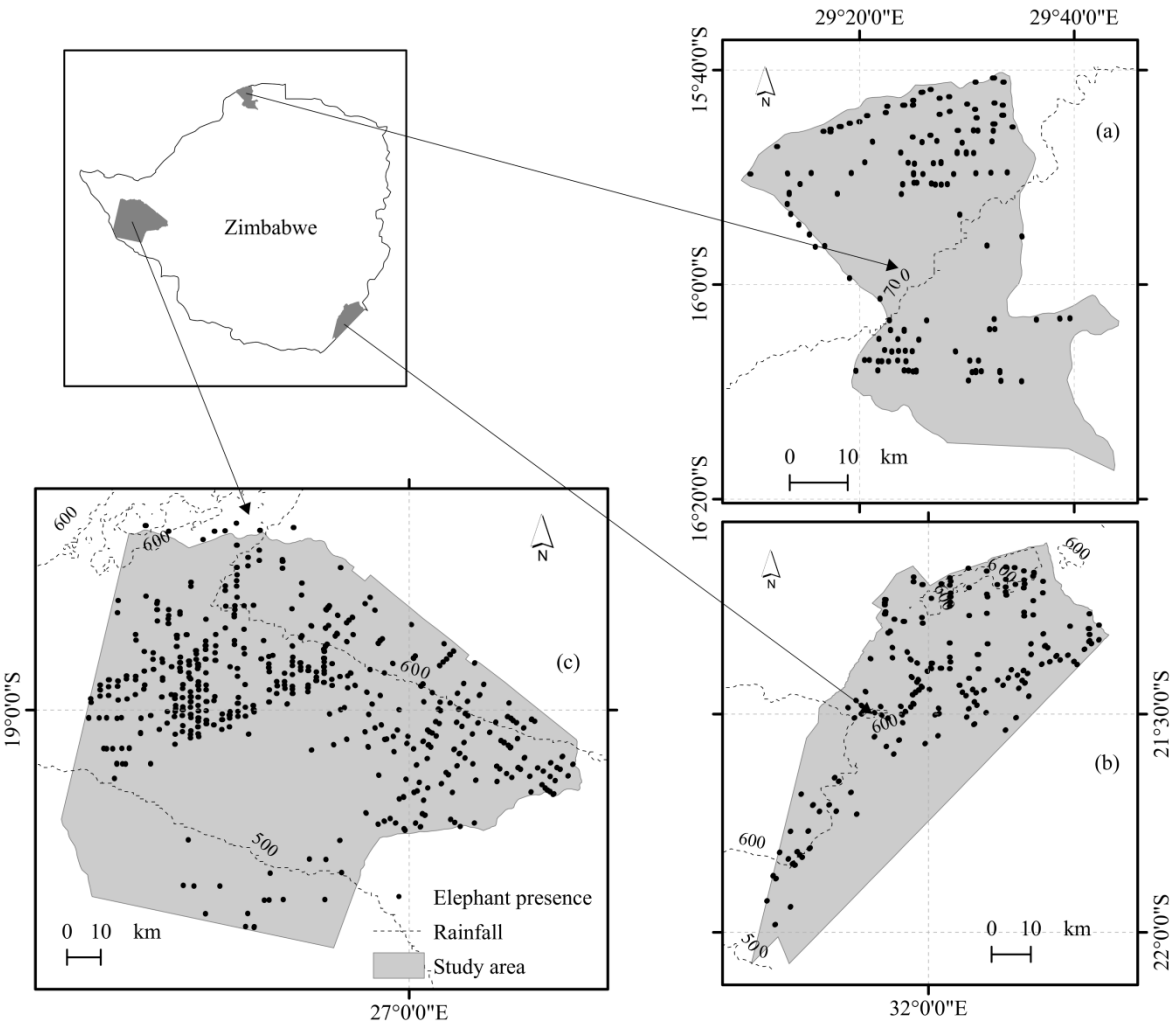

Figure 3-1: Location of (a) Mana Pools, (b) Gonarezhou, and (c) Hwange National Parks in Zimbabwe. Maps also show elephant sightings data from aerial surveys as well as rainfall from Bioclim data

The first study area lies in the Gonarezhou National Park (31.59°E-32.41°E, 21.11°S-22.07°S) located to the south-east of Zimbabwe (Figure 3-1(a)). The area is defined as that part of the park located within the Landsat scene defined by path 168 and row 075 and is 3,777 km^2 in size. Elevation ranges from 155 to 567 m while the mean slope is 2.78°. Total annual precipitation from long-term records is ~450 mm. Major soil groups are Cambic Arenosols, Luvic Arenolos and Lithosols. The vegetation found in the study area is predominantly dry deciduous savannah dominated by *Colophospermum mopane* and *Combretum apiculatum*. The park is home to ~11,000 elephants at a density of ~2.25 animals/km^2.

The second study area is ~11,389 km^2, lies in the Hwange National Park (26.07°E-27.46°E, 18.52°S-19.63°S) and is located to the north west of Zimbabwe (Figure 3-1(b)). This area is the part of the national park which is located in the Landsat scene defined by path 172 and row 073. Long-term annual rainfall ranges from 450 to 650 mm. Elevation ranges from 830 to 1128 m with a mean slope of 1.68°. Cambic Arenosols, Luvic Arenosols and Vertic Cambisols are the dominant soil groups found in the area. *Baikaea plurijuga* is the dominant vegetation type on Arenosols while *Terminalia sericea* and *Combretum spp* dominate the Cambisols. Elephant density is ~3.02 animals/km^2 and is the highest in the country.

The third study area is ~2124 km^2 and comprises the entire Mana Pools National Park (29.15°E-29.74°E, 15.67°S-16.29°S) found on the north of Zimbabwe (Figure 3-1(c)). Total annual precipitation from long-term data ranges from 450 to 650 mm. The area is characterised by elevation values of 268-1186 m and mean slope of 4.56°. Major soil groups include Chromic Luvisols, Ferralic Arenosols and Lithosols. *Colophospermum mopane* dominates on the Lithosols while *Brachystegia spp* are dominant on the Arenosols. Elephant densities are lower than in the other two sites (~0.38 animals/km^2).

3.2.2 Calibration flights

The calibration of flights was undertaken as described by Norton-Griffiths (1978b). Prior to aerial surveys in each of the three study sites, calibration flights were run with fixed wing aircraft, that is, Cessna 185 for Gonarezhou, Cessna 206 for Hwange and Cessna 206 for Mana Pools. This was necessary since the aircraft used and the observers who participated in each aerial survey were different. During calibration, the pilot flew the plane at right angles to an airstrip and above a windsock located at the centre of the airstrip. The pilot had to fly past the airstrip at a height of about 91.44 m (300 ft), which is the height used during the actual surveys. Meanwhile, observers seated at the rear right and left side of the aircraft visually scanned between streamers (a pair of parallel carbon fibre fishing rods) fixed on the struts of the aircraft and called out the maximum and minimum values of markers written in white paint on the airstrip visible from the air. The markers were numbered from zero to 35 on each side of the windsock and individual markers were separated by 10 m. The values for the maximum and minimum markers between the streamers on the side of each observer were later used to calculate the estimated strip width in metres for that observer. The total calibration runs were 31 in Gonarezhou, 33 in Hwange and 30 in Mana Pools.

3.2.3 Correction of the locational error

Strip width data collected during the calibration runs were used to derive the estimated correction factor (*D*) for each site (Figure 3-2). *D* is defined as the distance between the line of flight (marked by the windsock) and the centre of the average estimated strip width for the right and left observers.

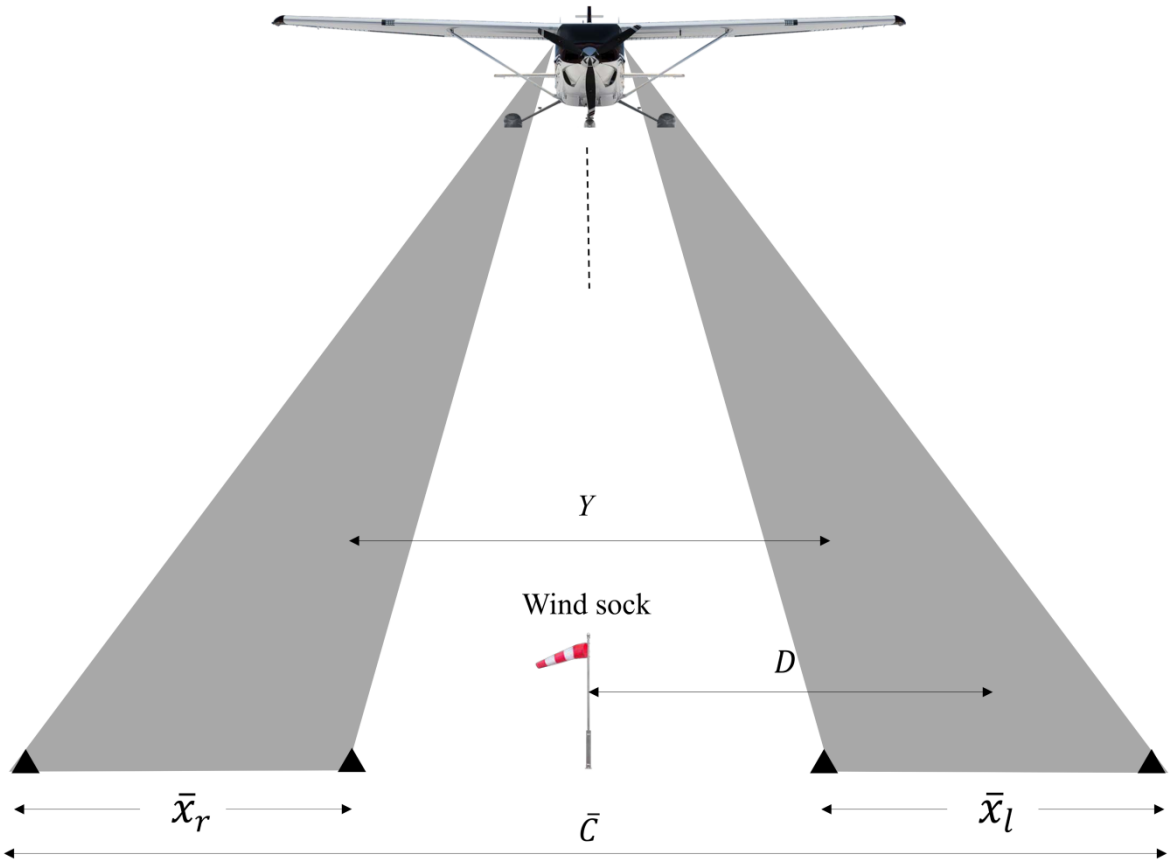

Figure 3-2: The correction factor (D) = estimated distance between the line of flight (marked by the windsock) and the centre of the average strip width for the right and left observers. C = distance between outer markers for both observers; x_r = average strip width for the right observer; x_l = average strip width for the left observer; and Y is the width of the invisible area underneath the aircraft and between the inner markers of both observers

A total of nine derived equations were used to correct the inherent error associated with aerial survey locational data.

First, the average combined distance between the left and right outer markers was calculated as:

$$\acute{C} = \frac{1}{n}\sum_{i=1}^{n} C_i \qquad \text{eqn 1}$$

where $\acute{C}$ is the average distance between the outer markers of the right and left observers; C_i is the distance between the outer markers of the right and left observers during an individual calibration run; and *n* is the total number of calibration runs for the site.

The average strip width for the right observer was calculated as:

$$\acute{x}_r = \frac{1}{n}\sum_{i=1}^{n} x_i \qquad \text{eqn 2}$$

where $\acute{x}_r$ is the average strip width for the right observer; x_i is the strip width for the ith calibration run; and n is the total number of calibration runs for the site.

Similarly, the average strip width for the left observer was calculated as:

$$\acute{x}_l = \frac{1}{n}\sum_{i=1}^{n} x_i \qquad \text{eqn 3}$$

where $\acute{x}_l$ is the average strip width for the left observer; x_i is the strip width for the ith calibration run; and n is the total number of calibration runs for the site.

To calculate the invisible strip underneath the aircraft and between the inner markers of the right and left observers, equation 4 was applied:

$$Y = \bar{C} - (\acute{x}_r + \acute{x}_l) \qquad \text{eqn 4}$$

where Y is the width of the invisible area underneath the aircraft; $\acute{C}$ is the average distance between the outer markers for the right and left observers; and $\acute{x}_r$ and $\acute{x}_l$ were described before.

Then, D was derived as follows:

$$D = \frac{Y}{2} + \frac{(\acute{x}_r + \acute{x}_l)}{2} \qquad \text{eqn 5}$$

After calculating the correction factor D, the next step was to calculate the bearing of an individual sighting located to the right of the flight path (θ_r) as :

$$\theta_r = \phi + 90° \qquad \text{eqn 6}$$

where ϕ is the bearing of the transect.

Equation 7 was used to calculate the bearing of an individual sighting located to the left of the flight path as given by:

$$\theta_l = \phi - 90° \qquad \text{eqn 7}$$

where θ_l is the bearing of the sighting to the right of the flight path.

Equations 8 and 9 were then used to calculate the longitude and latitude at the corrected location of the sighting, respectively.

$$x_2 = x_1 D sin\theta \qquad \text{eqn 8}$$

$y_2 = y_1 D cos\theta$ eqn 9

where x_1 is the longitude of the sighting along the flight path; x_2 is the estimated longitude of the sighting after correction; $y_1$is the latitude of the sighting along the flight path; y_2 is the estimated latitude of the sighting after correction; and D is the estimated correction factor.

The three sites have similar terrain ruggedness (Table 2-2). As a result, there was no need to correct for terrain differences using a Digital Elevation Model (DEM). In addition, the correction factors were less than 200 m, thus the effect of the earth's curvature on locational error was deemed negligible.

3.2.4 A comparison of the correction factors using real data sets

Data collected during calibration runs in Gonarezhou, Hwange and Mana Pools National Parks were used to estimate correction factors (D) based on our suggested method. We later tested whether the correction factors estimated for the three study sites were significantly different. One-way ANOVA was used to test whether there were any significant differences in the mean estimated values for the correction factors. ANOVA was used since data did not significantly deviate from a normal distribution (Gonarezhou: W= 0.967, p = 0.442; Hwange: W = 0.962, p = 0.286; Mana Pools: W = 0.969, p = 0.512). The null hypothesis tested was that $D_1=D_2=D_3$. The alternative hypothesis was that at least one of the mean D values differ. Following the rejection of H_o, Tukey's HSD tests were performed for pairwise comparisons.

3.2.5 Comparisons of elephant distribution models for corrected and uncorrected data

Elephant location data corrected for position error using the method described before were used to test whether the suggested correction method improves the performance of Species Distribution Models (SDMs). To achieve this, Maximum entropy modelling (MaxEnt) (Phillips et al., 2004) was used with elephant presence data as the response variable and NDVI as well as distance from water sources as the two predictor variables, to predict the potential

distribution of elephants in the three study sites. MaxEnt is a general-purpose machine learning method that predicts the presence of target species from presence-only data (Phillips et al., 2004). Multi-collinearity was not detected since the two predictor variables were observed to be weakly correlated (Gonarezhou: r = -0.162; Hwange: r = -0.085; Mana Pools: r = 0.168). Evidence from the literature suggests that multi-collinearity distorts model estimation when correlation coefficients (|r|) between predictor variables exceed 0.7 (Dormann et al., 2013). Correlation analysis was performed on raster data of the predictor variables using the Spatial Analyst Tools of ArcGIS 10.1 (ESRI, 2011).

Location data for elephants used for modelling were collected during a national survey conducted during the dry season in August of 2014 (Mana Pools) and during the month of October 2014 for both Gonarezhou and Hwange. Even though August and October occur in the dry season, visibility of animals might differ during these months because of potential differences in vegetation condition. Location data were collected along transects located within the individual stratum. Table 3-1 provides more detail on the sampling parameters.

Table 3-1: Details of the strata, sightings, transects and the dates on which data were collected in Gonarezhou, Hwange and Mana Pools National Parks (Adapted from Dunham et al.2014)

Site	Strata	Sightings	# Transects	Spacing (km)	Bearing	Dates
Gonarezhou	Chefu	53	14	2.8	42	29 Oct
	Chilojo A	81	15	1.7	45	26 Oct
	Chilojo B	82	24	2	134 (-46)	28 Oct
	Chipinda Pools	121	26	2.2	0	26 Oct
	Mabalauta NP	29	15	2.9	90	30 Oct
	Naivasha	22	12	3.5	134 (-46)	26 Oct
Hwange	Central A	64	10	4.4	66	15 Oct
	Central B	7	9	4.6	-26 (154)	23 Oct
	Dandari	199	29	2.5	0	16 Oct
	Dzivanini	114	15	4	90	18 Oct
	Main Camp	129	14	3.5	41	13 Oct
	Mtoa	97	20	2.7	0	13 Oct
	Ngamo	199	17	3.4	-52 (128)	22 Oct
	Robins	129	11	3.3	90	10 Oct
	Shakwanki	79	15	4.5	90	17 Oct
	Shapi	342	26	2.2	0	16 Oct
	Sinamatella	121	18	3.2	0	12 Oct
Mana Pools	Mana I	64	32	1.5	0	25 Aug
	Mana II	151	22	1.8	90	31 Aug

All elephant presence data falling outside the boundaries of the study sites were excluded from the analyses. The total number of elephant sightings used for analyses was 208 for Gonarezhou, 602 for Hwange and 160 for Mana Pools. Although the density of sightings later used for modelling differed significantly ($\chi^2 = 17.168$, df = 2, p = 0.000) in the three sites, there was no need to adjust the sample sizes since the MaxEnt algorithm is not sensitive to sample size (Wisz et al., 2008).

NDVI was selected for modelling elephant distribution as a proxy for forage quantity following Garroutte et al. (2016b). NDVI was calculated from Landsat 8 satellite data accessed from the

Glovis platform (www.glovis.usgs.gov). The acquisition dates for the images were 15/09/14 for Gonarezhou, 13/10/14 for Hwange and 20/09/14 for Mana Pools. We selected these dates because they represented cloud-free data acquired on dates closest to the time when aerial survey data were collected at each site. We could not obtain cloud-free scenes that cover the entire Gonarezhou and Hwange national parks and for that reason, we limited our analyses to the parts of the study sites covered by available scenes. Pre-processing of the data involved the conversion of radiance to Top-of-atmosphere (TOA) reflectance following the method described by Chavez Jr (1989). The actual conversion of radiance to TOA reflectance was implemented in ENVI version 5.1 (*Exelis Visual Information Solutions, Boulder, Colorado).* Later, we calculated NDVI using the standard formula (NIR-R/NIR+R).

Water is a key driver of elephant distribution hence its inclusion as a predictor variable in our models. We used the same Landsat 8 data described above to map water based on the Modified Normalised Difference Water Index (MNDWI) described by Xu (2006). Water pixels had MNDWI values of greater than zero. We later calculated the distance of individual pixels from surface water using the Euclidean distance calculation algorithm implemented in ArcGIS 10.1 (ESRI, 2011).

MaxEnt was run separately for corrected and uncorrected elephant presence data. The numbers of uncorrected points used for modelling were: Gonarezhou = 208, Hwange = 602 and Mana Pools = 160. Since correction was undertaken for all points falling inside study areas, the same numbers of corrected points were used for modelling. MaxEnt is a general utility presence only SDM that has been known to perform better than most presence-only models (Elith et al., 2006). We ran the MaxEnt models in the Biomeod2 package of the R software (Thuiller et al., 2016). For each study site, 30 model runs were performed using corrected data while the other 30 used uncorrected data to yield a total of 60 model runs per site. For each run, 70% of the presence

data were used to calibrate the model while the remaining 30% was set aside for model evaluation as recommended in the literature (Araujo and New, 2007). For each model run, 10,000 points were randomly generated and used as pseudo-absences. We selected 10,000 pseudo-absences because the number does not exceed the recommended maximum in all the three study sites (Thuiller et al., 2016).

The Relative Operating Characteristic (ROC) (Mason, 1982) and True Skill Statistic (TSS) (Woodcock, 1976) available in the Biomode2 were used to evaluate the performance of MaxEnt-based models in predicting elephant presence when ran with corrected or uncorrected data. Each of 60 model runs generated the ROC and TSS metrics per site. Thus, the student's t-test was used to compare whether ROC and TSS values differed significantly for MaxEnt models ran using corrected and uncorrected elephant presence data. This test is parametric and requires that the test variable follows a normal distribution. The data were tested for normality prior to statistical analysis and were found not to significantly ($p > 0.05$) deviate from a normal distribution. Tests for normality of distribution followed the procedure described by Shapiro and Wilk (1965) and were implemented in the R software (R Core Team, 2017).

We used the logistic threshold of equal training sensitivity and specificity to obtain a binary classification of the predictions for each model while continuous probabilities of presence were presented as maps. We later compared the size of the area classified as the potential distribution of elephants for both the corrected and uncorrected data.

3.2.6 Comparison of NDVI, distance from water and Terrain Ruggedness Index

We compared NDVI, distance from water and the Terrain Ruggedness Index (TRI) to establish whether there were differences in the values of the predictor variables at the corrected and uncorrected elephant presence sites. The TRI was calculated using the method suggested by

Riley et al. (1999). The method uses a DEM to calculate the absolute difference between elevation in a central pixel and its neighbouring pixels. The value obtained is later averaged to obtain the mean difference in elevation. The index measures the roughness of the landscape. The roughness of the landscape potentially has an effect on the calculation of a corrected position using our suggested method.

NDVI, distance from water sources and TRI at elephant location sites from both the corrected and uncorrected data sets were extracted using standard overlay functions implemented in ArcGIS 10.1 (ESRI, 2011). For each study site, the values extracted at the corrected and uncorrected sites were compared using the Mann-Whitney U statistic since data were not normally distributed. The significance of the results was inferred at an alpha level of 0.05.

3.2.7 Test for spatial autocorrelation of NDVI

Next, we tested the maximum distance at which spatial autocorrelation existed in the NDVI data. The existence of spatial autocorrelation at long distances is associated with more homogeneous vegetation cover than at shorter distances. The variogram method was used to establish the distances at which NDVI data showed spatial autocorrelation. First, NDVI values at corrected and uncorrected sites were extracted using the method described above. Second, the semi-variance of NDVI for coordinate pairs was calculated using the method described in detail by Clark (1979). Next, the semi-variance was plotted against lag distances at an interval of 500 metres to produce variogram clouds. Then, exponential functions were fitted to the variogram clouds using the eye fit function implemented using the geoR package in R Software (Ribeiro Jr and Diggle, 2001). Finally, the Nugget, Range and Sill were extracted from the analyses.

3.3 Results

We observe that the suggested correction method was successful in estimating corrected location in Gonarezhou, Hwange and Mana Pools (Figure 3-3). The correction was also successful in areas with different transect bearings. We also observe that the correction factor (D) differed significantly in the three study areas ($F_{2, 91} = 21.524$, $p < 0.0001$) (Figure 3-4). The following are the estimated correction factors: Gonarezhou (175.4 m); Hwange (142.7 m); and Mana Pools (177.9 m). Pairwise comparisons using the Tukey's HSD test illustrate significant differences in the estimated correction factor between Gonarezhou and Hwange ($p < 0.0001$); a significant difference between Hwange and Mana Pools ($p < 0.0001$); and no significant difference between Gonarezhou and Mana Pools ($p > 0.05$).

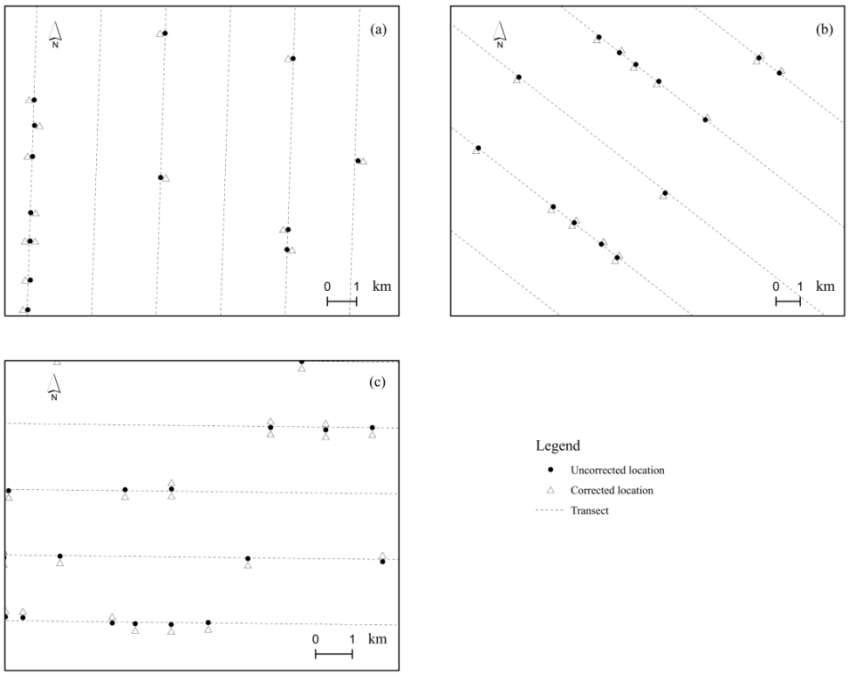

Figure 3-3: Location of selected uncorrected and corrected elephant presence points in (a) Gonarezhou; (b) Hwange; and (c) Mana Pools. Note that the transect bearing in (a) = 0°; (b) = 128°; and (c) = 90°

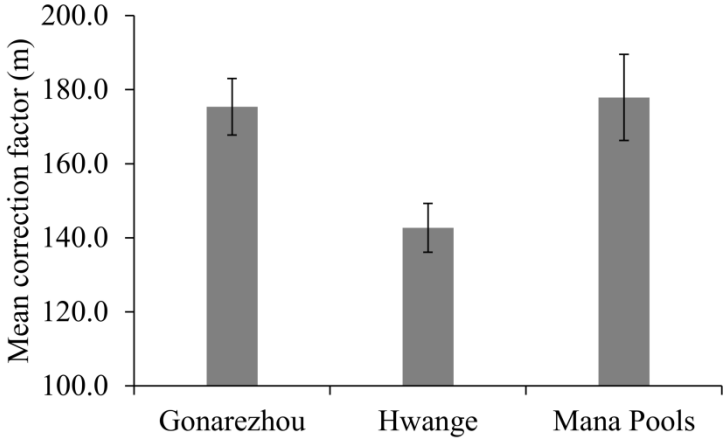

Figure 3-4: Comparison of estimated correction factors for Gonarezhou, Hwange and Mana Pools

We also observe that using ROC as the evaluation metric, the models from corrected data performed better than those from uncorrected data in Hwange (t = 8.817, df = 58, p = 0.000) while in Gonarezhou and Mana Pools their performance was not significantly different (Gonarezhou: t = 0.151, df = 58, $p > 0.05$; Mana Pools: t = 1.702, df = 58, $p > 0.05$) (Figure 3-5). When TSS was used as the evaluation metric, the models built using corrected data in Hwange and Mana Pools significantly differed from those built using uncorrected data (Hwange: t = 13.423, df = 58, p = 0.000; Mana Pools: t = 3.081, df = 58, p = 0.003) while in Gonarezhou we observed no significant difference (t = -1.137, df = 58, $p > 0.05$).

