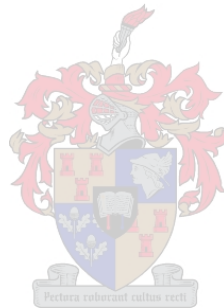


FACTORS AFFECTING LION (PANTHERA LEO) SPATIAL OCCURRENCE IN THE ZAMBEZI REGION, NAMIBIA

by
MICHELLE-LOUISE MOELLER (née Kastern)
(BSC HONOURS ENVIRONMENTAL STUDIES)

Thesis submitted in fulfilment of the requirements for the degree of Master of Science (in Geography and Environmental Studies) in the Faculty of Science at Stellenbosch University.



SUPERVISOR: DR HELEN MARGARET DE KLERK

December 2014

DEPARTMENT OF GEOGRAPHY AND ENVIRONMENTAL STUDIES

DECLARATION

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December 2014

ABSTRACT

Lion populations globally are on the decrease and their habitats are fragmenting. Despite their importance in the Zambezi Region in Namibia, very little research has yet been undertaken to understand their occurrence in this area. One of the primary motivations behind this study was the Kavango Zambezi Trans Frontier Conservation Area's (KAZA TFCA) need to identify trans-boundary movement of carnivores. The collaborative approach with the Ministry of Environment and Tourism in Namibia facilitated the collaring of lions in three National Parks. A number of species were collared and this study focuses on the occurrence of lions in the Zambezi Region.

From the lion home range analysis we could see that the home-range sizes of the collared lions varied greatly across the study area. The difference in home range size is largely due to human pressure surrounding the protected areas. Geographically weighted regression assisted in understanding which were the main drivers of lion occurrence, but further investigation was needed using the Maximum Entropy (MaxEnt) model for presence-only data.

The factors that were investigated as possibly affecting the occurrence of lions included the following: rivers, land cover, land use, elevation and human activity. After pursuing various research models and manipulating data among all these factors, no single factor or combination of factors was found to be reliable predictors on lion occurrence in the study area. As is discussed in recommendations for further research in Chapter 6, it became clear that quantitative data cannot be used in isolation to predict where lions may occur.

KEY WORDS

Panthera leo, home range, Zambezi Region, geographically weighted regression, tLoCoH, Environmental correlates, human factors, Namibia.

OPSOMMING

Leeu-bevolkings is wêreldwyd aan die afneem en hulle habitate fragmenteer al hoe meer. Ten spyte van hulle intrinsieke belang vir die Zambezi streek in Namibië is daar 'n gebrek aan navorsing om die voorkome van leeus in hierdie streek te verstaan. 'n Belangrike motivering vir hierdie studie was die vereiste van die "Kavango Zambezi Trans Frontier Conservation Area" (KAZA TFCA) om grensoorstekende bewegings te verstaan, in onder andere karnivore. In samewerking met KAZA TFCA is GPS-halsbande aangebring aan leeus in drie wildsparke, asook aan individue van ander spesies; hierdie studie fokus spesifiek op leeus in die Zambezi streek.

Analise van die leeus se loopgebied toon breë variasies oor die studiegebied, vir die individue met halsbande, hoofsaaklik te wyte aan menslike druk vanuit omliggende nedersettings. Hierdie studie gebruik geografies geweegde regressie om die belangrikste faktore in die teenwoordigheid van leeus te verstaan, terwyl Maximale Entropie modelle (MaxEnt) vir slegs teenwoordigheid data in verdere ondersoeke ingespan is.

Die volgende faktore is ondersoek ten opsigte van hulle moontlike bydrae tot die voorkome van leeus: riviere, land bedek, grondgebruik, hoogte en menslike aktiwiteite. Verskeie statistiese navorsingsmodelle is ondersoek, met inagneming van data vir al die faktore, maar geen betroubare aanwyser of aanwysers vir leeu-teenwoordigheid is gevind nie. Dit is duidelik dat bloot kwantitatiewe data ontoereikend is om leeu-teenwoordigheid te voorspel, soos uiteengesit in hoofstuk 6.

TREFWOORDE

Panthera leo, Zambezi Streek geografies Geweegde regressie, tLoCoH, omgewingskorrelate, menslike faktore, Namibië.

ACKNOWLEDGEMENTS

A special word of thanks goes to the following people and organisations for their exceptional help throughout the study.

Thank you to the Ministry of Environment and Tourism of Namibia for providing me with the data to do this study and for providing me with a permit. I would like to especially thank the following people; Mr Pierre du Preez for giving me valuable advice and guiding me throughout the MSc. Your support has always been timely and unconditional; Dr Ortwin Aschenborn for always being prepared and enthusiastic to do field work and giving me the opportunity to even get started on this project.; Mr Piet Beytell for keeping me focused on the topic and providing guidance for the project. You will always remain a good friend and colleague and your advice has always been appreciated, even if it's not what I wanted to hear.

I would like to sincerely thank Dr Helen de Klerk for her exceptional patience and supervision. Your endless support is much appreciated and without you I would not have been able to bring it all together.

The staff of the Namibian office of the World Wildlife Fund for Nature and Natural Resource Working Group, especially Greg Stuart-Hill, Sylvia Thompson and Dave Ward. Thank you for sharing your knowledge and experience with me.

A word of thanks goes to the Southern Africa Regional Environmental Program for funding the collection of spatial data, which is such an integral part of understanding human pressures on lion occurrence. Thank you to Craig Beech and Marina Faber from Peace Parks Foundation for providing data for the study.

I am most grateful to the National Geographic Young Explorers Grant for assisting with field costs and giving me the opportunity to do this fieldwork. Your interest has opened many doors for me.

Lise Hanssen, without you field work would not have been as fun.

Thank you to all the conservancies in the Mudumu North and Mudumu South Complex for allowing me to work in your areas.

And my dearest family and friends, especially Kora Holm, Heidi Kastern, Mark von Delft and Carl-Heinz for supporting me throughout this project. Danke!

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ACRONYMS AND ABBREVIATIONS

BNP	Bwabwata National Park
CBNRM	Community based natural resource management
CITES	Convention of International Trade of Endangered Species of Wild Fauna and Flora
GIS	Geographic Information Systems
GPS	Global positioning systems
GWR	Geographically weighted regression
HWC	Human-wildlife conflict
IRDNC	Integrated Rural Development and Nature Conservation
IUCN	International Union for Conservation of Nature
KAZA TFCA	Kavango Zambezi Trans Frontier Conservation Area
KDE	Kernel Density Estimation
MaxEnt	Maximum Entropy
MCP	Minimum Convex Polygon
MET	Ministry of Environment and Tourism
MNC	Mudumu North Complex
MNP	Mudumu National Park
MSC	Mudumu South Complex
NDVI	Normalized Difference Vegetation Index
NGO	Non-governmental organisation
NRNP	Nkasa Rupara National Park
OLS	Ordinary least squares
tLoCoH	Time Local Convex Hull
UTM	Universal Transverse Mercator
VHF	Very high frequency
VIF	Variance inflation factor
WWF	World Wide Fund for Nature

CHAPTER 1: GENERAL INTRODUCTION

“Everything you see exists together in a delicate balance. As king, you need to understand that balance and respect all the creatures, from the crawling ant to the leaping antelope.” (The Lion King)

1.1 BACKGROUND TO THE STUDY

Lions are an iconic African species and one of the Big Five, and draw local and international tourists to Namibia. Tourism can play an important role in the protection and conservation of wildlife and the natural environment (Frost & Bond 2008, Stander 2008). Income from tourism for local communities through the Community Based Natural Resource Management (CBNRM) program can compensate for livestock losses from lions.

Carnivore conservation is a global challenge; as human populations increase, suitable habitat for carnivores decreases (Winterbach et al. 2013, Bauer et al. 2014). Threats to large carnivores include habitat loss, declining natural prey populations, commercial exploitation, and killing due to human-wildlife conflict (Woodroffe & Ginsberg 1998, Bauer, Nowell & Packer 2008, Bauer et al. 2014).

Scientific knowledge about lions is limited in the Zambezi Region of Namibia (formerly known as the Caprivi Region) and studying the species has been complicated until recently due to their trans-boundary movement. With the advances in Global Positioning System (GPS) tracking devices, animals can now be studied in areas inaccessible by vehicle. GPS collars can also track animal movements when crossing the border into neighbouring countries, which was previously impossible. The most recent reported information available on lion density for the Zambezi Region is from the Ministry of Environment and Tourism, Namibia. This is an internal report co-published by this author (Stein et al. 2012) who updated the Large Carnivore Atlas for Namibia in 2012, building on the work previously done by Stander and Hanssen (Standar & Hanssen 2004).