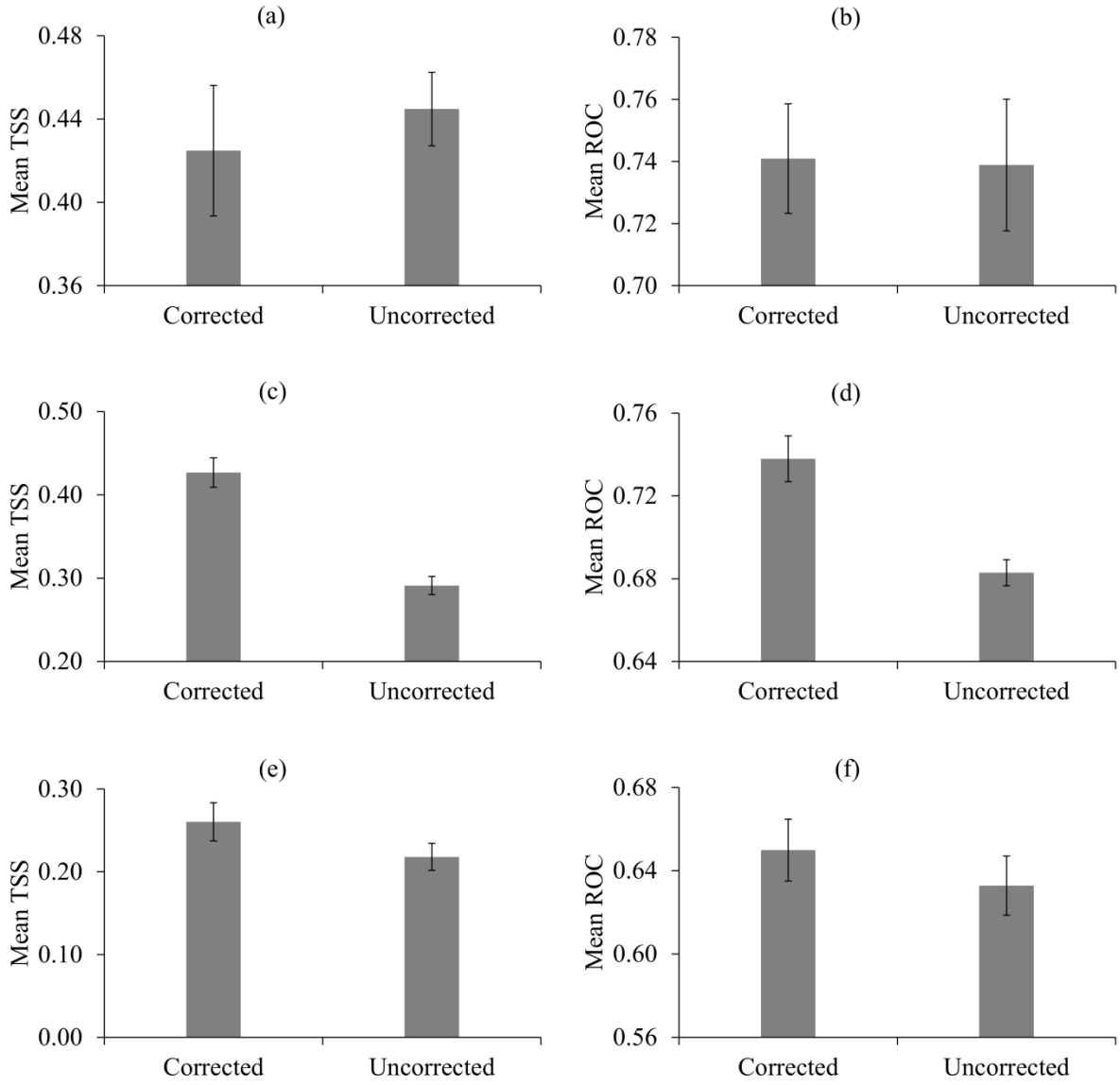

Figure 3-5: Comparison of models built using corrected and uncorrected data. Results illustrate; no significant difference in performance of both data sets in Gonarezhou based on (a) TSS and (b) ROC; significant difference in the models based on (c) TSS and (d) ROC in Hwange; and significant difference in the models based on (c) TSS and (d) ROC in Mana Pools

Results from our analysis illustrate that the predicted elephant habitat was consistently larger for corrected data than for uncorrected data. Predicted habitat in Gonarezhou using corrected data was 1690.78 km^2 while that for uncorrected data was 1630.10 km^2. In Hwange, the predicted habitat from the model using corrected data was 4385.31 km^2 while that predicted

using uncorrected data was 4333.65 km^2. The predicted habitat for elephants in Mana pools, from corrected data was 896.20 km^2 whereas that from uncorrected data was 853.22 km^2. Overall, we observe that uncorrected data underestimated the potential habitat of elephants by 60.68 km^2 in Gonarezhou, 51.66 km^2 in Hwange and 42.99 km^2 in Mana Pools.

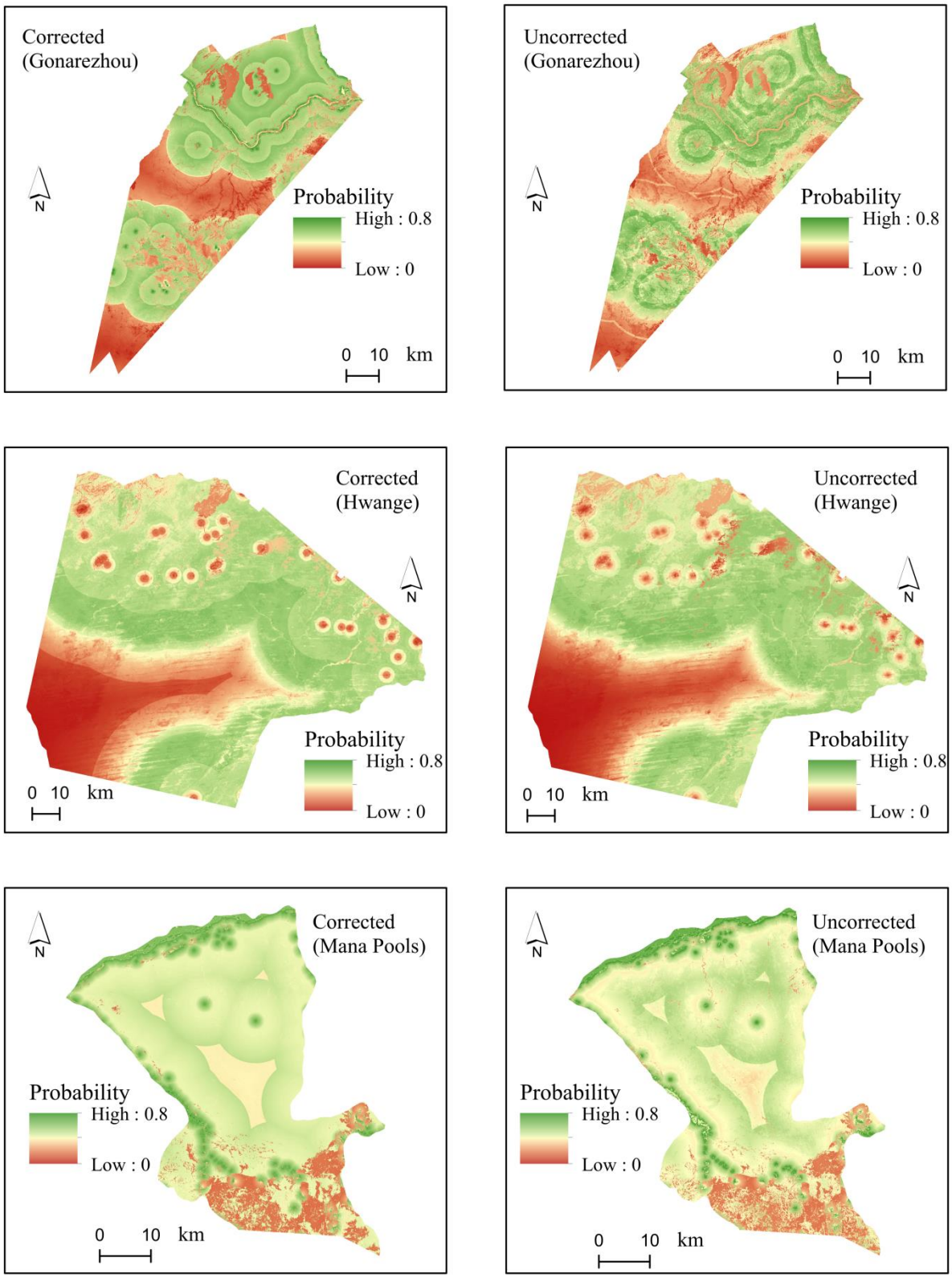

Figure 3-6: Probability of elephant presence predicted using corrected and uncorrected location data in Gonarezhou, Hwange and Mana Pools

Comparisons of extracted values of NDVI, distance to water and terrain ruggedness at elephant presence sites showed no significant difference ($p > 0.05$) between the corrected and uncorrected data (Table 3-2).

Table 3-2: Comparison of NDVI, distance to water and terrain ruggedness at corrected and uncorrected elephant presence sites

Study area	Variable	Mann-Whitney U	Wilcoxon W	Z	P-value
Gonarezhou	NDVI	21050	42786	-0.475	0.635
	Distance to water	21222	42958	-0.334	0.738
	Terrain ruggedness	20688	42424	-0.771	0.441
Hwange	NDVI	180323	361826	-0.146	0.884
	Distance to water	180557	362060	-0.107	0.915
	Terrain ruggedness	179764	361267	0.239	0.811
Mana Pools	NDVI	180323	361826	-0.146	0.884
	Distance to water	180557	362060	-0.107	0.915
	Terrain ruggedness	12790	25670	-0.012	0.990

Next, results illustrate that variogram clouds for NDVI data extracted at elephant presence sites corrected for locational error have spatial auto-correlation to distances of >=8 km in all the three study sites. Spatial autocorrelation was observed up to; 15 km in Gonarezhou (Nugget=0, Range = 15000 m, Sill=0.001); 10 km in Hwange (Nugget = 0, Range = 10000 m, Sill=0.01); and 8 km in Mana Pools (Nugget = 0, Range = 8000 m, Sill = 0.02).

3.4 Discussion

Results of this study indicate the utility of the correction in modelling wildlife habitat. In particular, results for Hwange and Mana Pools National Parks indicated that the corrected data improved the performance of the elephant distribution models. This is consistent with results reported in an earlier study that animal location data collected during aerial surveys consistently perform poorly in SDMs compared with GPS collar data (Ndaimani et al., 2016). The reported

improved performance of the corrected data in our study areas provides a basis for the need to use corrected data for modelling. Based on these results, it could be claimed that modelling elephant distribution using uncorrected data could possibly give results with lower levels of accuracy. Our suggested correction method shifts the supposed location closer to the actual location in the landscape. In other words, the shift in location introduced by the correction may be enhancing the probability that the sampled location closely resembles the actual location where the elephants were sighted thereby possibly improving model performance.

Although the corrected data generally improved habitat model performance, it did not improve model performance in the Gonarezhou National park. This could be explained by lower heterogeneity in the vegetation cover of Gonarezhou National Park. In fact, results from variogram models computed from NDVI data showed that the Gonarezhou landscape is more homogenous when compared to the other two landscapes. Thus, we speculate that failure by the corrected data to improve model performance in Gonarezhou could be linked to the homogeneity in GNP compared with the other study areas. These findings may suggest that the performance of corrected data in SDMs is better in more heterogeneous landscapes than homogeneous ones.

The calculated correction factor (D) estimated from calibration data was found to be different among the study areas. Particularly, the correction factors for Gonarezhou and Mana Pools were not significantly different ($p > 0.05$) whilst the correction factor for Hwange was significantly smaller. The same aircraft (Cessna 206) was used in Hwange and Mana Pools whereas a different one (Cessna 185) was used in the Gonarezhou National Park. We, therefore, claim that the model of the aircraft used has a limited effect on the magnitude of the correction factor. However, the pair of observers used in each of the three study areas were different. Thus, results

suggest that the observers potentially influence the correction factor since these were not the same in the three study areas.

Unlike previous studies that have used aerial survey data to model elephant habitat (Singh and Milner Gulland, 2011, Murwira and Skidmore, 2005), our study represents a novel attempt to use corrected aerial survey data to model elephant habitat. In fact, results indicate an improvement in the model quality based on these corrected data. This could further improve our understanding of wildlife distributions. However, we caution that while the correction is an important first step, it is not always precise as it shifts location to the centre of a search strip ~150 m wide. Therefore, related future work could involve further testing on whether and how the corrected data influences the performance of SDMs in more heterogeneous landscapes.

3.5 Conclusion

In this objective, we describe a simple method for correcting locational error inherent in animal presence data collected during aerial surveys. We found out that the magnitude of the correction factor (D) differs by study area. We also found out that the corrected data improved the performance of models predicting the potential distribution of elephants, especially in less homogenous landscapes. Our results are amongst the first attempts to improve the quality of animal presence data collected without the use of distance sampling during aerial surveys. Our findings are relevant to spatial ecologists and wildlife managers who use data collected from aerial surveys for research as well as for management. Although the suggested correction method significantly improved the performance of models that predict the potential distribution of elephants, we proceeded to use GPS collar data in the following objective. This is largely because GPS collar data possess both better locational accuracy and temporal coverage.

References

Araujo, M. B. & New, M. (2007) Ensemble forecasting of species distributions. Trends in Ecology & Evolution, 22, 42-47.

Buckland, S. T., Anderson, D. R., Burnham, K. P. & Laake, J. L. (2005) Distance sampling, Oxford University Press, Oxford

Chavez Jr, P. S. (1989) Radiometric calibration of Landsat Thematic Mapper multispectral images. Photogrammetric Engineering and Remote Sensing, 55, 1285-1294.

Child, G. (2004) Elephant culling in Zimbabwe. ZimConservation Opinion, 1, 1-6.

Clark, I. (1979). Practical Geostatistics, London, Applied Science Publishers.

Dormann, C. F., Elith, J., Bacher, S., Buchmann, C., Carl, G., Carré, G., Marquéz, J. R. G., Gruber, B., Lafourcade, B. & Leitão, P. J. (2013) Collinearity: a review of methods to deal with it and a simulation study evaluating their performance. Ecography, 36, 27-46.

Elith, J., Graham, C. H., Anderson, R. P., Dud, Xed, K, M., Ferrier, S., Guisan, A., Hijmans, R. J., Huettmann, F., Leathwick, J. R., Lehmann, A., Li, J., Lohmann, L. G., Loiselle, B. A., Manion, G., Moritz, C., Nakamura, M., Nakazawa, Y., Jacob Mc, C. O., Peterson, A. T., Phillips, S. J., Richardson, K., Scachetti-Pereira, R., Schapire, R. E., Sober, Xf, N, J., Williams, S., Wisz, M. S., Zimmermann, N. E. & Araujo, M. (2006) Novel methods improve prediction of species' distributions from occurrence data. Ecography, 29, 129-151.

ESRI (2011) ArcGIS Desktop: Release 10.1. Redlands, CA: Environmental Systems Research Institute.

Fedak, M., Lovell, P., Mcconnell, B. & Hunter, C. (2002) Overcoming the constraints of long range radio telemetry from animals: getting more useful data from smaller packages. Integrative and Comparative Biology, 42, 3-10.

Frair, J. L., Fieberg, J., Hebblewhite, M., Cagnacci, F., Decesare, N. J. & Pedrotti, L. (2010) Resolving issues of imprecise and habitat-biased locations in ecological analyses using

GPS telemetry data. Philosophical Transactions of the Royal Society of London B: Biological Sciences, 365, 2187-2200.

Garroutte, E. L., Hansen, A. J. & Lawrence, R. L. (2016) Using NDVI and EVI to map spatiotemporal variation in the biomass and quality of forage for migratory elk in the greater Yellowstone ecosystem. Remote Sensing, 8, 1-25.

Heezen, K. L. & Tester, J. R. (1967) Evaluation of radio-tracking by triangulation with special reference to deer movements. The Journal of Wildlife Management, 31, 124-141.

Mason, I. (1982) A model for assessment of weather forecasts. Australian Meteorological Magazine, 30, 291-303.

Moisen, G. G., Freeman, E. A., Blackard, J. A., Frescino, T. S., Zimmermann, N. E. & Edwards, T. C. (2006) Predicting tree species presence and basal area in Utah: a comparison of stochastic gradient boosting, generalized additive models, and tree-based methods. Ecological Modelling, 199, 176-187.

Murwira, A. & Skidmore, A. K. (2005) The response of elephants to the spatial heterogeneity of vegetation in a Southern African agricultural landscape. Landscape Ecology, 20, 217-234.

Ndaimani, H., Murwira, A., Masocha, M., Gara, T. W. & Zengeya, F. M. (2016) Evaluating performance of aerial survey data in elephant habitat modelling. African Journal of Ecology, 55, 270-281.

Norton-Griffiths, M. (1978) Counting animals, African Wildlife Leadership Foundation, Nairobi, Kenya.

Phillips, S. J., Dudík, M. & Schapire, R. E. (2004) A maximum entropy approach to species distribution modeling. In: Proceedings of the twenty-first international conference on Machine learning, 2004. ACM Press, New York, 655-662.

R Core Team (2017) R: A language and environment for statistical computing. Vienna, Austria: Foundation for Statistical Computing. URL https://www.R-project.org/.

Ribeiro Jr, P. J. & Diggle, P. J. (2001) geoR: a package for geostatistical analysis. R News, 1, 14-18.

Riley, S. J. (1999) Index that quantifies topographic heterogeneity. Intermountain Journal of Sciences, 5, 23-27.

Shapiro, S. S. & Wilk, M. B. (1965) An analysis of variance test for normality (Complete Samples). Biometrika, 52, 591-611.

Singh, N. J. & Milner Gulland, E. J. (2011) Conserving a moving target: planning protection for a migratory species as its distribution changes. Journal of Applied Ecology, 48, 35-46.

Thuiller, W., Georges, D., Engler, R., Breiner, F., Georges, M. D. & Thuiller, C. W. (2016) Package 'biomod2': Ensemble platform for species distribution modeling. R package version 2.1. 7/r560.

Wisz, M. S., Hijmans, R., Li, J., Peterson, A. T., Graham, C. & Guisan, A. (2008) Effects of sample size on the performance of species distribution models. Diversity and Distributions, 14, 763-773.

Woodcock, F. (1976) The evaluation of yes/no forecasts for scientific and administrative purposes. Monthly Weather Review, 104, 1209-1214.

Xu, H. (2006) Modification of normalised difference water index (NDWI) to enhance open water features in remotely sensed imagery. International Journal of Remote Sensing, 27, 3025-3033.

Chapter 4

Elephant (*Loxodonta africana*) GPS collar data show multiple peaks of occurrence farther from water sources

This chapter is based on:

Ndaimani, H., Murwira, A., Masocha, M. and Zengeya, F.M., 2017. Elephant (*Loxodonta africana*) GPS collar data show multiple peaks of occurrence farther from water sources. Cogent Environmental Science, 3(1), p.1-11.

4. Elephant (*Loxodonta africana*) GPS collar data show multiple peaks of occurrence farther from water sources

Abstract

The understanding of animal distribution in habitats located farther from water sources has not been dealt with adequately in literature, yet this knowledge enables better prediction of species occurrence across an entire landscape. We tested whether elephant occurrence peaks away from water in addition to the known peak that is associated with water sources. We used the Maximum Entropy Modelling (MaxEnt) algorithm to predict the potential distribution of elephants in the Gonarezhou National Park, Zimbabwe. Elephant tracking data from Global Positioning System (GPS) collars were used as the response variable while NDVI (a proxy for forage quantity) and water sources data were the environmental variables. Results showed multiple peaks of elephant occurrence with increasing distance from water sources. Additionally, results illustrated that the peaks occur in high NDVI areas. Our findings emphasise the utility of GIS and remote sensing in enhancing our understanding of animal occurrence driven by water sources.

4.1 Introduction

Drinking water and forage are generally understood to be key drivers of animal distributions in tropical landscapes. This is particularly true in savannah ecosystems where vegetation cover is heterogeneous (Roever et al., 2013) and drinking water largely limiting (Chamaille Jammes et al., 2007). Animals forage in order to meet their energy and protein requirements and drink water primarily for thermoregulatory purposes. Consequently, it is generally agreed that the movement of animals across landscapes is not random but rather follows the Optimal Foraging Theory which states that animals seek to get the most energy gain at the lowest cost as a strategy to maximise fitness (MacArthur and Pianka, 1966). Thus the accurate prediction of the potential distribution of animals in most landscapes depends on the inclusion of water and forage as predictor variables.

Several studies reported that animals forage near water sources in order to minimise the distances they travel to access water (Follett and Delgado, 2002, Epaphras et al., 2008). This behaviour has largely been reported among water-dependent species that need to drink daily (Wilson, 1966) and is common during the hot and dry months when heat stress is enhanced by high temperatures (Coleman et al., 2004, Wakefield and Attum, 2006). For instance, African elephants (*Loxodonta africana*) have been observed to drink water daily (De Beer et al., 2006) and also forage close to water throughout the year (Gaylard et al., 2003). When the probability of animal occurrence is relatively high in habitats close to water, we would expect density peaks to occur around water sources where distribution is linked to the availability of water (Redfern et al., 2003, Shannon et al., 2009). However, there is often a trade-off between access to water and forage as animals may have to weigh the benefits of foraging near water where the pressure on forage is high or travelling farther from the water where competition on forage resources is reduced (Redfern et al., 2003). Despite widespread knowledge of animal occurrence near water, knowledge on how they are distributed in those habitats farther from water remains largely

rudimentary. While the distribution of animals in habitats near water sources could be viewed as a strategy to maximise the intake of water, the habitat factors that drive the occurrence of animals in landscapes farther from water remain unclear. It is therefore important to also investigate the response of animals in habitats that are located farther from water sources in order to get a more complete view of animal distributions in the landscape.

In the past, studies that sought to understand the occurrence of animals in habitats near water sources relied to a great extent on point-based field measurements (e.g., Lange, 1969, e.g., Butler Jr et al., 1995). This approach virtually resulted in better understanding of more localised patterns that are limited to the sampled areas while ignoring those at the landscape scale. Consequently, understanding of animal occurrence dynamics near water sources has been well developed (Mukwashi et al., 2012b). Earlier studies widely reported the 'piosphere effect' which predicts that the pressure of herbivory on vegetation is higher near water than farther from water (Landman et al., 2012, James et al., 1999). As a result, animal-driven vegetation change near water points is well researched whilst the possible change farther from water has generally remained unclear. It is important to note that these earlier studies on the 'piosphere effect' mostly depended on point measurements possibly because large-scale spatial data that allows for a landscape view were not readily available. In more recent years, the developments in Geographical Information Systems (GIS), remote sensing and Global Positioning Systems (GPS) have allowed the testing of hypotheses related with the potential distribution of animals at large spatial scales (Phillips et al., 2006). For instance, it is now possible to obtain freely available remotely sensed data at the global scale and at relatively fine spatial resolutions which was impossible in the past (Hijmans et al., 2005). In addition, the developments in GPS collar tracking in recent years has made it possible to obtain fine grain movement data for target animal species. Thus GIS and remote sensing can now be applied to enhance our understanding of animal occurrence near waterholes as well as farther from the water.

In this study, we used elephant tracking data from GPS collars together with NDVI (a proxy for forage quantity) and water sources data to test whether elephant occurrence peaks away from water in addition to the known peak that is associated with water sources. We also tested whether the peaks of elephant occurrence away from water are associated with high forage quantity (estimated using NDVI). We specifically hypothesised that elephant occurrence peaks near water in a hypothetical landscape with homogeneous vegetation (Figure 4-1a). This hypothetical pattern is mainly because the availability of forage will be uniform across the landscape and therefore water will be expected to have more impact on the distribution of elephants than the other predictor variables. However, in a more realistic landscape with heterogeneous vegetation cover such as the tropical savannahs, the response would be intricate and typified by multiple peaks of occurrence at increasing distance from water (Figure 4-1b). The other peaks farther from water would be driven by other factors like forage abundance. Our study provides important insights into the precise response of elephants to the distribution of water within landscapes characterised by heterogeneous vegetation cover

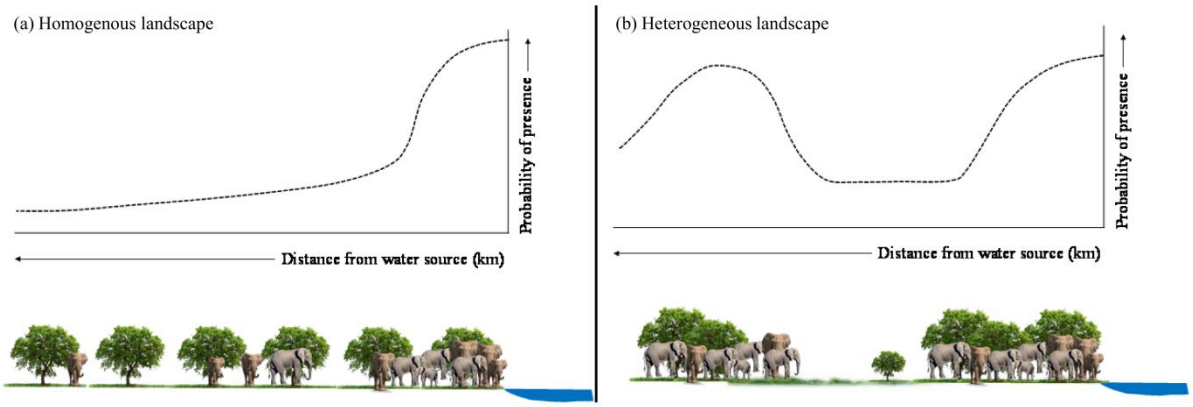

Figure 4-1: Hypothetical framework: the predicted response of elephants to water in (a) an imaginary homogeneous landscape characterised by uniform forage quantity and (b) a more realistic heterogeneous landscape characterised by non-uniform forage quantity

4.2 Materials and methods

4.2.1 Ethics statement

Handling of African elephants for GPS collaring was monitored by the Zimbabwe Parks and Wildlife Management Authority as well as licensed drug handlers approved by the Division of Veterinary Services in Zimbabwe. The two departments provide and enforce the wildlife collaring guidelines for research in the country.