Knowledge of the density of a lion population as well as the anthropogenic effects is relevant. However, environmental variables also play a role when understanding the occurrence of a species in a specific area. Changes in the environment locally can either disturb or enhance the habitat for lions and their prey. The key environmental drivers of the population need to be understood before one can understand how their change can affect the occurrence of a species. This study will investigate the intrinsic (environmental) and extrinsic (anthropogenic) factors, influencing lion movement in three National Parks situated in the Zambezi Region of Namibia.

The study area in the Zambezi Region consists of three National Parks; namely Bwabwata National Park, Mudumu National Park and Nkasa Rupara National Park (Figure 3.1 of study area can be seen in Chapter 3). These National Parks were all proclaimed around the time of Namibian independence in 1990. Bordering these National Parks are Communal Conservancies. Communal Conservancies were created for the protection of wildlife. These are managed by the communities of subsistence farmers and seasonal pastoralists who live within the conservancies. As such, these communities benefit from sustainable use of the natural resources. Communal Conservancies are declared by the government and differ from National Parks in that they are not managed by the government, but by the communities themselves.

The boundaries between park and conservancy are not fenced, but defined by two-spoor tracks. Each National Park has a river along one border as a natural barrier. Bwabwata National Park was a People's Park until 2007, meaning people were living within the park and could use it for grazing of their cattle but certain areas remained as core areas exclusively for wildlife. Although these core areas on the eastern side of the park are not fenced, there is still little movement of wildlife out of these areas. The Communal Conservancies are assisted by Integrated Rural Development and Nature Conservation (IRDNC) to take the Community based Natural Resource Management (CBNRM) approach to managing their areas. This encourages conservation of wildlife through joint venture tourism programs within conservancies to contribute to livelihoods locally as well as trophy hunting as an income.

In the light of the signing of the Kavango Zambezi Trans Frontier Conservation Area (KAZA TFCA) treaty - to which Namibia is a signatory - it was decided to collar lion, leopard, wild dog, spotted hyena, buffalo and elephant in the Zambezi Region with GPS tracking devices to show that this region is an important area of connectivity for many species crossing from Botswana to

Angola. TFCAs are protected areas connected by interspersed conservancies and other game protected areas. (Where a trans-frontier conversation park is two parks bordering each other, a trans-frontier conservation area includes other areas in which wildlife is protected such as conservancies). TFCAs are important in keeping animal movement open across international borders, and to re-open areas of connectivity to reduce habitat fragmentation.

Lions frequently cross into Botswana and Angola in the study site, and the project aims to investigate the factors influencing the movement of the lions. With the availability of new GPS satellite collar technology, it may be possible to track these animals, their movements, and study the environmental and human factors influencing their movements in more detail.

1.2 PROBLEM STATEMENT

Lion populations experience a range of ecological and human pressures (Celesia et al. 2009, Davidson et al. 2011). The purpose of the study is to determine which intrinsic factors (specifically environmental) and extrinsic factors (relating to humans) affect lion movement in the Zambezi Region in Namibia. The environmental factors investigated in this study are the effects of water availability, land cover, and land use on lion spatial selection. The anthropogenic factors investigated in this study are the effects of human infrastructure such as villages and corrals on lion spatial distribution.

1.3 RESEARCH AIM AND OBJECTIVES

To better understand the occurrence of lions in the Zambezi Region, the study aims to determine which intrinsic and extrinsic factors affect the spatial occurrence of lions using home range analyses and spatial statistics within geographic information systems.

To achieve the research aims, the following objectives were set:

1. Fit lions with GPS tracking devices and collect GPS location data from the devices.
2. Collect GPS locations of human activity, namely villages, corrals and water points, in the Communal Conservancies surrounding National Parks.

3. Collect secondary data of river, land use, land cover and lion mortalities.
4. Calculate the spatial-temporal extent of the home range of each collared lion using time Local Convex Hull analyses.
5. Calculate the frequency of occurrence in a 1 km x 1 km grid over the study area.
6. Calculate the distance of each grid cell to the nearest river, village, corral and water point and code each grid cell for categorical variables, namely land use and land cover.
7. Investigate the relationships between lion occurrence and the intrinsic and extrinsic factors, both individually and in combination, to determine the factors that influence their occurrence the most. This is done using geographically weighted regression and MaxEnt.

1.4 SIGNIFICANCE OF THE STUDY

The occurrence and movement of lions is not well understood in the Zambezi Region of Namibia. There has been very little research in this area and, although previous studies have covered certain fundamental elements, there was a need for more complex research of the species.

The study area lies in the centre of the Kavango-Zambezi trans-frontier conservation area (TFCA). This TFCA specifically encourages investigations into trans-boundary movement of wildlife; an understanding of the species at a local level can enable effective trans-boundary collaboration on the conservation of the species.

Time Local Convex Hull is a recent advancement in home range analysis. This technique will be applied to this study and it could aid in new understanding of how lions use their home range.

Evidence is limited on the use of geographically weighted regression and spatial statistics which will be used in this study. If the regression analysis method is shown to aid the conservation of lions in the Zambezi Region, this method can be applied to other regions within Namibia as well as to other species.

1.5 SCOPE AND LIMITATIONS OF THE STUDY

One of the limitations of the study will be to investigate the effect of prey density and movement on lion spatial occurrence. Prey is thought to have a large influence on lion movement in the dry or 'lean' season, although there is no consensus in the literature as to whether lions move after their prey during the rainy season or not. Results from previous studies found that rainfall and habitat affected prey density, which in turn plays a role in shifting patterns of lions' home range (Loveridge et al. 2009, Stander 2009, Valeix et al. 2012). To measure this accurately is difficult without intensive reliable data collection of prey-movements and prey-densities throughout the different times of the year. Prey preferences of lions in the study areas would also need to be determined, a topic beyond the scope of this study but a field for further research. Methods of determining prey preference of lions was explored in research done by Tambling (Tambling et al. 2010). It has been found that lion movements are usually affected by resources rather than social factors (Lehmann et al. 2008) and for that reason it was decided to focus on environmental correlates and human influence rather than factors relating to pride compositions and competition. Another environmental factor which could not be investigated as part of this study due to its complexity of time series analysis, is the effect of fire. NDVI, rainfall and temperature have also not been included in this study.

1.6 THESIS OUTLINE

This study uses information from various disciplines. In order to enhance understanding of the text ahead a short overview of the chapters is given below.

- Chapter 1 gave a brief background to the study as well as describing the aims and objectives. This sets the scene for the chapters to follow.
- Chapter 2 discusses what is current in the literature about lion biology and ecology as well as methods used to do similar studies. This broadens the reader's knowledge of the species and the study and gives motivation why this study chose the factors and techniques it has.
- Chapter 3 describes the design of the study and methodology used for the research. This is supported in the literature review as well as techniques which have not been applied before.

- Chapter 4 displays the results found from home range and species distribution modelling analyses.
- Chapter 5 interprets the results from analysis done.
- Chapter 6 gives a summary and recommendations for further research.

CHAPTER 2: LITERATURE REVIEW

This section reviews studies conducted on lion movement, spatial patterns, ecology and human-wildlife conflict to provide a clearer view of possible factors influencing their movements and spatial selection. Suitable methods and concepts will be applied to the proposed study of factors influencing lion occurrence in the Zambezi Region of Namibia.

2.1 STATUS AND LION ECOLOGY

Lions (*Panthera leo*) are listed as vulnerable under the International Union for Conservation of Nature (IUCN) Red List and the trend internationally of African Lion (*Panthera leo*) numbers is decreasing (Bauer, Nowell & Packer 2008). Lions are currently listed as a CITES Appendix II species (CITES 2012). Their status is currently under review and the outcome thereof could up their priority listing to an Appendix I species (CITES 2004, Lindsey et al. 2012).

The decline of lion populations is mainly due to habitat loss and human-lion conflict (Woodroffe, Thirgood & Rabinowitz 2005). If lions are better understood in their local environment, it can aid communities suffering from human-wildlife conflict to coexist successfully with these predators (Woodroffe, Thirgood & Rabinowitz 2005, Stander 2008, Bauer, de Iongh & Sogbohossou 2010, Chardonnet et al. 2010).