4.2.2 Study area

This study was carried out in northern Gonarezhou National Park, located between longitudes 31.75° - 32.41°E and latitudes 21.10° - 21.76° S in south-east Zimbabwe (Figure 4-2). The study area has a typical seasonal savannah climate with long-term annual rainfall averaging 600 mm. Data collected from a weather station in the study area shows that annual rainfall was 403 mm in 2009, 552 mm in 2010 and 580 mm in 2011. Rainfall is received from November to April while the rest of the year is dry (Gandiwa et al., 2011). Vegetation is dry deciduous savannah dominated by *Colophospermum mopane* and *Combretum apiculatum*.

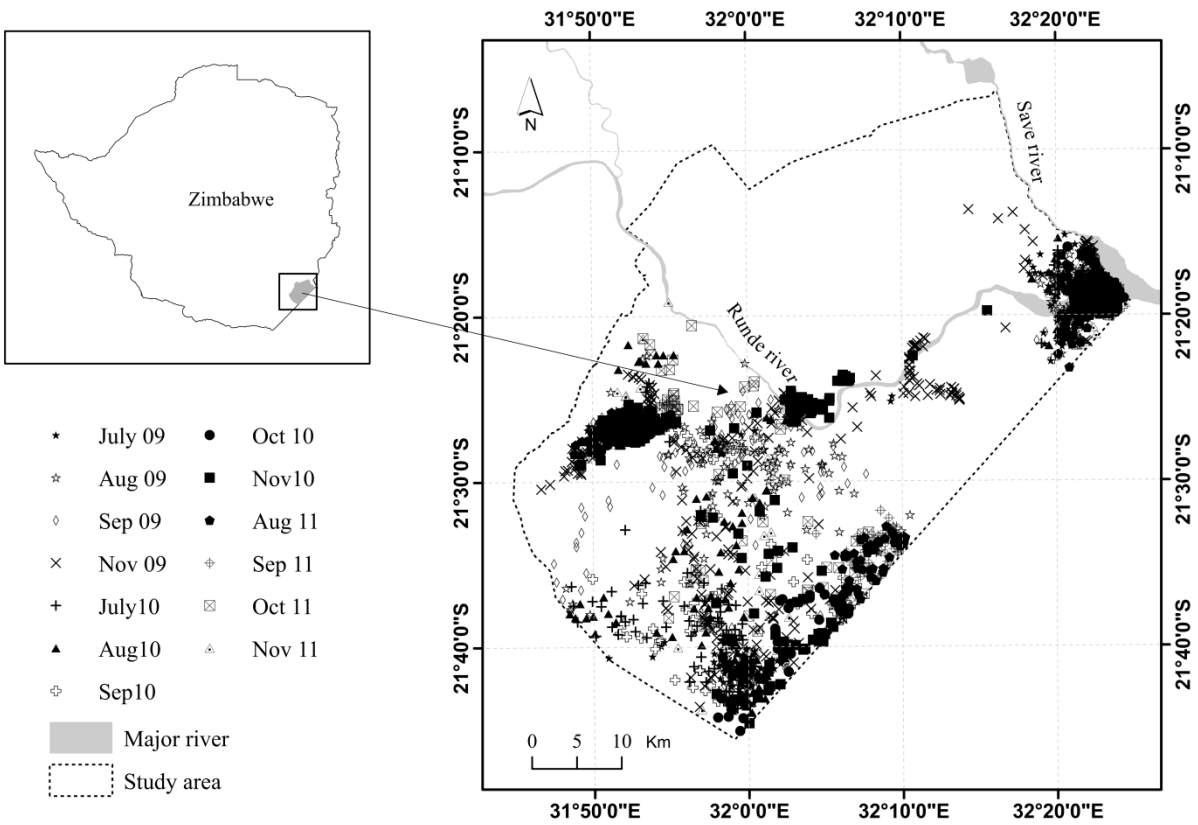

Figure 4-2: Elephant location data (from Global Positioning System (GPS) collars) collected from the eight elephants during 13 selected months between July 2009 and November 2011 in northern Gonarezhou National Park, south-east Zimbabwe

The study area lies within a protected area that has an estimated elephant population of about 10,000 (Dunham et al., 2013). We identified this area as ideal for answering our hypotheses because 1) data on the location of collared elephants is available for 3 years (2009, 2010 and 2011), allowing for analysis within three years of different rainfall amounts, and 2) perennial water is restricted to the major rivers especially during the dry season thus making water an important driver of animal distribution. No artificial water sources exist in the study area, thus rivers and natural pans are the only sources of drinking water for animals.

4.2.3 Elephant location data

Data on the location of elephants were collected during 13 selected months and the number of occurrence points used in the analyses is shown in Table 4-1. We selected the months used in the analyses based on the availability of data and those months with few occurrence points were left out.

Table 4-1: Elephant occurrence points used in the prediction of elephant habitat and the dates on which the terra/MODIS NDVI image was acquired.

Month	Elephant occurrence points	Date of Image acquisition
July 2009	175	28/07/09
August 2009	187	29/08/09
September 2009	170	30/09/09
November 2009	216	17/11/09
July 2010	136	28/07/10
August 2010	147	29/08/10
September 2010	128	30/09/10
October 2010	98	16/10/10
November 2010	138	17/11/10
August 2011	112	29/08/11
September 2011	103	30/09/11
October 2011	102	16/10/11
November 2011	85	17/11/11

Eight elephants were fitted with GPS collars in the study area in July 2009. The collars were programmed to take a minimum of three position fixes per day for a period of not less than 2 years depending on the battery life of the unit. The average fix success rate for the GPS collars during the 13 months selected for analyses was 81 %. For our analyses, we used only the data collected during the 13 months presented in Table 4-1. We were particularly interested in analysing elephant distribution during the dry months when surface water is limiting in the

study area. For this reason, the wetter months from December to June were not included in our analyses. Since our study area did not cover the entire range of the collared elephants, we masked out all position fixes that were located outside the study area boundary using the clip function implemented in a GIS.

4.2.4 Normalised difference vegetation index

NDVI data used to predict elephant habitat were extracted from the 16 days terra/MODIS data (MOD13Q1) freely available at the 250 m spatial resolution. These data are provided already corrected for water, clouds, heavy aerosols and cloud shadows (Olofsson et al., 2007). We downloaded the data from the www.glovis.usgs.gov website where they are available for download free of charge. The dates on which these data were acquired are presented in Table 4-1. Since two composites of the 16 days data are available during each month, we selected the data acquired during the latter half of the month for consistency. Geometric corrections included conversion from the sinusoidal (SIN) to the Universal Transverse Mercator (UTM, WGS 84 Zone 36S) projection to ensure compatibility with the elephant location data. Two tiles (h20v11 and h21v11) were required to cover the entire study area. We later mosaicked and clipped the images to the size of the study area. In this study, we used NDVI as a proxy for forage quantity following Garroutte et al. (2016a). Forage quantity is an important habitat variable for elephants during the drier months of the year because it is largely limiting at that time especially in savannah landscapes.

4.2.5 Distance from water sources

In order to determine the water sources available in the study area during the months included in the analyses, we used 16 days MODIS NDVI data described above. The data are provided at the 250m spatial resolution. It was least likely that some water sources were missed during mapping since no artificial water is supplied in the study area and the sources that have water

during the dry season are big enough to be picked even at the spatial resolution of 250m. NDVI values range from -1 to +1, where negative values are generally associated with water bodies and positive values with vegetation. Thus it is possible to use a threshold approach to extract water surfaces from NDVI data. We extracted water surfaces from the monthly generated NDVI following the method described by Huang et al (2012), where a pixel is considered water when NDVI is less than zero. Although other indices for extracting water sources have been proposed such as the Modified Normalised Difference Water Index (Xu, 2006) we could not use the index since it uses the green and mid-infrared bands which are not available on the MOD13Q1 product. While Landsat images have these bands, non-availability of cloud-free images limited our analysis to MODIS images whose availability is enhanced by their high temporal resolution. We did not evaluate the accuracy of the resultant classification since we did not have an independent field-based data set for validation. However, the method used in our study has been used elsewhere (e.g Kameyama et al., 2004) and has yielded reasonably accurate results in those landscapes thus justifying its use.

After extracting the water surfaces for each of the study months, we then calculated the distance of individual pixels from the nearest water sources using the Euclidian distance calculation algorithm implemented in a GIS.

4.2.6 Modelling probability of elephant occurrence

We modelled the potential distribution of elephants in the study area using the Maximum Entropy Modelling (MaxEnt) algorithm. MaxEnt is a general purpose machine learning method that has widely been used in species distribution modelling and has been observed to perform better than other methods (Elith and Graham, 2009). We used elephant occurrence data from the eight GPS collars described above as the response variable while NDVI and distance from the water were used as the predictor variables. The two predictor variables were used in the

models since they are widely accepted as key drivers of elephant distribution in most landscapes. Overall, we built 13 models, a model for each of the selected 13 months. The option for removing duplicate presence records was selected to ensure that MaxEnt does not sample the same pixel several times.

The Area Under Curve (AUC) of the Receiver Operating Curve (ROC) was used to validate the ability of individual models to predict elephant occurrence. A model was observed as adequate, very good and excellent when the AUC was 0.70 – 0.80, 0.80 – 0.90 and AUC = 0.90 -1.00 respectively (Panczykowski et al., 2012).

Graphs showing the response of elephants to distance from water sources were used to determine peaks of elephant occurrence farther from water sources. The peaks were defined as the points where the predicted probability of occurrence was above the logistic threshold of equal training sensitivity and specificity. The distance from water at which elephant occurrence peaked was extracted from the response curves. The same procedure was followed for detecting peaks of elephant occurrence in relation to NDVI. Next, we extracted NDVI and elephant probability of occurrence values at the elephant position fixes used for modelling. The extracted NDVI values were then plotted against extracted probabilities of elephant occurrence and polynomials fitted to the data. To establish whether the peaks of elephant occurrence coincided with high NDVI, we plotted elephant response to water on the same axis with the polynomials relating NDVI to distance from water.

4.3 Results

Results show that the two predictors, distance from water sources and NDVI explained most of the variation in the probability of occurrence of elephants across the landscape (Table 4-2). However, it can be observed that distance from water consistently predicts elephant distribution

better than NDVI over the three year period. We observe that the AUC of the ROC curves from the models can be rated adequate (August 2009, September 2009, November 2009, August 2010, September 2010 and October 2010), very good (July 2009, July 2010, November 2010, August 2011, October 2011 and November 2011) and excellent (September 2011).

Table 4-2: Performance and variable contribution of the MaxEnt models predicting the geographical distribution of elephants in the GNP during the dry season months of 2009, 2010 and 2011

Month	Test data AUC ± SD‡	Model quality†	The contribution of the variable (%)	
			Distance from the water source	NDVI‡
July 2009	0.832 ± 0.022	Very good	72.8	27.2
August 2009	0.796 ± 0.029	Adequate	69.2	30.8
September 2009	0.740 ± 0.030	Adequate	57.3	42.7
November 2009	0.775 ± 0.022	Adequate	54.3	45.7
July 2010	0.854 ± 0.020	Very good	65.9	34.1
August 2010	0.722 ± 0.029	Adequate	55.4	44.6
September 2010	0.719 ± 0.033	Adequate	75.3	24.7
October 2010	0.780 ± 0.038	Adequate	68.5	31.5
November 2010	0.838 ± 0.022	Very good	64.7	35.3
August 2011	0.855 ± 0.022	Very good	65.2	34.8
September 2011	0.912 ± 0.015	Excellent	53.0	47.0
October 2011	0.806 ± 0.030	Very good	72.8	27.2
November 2011	0.864 ± 0.024	Very good	78.8	21.2

† Model quality thresholds based on the AUC: Adequate = 0.70 – 0.80, Very good = 0.80 – 0.90, Excellent = 0.90 -1.00 (Panczykowski et al., 2012).

‡ Abbreviations used: AUC, SD, and NDVI refer to Area Under Curve, Standard Deviation and Normalised Difference Vegetation Index.

Response curves illustrate that elephant occurrence consistently peaked twice with distance from water sources (Figure 4-3). However, this pattern is not observed in October 2010 and September 2011 where elephant occurrence peaks three times and once respectively. Overall,

the first peak is located near water (not more than 9 km away) while the other is farther from water (more than 50 km away)(Table 4-3).

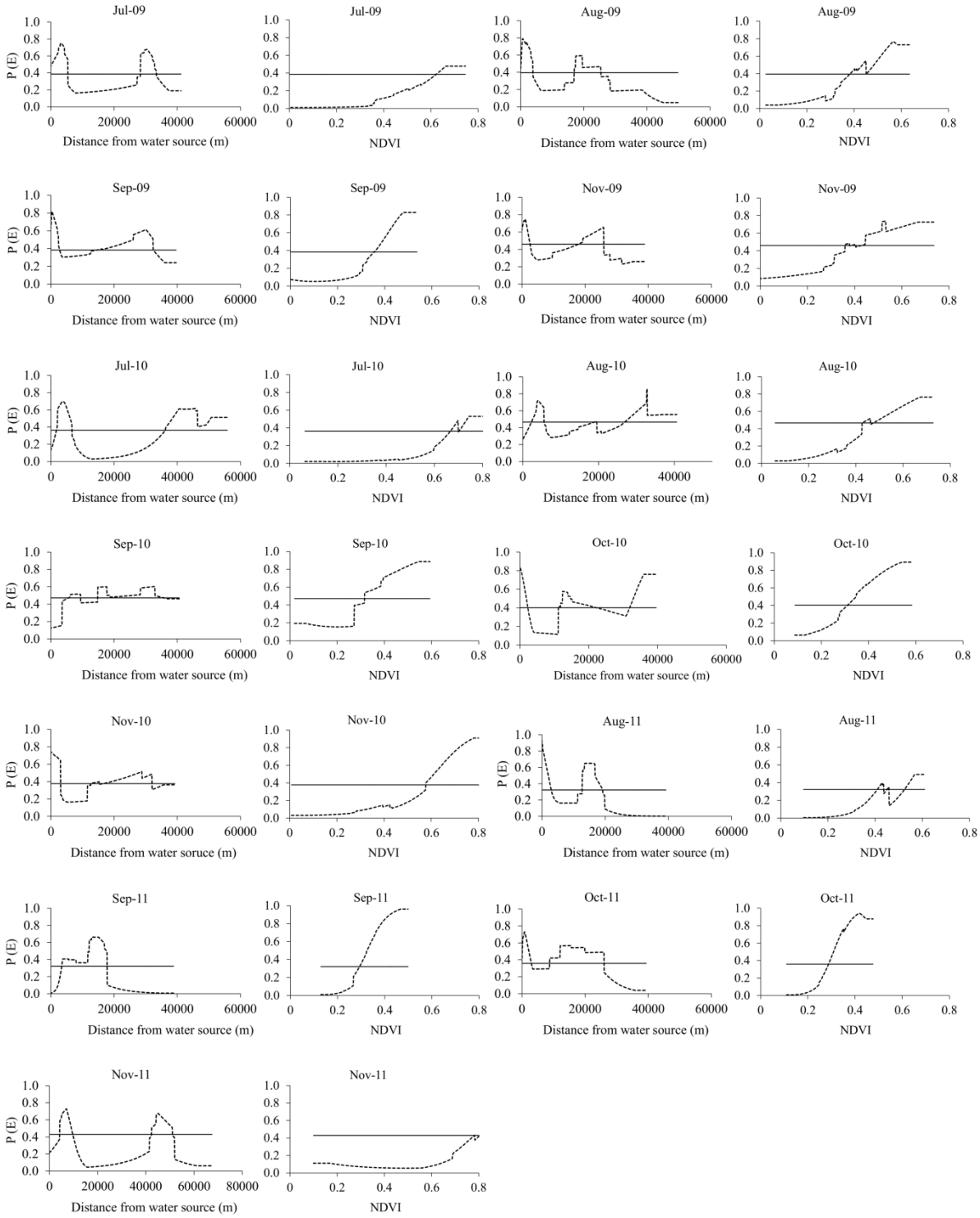

Figure 4-3: Probability of elephant occurrence (P (E)) plotted against distance from water sources and NDVI from July 2009 to November 2011. Elephant occurrence generally peaked at least twice with distance from water sources. The continuous horizontal line represents the

logistic threshold value of equal training sensitivity and specificity (values above the line represent elephant habitat while those below represent non-habitat).

Table 4-3: Peaks of elephant occurrence away from water sources and minimum NDVI within elephant habitat (habitat = probability values > the logistic threshold of equal training sensitivity and specificity)

Month	The distance at which elephant probability of occurrence peaked away from water sources (km)	Number of peaks	Minimum NDVI within elephant habitat	Logistic threshold
July 2009	0-4.5 & 7.1-32.4	2	0.614	0.386
August 2009	0-2.9 & 15.9-24.6	2	0.369	0.395
September 2009	0-2.0 & 14.1-31.5	2	0.343	0.383
November 2009	0-2.5 & 17.0-26.0	2	0.348	0.460
July 2010	0.5-5.8 & 35.2-	2	0.654	0.362
August 2010	1.4-5.0 & 26.2-	2	0.415	0.466
September 2010	4.9-8.4 & 13.6-34.8	2	0.304	0.473
October 2010*	0-1.6 & 10.4-21.6 & 31.1-	3	0.298	0.402
November 2010	0-2.0 & 11.9-30.9	2	0.564	0.377
August 2011	0-2.2 & 11.8-18.3	2	0.393	0.322
September 2011*	2.5-16.8	1	0.280	0.322
October 2011	0-2 & 7.5-24.8	2	0.275	0.358
November 2011	2.6-8.4 & 41.1-49.9	2	0.800	0.428

It can also be observed that the high probability of elephant occurrence coincides with high NDVI values (Figure 4-3). In addition to this observation, response curves illustrating elephant occurrence plotted against distance from water peaked consistently with those showing NDVI plotted against distance from water (Figure 4-4). NDVI values in areas predicted as suitable for elephants range from a minimum of 0.28 in October 2011 to 0.80 in November 2011 (Table 4-3). These NDVI values are observed to be generally higher in July and November than the rest of the months under study.

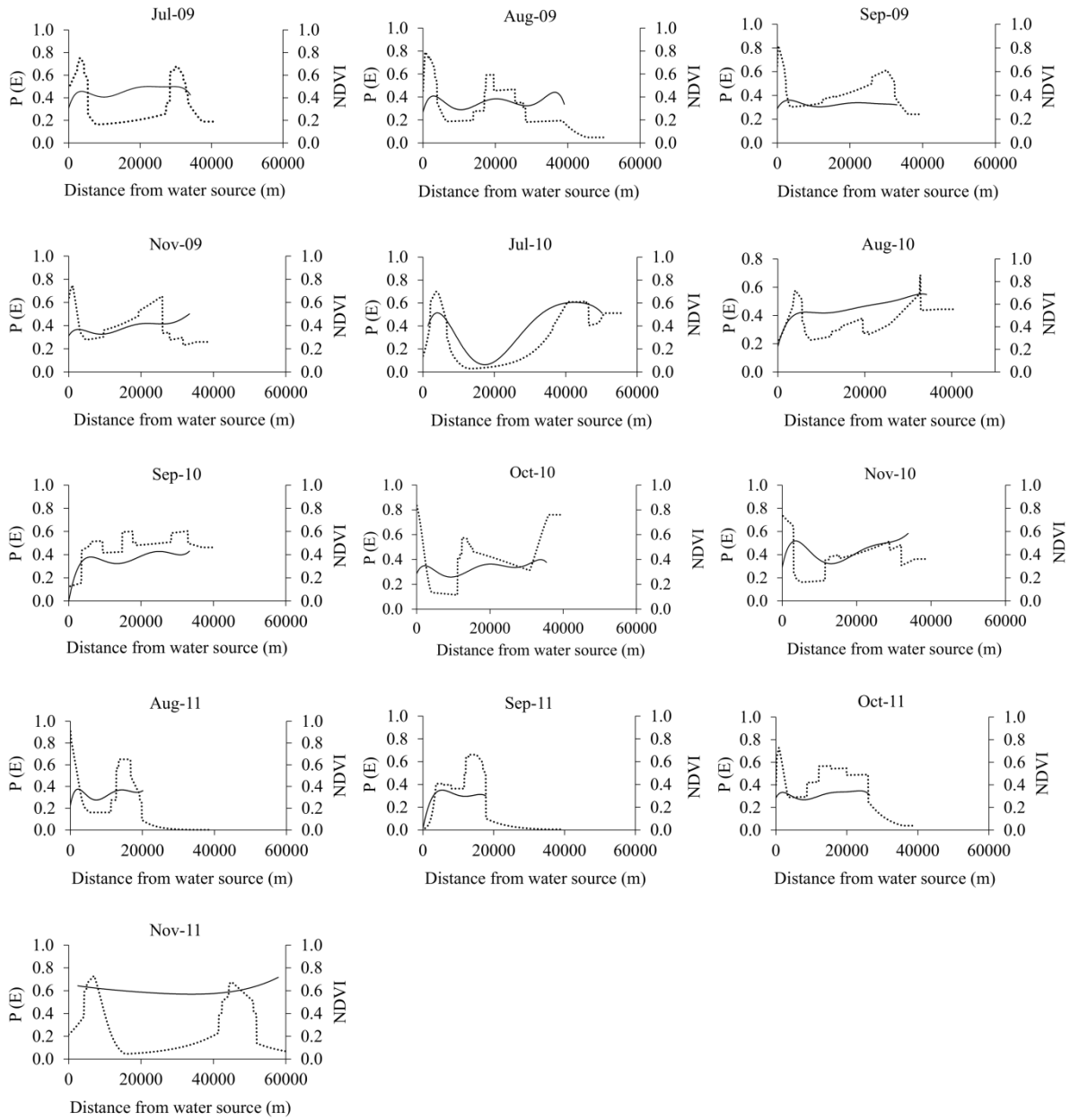

Figure 4-4: Probability of elephant occurrence (P (E)) – dotted line, and NDVI – continuous line plotted against distance from water sources, from July 2009 to November 2011.

4.4 Discussion

Results in this study seem to suggest that elephant occurrence peaks farther from water in addition to the expected peak near water sources. This, therefore, confirms our main hypothesis that in a heterogeneous landscape characterised by patchy vegetation cover, elephant occurrence peaks more than once with distance from water sources in response to forage

resource clustering. This is because evidence from our analyses suggests that the patches selected by elephants farther from water are characterised by high NDVI values, i.e., high forage (Figure 4-4). In fact, elephant occurrence peaked in patches with minimum NDVI values of about 0.44 and these areas are generally classified as forests (Nemani and Running, 1997). This is not surprising as elephants are non-selective bulk feeders that often select highly productive patches (i.e., high NDVI) either for foraging (Ruggiero, 1992) or for thermoregulation under tree canopies (i.e., high NDVI) (Kinahan et al., 2007). Our results seem to contradict earlier studies that reported that elephants select landscapes of intermediate vegetation cover (Roever et al., 2013, Gara et al., 2016). Based on our findings, we thus deduce that elephant occurrence peaks in areas with high forage quantity farther from water and this could be for foraging purposes.

Our results also suggest that while both water and forage are key predictors of elephant occurrence, the availability of water explains the distribution of elephants better than vegetation cover (estimated by NDVI) (Table 4-2). This finding is supported by earlier studies where elephants have been reported to drink water daily (Viljoen, 1989, De Beer et al., 2006) and stay within 20 km of water (Loarie et al., 2009). This is particularly common during the hotter months of the year when demand for water is high. In this regard, data used in our analyses were also collected during hotter months of the year making the reported importance of water not surprising. Our findings therefore unsurprisingly reinforce the notion that elephants are water dependent since the first peak in elephant occurrence was generally observed at less than 9 km away from water although during selected months they ventured further than 50 km away (Table 4-3).

The finding that elephant occurrence peaks farther from water in addition to the peak close to water is of particular interest to landscape ecologists since elephant-induced vegetation change

has historically been well explained in landscapes close to water than those farther away. Owing to a local overabundance of elephants near water, most studies have reported elephant-induced vegetation change linked to water sources (De Beer et al., 2006, Chamaille James et al., 2007). However, following our findings, attention could now be directed to the hotspots of elephant occurrence farther from water to test whether these landscapes could also be experiencing elephant-induced vegetation change in a similar way to those landscapes closer to water. Our findings, therefore, form the basis for formulating hypotheses that test for elephant-induced vegetation change in landscapes located farther from water.

Results from our study represent observations largely made during the dry season. Application of the findings to the wet season should, therefore, be done with caution. Even though our observations pertain to the dry season, we, however, emphasise that an understanding of elephant distribution during that time of the year is critical since their ranging behaviour is highly influenced by the availability of surface water (de Beer and van Aarde, 2008). In addition, while our study has been successful in reporting multiple peaks of elephant occurrence farther from water using dry season data, future studies could extend this analysis to the wet season to establish whether similar findings can be made when surface water is abundant. Other work could involve tracking elephants in the field to establish whether they select high NDVI patches for forage, thermoregulation or any other purpose. Despite our effort to remove spatial dependence in elephant occurrence data using the 'remove duplicate presence points' option in MaxEnt, future work could use more robust methods (e.g., spatial filtering) to deal with spatial bias.

4.5 Conclusion

In this chapter, we reported multiple peaks of elephant occurrence farther from water. We also reported that these areas of peak occurrence are associated with high NDVI. Our findings are

amongst the first to provide empirical evidence for the existence of multiple peaks of elephant occurrence farther from water during the dry season. Results from our study provide the basis for formulating hypotheses that test for elephant-induced vegetation change in peak elephant occurrence patches located farther from water sources.