Communities tolerate the losses caused by lions if there is an economic benefit, but this tolerance needs to be developed over time (Stander 2009, Chardonnet et al. 2010). There are a number of initiatives whose goals include supporting sustainable human-wildlife coexistence. The Community Based Natural Resource Management (CBNRM) program in Namibia encourages sustainable wildlife utilisation in the form of trophy hunting and tourism as income for the Communal Conservancies (Naidoo et al. 2011). CBNRM forms the basis of conservancy management whereby communities become responsible for managing their own resources.

This CBNRM program also aims to improve sustainable use of biodiversity and management of communal lands (Stuart-Hill et al. 2005). The Namibian Government, with the help of Non-

governmental Organizations (NGOs), assists willing communal conservancies with the re-establishment of wildlife populations by relocating game to areas where they previously occurred (Paterson et al. 2008).

Home ranges of lions varied across studies with arid regions revealing larger home ranges and moist savannahs revealing smaller home ranges (Spong 2002, Celesia et al. 2009, Loveridge et al. 2009, Power & Compion 2009, Stander 2009, Davidson et al. 2011, Bissett, Bernard & Parker 2012, Valeix et al. 2012).

In the tree savannahs of Kruger National Park, male lions were found to hunt and reside in the same habitat as buffalo (*Syncerus caffer*) (Funston et al. 2003), and a similar pattern was found in Addo Elephant Park (Hayward et al. 2009). The biggest challenge for all predator-prey studies is to determine the prey preference of the carnivore in question and the effect of predators on prey behaviour and populations (Fryxell et al. 2007, Valeix et al. 2009). Lions are Africa's largest carnivores and are thought to structure terrestrial ungulate populations (Mills, Biggs & Whyte 1995, Sinclair 2003). This is noticed on small reserves but in larger National Parks it is difficult to quantify the effect.

Prey preference of lions has been determined using various methods (Tambling et al. 2010, Hayward et al. 2011, Klare, Kamler & Macdonald 2011, Tambling et al. 2012). Tambling et al. (2012) considered the various ways of determining prey preference of lions by comparing positional clusters and scat analyses. They found that neither method can be used in isolation and suggest that, if prey preference needs to be determined, a combination of the two methods needs to be used. This is because GPS clusters alone do not account for resting periods which could be misinterpreted as a kill. The cluster method does not allow for inclusion of small prey if, for example, lions move on rapidly after a warthog kill. Both methods sometimes miss small prey eaten. Scat analyses are subdivided into a further 11 different methods for analysing scat and the significance thereof. A review and critique of these methods can be seen in (Klare, Kamler & Macdonald 2011).

Cub production of lions is a factor which can be affected by human influences. This was evidenced in the Laikipia study where cub production and mortality was higher among female lions with a stock raiding history (Woodroffe & Frank 2005). Another reason for cub mortality is

infanticide, as was observed in Northern KwaZulu-Natal (Hunter et al. 2007). This is a natural process in lion territory establishment where males kill existing cubs when they take over a territory (Schaller 1972).

2.2 CAPTURING AND COLLARING OF LIONS

In order to fit telemetry collars, lions are darted using standard veterinary procedures (Mills 1996). This is usually done from a vehicle at night, as this is when lions are most active (Hayward & Hayward 2006, Ferreira & Funston 2010). Drug combinations used for the darting of free range lions have improved over the years. Original combinations for immobilisation of lions used drugs which could not be reversed (Stander & Morkel 1991) or reversals which took between 20 to 60 minutes for full recovery of lions (van Wyk & Berry 1986). Such combinations put the animal in danger since it could not defend itself soon after the necessary sample collection had been done. This resulted in a lengthy wait for the researcher who had to remain close to the darted animal until the drug wore off. Newer combinations use a tranquiliser (Zolazepam-Tiletamine or Zoletil) together with a reversible sedative (Medetomidine) (Fahlman et al. 2005, Jacquier et al. 2006). Both studies used Antipamazole (Antisedan) to reverse the Medetomidine leading to a faster recovery of the immobilised lion. Dosages described by Fahlmana et al. (2005) are the preferred choice for the study in the Zambezi Region. The mixture uses less Zoletil and more Medetomidine than Jacquier et al. (2006), making the recovery quicker after the antidote is administered. This is important in the Zambezi Region as there is a high elephant density, causing complications during field work, therefore the quicker the recovery of the lion the better.