References

Butler Jr, W. I., Stehn, R. A. & Balogh, G. R. (1995) GIS for mapping waterfowl density and distribution from aerial surveys. Wildlife Society Bulletin, 23, 140-147.

Chamaille Jammes, S., Valeix, M. & Fritz, H. (2007) Managing heterogeneity in elephant distribution: interactions between elephant population density and surface water availability. Journal of Applied Ecology, 44, 625-633.

Coleman, S. W., Moore, J. E. & Wilson, J. R. (2004) Quality and utilization. Warm-season (C4) grasses, Agronomy Monograph, 45, 267-308.

De Beer, Y., Kilian, W., Versfeld, W. & Van Aarde, R. J. (2006) Elephants and low rainfall alter woody vegetation in Etosha National Park, Namibia. Journal of Arid Environments, 64, 412-421.

De Beer, Y. & Van Aarde, R. J. (2008) Do landscape heterogeneity and water distribution explain aspects of elephant home range in southern Africa's arid savannas? Journal of Arid Environments, 72, 2017-2025.

Dunham, K., Van Der Westhuizen, E., Van Der Westhuizen, H. & Ndaimani, H. (2013) Aerial survey of elephants and other large herbivores in Gonarezhou National Park (Zimbabwe), and surrounding areas: 2013. Zimbabwe Parks and Wildlife Management Authority.

Elith, J. & Graham, C. H. (2009) Do they? How do they? WHY do they differ? On finding reasons for differing performances of species distribution models. Ecography, 32, 66-77.

Epaphras, A., Gereta, E., Lejora, I., Meing'ataki, G. O., Ng'umbi, G., Kiwango, Y., Mwangomo, E., Semanini, F., Vitalis, L. & Balozi, J. (2008) Wildlife water utilization and importance of artificial waterholes during dry season at Ruaha National Park, Tanzania. Wetlands Ecology and Management, 16, 183-188.

Follett, R. & Delgado, J. (2002) Nitrogen fate and transport in agricultural systems. Journal of Soil and Water Conservation, 57, 402-408.

Gandiwa, P., Matsvayi, M., Ngwenya, M. M. & Gandiwa, E. (2011) Assessment of livestock and human settlement encroachment into northern Gonarezhou National Park, Zimbabwe. Journal of Sustainable Development in Africa, 13, 19-33.

Gara, T. W., Wang, T., Skidmore, A. K., Zengeya, F. M., Ngene, S. M., Murwira, A. & Ndaimani, H. (2016) Understanding the effect of landscape fragmentation and vegetation productivity on elephant habitat utilization in the Amboseli ecosystem, Kenya. African Journal of Ecology, 55, 259-269.

Garroutte, E. L., Hansen, A. J. & Lawrence, R. L. (2016) Using NDVI and EVI to Map Spatiotemporal Variation in the Biomass and Quality of Forage for Migratory Elk in the Greater Yellowstone Ecosystem. Remote Sensing, 8, 404.

Gaylard, A., Owen-Smith, N. & Redfern, J. (2003) Surface water availability: implications for heterogeneity and ecosystem processes, The Kruger experience: ecology and management of savanna heterogeneity. Washington: Island Press.

Hijmans, R. J., Cameron, S. E., Parra, J. L., Jones, P. G. & Jarvis, A. (2005) Very high resolution interpolated climate surfaces for global land areas. International Journal of Climatology, 25, 1965-1978.

Huang, S., Li, J. & Xu, M. (2012) Water surface variations monitoring and flood hazard analysis in Dongting Lake area using long-term Terra/MODIS data time series. Natural Hazards, 62, 93-100.

James, C. D., Landsberg, J. & Morton, S. R. (1999) Provision of watering points in the Australian arid zone: a review of effects on biota. Journal of Arid Environments, 41, 87-121.

Kameyama, S., Zhang, J., Wang, Q., Xu, K., Katoh, T. & Watanabe, M. (2004) An approach to estimate the water level and volume of Dongting Lake using Terra/MODIS data. Acta Geographica Sinica-Chinese Edition, 59, 88-94.

Kinahan, A., Pimm, S. L. & Van Aarde, R. J. (2007) Ambient temperature as a determinant of landscape use in the savanna elephant, *Loxodonta africana*. Journal of Thermal Biology, 32, 47-58.

Landman, M., Schoeman, D. S., Hall-Martin, A. J. & Kerley, G. I. (2012) Understanding long-term variations in an elephant piosphere effect to manage impacts. PloS one, 7, e45334.

Lange, R. T. (1969) The piosphere: sheep track and dung patterns. Journal of Range Management, 22, 396-400.

Loarie, S. R., Van Aarde, R. J. & Pimm, S. L. (2009) Fences and artificial water affect African savannah elephant movement patterns. Biological Conservation, 142, 3086-3098.

Macarthur, R. H. & Pianka, E. R. (1966) On optimal use of a patchy environment. American Naturalist, 100, 603-609.

Mukwashi, K., Gandiwa, E. & Kativu, S. (2012) Impact of African elephants on *Baikiaea plurijuga* woodland around natural and artificial watering points in northern Hwange National Park, Zimbabwe. International Journal of Environmental Sciences, 2, 1355-1368.

Nemani, R. & Running, S. (1997) Land cover characterization using multitemporal red, near-IR, and thermal-IR data from NOAA/AVHRR. Ecological Applications, 7, 79-90.

Olofsson, P., Eklundh, L., Lagergren, F., Jönsson, P. & Lindroth, A. (2007) Estimating net primary production for Scandinavian forests using data from Terra/MODIS. Advances in Space Research, 39, 125-130.

Panczykowski, D. M., Puccio, A. M., Scruggs, B. J., Bauer, J. S., Hricik, A. J., Beers, S. R. & Okonkwo, D. O. (2012) Prospective independent validation of IMPACT modeling as a prognostic tool in severe traumatic brain injury. Journal of Neurotrauma, 29, 47-52.

Phillips, S. J., Anderson, R. P. & Schapire, R. E. (2006) Maximum entropy modeling of Species Geographic Distributions. Ecological Modelling, 190, 231-259.

Redfern, J. V., Grant, R., Biggs, H. & Getz, W. M. (2003) Surface-water constraints on herbivore foraging in the Kruger National Park, South Africa. Ecology, 84, 2092-2107.

Roever, C. L., Van Aarde, R. J. & Leggett, K. (2013) Functional connectivity within conservation networks: Delineating corridors for African elephants. Biological Conservation, 157, 128-135.

Ruggiero, R. (1992) Seasonal forage utilization by elephants in central Africa. African Journal of Ecology, 30, 137-148.

Shannon, G., Matthews, W. S., Page, B. R., Parker, G. E. & Smith, R. J. (2009) The effects of artificial water availability on large herbivore ranging patterns in savanna habitats: a new approach based on modelling elephant path distributions. Diversity and Distributions, 15, 776-783.

Viljoen, P. (1989) Spatial distribution and movements of elephants (*Loxodonta africana*) in the northern Namib Desert region of the Kaokoveld, South West Africa/Namibia. Journal of Zoology, 219, 1-19.

Wakefield, S. & Attum, O. (2006) The effects of human visits on the use of a waterhole by endangered ungulates. Journal of Arid Environments, 65, 668-672.

Wilson, A. (1966) The intake and excretion of sodium by sheep fed on species of Atriplex (saltbush) and Kochia (bluebush). Crop and Pasture Science, 17, 155-163.

Xu, H. (2006) Modification of normalised difference water index (NDWI) to enhance open water features in remotely sensed imagery. International Journal of Remote Sensing, 27, 3025-3033.

Chapter 5

GPS-collar data confirm the selective use of a protected patchy African savannah landscape by elephants (*Loxodonta africana*)

This chapter is based on:

Ndaimani, H., Murwira, A., Masocha, M. and Gara, T. W., 2017. GPS-collar data confirm the selective use of a protected patchy African savannah landscape by elephants (*Loxodonta africana*). *Submitted to PlosOne*.

5. GPS-collar data confirm the selective use of a protected patchy African savannah landscape by elephants (*Loxodonta africana*)

Abstract

Understanding the influence of landscape patch heterogeneity on habitat utilisation by megaherbivores such as the African elephant (*Loxodonta africana*) in the patchy savannah landscape is an important objective in conservation ecology. To date, existing knowledge on whether the African elephant utilises a heterogeneous landscape uniformly or selectively is largely based on data collected via observing selected individual elephants for a few daytime hours in the field and recording what they eat. Thus the knowledge generated from those data remains inconclusive because the window of observation is limited in space and time. Enhanced availability of satellite data and Global Positioning System (GPS) tracking of collared animals enables observation at a wider spatial and temporal window. In this study, GPS-collar data from 15 elephants, collected over two years in Gonarezhou National Park, Zimbabwe, were used to test whether elephant length of stay (estimated with Linear Time Density), the speed of movement as well as patch selection differed significantly among vegetation types. Comparative use of vegetation type by elephants was tested using the Compositional Analysis algorithm of the adehabitatHS package in R software. Elephants (1) selectively used the patchy savannah landscape; (2) moved fastest in mixed woodland on clay and *Brachystegia-Julbernadia* woodland; (3) moved slowest in *Combretum apiculatum* and *Androstachys* woodland; and (4) stayed longest in *C. apiculatum* and mixed *Brachystegia* vegetation types. These findings provide the basis for formulating hypotheses which test whether elephant-driven vegetation change could be differentiated by vegetation type while also underscoring the utility of GPS-collar tracking and satellite remote sensing in elephant conservation in the African savannah landscape.

5.1 Introduction

Megaherbivores such as the African savannah elephant (*Loxodonta africana* hereinafter elephant) are known to be less selective when foraging (Osborn, 2005, Wittemyer et al., 2007). This foraging strategy has been attributed to its inherently high daily energy requirements. Thus, in a patchy landscape where forage resources are limited, the elephant is expected to feed on any vegetative material that is abundant. In fact, existing knowledge shows that in biomes characterised by seasonal water availability like the savannah, elephants prefer to graze during the wet-season when grasses occur in abundance, but browse more during the dry-season when fresh grass biomass is in short supply (Codron et al., 2006, Tangley, 1997). Assuming this observation to be valid, it is therefore expected that plant communities that contribute to the bulk of community biomass are utilised more by elephants when foraging in a habitat with patchily distributed food resources. In light of this background, it is logical to assume that elephants roam the landscape in search of food at random without being particularly selective. Whether elephants selectively or uniformly utilise a heterogeneous landscape has been questioned in several studies. For instance, Okello et al (2015) reported that elephants exhibited a preference for bushland and woodland habitats in the Amboseli ecosystem, Kenya. In a separate study, Duffy et al (2011) also provided evidence on the selective use of habitat by elephants. Based on these conflicting viewpoints on feeding behaviour, we, therefore, seek to revisit the question, ‘do elephants selectively or uniformly utilise a heterogeneous landscape?’

Savannahs are typically characterised by a mosaic of grass and woody vegetation communities in the same landscape (Scholes and Archer, 1997). Hence, key resources such as forage are also patchily distributed. If elephants non-selectively utilise the landscape, then their selection of foraging spots is predicted to be uniform across all vegetation types as shown in the conceptual framework presented in Figure 5-1(a). On the other hand, if the elephant is selective as some studies have suggested, then a discernible preference for certain vegetation types is inevitable

and this can be characterised (see Figure 5-1(b)). Thus, it is critical to investigate whether the selection of vegetation types by elephants is random across a heterogeneous landscape in an effort to better understand their potential impact on ecosystems.

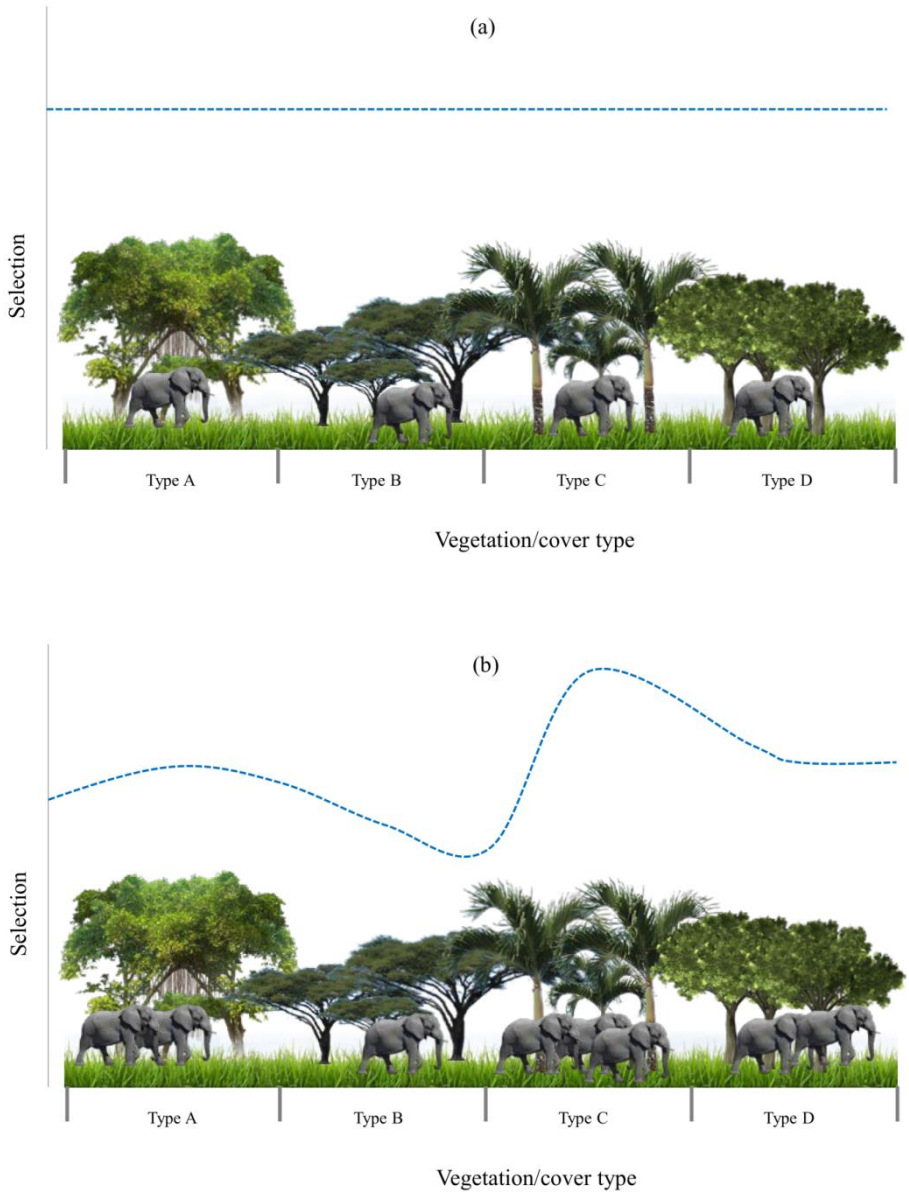

Figure 5-1: Conceptual framework indicating habitat selection by elephants if they (a) uniformly; and (b) selectively utilise the landscape.

Previous work investigating how elephants utilise the landscape showed that they selected certain plant species while avoiding others when foraging. For instance, in a recent study

conducted in the Chobe National Park in Botswana, Owen-Smith and Chafota (2012) reported that 30-50% of 27 woody species were preferred by elephants for their dietary needs. A limitation of these earlier studies is that they were based on physically tracking individual animals in the field and observing and recording what they eat during the day (Wyatt and Eltringham, 1974, Kalemera, 1989). As a result, conclusions drawn were thus limited to observations made on a few animals tracked over a few hours. In addition to basing conclusions from a few tracked animals, observations for night feeding were overlooked owing to limited visibility as well as the dangers associated with night tracking (Guy, 1976). Although these earlier studies laid a foundation for current understanding of elephant distribution, they offered snapshots of how elephants selected plants for foraging and selections made outside the narrow window of observation remained unknown.

In recent years, increased use of Global Position System (GPS) technology in wildlife tracking, combined with enhanced availability of freely acquired remotely sensed data, has made it possible to acquire GPS tracking data for both day and night (e.g., De Boer et al., 2005, Loarie et al., 2009b). Apart from providing the capability to track nighttime movement, the current GPS technology allows researchers to track animals over longer periods depending on the battery life of the tracking devices (Ndaimani et al., 2017). For instance, it is now possible to remotely track collared animals over periods exceeding two years (Birkett et al., 2012). In addition, knowledge on the vegetation types visited by the study animals is no longer limited spatially since position fixes for the entire home range can now be obtained by overlying these point data on high-resolution vegetation maps (Leggett, 2006). Such accurate vegetation maps are derived from freely available data retrieved from satellite sensors that take repeated measurements of the same area giving a synoptic view of the landscape (Masocha and Skidmore, 2011). Therefore, with these improvements in GPS-collar tracking and satellite

sensing technologies, it is important to revisit hypotheses that investigate how elephants utilise the landscape.

Knowledge of the vegetation communities preferred by elephants is not only important for understanding their feeding patterns but could be useful in explaining patterns of vegetation change driven by the megaherbivore (Laws, 1970). Elephants are known to break and uproot trees when browsing (Kohi et al., 2011, Lamprey et al., 1967). Thus, rates of change in vegetation structure could be expected to be higher in landscapes used more often than those less visited. For instance, in an earlier study, Ndaimani et al (2017) reported peaks of elephant presence farther from water sources, thus demonstrating that improvements in GPS and satellite remote sensing technology give some insight into how water and vegetation use could be differentiated in a heterogeneous landscape.

In this study, movement data from 15 GPS-collared elephants were used to test whether elephants utilise a heterogeneous landscape uniformly or selectively. This is different from relying on field observations that are limited to a few individuals monitored during daylight. In particular, the study tested whether elephant speed of movement, selection and time of stay (estimated by Linear Time Density) differed significantly among vegetation types in a savannah ecosystem in Gonarezhou National Park, Zimbabwe. The motivation for these tests was to gather evidence in support or against the widely held view that elephants selectively utilise the landscape. This information is required for the later formulation of hypotheses that test whether the impact of elephants on vegetation structure is uniform across vegetation types.

5.2 Materials and methods

5.2.1 Ethics statement

Handling of elephants for GPS collaring and data collection for this research was approved

under permits: 23(1)(C)(II)31/2015; 23(1)(C)(II)21/2016; and 23(1)(C)(II)22/2016 issued by the Zimbabwe Parks and Wildlife Management Authority.

5.2.2 Study area

The study was conducted in Gonarezhou National Park (GNP) located to the southeast of Zimbabwe between longitudes 31.32° and 32.41° East and latitudes 21.11° and 22.15° South (Figure 5-2). GNP is approximately 5,000 km^2 in area. Elevation ranges from 155 to 567 m above sea level (Ndaimani et al., 2016). The terrain is flat to gently undulating with an average slope of 0.98°. Climate is typical subtropical savannah with a long-term annual rainfall of 466 mm (Gandiwa and Kativu, 2009). Rainfall is normally received from November to March with the rest of the year being dry. Mean monthly temperatures range from 9°C in winter to 36°C in summer. The park has an estimated elephant population of ~10 000 (Dunham et al., 2013), which converts to ~2 elephants/km^2. This makes GNP one of the key elephant conservation areas in the country.

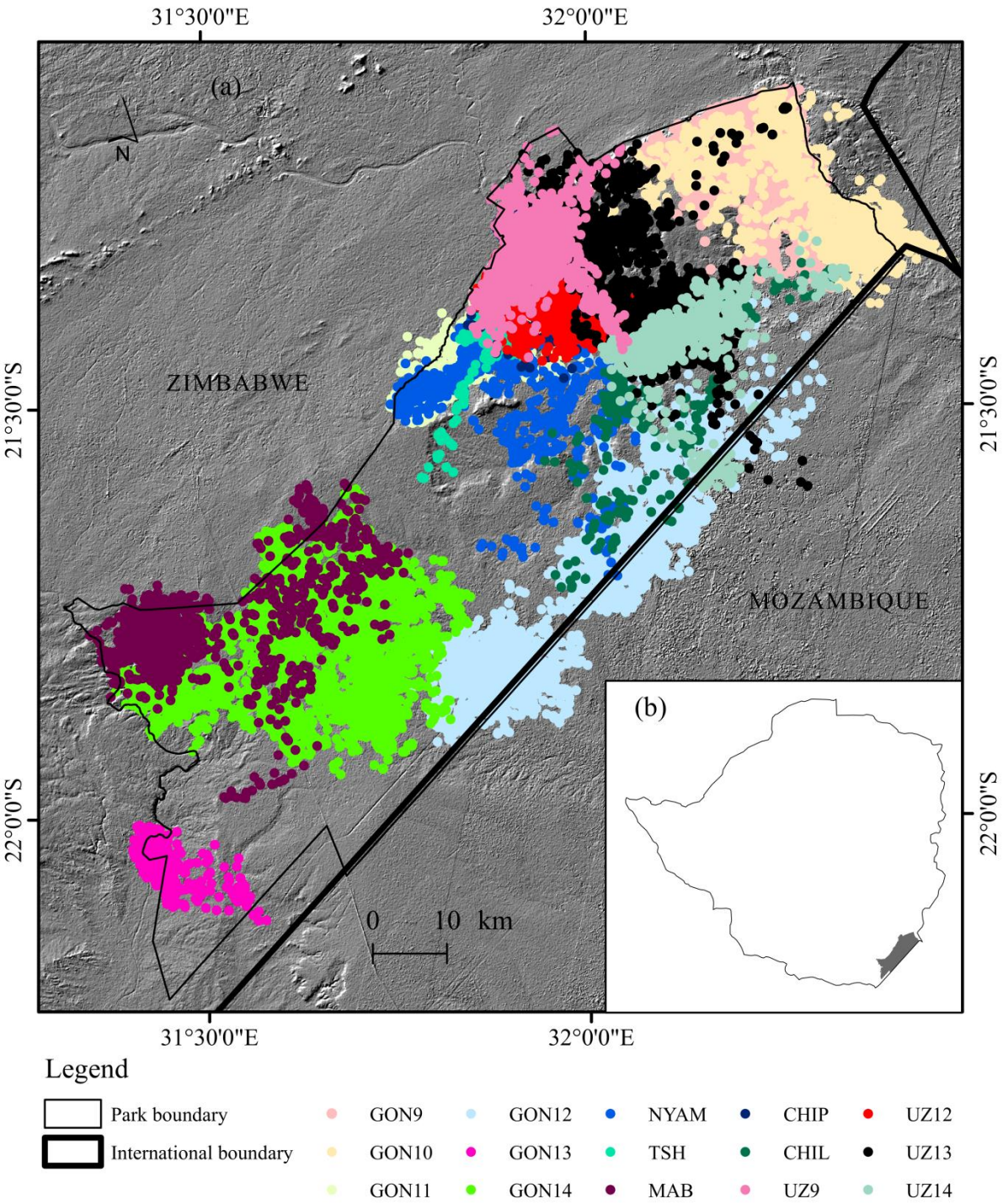

Figure 5-2: Location of (a) position fixes for 15 elephants fitted with GPS collars and; (b) Gonarezhou in Zimbabwe.

Vegetation is typical dry deciduous savannah dominated by *Combretum* spp combined with *Colophospermum mopane* woodland. Together, these woody species account for ~85% of the tree biomass in the study area (Martini et al., 2016).

5.2.3 Elephant movement data

Fifteen adult elephants (10 bulls and 5 cows) were immobilised and fitted with GPS collars from 1 May 2015 to 20 August 2016 (Table 5-1). The bulls were selected from bachelor herds while the cows were selected from family herds. The collars were programmed to take position fixes every 4 hours resulting in 6 fixes per day. The error in the GPS location was +/-15m as stipulated by the supplier. The success rate of fixes ranged from 85% to 99% which is within acceptable limits (Frair et al., 2010).

Table 5-1: Details of the collared elephants (♂ = male and ♀ = female)

Elephant ID	Date of collaring	Fix end date	GPS fixes used	% Missing GPS fixes
GON9♀	5/1/2015	6/30/2017	4369	8
GON10♂	5/1/2015	8/24/2016	2871	1
GON11♀	5/1/2015	6/30/2017	4470	6
GON12♂	5/1/2015	6/30/2017	4262	10
GON13♂	5/1/2015	11/28/2015	1256	1
GON14♀	5/2/2015	6/30/2017	4060	14
NYAM♂	8/12/2016	6/30/2017	1685	13
TSH♂	8/13/2016	6/30/2017	1706	11
MAB♂	8/20/2016	6/30/2017	1672	11
CHIP♂	8/15/2016	6/30/2017	1627	15
CHIL♂	8/13/2016	6/30/2017	1637	15
UZ9♀	12/28/2015	6/30/2017	3232	2
UZ12♂	12/28/2015	6/30/2017	3233	2
UZ13♀	12/30/2015	6/30/2017	3215	2
UZ14♂	12/30/2015	6/30/2017	3211	2

5.2.4 Selection of vegetation type

The selection of vegetation types by collared elephants was estimated using the resource selection ratio (Neu et al., 1974) calculated as:

$$W_i = (U_i/U_+)/(A_i/A_+) \qquad \text{eqn 1}$$

where; U_i = number of position fixes in vegetation type *i*; U_+ = total number of position fixes for the individual animal; A_i = size of vegetation type *i* within the elephant home range; and A_+ = Total size of the elephant home range.

For each collared elephant, the position fixes collected during the study period were retrieved from the tracking site as text files and later converted to a point map. The home range of individual elephants was estimated using the Minimum Convex Polygon (MCP) based on the point map. Vegetation types located within the home range of each collared elephant were later extracted by masking out the areas outside the MCP. The area covered by each vegetation type within the home range of individual elephants was estimated using the area calculation algorithm.

5.2.5 Elephant speed

The speed of movement of each collared elephant (in km/hr) within a 500 m grid cell was calculated using the formula:

$$S_G = \sum_{k=1}^{N} \frac{d_k}{t_k} \qquad \text{eqn 2}$$

Where S_G = speed in grid cell G; d_k = fractional length of track segment k intersecting G, N = number of track segments in the elephant's trajectory; and t_k = time spent by an elephant in track segment k.

The calculation was implemented in the Movement Ecology Tools for ArcGIS (Wall et al., 2013). The average speed of movement was not segregated between male and female elephants since it was not the objective of this study to test for differences in speed between the sexes. In addition, Wall et al (2013) reported no significant difference in the speed of male and female elephants studied in Mali. Elephant speed within particular grid cells was later extracted using standard overlay functions.

It was predicted that elephants would move slowly in preferred vegetation types than those less preferred.

5.2.6 Elephant time of stay in a grid cell

The time (in hours) spent by a collared elephant in a 500 m grid cell was calculated using the formula:

$$T_G = \sum_{k=1}^{N} \frac{d_k}{s_k} \qquad \text{eqn 3}$$

Where T_G = time spent in grid cell G; d_k = fractional length of track segment k intersecting G; N = number of track segments in the elephant's trajectory; and s_k = animal's linear speed for track segment k (Wall et al., 2013).

All the track segments that originated in a particular grid cell were used to calculate the mean time spent by the target elephant within the grid. The time spent in each grid cell was later divided by total tracking time for the entire study period to get a normalised Linear Time Density (LTD) value for each elephant. These calculations were implemented in the Movement Ecology Tools for ArcGIS (Wall et al., 2013). Similar to speed calculation, LTD values for both male and female elephants were aggregated and average values extracted for all the grid cells located along the movement trajectories.

It was predicted that elephants spent more time in preferred vegetation types than those less preferred. Preference of vegetation type is not limited to the need to forage but could linked to other reasons like predator avoidance as well as other forms of disturbance.

5.2.7 Vegetation type

Variation in the speed, selection, and LTD of elephants was assessed per vegetation type. A thematic vegetation map with fourteen dominant vegetation types produced by Cunliffe et al (2012) was converted to a 500 m raster to match other spatial datasets (Figure 5-3). The vegetation map was deemed reliable for use in this study since it has low out-of-bag prediction error (0.000-0.048). Elephant speed and LTD within particular vegetation types were extracted from grid cells using standard overlay functions.

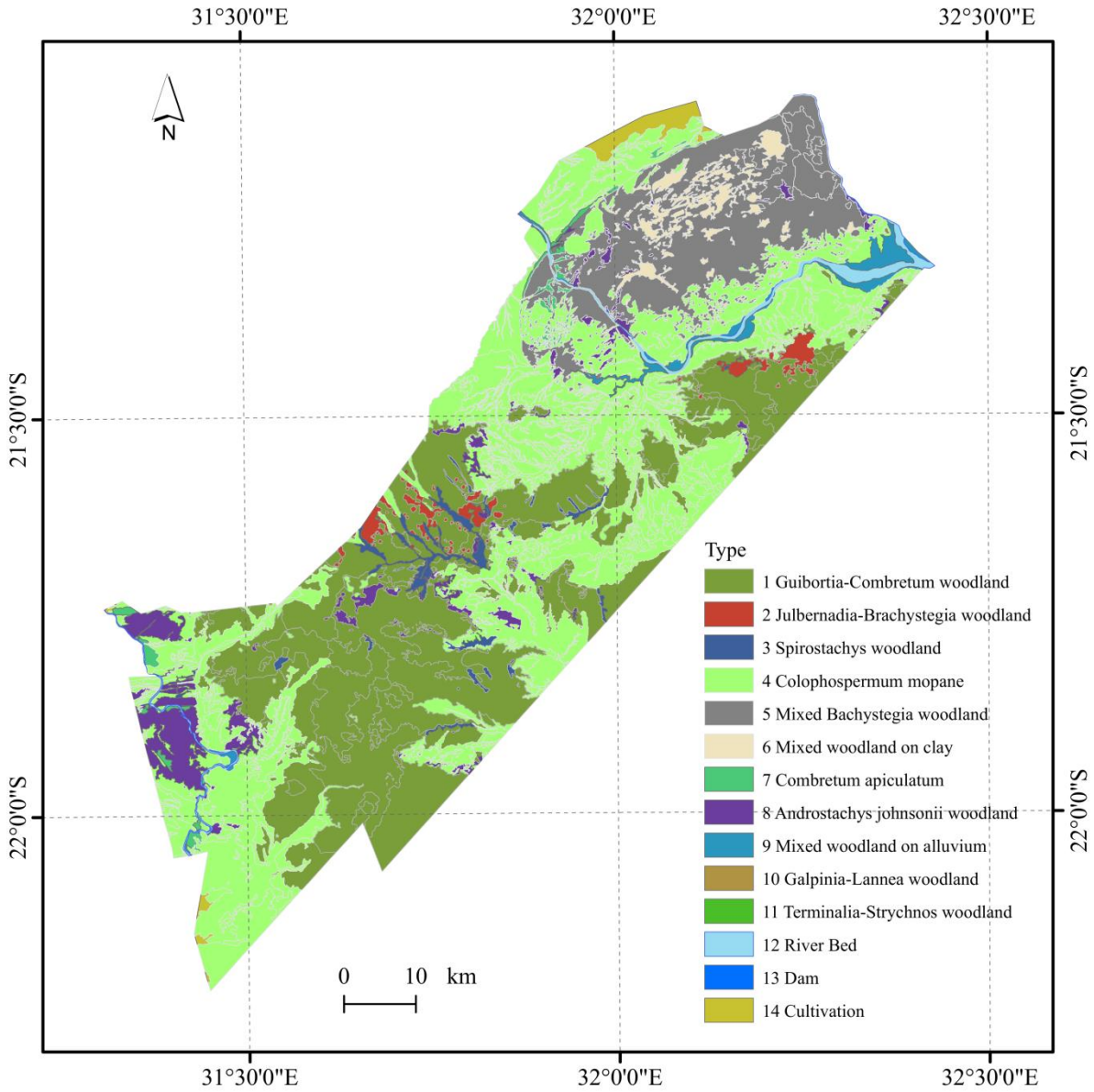

Figure 5-3: Major vegetation/cover types in the Gonarezhou National Park (adapted from Cuniliffe et al (2012))

5.2.8 Data analysis

Variation in the selection of vegetation types by the pooled study elephants was tested using the Wilks lambda at an alpha level of 0.05. The test was run using the Compositional Analysis algorithm of the adehabitatHS package implemented in R software (Calenge, 2015). Compositional analysis performs pairwise comparisons of habitat use in landscapes characterised by several habitat types. As part of the output, a ranking matrix was built

indicating whether the vegetation type in the row is significantly used more than the type in the column (see Table 5-2). For each study elephant, selection of vegetation type (estimated from habitat selection ratios) was presented as bar plots to show whether the selection was uniform.

The difference in the speed and LTD of elephants in the various vegetation types was tested using the Kruskal Wallis test since data significantly deviated from normality ($p<0.05$). There was no need to test for spatial autocorrelation in elephant speed and LTD since the data were not drawn from continuous phenomena. Pairwise comparisons of elephant speed and LTD within the different vegetation types was based on the Tamhane test since residuals significantly deviated from normality. Vegetation types covering less than 3 pixels were left out in the comparison of speed and LTD since observations were deemed too few for analysis.

The median speed of elephants per vegetation type was later calculated and ranked in descending order. This analysis helped to illustrate the variation in elephant speed within the different vegetation types. Similarly, the median LTD per vegetation type was calculated and ranked to visually illustrate the variation in the time spent by elephants in the different vegetation types. Mean values were not used since data were not normally distributed.

5.3 Results

Use of vegetation types by the pooled 15 elephants differed significantly (Lambda=0.029, df=13, p=0.000) in the study area. Results from compositional analysis illustrate that the elephants used open water and riverbeds more than all the other available vegetation types (Table 5-2). Both these types are located close to open water sources. Among the vegetation types located away from the piosphere, *Mopane, Terminalia-Strychnos* and *Combretum* woodlands were most used. The types least used by the elephants were *Guibortia, Brachystegia-Julbernardia* and mixed woodland on clay.

Table 5-2: Results of compositional analysis showing more use of open water (13) and riverbed (12) by elephants in the Gonarezhou National Park. A "+" is used when the vegetation type in the row is used more than the type in a column, and "-" otherwise. When the difference is significant, the sign is tripled.

Type	1	2	3	4	5	6	7	8	9	10	11	12	13	14	Total
1	0	-	-	---	-	-	---	---	---	---	---	---	---	---	0
2	+	0	---	---	---	+	---	---	---	---	---	---	---	---	2
3	+	+++	0	---	-	+	---	---	-	---	---	---	---	-	5
4	+++	+++	+++	0	+++	+++	+	+	+	+	+	-	---	+++	23
5	+	+++	+	---	0	+++	-	-	-	-	-	---	---	+	9
6	+	-	-	---	---	0	---	---	---	---	---	---	---	---	1
7	+++	+++	+++	-	+	+++	0	+	+	+	-	-	---	+++	19
8	+++	+++	+++	-	+	+++	-	0	+	-	-	-	---	+	15
9	+++	+++	+	-	+	+++	-	-	0	-	-	---	---	+	12
10	+++	+++	+++	-	+	+++	-	+	+	0	-	---	---	+++	18
11	+++	+++	+++	-	+	+++	+	+	+	+	0	-	---	+++	20
12	+++	+++	+++	+	+++	+++	+	+	+++	+++	+	0	---	+++	28
13	+++	+++	+++	+++	+++	+++	+++	+++	+++	+++	+++	+++	0	+++	39
14	+++	+++	+	---	-	+++	---	-	-	---	---	---	---	0	10

Analysis of vegetation type use by individual elephants showed that 11 selected types found in the piosphere while four selected those away from the piosphere (Figure 5-4). In total, five elephants preferred mixed woodland on alluvial soils (elephants: GON10, chil, chip, UZ13, uz14); four preferred the riverbed (elephants: GON14, mab, tsh, UZ9); and two preferred open water habitat (elephants: UZ11 and nyam). The rest of the elephants preferred vegetation types located away from the piosphere: two preferred *Spyrostachys africanus* woodland; one preferred *C. mopane* woodland and one preferred *Combretum apiculatum* woodland.

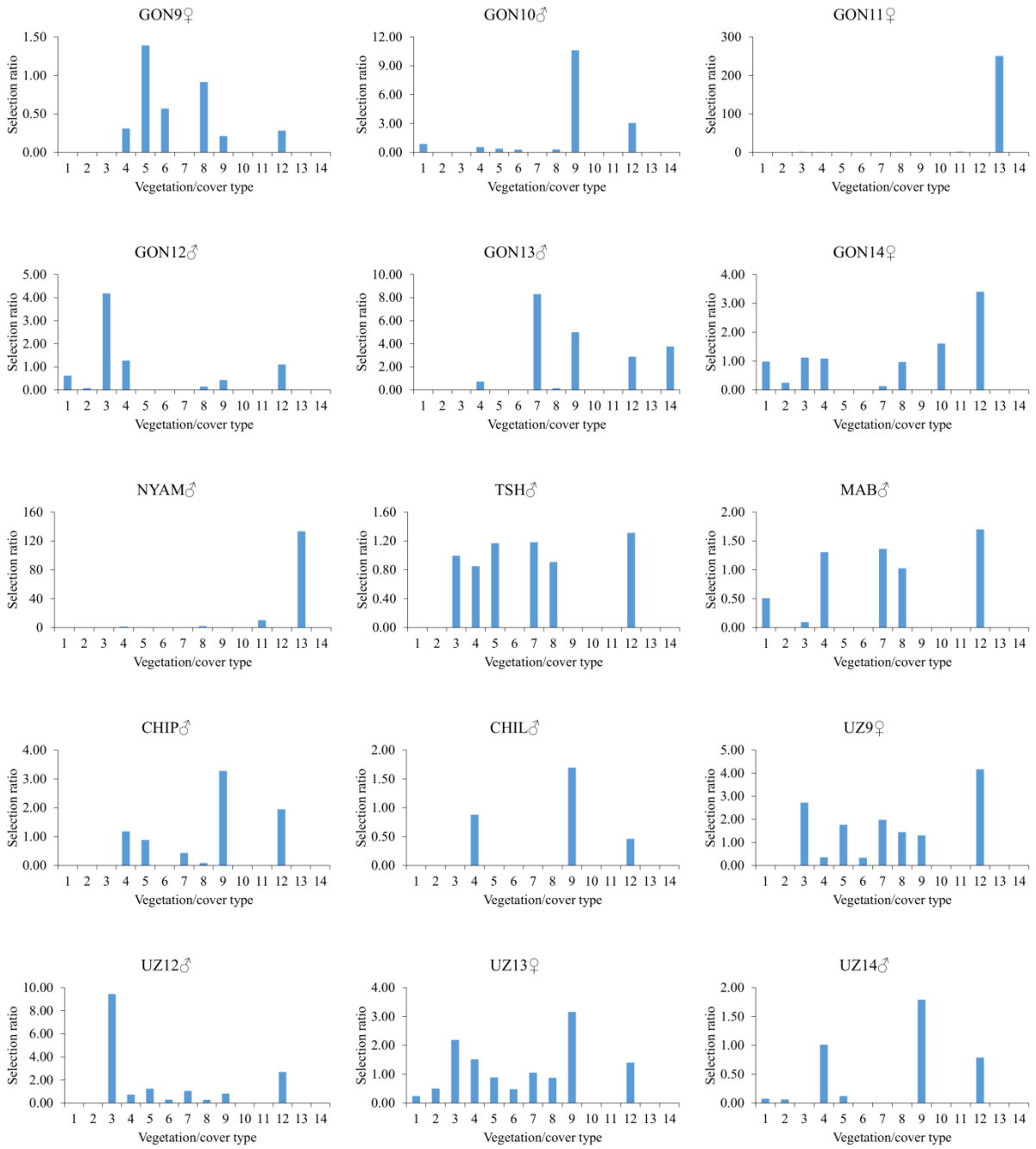

Figure 5-4: Selective use of vegetation /cover type by elephants in the Gonarezhou National Park, Zimbabwe. Cover type: 1=*Guibortia*; 2=*Brachystegia-Julbernadia*; 3=*Spyrostachys*; 4=Mopane; 5=mixed *Brachystegia*; 6=mixed woodland on clay; 7=*Combretum apiculatum*; 8=*Androstachys*; 9=mixed woodland on alluvium; 10-mixed *Galpinia-Lannea*; 11=*Terminalia-Strychnos*; 12=riverbed; 13=dam; 14=cultivation.

Elephants were observed to move at significantly different speeds (χ^2 =99.970, df = 9, p=0.000) across the vegetation types.

The speed of elephants in *Guibortia* woodland significantly differed from that in *C. mopane*; mixed *Brachystegia*; *C. apiculatum*; mixed woodland on alluvium; and riverbed habitat (Table 5-3). Elephant speed in *C. mopane* significantly differed from that recorded in mixed *Brachystegia* and *C. apiculatum* woodland. In addition, speed in mixed *Brachystegia* differed significantly from that in mixed woodland on clay habitat while speed in mixed woodland on clay habitat differed significantly from that observed in *C. apiculatum* woodland. Elephant speed was the same over the rest of the vegetation type pairs.

Table 5-3: Pairwise comparisons of elephant speed in the vegetation types (values represent mean difference while * shows significant difference at the 0.05 alpha level)

Type	1	2	3	4	5	6	7	8	9	12
1	1	-0.014	0.048	0.040*	0.094*	0.010	0.124*	0.058	0.068*	0.070*
2		1	0.062	0.053	0.108	0.024	0.138	0.072	0.082	0.083
3			1	-0.008	0.046	-0.038	0.076	0.010	0.020	0.022
4				1	0.054*	-0.029	0.085*	0.019	0.029	0.030
5					1	-0.084*	0.030	-0.036	-0.026	-0.024
6						1	0.114*	0.048	0.058	0.059
7							1	-0.066	-0.056	-0.055
8								1	0.010	0.011
9									1	0.001
12										1

The highest median speed of elephant movement was recorded in mixed woodland on clay and *Brachystegia-Julbernadia* while the lowest was recorded in *C. apiculatum* and *Androstachys* woodland (Table 5-4).

Table 5-4: Ranked median speed of elephant movement, range, and number of samples in different vegetation types

Vegetation	Median Speed	Range	N
7	0.203	1.874	124
8	0.243	1.573	237
5	0.260	2.163	1686
3	0.271	1.929	117
12	0.280	1.485	168
4	0.286	3.074	3271
9	0.292	0.974	211
1	0.299	2.729	1996
2	0.306	1.331	42
6	0.329	1.343	199

The percentage time spent by elephants in individual vegetation types (as estimated by LTD) differed significantly (χ^2 =1640.782, df=10, p=0.000). Elephant LTD differed significantly in all of the vegetation types except for the following pairs: *Brachystegia/Julbernardia*-mixed *Galpinia/Lannea*; *Spyrostachys*-mixed woodland on clay; *C. Mopane-Androstachys; C. Mopane*-mixed woodland on alluvium; mixed *Brachystegia*-mixed woodland on alluvium; mixed *Brachystegia*-riverbed; and *Androstachys*- mixed woodland on alluvium (Table 5-5).

Table 5-5: Pairwise comparisons for LTD among vegetation types (values represent mean difference while * shows significant difference)

Vegetation	1	2	3	4	5	6	7	8	9	10	12
1	1	-0.000004	-0.000017*	-0.000037*	-0.000062*	-0.000015*	-0.000121*	-0.000036*	-0.000055*	0.000026	-0.000067*
2		1	-0.000013*	-0.000033*	-0.000059*	-0.000011*	-0.000117*	-0.000032*	-0.000051*	0.000030*	-0.000063*
3			1	-0.000020*	-0.000046*	0.000002	-0.000105*	-0.000020*	-0.000038*	0.000043*	-0.000050*
4				1	-0.000025*	0.000022*	-0.000084*	0.000001	-0.000018	0.000063*	-0.000030*
5					1	0.000048*	-0.000059*	0.000026*	0.000007	0.000089*	-0.000005
6						1	-0.000107*	-0.000022*	-0.000040*	0.000041*	-0.000052*
7							1	0.000085*	0.000066*	0.000148*	0.000054*
8								1	-0.000019	0.000063*	-0.000031*
9									1	0.000082	-0.000012*
10										1	-0.000094*
12											1

In fact, elephants were observed to spend more time in *C. apiculatum* and mixed *Brachystegia*, while the shortest time was spent in *Guibortia* and in mixed *Galpinia-Lannea* vegetation types (Table 5-6).

Table 5-6: Ranked median LTD of elephant, range, and number of samples in different vegetation types

Vegetation	Median LTD	Range	N
10	0.000002	0.000002	2
1	0.000023	0.000144	4883
2	0.000030	0.000084	178
6	0.000032	0.000166	345
8	0.000035	0.000345	400
9	0.000036	0.000395	241
4	0.000042	0.000546	5768
12	0.000045	0.000422	208
3	0.000047	0.000098	231
5	0.000066	0.000671	2565
7	0.000169	0.000450	127

5.4 Discussion

The speed of movement and the time spent by elephants in major vegetation types differed significantly. Elephants moved fastest in mixed woodland on clay and *Brachystegia-Julbernardia* woodland but slowest in *C. apiculatum* and *Androstachys* woodland. In addition, elephants spent more time in *C. apiculatum* and mixed *Brachystegia* woodland while the least time was spent in *Guibortia* and in mixed *Galpinia-Lannea* vegetation types. The findings confirm that savannah elephants utilise heterogeneous savannah landscapes selectively.

The preference or avoidance of certain vegetation types by the elephant has been reported before in other landscapes outside our study area. For example, preference of habitats close to water (Harris et al., 2008), high vegetative cover (Harris et al., 2008, De Boer et al., 2005) and patches with abundant particular fruit trees (Short, 1983) has been reported before in literature. At the much smaller scale of the plant species, a study by Owen-Smith and Chafota (2012) reported that up to two-thirds of species were not used as food items by the elephant. However, despite the existence of these studies, it is generally accepted that elephants are not selective when foraging (Spanbauer and Adler, 2015, Campos-Arceiz and Blake, 2011). Taken together, evidence provided in this study suggests that the savannah elephant does not roam the landscape at random since its movement is clearly influenced by vegetation type in addition to surface water (Ndaimani et al., 2017).

The main ecological mechanism proposed to explain the importance of vegetation in regulating elephant movement relates to the need to balance forage intake (Nellemann et al., 2002, Loarie et al., 2009a) and thermal regulation, which is achieved through seeking shade (Midgley et al., 2005). Therefore the observed lowest speed in *C. apiculatum* and *Androstachys* woodland imply that elephants either reduce their speed in these vegetation types while foraging or sheltering from the heat under the trees. Similarly, elephants were found to spent more time

(LTD) in *C. apiculatum* and mixed *Brachystegia* woodlands possibly implying that these patches might also be important for foraging and shade. In protected landscapes, the combined influence of forage and shade on elephant movement and habitat use has been reported previously (Joshi and Singh, 2008). Variation in the time spent by elephants in patchy landscapes has also been reported in human-dominated landscapes. For instance, in a human-dominated east African savannah, elephants were reported to spend more time in less fragmented landscapes (Gara et al., 2017). In another study, Ngene et al (2012) found that elephants walked fastest in the early morning when moving from livestock dominated landscapes. Taken together, these studies confirm the selective use of patchy human-dominated landscapes.

Findings from this study are based on data with better spatial and temporal coverage as opposed to earlier studies that relied on following few animals in the field. In fact, elephant movement data used in this study cover an area ~4,000km^2 in extent and were collected both during the day and night. These findings possibly represent an enhanced picture of how elephants utilise the landscape. Overall, our study underscores the importance of satellite GPS tracking, spatial analysis and remote sensing in enhancing understanding of wildlife movement in general and the savannah elephant in particular. The limitation of our study is that position fixes of the collared elephants were taken at long intervals (every 4 hours). Fine-grained movement data give a better picture of movement patterns than the coarse-grained since in the former more habitats are sampled. However, in most studies, the GPS-collar fix rate is often a trade-off between a high number of fixes per day and the battery life of the tracking device (Rempel and Rodgers, 1997). More fixes per day shorten the battery life thus reducing the total tracking time. Nevertheless, our results could be treated with confidence since we consistently found the selective use of vegetation type from three different acceptable metrics of habitat use (selection, speed, and LTD). The consistency of our results could imply that the findings are not by chance

but are a result of a fixed pattern. This study provides additional evidence for the selective use of a savannah landscape by elephants from a huge data set.

Future studies testing similar hypotheses could, therefore, use fine-grained elephant location data to get a better picture of how the herbivore utilises the landscape. More fixes per day reveal elements of elephant movement that otherwise might be missed at the coarser fix interval of four hours. In addition, collaring more elephants might also confirm whether our findings are not confounded by the smaller number of collared individuals. Other hypotheses might centre on whether the selection of vegetation type by elephants is not confounded by the sex and age of collared individuals as well as season.

The finding that elephants selectively utilise a heterogeneous landscape is critical for ecologists and wildlife managers since it could imply that their impact on vegetation is also selective. Elephants are known to transform the structure of vegetation as they push and pull trees when foraging (O'Connor and Page, 2014). To date, their impact on vegetation in the piosphere is well documented (Landman et al., 2012, Mukwashi et al., 2012). However, the impact that could possibly occur away from the piosphere remains largely unconfirmed. Our findings could, therefore, form the basis for hypothesizing that away from the piosphere, elephant impact on vegetation structure is more pronounced within preferred vegetation types than those that are avoided.

5.5 Conclusion

In conclusion, we report that elephants utilise a heterogeneous savannah landscape selectively. While this has been reported in other landscapes, our results provide additional evidence on how elephants utilise a protected savannah landscape. We particularly found out that the elephant prefers *C. apiculatum*, *Androstachys* and *Brachystegia* woodlands in addition to the

traditionally preferred piosphere habitats. Selective use of vegetation types by elephants could imply that the rate of transformation of the vegetation differs by vegetation type. Going forth, studies that test the effect of elephants on vegetation no longer need to be limited to the piosphere alone but could include other preferred vegetation types located away from water.

References

Birkett, P. J., Vanak, A. T., Muggeo, V. M., Ferreira, S. M. & Slotow, R. (2012) Animal perception of seasonal thresholds: changes in elephant movement in relation to rainfall patterns. PLoS One, 7, e38363.

Calenge, C. (2015) adehabitatHS: analysis of habitat selection by animals. R Package version 0.3. 12.

Campos-Arceiz, A. & Blake, S. (2011) Megagardeners of the forest–the role of elephants in seed dispersal. Acta Oecologica, 37, 542-553.

Codron, J., Lee-Thorp, J. A., Sponheimer, M., Codron, D., Grant, R. C. & De Ruiter, D. J. (2006) Elephant (*Loxodonta africana*) diets in Kruger National Park, South Africa: spatial and landscape differences. Journal of Mammalogy, 87, 27-34.

Cunliffe, R., Muller, T. & Mapaura, A. (2012) Vegetation survey of Gonarezhou National Park, Zimbabwe. Zimbabwe Parks and Wildlife Management Authority, Harare.

De Boer, W. F., Fairall, N., Van Aarde, R. J. & Ntumi, C. P. (2005) Use of space and habitat by elephants (*Loxodonta africana*) in the Maputo Elephant Reserve, Mozambique. South African Journal of Wildlife Research-24-month delayed open access, 35, 139-146.

Duffy, K. J., Dai, X., Shannon, G., Slotow, R. & Page, B. (2011) Movement patterns of African elephants (*Loxodonta africana*) in different habitat types. South African Journal of Wildlife Research, 41, 21-28.

Dunham, K., Van Der Westhuizen, E., Van Der Westhuizen, H. & Ndaimani, H. (2013) Aerial survey of elephants and other large herbivores in Gonarezhou National Park (Zimbabwe) and surrounding areas: 2013. Frankfurt Zoological Society, Chiredzi.

Frair, J. L., Fieberg, J., Hebblewhite, M., Cagnacci, F., Decesare, N. J. & Pedrotti, L. (2010) Resolving issues of imprecise and habitat-biased locations in ecological analyses using

GPS telemetry data. Philosophical Transactions of the Royal Society of London B: Biological Sciences, 365, 2187-2200.

Gandiwa, E. & Kativu, S. (2009) Influence of fire frequency on Colophospermum mopane and *Combretum apiculatum* woodland structure and composition in northern Gonarezhou National Park, Zimbabwe. Koedoe, 51, 0-13.

Gara, T. W., Wang, T., Skidmore, A. K., Zengeya, F. M., Ngene, S. M., Murwira, A. & Ndaimani, H. (2017) Understanding the effect of landscape fragmentation and vegetation productivity on elephant habitat utilization in Amboseli ecosystem, Kenya. African Journal of Ecology, 55, 259-269.

Guy, P. (1976) Diurnal activity patterns of elephant in the Sengwa Area, Rhodesia. African Journal of Ecology, 14, 285-295.

Harris, G. M., Russell, G. J., Van Aarde, R. I. & Pimm, S. L. (2008) Rules of habitat use by elephants *Loxodonta africana* in southern Africa: insights for regional management. Oryx, 42, 66-75.

Joshi, R. & Singh, R. (2008) Feeding behaviour of wild Asian elephants (*Elephas maximus*) in the Rajaji National Park. Journal of American Science, 4, 34-48.

Kalemera, M. (1989) Observations on feeding preference of elephants in the *Acacia tortilis* woodland of Lake Manyara National Park, Tanzania. African Journal of Ecology, 27, 325-333.

Kohi, E. M., De Boer, W. F., Peel, M. J., Slotow, R., Van Der Waal, C., Heitkönig, I., Skidmore, A. & Prins, H. H. (2011) African elephants *Loxodonta africana* amplify browse heterogeneity in African savanna. Biotropica, 43, 711-721.

Lamprey, H., Glover, P. E., Turner, M. I. & Bell, R. H. (1967) Invasion of the Serengeti National Park by elephants. African Journal of Ecology, 5, 151-166.

Landman, M., Schoeman, D. S., Hall-Martin, A. J. & Kerley, G. I. (2012) Understanding long-term variations in an elephant piosphere effect to manage impacts. PLoS One, 7, e45334.

Laws, R. M. (1970) Elephants as agents of habitat and landscape change in East Africa. Oikos, 21, 1-15.

Leggett, K. E. (2006) Home range and seasonal movement of elephants in the Kunene Region, northwestern Namibia. African Zoology, 41, 17-36.

Loarie, S. R., Van Aarde, R. J. & Pimm, S. L. (2009a) Elephant seasonal vegetation preferences across dry and wet savannas. Biological Conservation, 142, 3099-3107.

Loarie, S. R., Van Aarde, R. J. & Pimm, S. L. (2009b) Fences and artificial water affect African savannah elephant movement patterns. Biological Conservation, 142, 3086-3098.

Martini, F., Cunliffe, R., Farcomeni, A., De Sanctis, M., D'ammando, G. & Attorre, F. (2016) Classification and mapping of the woody vegetation of Gonarezhou National Park, Zimbabwe. Koedoe, 58, 1-10.

Masocha, M. & Skidmore, A. K. (2011) Integrating conventional classifiers with a GIS expert system to increase the accuracy of invasive species mapping. International Journal of Applied Earth Observation and Geoinformation, 13, 487-494.

Midgley, J., Balfour, D. & Kerley, G. (2005) Why do elephants damage savanna trees?: commentary. South African Journal of Science, 101, 213-215.

Mukwashi, K., Gandiwa, E. & Kativu, S. (2012) Impact of African elephants on *Baikiaea plurijuga* woodland around natural and artificial watering points in northern Hwange National Park, Zimbabwe. International Journal of Environmental Sciences, 2, 1355-1368.

Ndaimani, H., Murwira, A., Masocha, M., Gara, T. W., Zengeya, F. M. (2016) Evaluating performance of aerial survey data in elephant habitat modelling. African Journal of Ecology, 55, 270-281.

Ndaimani, H., Murwira, A., Masocha, M. & Zengeya, F. M. (2017) Elephant (*Loxodonta africana*) GPS collar data show multiple peaks of occurrence farther from water sources. Cogent Environmental Science, 3, 1420364.

Nellemann, C., Moe, S. R. & Rutina, L. P. (2002) Links between terrain characteristics and forage patterns of elephants (*Loxodonta africana*) in northern Botswana. Journal of Tropical Ecology, 18, 835-844.

Neu, C. W., Byers, C. R. & Peek, J. M. (1974) A technique for analysis of utilization-availability data. The Journal of Wildlife Management, 38, 541-545.

Ngene, S., Skidmore, A., Van Gils, H., Prins, H., Toxopeus, A. & Douglas-Hamilton, I. (2012) Walk or stride? a question for roaming herds of elephants in Marsabit, protected area. Elephants: ecology, behavior and conservation. New York: NOVA Publishers.

O'connor, T. & Page, B. (2014) Simplification of the composition, diversity and structure of woody vegetation in a semi-arid African savanna reserve following the re-introduction of elephants. Biological Conservation, 180, 122-133.

Okello, M. M., Njumbi, S. J., Kiringe, J. W. & Isiiche, J. (2015) Habitat use and preference by the African elephant outside of the protected area, and management implications in the Amboseli landscape, Kenya. International Journal of Biodiversity and Conservation, 7, 211-226.

Osborn, F. V. (2005) Habitat selection by bull elephants in central Zimbabwe. IUCN, 63.

Owen-Smith, N. & Chafota, J. (2012) Selective feeding by a megaherbivore, the African elephant (*Loxodonta africana*). Journal of Mammalogy, 93, 698-705.

Rempel, R. S. & Rodgers, A. R. (1997) Effects of differential correction on accuracy of a GPS animal location system. The Journal of Wildlife Management, 61, 525-530.

Scholes, R. & Archer, S. (1997) Tree-grass interactions in savannas. Annual Review of Ecology and Systematics, 28, 517-544.

Short, J. (1983) Density and seasonal movements of forest elephant (*Loxodonta africana cyclotis*, Matschie) in Bia National Park, Ghana. African Journal of Ecology, 21, 175-184.

Spanbauer, B. R. & Adler, G. H. (2015) Seed protection through dispersal by African savannah elephants (*Loxodonta africana africana*) in northern Tanzania. African Journal of Ecology, 53, 496-501.

Tangley, L. (1997) In search of Africa's forgotten forest elephant. Science, 275, 1417-1419.

Wall, J., Wittemyer, G., Klinkenberg, B., Lemay, V. & Douglas-Hamilton, I. (2013) Characterizing properties and drivers of long-distance movements by elephants (*Loxodonta africana*) in the Gourma, Mali. Biological Conservation, 157, 60-68.

Wittemyer, G., Getz, W., Vollrath, F. & Douglas-Hamilton, I. (2007) Social dominance, seasonal movements, and spatial segregation in African elephants: a contribution to conservation behavior. Behavioral Ecology and Sociobiology, 61, 1919-1931.

Wyatt, J. & Eltringham, S. (1974) The daily activity of the elephant in the Rwenzori National Park, Uganda. African Journal of Ecology, 12, 273-289.

Chapter 6

GPS-collar data show a correlation between elephant movement (*Loxodonta africana)* and tree cover change in a protected patchy African savannah landscape

This chapter is based on:

Ndaimani, H., Murwira, A., Masocha, M., 2017. GPS-collar data show a correlation between elephant movement (*Loxodonta africana*) and tree cover change in a protected patchy African savannah landscape. *Submitted to Geocarto International*.

6. GPS-collar data show a correlation between elephant movement (*Loxodonta africana*) and tree cover change in a protected patchy African savannah landscape

Abstract

Knowledge on the impact of elephant foraging on tree cover is important for conservation. Although ecologists generally agree that elephants drive change in vegetation structure, knowledge on where exactly in the landscape the change occurs remains largely underdeveloped. In this study, movement data from 16 GPS-collared elephants are used together with percentage tree cover (MOD44B) and NDVI (MOD13Q1) data to test (1) whether rates of change in structure differ by vegetation/cover type, and (2) whether the change is correlated with elephant movement in the Gonarezhou national park, Zimbabwe. From 2000 to 2016, tree cover significantly changed in ~24% of the entire study area. The observed proportions of vegetation/cover type showing a change in tree cover were observed to be significantly different ($\chi^2 = 596.35$, df = 13, p = 0.000). Results seem to suggest that change in percentage tree cover was positively correlated with elephant KDE in 2015, 2016 and 2017. It was however not correlated with LTD and speed of elephant movement during the three years of elephant tracking. Finer temporal resolution MODIS NDVI data (MOD13Q1) were significantly correlated with KDE in 2015, 2016 and 2017; significantly correlated with LTD in 2016 and 2017; and significantly correlated with speed in 2017 only. The results are important to park managers since the change in vegetation structure could drive change in the distribution of wild animals. The study further reinforces the utility of elephant tracking from GPS collars combined with remotely sensed data in enhancing knowledge on how they utilise the landscape and also their potential as drivers of change in certain vegetation/cover types.

6.1 Introduction

The modification of vegetation structure by African elephants (*Loxodonta africana*), especially in landscapes where they occur at high densities is a well-supported hypothesis (e.g., Davies et al., 2018, Asner et al., 2016, Valeix et al., 2011). It is also generally accepted that when foraging, elephants push, debark and uproot trees (Ihwagi et al., 2010, Nasseri et al., 2011). Thus, the prolonged use of a foraging spot by the mega-herbivore will mostly lead to change, especially from more closed to more open vegetation types (van Staden et al., 2017, Goheen and Palmer, 2010). However, the densification of vegetation as a result of elephant use has also been reported in other landscapes (Kalwij et al., 2010, Rutina et al., 2005). It is, therefore, logical to predict that the areas used the most by elephants are associated with a higher rate of change in vegetation structure than those least used. Thus, it can be hypothesised that in a heterogeneous savannah landscape, selective use of vegetation/cover type by elephants translates to differential impact on vegetation structure and that change can be conceptualised (Figure 6-1). Overall, understanding where vegetation change occurs in the landscape and to what extent is critical because the change often alters the use of the landscape by other wildlife species (Herremans, 1995, Valeix et al., 2011). For instance, change in structure from woodland to grassland could result in the landscape being used more by grassland species than woodland species.

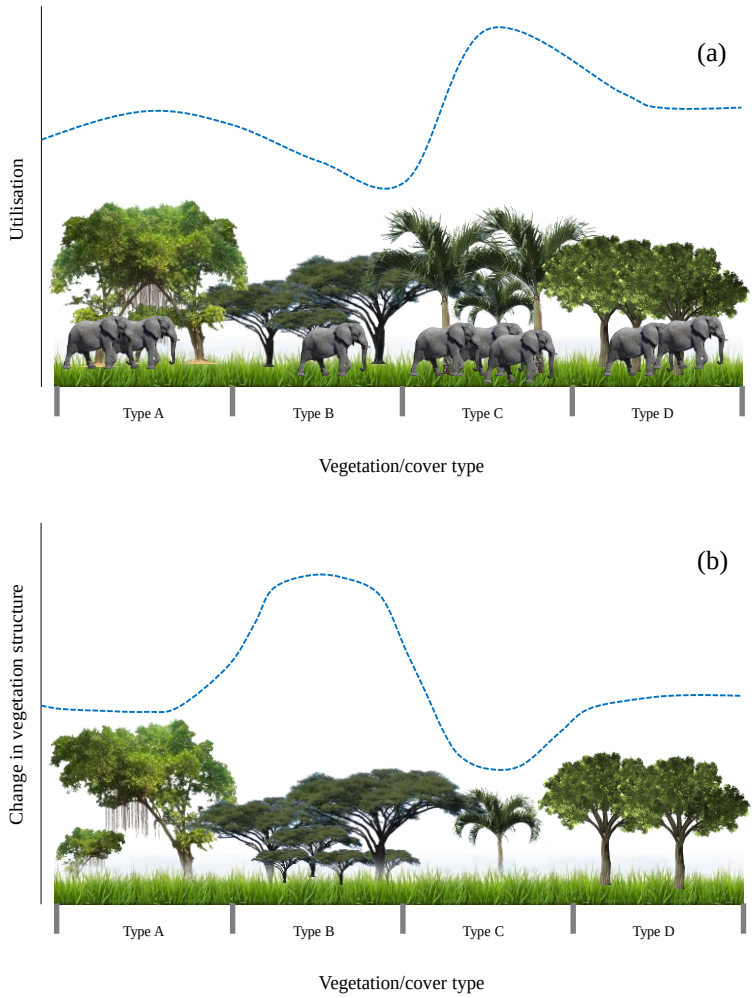

Figure 6-1: Conceptual diagram showing: (a) elephant selective use of a heterogeneous landscape; and (b) differential rates of change in vegetation structure

While there is a general consensus that elephants drive change in landscapes where they occur at high densities (Holdo et al., 2009, Mosugelo et al., 2002), knowledge of landscape sections where rates of change are highest remains largely inconclusive. Alteration of vegetation by elephants in areas around waterholes (i.e., piospheres) is well described in the literature (Fullman and Child, 2013, Landman et al., 2012, Mukwashi et al., 2012). These landscapes are constantly used by elephants as they access the water points for drinking and other thermoregulatory purposes (Ndaimani et al., 2017b). Consequently, it has been reported that the piosphere is characterised by different vegetation structure from that found in landscapes

located further away. Literature is replete with descriptions of the piosphere effect especially in African savannahs (Chamaillé-Jammes et al., 2009). Earlier descriptions of the piosphere were largely based on comparisons of tree cover data collected in plots located at increasing distances from waterholes (e.g., Mukwashi et al., 2012, Ndoro et al., 2016, Gandiwa et al., 2011). While these studies have been critical in laying the foundation for the current understanding of the piosphere effect, the window of observation was limited both in space and time. Thus, field-work based studies were largely limited in that they could not offer landscape-scale data to test whether the rate of change in vegetation structure driven by elephants differs by vegetation/cover type. These shortcomings can be overcome by using remotely sensed data.

Advances in remote sensing and the continued availability of freely available satellite data offer a synoptic view of the landscape (Zhang et al., 2003, Gu et al., 2007) and enable repetitive observations (Mas, 1999) of the same landscape hence providing an enhanced picture of any changes that might occur in the vegetation. To date, landscape-scale change in vegetation structure has been successfully mapped from remotely sensed data (Gandhi et al., 2015, Thenkabail and Lyon, 2016). However, in landscapes characterised by high densities of elephants, the rate of change in vegetation structure could differ by vegetation type since the mega-herbivore has been reported to be selective when foraging. Thus, remote sensing coupled with GPS-collar tracking opens new opportunities for investigating elephant driven vegetation change within individual vegetation/cover types further away from the piosphere in cost-effective ways that require minimal fieldwork.

In this study, movement data from 16 GPS-collared elephants are used together with percentage tree cover (MOD44B) and NDVI (MOD13Q1) data to test (1) whether rates of change in structure differ by vegetation/cover type, and (2) whether the change is correlated with elephant

movement in the Gonarezhou national park, Zimbabwe. The study seeks to enhance knowledge on whether and how elephants drive change in vegetation structure within savannah landscapes

6.2 Materials and methods

6.2.1 Study area

The study was conducted in the Gonarezhou National Park (GNP) located between longitudes 31.32° and 32.41° East and latitudes 21.11° and 22.15° South in Zimbabwe (Figure 6-2). GNP is the second largest national park in the country, covers ~5000km^2 and is a key elephant range area with an estimated population of ~10 000 (Dunham et al., 2013). Between 2001 and 2014, the elephant population in the GNP increased by 123%, representing the highest population growth in the country (Dunham, 2015). GNP was selected for testing our hypothesis because high densities of elephants have been reported to result in a change in vegetation structure in other landscapes (Valeix et al., 2011), thus it is logical to predict that elephants in the national park might also be driving vegetation change.

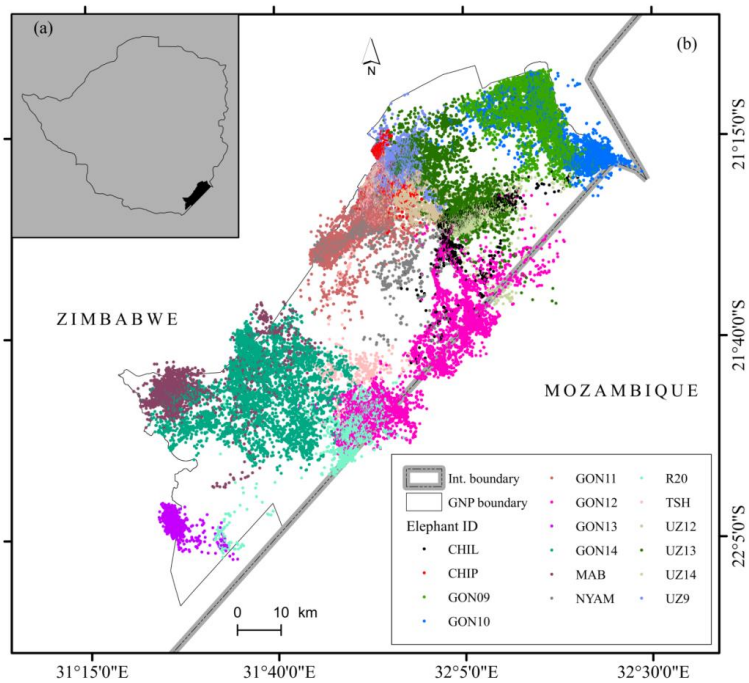

Figure 6-2: Study area: (a) location of the Gonarezhou National Park in Zimbabwe, and (b) location data for collared elephants (GNP = Gonarezhou National Park)

Vegetation in the national park is dry deciduous; dominated by *Colophospermum mopane* and *Combretum apiculatum* occurring on granophytic and basaltic clays (Figure 6-3). Climate is subtropical savannah characterised by hot wet summers and cool dry winters. Rainfall is largely received from November to April with a long tern annual precipitation of ~600mm/year (Ndaimani et al., 2017b). The terrain is flat to undulating and altitude ranges from 155m to 567m above sea level (Ndaimani et al., 2017a).

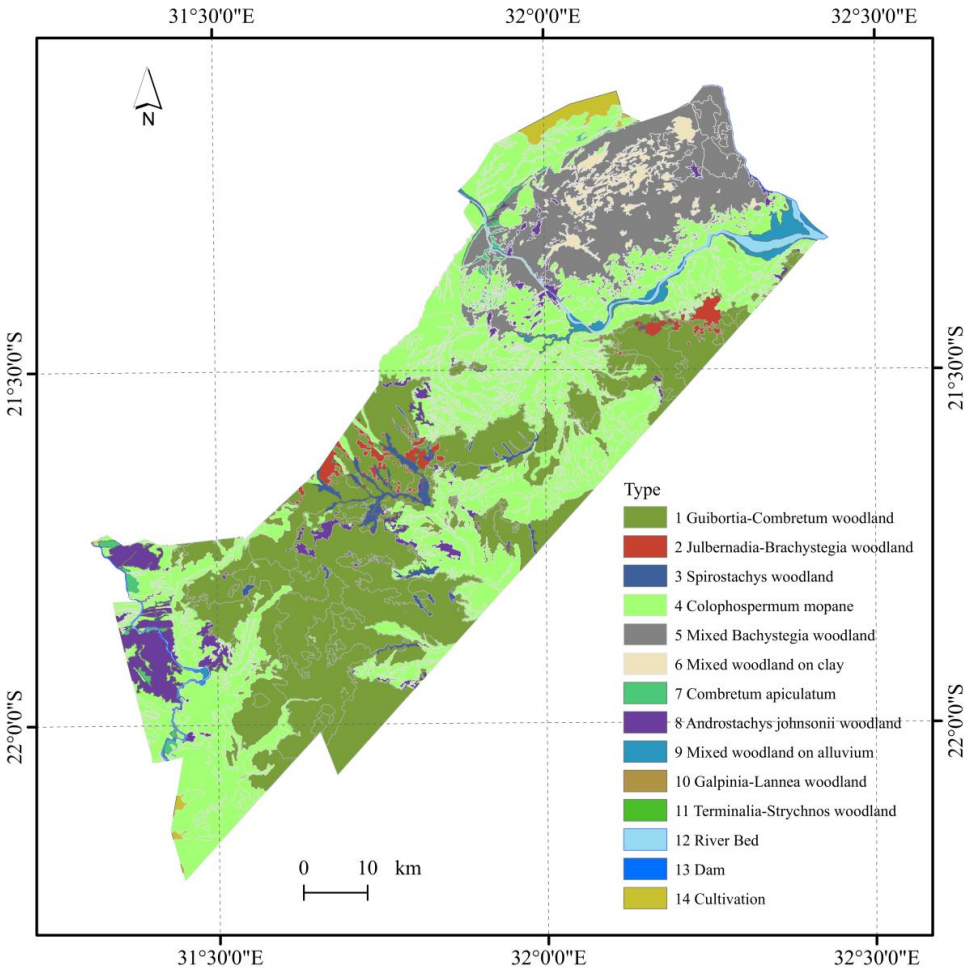

Figure 6-3: Vegetation/cover types in the Gonarezhou National Park, Zimbabwe (adapted from Cunliffe (2012))

6.2.2 Elephant location data

From 1 May 2015 to 31 December 2017, 16 elephants (11 bulls and 5 cows) were fitted with satellite-based GPS collars and tracked for periods ranging from 211 to 975 days (Table 6-1). Candidate elephants for collaring were selected from different parts of GNP to ensure that their combined movement data covered the entire national park. The collars were programmed to take position fixes every four hours adding up to six fixes per day if fixes were not missed. The fix success rate ranged from 64% to 90% and that was deemed adequate (Frair et al., 2010).

Table 6-1: Details of the collared elephants (♂ = male, ♀ = female)

Elephant ID	Start date	End date	Tracking days	Fixes	Fix success rate
CHIL♂	8/13/2016	12/31/2017	505	1974	65%
CHIP♂	8/15/2016	12/31/2017	503	1941	64%
GON09♀	5/1/2015	12/31/2017	975	5224	89%
GON10♂	5/1/2015	8/24/2016	481	2871	99%
GON11♀	5/1/2015	12/31/2017	975	5380	92%
GON12♂	5/1/2015	9/20/2017	873	4612	88%
GON13♂	5/1/2015	11/28/2015	211	1256	99%
GON14♀	5/2/2015	12/31/2017	974	4971	85%
MAB♂	8/20/2016	12/31/2017	498	2457	82%
NYAM♂	8/12/2016	12/31/2017	506	2593	85%
R20♂	1/14/2017	12/31/2017	351	1723	82%
TSH♂	8/13/2016	12/31/2017	505	2500	83%
UZ12♂	12/28/2015	12/31/2017	734	4142	94%
UZ13♀	12/30/2015	12/31/2017	732	4125	94%
UZ14♂	12/30/2015	12/2/2017	703	3868	92%
UZ9♀	12/28/2015	12/31/2017	734	4143	94%

Location data for the collared elephants were downloaded via a user interface available on the internet. Data were then cleaned for missing or erroneous coordinates before being converted

to csv format for later input into ArcGIS. Point maps of elephant location were then produced for later estimation of selected movement metrics.

6.2.3 Elephant utilisation of vegetation/cover type

Yearly utilisation of individual 250m grid cells by elephants was estimated using the Kernel Density Estimator (KDE). Firstly, point maps of the 16 collared elephants were displayed in ArcGIS. Secondly, their trajectories of movement were extracted using the Movement Ecology Tools for ArcGIS (Wall et al., 2013). Lastly, per year Kernel Density estimation was undertaken based on h-ref smoothening. Average elephant KDE per vegetation/cover type was calculated from values extracted using zonal statistics

6.2.4 Elephant speed of movement

The speed of movement of the collared elephants (in km/hour) was calculated by dividing the distance between two successive fixes by the time. The coordinates of the position fixes were used to calculate straight line distance based on the Pythagoras theorem while the data stored in the location files were used to calculate time. All the trajectories intersecting 250m grid cells were used to calculate average speed per cell. Calculations were implemented in the Movement Ecology Tools for ArcGIS. Per year files of elephant-speed were created for 2015, 2016 and 2017. Average elephant speed per vegetation/cover type was calculated from values extracted using zonal statistics.

6.2.5 Elephant Linear Time Density

The length of stay of collared elephants in particular grid cells (in hours) was estimated using Linear Time Density (LTD). Elephant position fixes come with time data. Thus, the time spent between successive fixes is obtained from simple subtraction. All the trajectories intersecting a 250m grid cell were used to calculate the total time spent by collared elephants in the target

cell. These calculations were also implemented in the Movement Ecology Tools for ArcGIS. Similar to speed, yearly files for LTD were produced. The LTD of elephant movement per vegetation/cover type was extracted using zonal statistics.

6.2.6 Vegetation/cover type

Classification of vegetation/cover types was based on 14 main types adapted from Cunliffe et al (2012) (Figure 6-3). The authors of the map produced it from remotely sensed data combined with extensive field data collection. The map has low out-of-bag prediction error (0.000-0.048). Variations in elephant movement (KDE, LTD and speed) and vegetation condition (tree cover and NDVI) were analysed within individual vegetation/cover types.

6.2.7 Tree cover data

Yearly data on tree cover were obtained from the freely available MOD44B product at the 250m spatial resolution and downloadable from the earthexplorer portal (http://earthexplorer.usgs.gov/). Data were downloaded for the years 2000 to 2016. Pre-processing of the data included re-projection from the Sinusoidal to the UTM WGS84 Zone 36 South coordinate reference system to be compatible with the other data sets used in the analyses. Two tiles (h21v10 and h21v11) cover the study area and these were first mosaicked and later masked to exclude pixels located outside the study area. The Modis Reprojection Tool downloadable from https://lpdaac.usgs.gov/tools/ was used to re-project; mosaic and mask the MODIS layers.

Following pre-processing, the yearly data were stacked using functions made available through the rgdal package of R software (Bivand et al., 2018). Pixel-based change in percentage tree cover over the 17 years was estimated from regression models that used the years as the predictor variable. For each pixel, all model parameters from regression analysis were estimated

but only the slope of the relationship (β-value) and the significance (*p*-value) was presented in raster format. Pixels that did not exhibit a significant change in tree cover (p>0.05) were masked out from the final output. Later, slope a values (β) for the pixels exhibiting a significant change in tree cover per vegetation/cover type were extracted usinthe g the zonal statistics. In addition, the the size of the area exhibiting a significant change in tree cover per vegetation/cover type was later estimated using the area calculation algorithm in ArcGIS. The size of the area exhibiting significant change per vegetation/cover type was later divided by the total size of the vegetation/cover type to get change as a proportion.

6.2.8 NDVI data

NDVI data were based on MODIS 16 days composites (MOD13Q1) freely downloadable from earthexplorer (http://earthexplorer.usgs.gov/) and available at the 250m resolution. Pre-processing of the data included re-projection, mosaicking and masking following the procedure described earlier for MOD44B. Additional pre-processing included data smoothening using the Savitzky-Golay filter to reduce noise inherent in MODIS time series data. Firstly, the data were imported into R software as an image stack with 23 images per year for the years 2015, 2016 and 2017. The acquisition dates for these data coincided with the time when location data from the collared elephants were collected. Data smoothening was implemented in the R software.

Yearly NDVI images were produced by averaging the 23 smoothened 16 days composites. The average per year NDVI for individual vegetation/cover types was later extracted using zonal statistics in ArcGIS.

6.2.9 Data analysis

The proportion of the study area exhibiting a significant positive change in percentage tree cover was compared to that showing negative change using the Chi-square test of proportions.

Significance was inferred at the alpha level of 0.05. Bar graphs illustrating variation in the size as well as the proportion of area displaying a significant change in tree cover per vegetation/cover type were also plotted.

The Spearman's correlation test was used to test for correlation between pixel-based change in tree cover and elephant movement (KDE, LTD and speed). The test was selected since data were observed to significantly deviate from a normal distribution ($p<0.05$). Values of change in tree cover, KDE, LTD and speed were first extracted from raster data described earlier. Grid cells that did not have at least one value from the four variables were left out of the analysis. After removal of grid cells with incomplete data, 109 cells were then used for analysis.

For each of the years 2015, 2016 and 2017, values for NDVI, KDE, LTD and speed were extracted in individual grid cells. Only the grid cells with values for all the four variables were considered for later analyses. After removing grid cells with missing data, 785 cells were later used for analyses. Per year correlations of NDVI and each of KDE, LTD and speed were computed using the Spearman correlation since data were not normally distributed ($p<0.05$). Per year graphs showing NDVI plotted together with KDE, LTD and speed were also produced.

6.3 Results

6.3.1 Long term change in tree cover

Results from pixel-based regression illustrate that percentage tree cover changed significantly in an area ~1218km^2 in size from 2000 to 2016. The area exhibiting significant change was, therefore, ~24% of the entire study area. Percentage tree cover was observed to significantly decrease in an area ~1186km^2 in size while it increased significantly in 32km^2, and remained unchanged in 3755km^2 of the study area. In fact, percentage tree cover decreased significantly in 23.8% of the study area while it increased significantly in 0.6% of the area.

Results further illustrate that the proportion of the study area showing a positive change in percentage tree cover significantly differed from that showing negative change (χ^2 = 1243, df =1, p = 0.000). Figure 6-4 shows spatial variation in the slope of change in tree cover (β); significance of the change (p-value); and a mask of the pixels where significant change was observed.

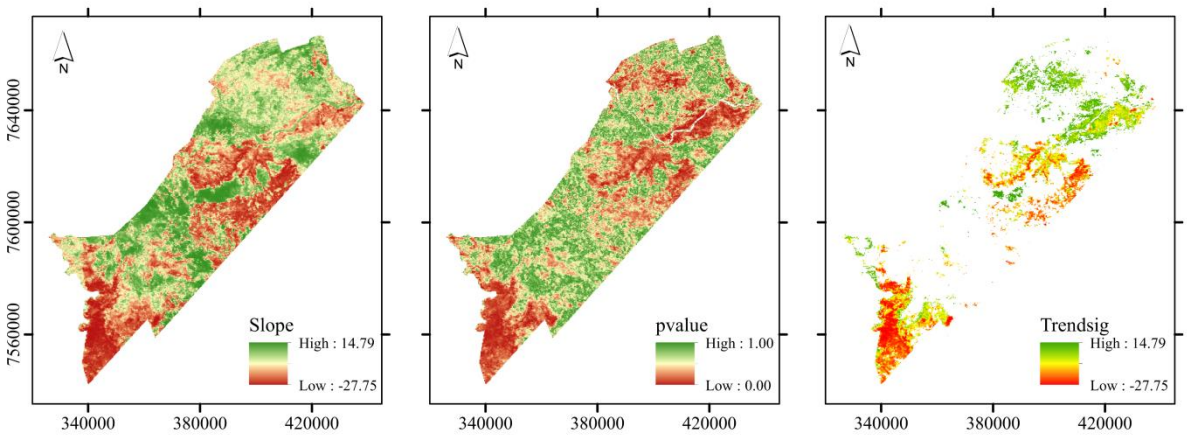

Figure 6-4: Results of pixel-based regression for tree cover change estimated from MOD44B data in the Gonarezhou national park (2000-2016): (a) Slope of the regression, (b) p-value, and (c) pixels where change is significant.

6.3.2 Magnitude of long-term tree cover change by vegetation/cover type

Vegetation/cover types with the largest areas that changed significantly in percentage tree cover include *Colophospermum mopane* (859km^2), *Guibortia-Combretum* (149km^2); and mixed *Brachystegia* (106km^2) (Figure 6-5(a)). The vegetation/cover types with the smallest areas that changed significantly include, *Galpinia-Lannea* (0.06km^2); *Terminalia-strychnos* (0.13km^2); and dam (0.06km^2). Results from comparison of the proportions of vegetation/cover type showing change in tree cover illustrated significant difference (χ^2 = 596.35, df = 13, p = 0.000) (Figure 6-5(b)).

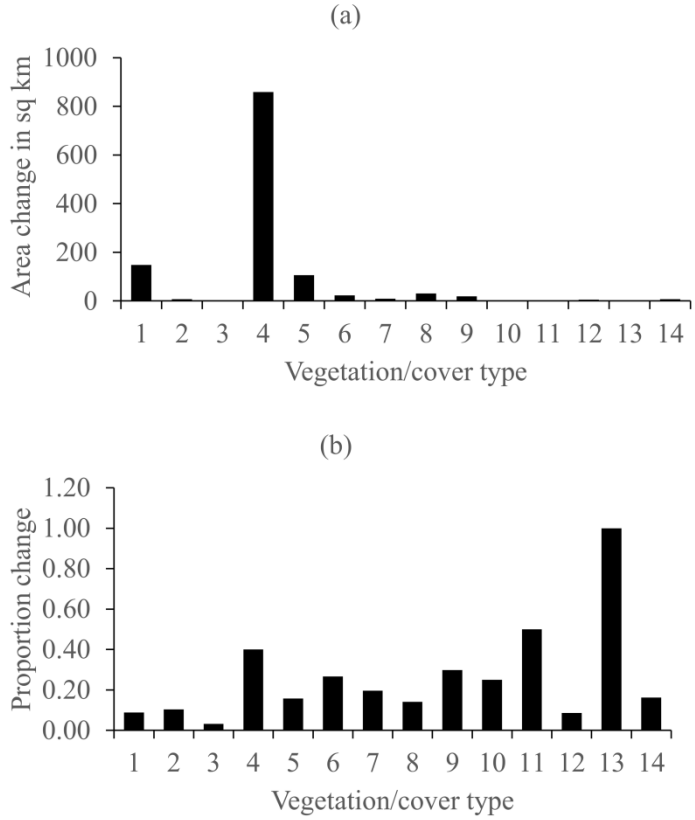

Figure 6-5: Tree cover change in major vegetation/cover types of Gonarezhou National Park: (a) area change per vegetation/cover type, and (b) proportion of the vegetation/cover type changed.

Apart from the dam cover type, the largest proportion change in percentage tree cover was observed in *Terminalia-strychnos* (50.00%), *Colophospermum mopane* (40.06%), mixed woodland on alluvium (29.79%), and mixed woodland on clay (26.60%) whilst the smallest change was observed in *Spyrostachys* (0.03%); riverbed (0.09%); and *Guibortia-Combretum* vegetation (0.09%) (Figure 6-5(b)).

6.3.3 Direction of long term tree cover change

Results illustrate that positive change in percentage tree cover was only observed in *Julbernadia-Brachystegia* woodland while in the rest of the vegetation/cover types change was

negative (i.e., a reduction in percentage tree cover over time) (Figure 6-6(a)). Data in Figure 6-6(b) also illustrate a negative change in percentage tree cover for most of the pixels were significant change was observed.

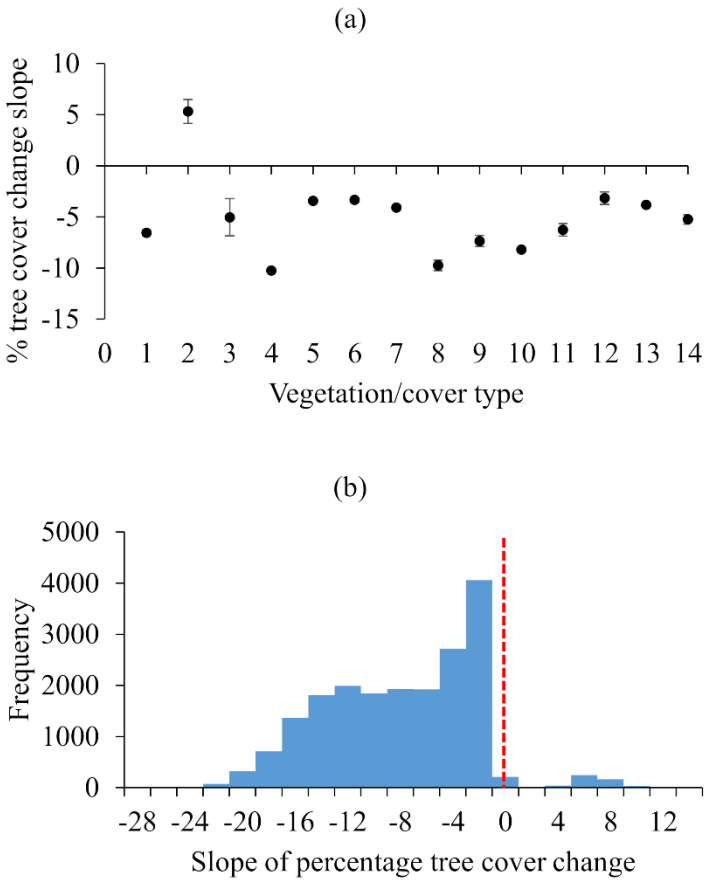

Figure 6-6: Mean slope of tree cover change in 14 vegetation/cover types in the Gonarezhou National Parks: (a) mean change and 95% confidence interval; and (b) histogram of the slope of change in pixels where change is significant (red dotted line separates negative and positive change). Change is based on MOD44B data (2000-2016).

Results from correlation analyses illustrate that change in percentage tree cover was positively correlated with elephant KDE for 2015 ($r = 0.227$, $df = 109$, $p = 0.018$); 2016 ($r = 0.240$, $df = 109$, $p = 0.012$); and 2017 ($r = 0.238$, $df = 109$, $p = 0.013$). It was however not correlated with LTD and speed of elephant movement during the entire study period.

6.3.4 Correlation of short term tree cover (NDVI) and elephant movement

NDVI data for 2015 were significantly correlated with elephant KDE ($r = 0.075$, $df = 785$, $p = 0.034$) but not with LTD and speed.

Results for 2016 illustrate significant correlation between: NDVI and KDE ($r = -0.231$, $df = 785$, $p = 0.000$); and between NDVI and LTD ($r = -0.146$, $df = 785$, $p = 0.000$). NDVI and speed were not correlated.

In 2017, NDVI was significantly correlated with KDE ($r = -0.534$, $df = 785$, $p = 0.000$); LTD ($r = -0.512$, $df =785$, $p = 0.000$) and speed in 2017 ($r = 0.081$, $df =785$, $p =0.023$).

Figure 6-7 shows variation in NDVI, KDE, LTD and speed of elephants by vegetation/cover type.

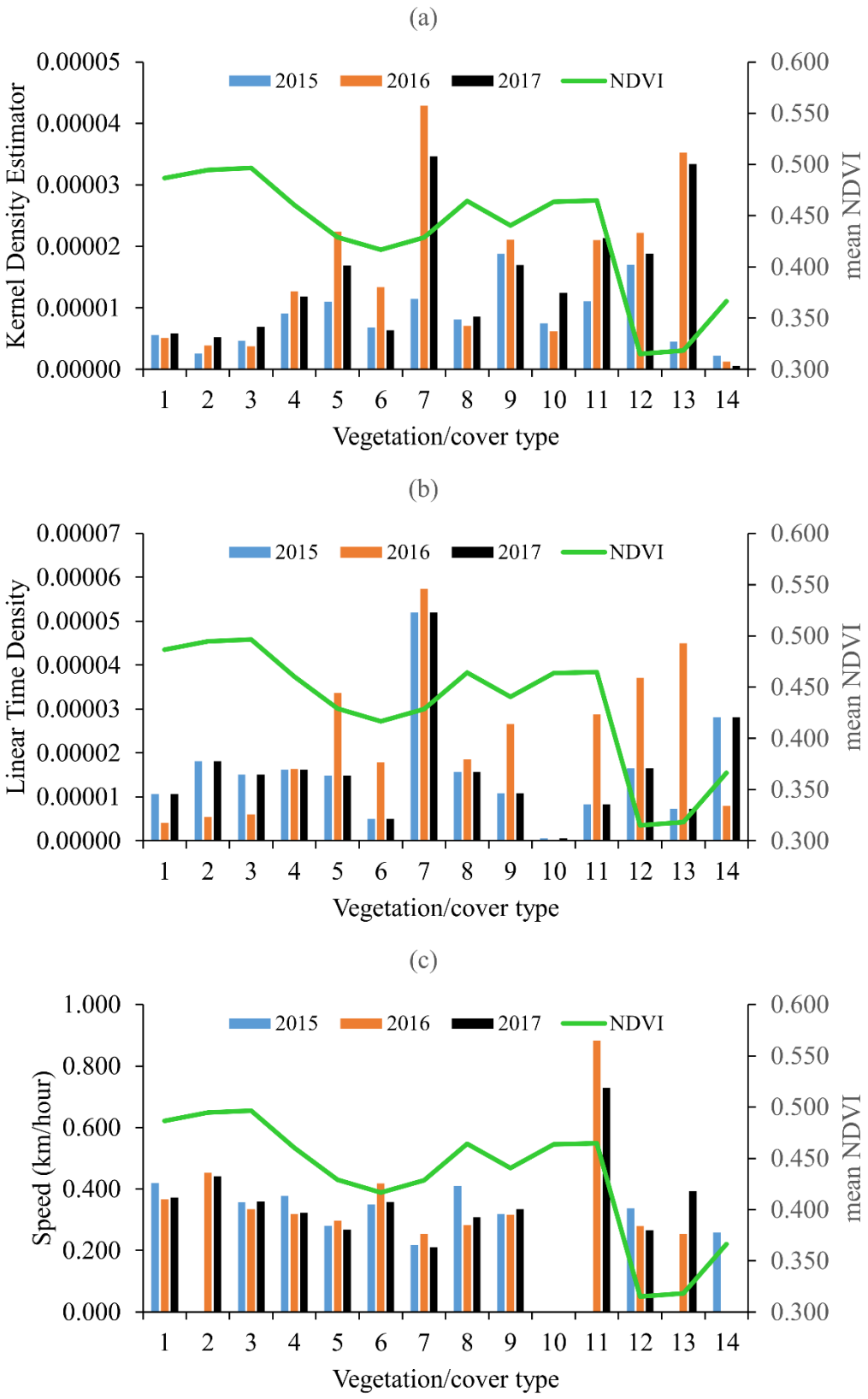

Figure 6-7: Change in MOD13Q1-derived NDVI per vegetation/cover type plotted together with: (a) KDE; (b) LTD; and (c) speed of collared elephants in the Gonarezhou national park.

6.4 Discussion

Percentage of tree cover decreased significantly in the GNP from the year 2000 to 2016. The greatest decrease in absolute values was observed in *Colophospermun mopane* and *Terminalia-Strychnos* woodlands. The only increase in percentage tree cover was observed in *Julbernadia-Brachystegia* woodland. In all, percentage tree cover decreased significantly in 23.8% of the study area while it increased significantly in 0.6% of the area. Results seem to suggest that change in percentage tree cover was positively correlated with elephant KDE in 2015, 2016 and 2017. It was however not correlated with LTD and speed of elephant movement during the three years of elephant tracking. Finer temporal resolution MODIS NDVI data (MOD13Q1) were significantly correlated with KDE in 2015, 2016 and 2017; significantly correlated with LTD in 2016 and 2017; and significantly correlated with speed in 2017 only. However, the direction of the correlations differed by year. For instance, there was a significant positive correlation between NDVI and KDE in 2015 but the correlation was negative in 2016 and 2017.

The reported decrease in tree cover, which can be differentiated by vegetation/cover type; and the correlation of tree cover with elephant utilisation (KDE) might imply that the impact of elephants on vegetation is not uniform but selective. Findings from this study represent the first few attempts to apply elephant tracking data and remotely sensed data to understand whether a change in vegetation structure could be differentiated by vegetation/cover type, and also whether that change could be related to the use of the landscape by the mega-herbivore. In fact, the results are amongst the first to report evidence of differential change in vegetation structure at the landscape scale. That change could be related to selective use of vegetation by elephants as reported in earlier studies (Stokke and Du Toit, 2002, Codron et al., 2006). As elephants forage, they are known to push and uproot trees thus leading to possible structural changes in vegetation (Ihwagi et al., 2010, Nasseri et al., 2011). Following this logic, it can thus be expected that the rates of change would differ by vegetation/cover type since the rates of use

also differ. However, veld fires and rainfall variability have an equally important impact on vegetation (Holdo et al., 2009, Dublin et al., 1990). For instance, variability in long-term rainfall is known to drive vegetation change in other landscapes (De Beer et al., 2006). Similarly, frequent veld fires in an area might result in the selection of fire-tolerant species; controls bush encroachment; and leads to major changes in structure in the long-term (Bond et al., 2003, Kruger, 1984). While the impact of veld fires is largely limited to areas where they occur often, rainfall variability might affect entire landscapes. Thus, similar to what has been reported for elephants in this study, the impact of veld fires might also differ by vegetation type.

The finding that elephants are selective when foraging and might, therefore, drive change differently in dissimilar vegetation/cover types are in tandem with earlier studies (Owen-Smith and Chafota, 2012, Guy, 1976, Ihwagi et al., 2010). However, in most of those studies, conclusions were based on data collected in a few randomly selected plots thus giving a more localised view. In the current study, conclusions are based on remotely sensed data that give a repetitive and synoptic view of entire landscapes.

The major strength of this study lies in the fact that results are based on tracking GPS-collared elephants for periods up to two and a half years thus giving a broad view of how they utilise the landscape. In addition, vegetation change was analysed over 17 years as opposed to once-off observations made in the field, thus giving a more complete picture of the trends. Fine temporal scale (16 days NDVI composites) data were also used to test for correlation with elephant utilisation of the landscape thus capturing fine scale detail on how elephants possibly interact with vegetation. Moreover, the study tests a new hypothesis and findings open a new window to enhance knowledge on how elephants might be driving change in vegetation structure at different rates in heterogeneous savannah landscapes. However, results are based on observations made in one study area hence making it difficult to generalise. Thus, in future

similar hypotheses need to be tested in other landscapes to seek generalisation of results. While elephants are an important driver of vegetation change, it is important to note that vegetation might also drive elephant movement. Whether elephants are driving change in vegetation or it is the vegetation driving change in elephant movement remains an unanswered question which requires further investigation. Future studies could also test the combined effect of elephants, veld fires and rainfall variability on vegetation, as well as their relative importance as drivers of change.

6.5 Conclusion

The major finding of this chapter is that change in tree cover can be differentiated by vegetation/cover type in the GNP. The magnitude of change was higher in certain vegetation/cover types than others. In most vegetation/cover types, tree cover decreased significantly over the study area resulting in overall opening up of habitats. Results further report on the possible association between utilisation of vegetation by elephants and change in vegetation structure. The results are important to park managers since the change in vegetation structure could drive change in the distribution of wild animals. The study further reinforces the utility of elephant tracking from GPS collars combined with remotely sensed data in enhancing knowledge on how they utilise the landscape and also their potential as drivers of change in certain vegetation/cover types.

References

Asner, G. P., Vaughn, N., Smit, I. P. & Levick, S. (2016) Ecosystem-scale effects of megafauna in African savannas. Ecography, 39**,** 240-252.

Bivand, R., Keitt, T., Rowlingson, B., Pebesma, E., Sumner, M., Hijmans, R., Rouault, E. & Bivand, M. R. (2018) Package 'rgdal'.

Bond, W., Midgley, G., Woodward, F., Hoffman, M. & Cowling, R. (2003) What controls South African vegetation-climate or fire? South African Journal of Botany, 69**,** 79-91.

Chamaillé-Jammes, S., Fritz, H. & Madzikanda, H. (2009) Piosphere contribution to landscape heterogeneity: a case study of remote-sensed woody cover in a high elephant density landscape. Ecography, 32**,** 871-880.

Codron, J., Lee-Thorp, J. A., Sponheimer, M., Codron, D., Grant, R. C. & De Ruiter, D. J. (2006) Elephant (*Loxodonta africana*) diets in Kruger National Park, South Africa: spatial and landscape differences. Journal of Mammalogy, 87**,** 27-34.

Cunliffe, R., Muller, T. & Mapaura, A. (2012) Vegetation survey of Gonarezhou National Park, Zimbabwe. Zimbabwe Parks and Wildlife Management Authority, Harare.

Davies, A. B., Gaylard, A. & Asner, G. P. (2018) Megafaunal effects on vegetation structure throughout a densely wooded African landscape. Ecological Applications, 28**,** 398-408.

De Beer, Y., Kilian, W., Versfeld, W. & Van Aarde, R. J. (2006) Elephants and low rainfall alter woody vegetation in Etosha National Park, Namibia. Journal of Arid Environments, 64**,** 412-421.

Dublin, H. T., Sinclair, A. R. & Mcglade, J. (1990) Elephants and fire as causes of multiple stable states in the Serengeti-Mara woodlands. The Journal of Animal Ecology**,** 59, 1147-1164.

Dunham, K. (2015) National summary of Aerial Survey Results for Elephant in Zimbabwe: 2014. Great Elephant Census Vulcan Inc., Washington, USA.

Dunham, K., Van Der Westhuizen, E., Van Der Westhuizen, H. & Ndaimani, H. (2013) Aerial survey of elephants and other large herbivores in Gonarezhou National Park (Zimbabwe), and surrounding areas: 2013. Zimbabwe Parks and Wildlife Management Authority.

Frair, J. L., Fieberg, J., Hebblewhite, M., Cagnacci, F., Decesare, N. J. & Pedrotti, L. (2010) Resolving issues of imprecise and habitat-biased locations in ecological analyses using GPS telemetry data. Philosophical Transactions of the Royal Society of London B: Biological Sciences, 365**,** 2187-2200.

Fullman, T. J. & Child, B. (2013) Water distribution at local and landscape scales affects tree utilization by elephants in Chobe National Park, Botswana. African Journal of Ecology, 51**,** 235-243.

Gandhi, G. M., Parthiban, S., Thummalu, N. & Christy, A. (2015) NDVI: vegetation change detection using remote sensing and GIS–A case study of Vellore District. Procedia Computer Science, 57**,** 1199-1210.

Gandiwa, E., Magwati, T., Zisadza, P., Chinuwo, T. & Tafangenyasha, C. (2011) The impact of African elephants on *Acacia tortilis* woodland in northern Gonarezhou National Park, Zimbabwe. Journal of Arid Environments, 75**,** 809-814.

Goheen, J. R. & Palmer, T. M. (2010) Defensive plant-ants stabilize megaherbivore-driven landscape change in an African savanna. Current Biology, 20**,** 1768-1772.

Gu, Y., Brown, J. F., Verdin, J. P. & Wardlow, B. (2007) A five-year analysis of MODIS NDVI and NDWI for grassland drought assessment over the central Great Plains of the United States. Geophysical Research Letters, 34. 1-6.

Guy, P. (1976) The feeding behaviour of elephant (*Loxodonta africana*) in the Sengwa area Rhodesia. South African Journal of Wildlife Research-24-month delayed open access, 6**,** 55-63.

Herremans, M. (1995) Effects of woodland modification by African elephant *Loxodonta africana* on bird diversity in northern Botswana. Ecography, 18**,** 440-454.

Holdo, R. M., Holt, R. D. & Fryxell, J. M. (2009) Grazers, browsers, and fire influence the extent and spatial pattern of tree cover in the Serengeti. Ecological Applications, 19**,** 95-109.

Ihwagi, F. W., Vollrath, F., Chira, R. M., Douglas-Hamilton, I. & Kironchi, G. (2010) The impact of elephants, *Loxodonta africana*, on woody vegetation through selective debarking in Samburu and Buffalo Springs National Reserves, Kenya. African Journal of Ecology, 48**,** 87-95.

Kalwij, J., De Boer, W., Mucina, L., Prins, H., Skarpe, C. & Winterbach, C. (2010) Tree cover and biomass increase in a southern African savanna despite growing elephant population. Ecological Applications, 20**,** 222-233.

Kruger, F. (1984) Effects of fire on vegetation structure and dynamics. Ecological effects of fire in South African ecosystems. Springer, Berlin.

Landman, M., Schoeman, D. S., Hall-Martin, A. J. & Kerley, G. I. (2012) Understanding long-term variations in an elephant piosphere effect to manage impacts. PLoS One, 7**,** e45334.

Mas, J. F. (1999) Monitoring land-cover changes: a comparison of change detection techniques. International Journal of Remote Sensing, 20**,** 139-152.

Mosugelo, D. K., Moe, S. R., Ringrose, S. & Nellemann, C. (2002) Vegetation changes during a 36-year period in northern Chobe National Park, Botswana. African Journal of Ecology, 40**,** 232-240.

Mukwashi, K., Gandiwa, E. & Kativu, S. (2012) Impact of African elephants on *Baikiaea plurijuga* woodland around natural and artificial watering points in northern Hwange

National Park, Zimbabwe. International Journal of Environmental Sciences, 2**,** 1355-1368.

Nasseri, N. A., Mcbrayer, L. D. & Schulte, B. A. (2011) The impact of tree modification by African elephant (*Loxodonta africana*) on herpetofaunal species richness in northern Tanzania. African Journal of Ecology, 49**,** 133-140.

Ndaimani, H., Murwira, A., Masocha, M., Gara, T. W. & Zengeya, F. M. (2017a) Evaluating the performance of aerial survey data in elephant habitat modelling. African Journal of Ecology, 55**,** 270-281.

Ndaimani, H., Murwira, A., Masocha, M. & Zengeya, F. M. (2017b) Elephant (*Loxodonta africana*) GPS collar data show multiple peaks of occurrence farther from water sources. Cogent Environmental Science, 3**,** 1420364.

Ndoro, O., Mashapa, C., Kativu, S. & Gandiwa, E. (2016) Impact of African elephant on baobab along a surface water availability gradient in Mana Pools National Park, Zimbabwe. Tropical Ecology, 57**,** 333-341.

Owen-Smith, N. & Chafota, J. (2012) Selective feeding by a megaherbivore, the African elephant (*Loxodonta africana*). Journal of Mammalogy, 93**,** 698-705.

Rutina, L. P., Moe, S. R. & Swenson, J. E. (2005) Elephant *Loxodonta africana* driven woodland conversion to shrubland improves dry-season browse availability for impalas *Aepyceros melampus*. Wildlife Biology, 11**,** 207-213.

Stokke, S. & Du Toit, J. T. (2002) Sexual segregation in habitat use by elephants in Chobe National Park, Botswana. African Journal of Ecology, 40**,** 360-371.

Thenkabail, P. S. & Lyon, J. G. (2016) Hyperspectral remote sensing of vegetation, CRC Press, Boca Raton.

Valeix, M., Fritz, H., Sabatier, R., Murindagomo, F., Cumming, D. & Duncan, P. (2011) Elephant-induced structural changes in the vegetation and habitat selection by large herbivores in an African savanna. Biological Conservation, 144**,** 902-912.

Van Staden, P. J., Bezuidenhout, H., Ferreira, S. & Bredenkamp, G. J. (2017) The effects of elephants and fire on vegetation at Marakele National Park, South Africa. Pachyderm**,** 58, 107-122.

Wall, J., Wittemyer, G., Klinkenberg, B., Lemay, V. & Douglas-Hamilton, I. (2013) Characterizing properties and drivers of long-distance movements by elephants (*Loxodonta africana*) in the Gourma, Mali. Biological Conservation, 157**,** 60-68.

Zhang, X., Friedl, M. A., Schaaf, C. B., Strahler, A. H., Hodges, J. C., Gao, F., Reed, B. C. & Huete, A. (2003) Monitoring vegetation phenology using MODIS. Remote Sensing of Environment, 84**,** 471-475.

Chapter 7

Synthesis

7. Introduction

Although scientists generally agree that African elephants (*Loxodonta africana*) transform vegetation structure when foraging, knowledge on differences in their impact across heterogeneous landscapes remains largely inconclusive. For instance, it has long been known that intense elephant foraging around water points leads to opening up (Laws, 1970, Beuchner and Dawkins, 1961, van Staden et al., 2017) or alternatively densification of woody vegetation (Mueller-Dombois, 1972, Valeix et al., 2007) in those landscapes (i.e., the piosphere effect). Nevertheless, patterns of change farther from the water points remain least understood (Ben-Shahar, 1996). In addition, earlier attempts to investigate the impact of elephants on vegetation were largely based on observing elephant-driven tree damage in localised monitoring plots (e.g., Ben-Shahar, 1998, Ben-Shahar, 1993, Holdo, 2007). Although these studies provided useful insights on how elephant foraging might drive vegetation change, they remained largely limited in spatial extent, therefore largely inconclusive To date, advances in Geographical Information Science, combined with enhanced availability of freely downloadable remotely sensed data makes it imperative to revisit hypotheses predicting elephant impact on vegetation at larger spatial extents, thus providing more complete insights into this phenomenon with the final aim of enhancing ecosystem management.

In this thesis, the main aim was to develop, test and apply Geographical Information Systems (GIS) and remote sensing methods to understand whether and how elephant foraging drives change in vegetation structure across a largely heterogeneous savannah landscape. The specific objectives of the thesis were to 1) develop elephant distribution models from presence data collected using GPS collars and compare their predictive ability to those developed from aerial survey data; 2) propose a new method for correcting locational error in aerial survey data and to test whether the correction improves elephant distribution modelling results; 3) determine

whether elephant presence peaks farther from water points in addition to the known peak near water; 4) validate selective utilisation of a heterogeneous landscape by elephants; and 5) investigate whether and how the rate of change in vegetation structure differs across a heterogeneous landscape.

7.1 How do elephant distribution models built from GPS collar data compare to those built from aerial survey data?

The understanding of how elephants are distributed across any landscape to a large extent depends on the quality of presence data used in modelling (Phillips et al., 2004, Elith et al., 2006). Although presence data from aerial surveys have been used extensively in modelling (Scheidat et al., 2012, Chamaille Jammes et al., 2007), their accuracy has been questioned (e.g., Murwira and Skidmore, 2005). However, to the best of our knowledge, no studies have ever provided empirical evidence on how the data would affect modelling output.

The thesis compared the predictive ability of elephant distribution models built from presence data collected using GPS collars to those built from data collected during aerial surveys Findings in this thesis (Chapter 2) demonstrate that elephant distribution models built using GPS collar data as the response variable; and distance from water and NDVI as the two predictor variables; consistently have better predictive ability when compared to those based on data collected from aerial survey data. However, increasing the spatial resolution of the predictor variable data to 1000m improves the predictive ability of models based on aerial survey data. The prediction of elephant distribution from aerial survey data yielded better results in more open habitats than in the closed habitats.

Although GPS collar data lack adequate spatial spread when compared to aerial survey data, they have better locational accuracy when compared to the latter. Thus, even when used

together with finer resolution predictor variable data (e.g. at 30m), it is most likely that the location coordinates collected from GPS collars sample the exact grid cell where the elephant was at the time of the fix. Increasing the size of the grid cell for the predictor variable to 1000m implies that points with substantial locational error could still be found in the same cell where the elephant was at the time of sampling and this explains why models built using coarser data perform better than those built using finer data. Additionally, position fixes from GPS collars are collected even when collared elephants are under tree canopies thus allowing for adequate sampling of the entire range of habitats visited by the elephant. Adequate sampling would allow for the building of spatial models that better represent the true distribution of the elephant (Araujo and Guisan, 2006).

On the other hand, aerial survey data are associated with a locational error since position data are collected along the line of flight of the aircraft when in actual fact the sighting is located within a 150m wide search strip located several metres from the line of flight. This possibly introduces error that might affect model performance. More so, detectability of elephants from the air could be inhibited by tree canopies and shade (Ancrenaz et al., 2004). Thus, the chance of missing an elephant during an aerial survey is higher than that of missing position fixes from the GPS collars. The finding that detectability of animals under tree canopies is reduced when sampling using aerial surveys is in line with earlier studies (Pollock and Kendall, 1987, Jachmann, 2002). Thus, findings in this thesis (Chapter 2) report on the superiority of elephant distribution models based on GPS collar data over those based on aerial survey data, especially when used together with finer resolution predictor variable data. The study is amongst the earliest attempts to provide evidence of the shortcomings of aerial survey data in modelling the distribution of elephants.

7.2 A new method for correcting the locational error in aerial survey data

The development of novel approaches for improving the locational accuracy of elephant presence data collected from aerial surveys opens opportunities for enhancing our understanding of their ranging behaviour.

Chapter 3 of this thesis proposes a new method for correcting locational error of aerial survey data. Testing the corrected data against uncorrected data provided evidence that the correction improves the performance of species distribution models. However, the correction improved the predictive ability of models better in heterogeneous landscapes than in the homogenous landscapes. This is possibly because a slight change in location in a heterogeneous landscape could enable sampling of a different habitat from the original location. The magnitude of the correction was found to be different in all the three study areas (Gonarezhou, Hwange and Mana Pools National Park). Based on the results, it was suggested that using different observers possibly resulted in differences in the magnitude of the correction.

The finding that the locational error of aerial survey data can be corrected to yield better modelling results (see Figure 3-5) is critical since it enables a better understanding of how elephants and other animals utilise the landscape from data collected during aerial surveys. Elephant location data collected from aerial surveys are more widespread than GPS collar data since in the former sampling is systematic. Thus, the data from aerial surveys enable sampling of the entire landscape hence they possibly sample the full range of habitats represented in the survey region. However, the major weakness of location data collected from aerial surveys is that it is associated with the error and that error has been found to range up to 177m. Even with the correction suggested in Chapter 3 of this thesis, the new location is found at the centre of a 150m wide search strip. The correction, in its current state, thus fails to outrightly remove the error. This is perhaps explained by the failure of the corrected data to improve model

performance in homogenous landscapes since the new position is likely to sample the same habitat as that sampled by the uncorrected position. However, it is imperative that the correction could be useful in heterogeneous landscapes where the new position possibly samples a different habitat.

The other weakness of aerial surveys when pitted against using GPS collars is their failure to provide data covering long periods (Ferreira and Aarde, 2009). At the best, aerial surveys provide a snapshot of how animals are distributed across an entire landscape at a specific time. Changes in patterns of use with time are largely missed by aerial surveys (Vermeulen et al., 2013). For instance, dry season and wet season use of the landscape by elephants has been observed to differ significantly in savannah landscapes. Thus, even with the suggested correction, aerial survey data lack temporal coverage of the ranging behaviour of elephants. GPS collar data, on the other hand, are much more precise since the error in location readings has been observed to rarely exceed 100m (Rempel et al., 1995). In addition, position fixes located under tree canopies are often captured while these are largely missed during aerial surveys. More so, at the fix interval of four hours used in this thesis, GPS collars capture temporal variations in the ranging behaviour of elephants better than aerial surveys with data covering a few days.

Taken together, results in Chapter 3 provide a basis for using corrected aerial survey data in modelling the distribution of elephants at a particular time of the year. However, when GPS collar data are available, it would be logical to use them, especially in the case where the objective is to test for temporal changes in distribution. Chapters 4, 5 and 6, therefore, use GPS collar data to explain the distribution of elephants in the Gonarezhou National Park.

Findings presented in Chapter 3 are amongst the first to report correction of locational error from aerial surveys to improve modelling output. The results lay the basis for further correction of aerial survey data with the aim of enhancing knowledge on the ranging behaviour of the megaherbivore; especially where GPS collar data are not available.

7.3 Does elephant presence peak farther from water?

Knowledge on the impact of elephants on vegetation in landscapes located near water points (i.e., the piosphere effect) is well developed (Loarie et al., 2009, Chamaille Jammes et al., 2007). In fact, the earliest description of the piosphere dates back to the 1960s (Lange, 1969); and ever since interest on the subject has intensified (Thrash et al., 1995, Morris, 2017). To date, evidence that elephant presence peaks at water is abundant and that peak has been linked to the fact that the mega-herbivore is water-dependent (Smuts, 1974). However, whether elephant presence also peaks farther from water is not well described in the literature.

Results in Chapter 4 demonstrate that elephant presence peaks first at water points and then at other sites located further away from water. The peaks located farther from the water were characterised by high tree cover (high NDVI). These findings represent one of the earliest attempts to describe peaks of elephant utilization that are not linked to drinking points at the landscape level; from remotely sensed data; as opposed to localised observations from fieldwork.

The finding relating to enhanced use of habitats located near water reinforces the idea that the elephant is a water-dependent herbivore. Although elephants range far when foraging in order to meet daily energy and protein needs, evidence from existing literature suggests that they rarely go beyond 10km and will often visit drinking points daily to drink and for other thermoregulatory purposes (Chamaillé-Jammes et al., 2013). This is especially true for cow

herds which are in the attendance of young calves. The cow herds are reported not to range far from water to avoid walking long distances with the calves (Barnes, 1983). Water dependency is not only reported for elephants, but also for other animals found in the savannah landscape. Knowledge of the peak located close to water is important for management since this is usually a hotspot of foraging and often results in high rates of change in vegetation structure (De Beer et al., 2006). Overall, that the elephant intensely utilises piosphere habitats (habitats located close to water) is well known from observations made from sampling plots in the field (Gaylard et al., 2003, Mukwashi et al., 2012). Findings in this thesis add to that knowledge by providing landscape level evidence from remotely sensed data.

The other peaks of elephant presence located farther from water sources; described in this thesis; are not adequately explained in existing literature. This finding provides a platform for hypothesizing that away from water, elephants also have hotspots of presence not linked to the need to drink water but possibly linked to foraging and standing under the shade for thermoregulation. These peaks were observed to be associated with high tree cover (high NDVI). Knowledge on the existence of peaks in elephant presence farther from water, especially provided at the landscape level, points to the need to test for possible change in vegetation structure in those landscapes. Taken together, results presented in Chapter 3 of this thesis provide evidence for the utility of remote sensing and GPS-collar tracking of elephants in providing a broad landscape view on how the mega-herbivore utilises the landscape and possibly transforms vegetation structure in the process.

Findings in Chapter 4 are amongst the earliest descriptions of peaks of elephant presence farther from water points.

7.4 Additional evidence for selective use of a heterogeneous savannah landscape by elephants

Studies that test whether elephants selectively utilise heterogeneous landscapes provide the impetus for testing whether their impact on vegetation could also be differentiated. To date, selective utilisation of the landscape by elephants is not adequately described at the landscape level.

Results in Chapter 5 demonstrate that; 1) the speed of movement of elephants differs by vegetation/cover type, and 2) the time spent by elephants in the dissimilar vegetation/cover types also differs significantly. The findings reinforce the notion that elephants are selective when foraging, in tandem with earlier studies.

In earlier studies, elephants were reported to move at fast speeds along corridors connecting key resources like water and forage while the slow movement has been linked to foraging (Douglas-Hamilton et al., 2005, Galanti et al., 2000). Additionally, elephants might also move slowly in landscapes where they utilise salt licks (Holdø et al., 2002) and stand under trees for shade (Kinahan et al., 2007). Moreover, elephants utilised human-settled landscapes during the night but relocated to the more peaceful protected areas during early morning hours and fast speeds (Graham et al., 2009). This behaviour was linked to avoidance of disturbance.

In this thesis, although data were not adequate for investigating why elephants change their speed of movement in different vegetation/cover types, results confirm selective use of a heterogeneous landscape by the mega-herbivore. The finding could imply that the impact of elephants on vegetation can be differentiated by vegetation/cover type. Elephants push, debark and uproot trees when foraging (Guy, 1976). Thus, they potentially modify vegetation structure in landscapes where they spent most of their time. Taken together, findings presented in Chapter

5 provide the basis for hypothesising that selective use of the landscape also leads to a selective impact on vegetation.

Findings in this thesis represent one of the first few attempts to apply GIS and remote sensing to understand whether elephants select certain vegetation/cover types while avoiding others. That was particularly made possible by the availability of a schematic vegetation map which divides the landscape into distinct units in which use by the elephant differs. In the past, most studies testing the impact of elephants on vegetation looked at the gradient of elephant-induced change at increasing distance from water points (i.e. the piosphere effect) (e.g., Fullman and Child, 2013). In this thesis, we shift attention to other landscapes located further from water in an effort to provide a more complete picture of elephant impact on vegetation.

7.5 Different rates of vegetation change in vegetation/cover types

The general consensus amongst ecologists is that elephants and other mega-herbivores drive change in vegetation structure, especially in landscapes where they occur in abundance (e.g., Dublin et al., 1990). However, descriptions of difference in the rates of change in heterogeneous landscapes are few.

Results in Chapter 6 demonstrate that tree cover decreased significantly in the Gonarezhou national park between 2000 and 2016. The rates of decrease were observed to be different in the fourteen major vegetation/cover types. Elephant occupancy, calculated from Kernel Density Estimation, was found to be significantly correlated with long-term tree cover change (MOD44B data). Elephant KDE was also found to be significantly correlated with fine-scale vegetation cover data (MOD13Q1) during the years 2015, 2016 and 2017.

The reported decrease in tree cover in about 24% of the Gonarezhou national park provides evidence for a changing landscape. A changing landscape is of interest to park managers it will drive change in the distribution of other wildlife species. While it is not yet clear whether the change observed in the Gonarezhou national park is solely attributable to elephant browsing, positive correlation with elephant occupancy provides the impetus for further testing how elephant foraging contributes to vegetation change. Evidence from existing literature suggests that in addition to elephant foraging, climate change and veld fires (Frost and Robertson, 1985, Lykke, 2000) drive change in vegetation structure, especially in African savannahs. Although it was not the objective of this study to test the impact of the other two variables, it can be reasoned that the study area is fairly homogenous in terms of climate; hence the different rates of change reported in the different vegetation/cover types are not easily attributable to climate variables. In addition, veld fires are largely non-selective when they burn. Thus, it would be erroneous to assume that their effect on vegetation can be differentiated by vegetation/cover type. Therefore it is logical to propose that elephants are driving tree cover change in the Gonarezhou national park. This assertion is based on the significant correlations between elephant utilization and tree cover, and the finding reported in Chapter 5 that elephants selectively utilise heterogeneous savannah landscapes.

Findings of this thesis are amongst the first to report different rates of vegetation change in a heterogeneous savannah landscape where elephants occur at high densities.

7.6 Contributions of this thesis to knowledge

This thesis provides the following insights in relation to spatial ecology with a focus on semi-arid savannah ecosystems:

1. Predicting elephant distribution from GPS collar data provides better modelling output than using data collected from aerial surveys (Chapter 2). This finding represents one

of the earliest attempts to compare the predictive ability of models built from aerial survey data to those built from GPS collar data.

2. Predicting elephant distribution from aerial survey data corrected for locational error improves modelling results (Chapter 3). The proposed correction method is new and thus represents an early attempt to improve the locational accuracy of aerial survey data in habitat modelling. However, aerial survey data are useful where GPS collar data are not available.
3. Elephant presence peaks farther from water in addition to the known peak located at water or near water points (Chapter 4). The finding represents one of the earliest evidence of elephant peaks of presence further from water sources.
4. Elephants selectively utilise a heterogeneous savannah landscape (Chapter 5). In fact, some vegetation types are selected while others are avoided. Although this has been reported before in literature, the finding serves to reinforce existing evidence that elephants are selective herbivores.
5. The impact of elephants on vegetation structure could be differentiated by vegetation/cover type (Chapter 6). This finding is new in that it provides a broad landscape view of possible elephant-vegetation dynamics as opposed to limited observations made in localised areas.

7.7 Recommendations for future research

Although we developed, tested and applied GIS, GPS and Remote sensing methods to provide evidence of a changing landscape characterised by high elephant utilisation, future research should test whether the observed decrease in tree cover could be altering habitat use by other animal species found in the study area. Such a study could provide insight into possible future local extinctions of animal species that is driven by modification of habitats by elephants.

Secondly, it is recommended that future studies should predict the further change that is likely to occur in tree cover in the different vegetation/cover types in the future. Results from the study will enhance knowledge on possible local extinctions of plant communities driven by elephant utilisation.

Thirdly, testing the combined effect of elephant browsing, climate and veld fires on vegetation structure is recommended for future studies. It is well known that these three are the major drivers of change, especially in protected African savannahs. Results from such study will firstly provide evidence on the combined effect of the predictors and secondly give insight on how each predictor contributes to variability in vegetation cover.

Finally, future studies could also test the optimum density of elephants in protected areas that will not result in major alteration of ecosystem structure and function. Existing thresholds are largely based on observations made in the field and these often lack good spatial and temporal coverage. In future determining the thresholds from remotely sensed data will provide a landscape view as opposed to the localised observations made from labour- intensive fieldwork.

References

Ancrenaz, M., Goossens, B., Gimenez, O., Sawang, A. & Lackman-Ancrenaz, I. (2004) Determination of ape distribution and population size using ground and aerial surveys: a case study with orang-utans in lower Kinabatangan, Sabah, Malaysia. *In:* Animal Conservation Forum, 2004. Cambridge University Press, 375-385.

Araujo, M. B. & Guisan, A. (2006) Five (or so) challenges for species distribution modelling. Journal of Biogeography, 33**,** 1677-1688.

Barnes, R. (1983) Elephant behaviour in a semi-arid environment. African Journal of Ecology, 21**,** 185-196.

Ben-Shahar, R. (1993) Patterns of elephant damage to vegetation in northern Botswana. Biological Conservation, 65**,** 249-256.

Ben-Shahar, R. (1996) Do elephants over-utilize mopane woodlands in northern Botswana? Journal of Tropical Ecology, 12**,** 505-515.

Ben-Shahar, R. (1998) Changes in structure of savanna woodlands in northern Botswana following the impacts of elephants and fire. Plant Ecology, 136**,** 189-189.

Beuchner, H. & Dawkins, H. C. (1961) Vegetation change induced by elephants and fire in Murchison Falls National Park, Uganda. Ecology, 42**,** 752-766.

Chamaillé-Jammes, S., Mtare, G., Makuwe, E. & Fritz, H. (2013) African elephants adjust speed in response to surface-water constraint on foraging during the dry-season. PloS one, 8**,** e59164.

Chamaille Jammes, S., Valeix, M. & Fritz, H. (2007) Managing heterogeneity in elephant distribution: interactions between elephant population density and surface-water availability. Journal of Applied Ecology, 44**,** 625-633.

De Beer, Y., Kilian, W., Versfeld, W. & Van Aarde, R. J. (2006) Elephants and low rainfall alter woody vegetation in Etosha National Park, Namibia. Journal of Arid Environments, 64**,** 412-421.

Douglas-Hamilton, I., Krink, T. & Vollrath, F. (2005) Movements and corridors of African elephants in relation to protected areas. Naturwissenschaften, 92**,** 158-163.

Dublin, H. T., Sinclair, A. R. & Mcglade, J. (1990) Elephants and fire as causes of multiple stable states in the Serengeti-Mara woodlands. The Journal of Animal Ecology**,** 59, 1147-1164.

Elith, J., Graham, C. H., Anderson, R. P., Dudík, M., Ferrier, S., Guisan, A., Hijmans, R. J., Huettmann, F., Leathwick, J. R. & Lehmann, A. (2006) Novel methods improve prediction of species' distributions from occurrence data. Ecography**,** 29, 129-151.

Ferreira, S. M. & Aarde, R. J. V. (2009) Aerial survey intensity as a determinant of estimates of African elephant population sizes and trends. South African Journal of Wildlife Research, 39**,** 181-191.

Frost, P. & Robertson, F. (1985) Fire the ecological effects of fire in savannas. Determinants of Tropical Savannas; Walker, TS, Walker, BH, Eds**,** 93-140.

Fullman, T. J. & Child, B. 2013. Water distribution at local and landscape scales affects tree utilization by elephants in Chobe National Park, Botswana. African Journal of Ecology, 51**,** 235-243.

Galanti, V., Tosi, G., Rossi, R. & Foley, C. (2000) The use of GPS radio-collars to track elephants (*Loxodonta africana*) in the Tarangire National Park (Tanzania). Hystrix-the Italian Journal of Mammalogy, 11, 27-37.

Gaylard, A., Owen-Smith, N. & Redfern, J. (2003) Surface water availability: implications for heterogeneity and ecosystem processes. The Kruger experience: Ecology and management of savanna heterogeneity**,** Island Press, Washington, D.C., USA.

Graham, M. D., Douglas-Hamilton, I., Adams, W. M. & Lee, P. C. (2009) The movement of African elephants in a human-dominated land-use mosaic. Animal Conservation, 12**,** 445-455.

Guy, P. (1976) The feeding behaviour of elephant (*Loxodonta africana*) in the Sengwa area Rhodesia. South African Journal of Wildlife Research-24-month delayed open access, 6**,** 55-63.

Holdo, R. M. (2007) Elephants, fire, and frost can determine community structure and composition in Kalahari woodlands. Ecological Applications, 17**,** 558-568.

Holdø, R. M., Dudley, J. P. & Mcdowell, L. R. (2002) Geophagy in the African elephant in relation to availability of dietary sodium. Journal of Mammalogy, 83**,** 652-664.

Jachmann, H. (2002) Comparison of aerial counts with ground counts for large African herbivores. Journal of Applied Ecology, 39**,** 841-852.

Kinahan, A., Pimm, S. L. & Van Aarde, R. J. (2007) Ambient temperature as a determinant of landscape use in the savanna elephant, *Loxodonta africana*. Journal of Thermal Biology, 32**,** 47-58.

Lange, R. T. (1969) The piosphere: sheep track and dung patterns. Journal of Range Management**,** 22, 396-400.

Laws, R. M. (1970) Elephants as agents of habitat and landscape change in East Africa. Oikos**,** 21, 1-15.

Loarie, S. R., Van Aarde, R. J. & Pimm, S. L. (2009) Fences and artificial water affect African savannah elephant movement patterns. Biological Conservation, 142**,** 3086-3098.

Lykke, A. (2000) Local perceptions of vegetation change and priorities for conservation of woody-savanna vegetation in Senegal. Journal of Environmental Management, 59**,** 107-120.

Morris, C. (2017) Vegetation gradients around cattleposts in the eastern mountains of Lesotho. African Journal of Range & Forage Science, 34**,** 219-225.

Mueller-Dombois, D. (1972) Crown distortion and elephant distribution in the woody vegetations of Ruhuna National Park, Ceylon. Ecology, 53**,** 208-226.

Mukwashi, K., Gandiwa, E. & Kativu, S. (2012) Impact of African elephants on *Baikiaea plurijuga* woodland around natural and artificial watering points in northern Hwange National Park, Zimbabwe. International Journal of Environmental Sciences, 2**,** 1355-1368.

Murwira, A. & Skidmore, A. K. (2005) The response of elephants to the spatial heterogeneity of vegetation in a Southern African agricultural landscape. Landscape Ecology, 20**,** 217-234.

Phillips, S. J., Dudík, M. & Schapire, R. E. (2004) A maximum entropy approach to species distribution modeling. *In:* Proceedings of the twenty-first international conference on Machine learning, 2004. ACM Press, New York, 655-662.

Pollock, K. H. & Kendall, W. L. (1987) Visibility bias in aerial surveys: a review of estimation procedures. The Journal of Wildlife Management**,** 51, 502-510.

Rempel, R. S., Rodgers, A. R. & Abraham, K. F. (1995) Performance of a GPS animal location system under boreal forest canopy. The Journal of Wildlife Management**,** 59, 543-551.

Scheidat, M., Verdaat, H. & Aarts, G. (2012) Using aerial surveys to estimate density and distribution of harbour porpoises in Dutch waters. Journal of Sea Research, 69**,** 1-7.

Smuts, G. (1974) Game movements in the Kruger National Park and their relationship to the segregation of sub-populations and the allocation of culling compartments. South African Journal of Wildlife Research-24-month delayed open access, 4**,** 51-58.

Thrash, I., Theron, G. & Bothma, J. D. P. (1995) Dry season herbivore densities around drinking troughs in the Kruger National Park. Journal of Arid Environments, 29**,** 213-219.

Valeix, M., Fritz, H., Dubois, S., Kanengoni, K., Alleaume, S. & Said, S. (2007) Vegetation structure and ungulate abundance over a period of increasing elephant abundance in Hwange National Park, Zimbabwe. Journal of Tropical Ecology, 23**,** 87-93.

Van Staden, P. J., Bezuidenhout, H., Ferreira, S. & Bredenkamp, G. J. (2017) The effects of elephants and fire on vegetation at Marakele National Park, South Africa. Pachyderm**,** 58, 107-122.

Vermeulen, C., Lejeune, P., Lisein, J., Sawadogo, P. & Bouché, P. (2013) Unmanned aerial survey of elephants. PloS one, 8**,** e54700.