A completely different combination is used in South Africa which includes three drugs, all of which can be reversed (Wenger et al. 2010). This combination has the best recovery time from the moment that the antidote is given, but the disadvantage is that it requires three drugs for induction and three for reversal, making it logistically more difficult and expensive. This has not been tested and will not be used for the study as not all drugs can easily be acquired in Namibia.

2.3 ENVIRONMENTAL VARIABLES AFFECTING LION AND OTHER SPECIES

A review done on environmental correlates of lion demography found that lion density is correlated with rainfall, soil nutrients and annual mean temperature (Celesia et al. 2009). However, this review was very broad and cannot reliably be used to determine environmental correlates of lion density for a specific study site. There are further reviews which indicate that certain environmental correlates can be considered with greater certainty when considering particular study sites.

2.3.1 Water

An environmental factor which can be considered is surface water or water hole availability. Valeix et al. (2010) studied the influence of water holes on lion movement in Hwange National Park and found that lions spend a significant amount of time within two kilometres of a water hole. The study also found that the habitat associated with water is a determining factor of lion habitat selection. The study area of Valeix et al. (2010) is comparable to that of this study and suggests it would be relevant to include the effect of water availability as one of the factors affecting lion spatial occurrence in the Zambezi Region.

Bwabwata National Park, Mudumu National Park and Nkasa Rupara National Park have the same amount of average rainfall, 600-700mm ((Mendelsohn & Roberts 1997) in (O'Connell-Rodwell et al. 2000)) as Hwange National Park, but differ in that the permanent water sources are rivers and floodplains, rather than water holes. Lions in Hwange National Park changed their habitat use to denser vegetation classes during a hunting moratorium (Davidson et al. 2011).

In Etosha National Park, artificial water points were constructed and this led to a higher carrying capacity of lions in the studied area. This was due to the increase of prey density through creating water availability (Stander 1991).

Woodroffe and Frank (2005) investigated the effect of rainfall on lion mortality. The study focused on months where at least 20 lions were monitored per month. The factors were broken into two categories, months where zero lions were killed by humans and months where more than one lion was killed by humans. This was correlated to months with less than 50mm rain to months with more than 50mm of rain. It was found that there was more lion mortality in wetter months. Rainfall will not be investigated at in this study as there is insufficient data, but the study explore the levels of lion mortality in the rainy seasons compared to the dry season. This analysis will be carried out when considering human factors influencing lion spatial selection; this sub-area of research was done with the intention of investigating human-wildlife conflict. However, the environmental correlate in this instance was found to be the rainfall.

Further literature search done on environmental correlates affecting species distribution revealed information on a study undertaken in the Serengeti National Park in Tanzania. The study investigated whether there was a correlation between reproductive successes in female lions and six landscape variables, namely; distance to rivers, distance to river confluences, distance to rocky outcrops, vegetation type, prey density and rainfall (Mosser & Packer 2009). Distance to river confluences (the meeting of two or more bodies of water) was significantly correlated with reproductive success (Mosser & Packer 2009). In similar research done in the same study area, it was found that lions prefer to hunt in landscapes where it is easier to catch prey rather than in areas of high prey density. In this case it was the distance to river confluences that showed the strongest correlation to hunts (Hopcraft, Sinclair & Packer 2005).

2.3.2 Land Cover

Habitat (or land cover) also influences the abundance and density of prey (Funston et al. 1998, Funston 2011). The main reason for this is that water dependant prey, such as grazers, are drawn to and influenced by surface water availability (Redfern, Grant & Biggs 2003, Valeix 2009, Valeix et al. 2009). This supports the idea that lions utilise areas where prey resources are abundant rather than scarce (Valeix et al. 2010). Funston et al. (1998) suggested that vegetation influencing prey availability and hunting success in turn affected lion territory (Funston et al. 1998).

2.3.3 Moonlight

Another factor influencing lion movement found in some literature is the effect of moonlight (Power & Compion 2009, Polansky et al. 2010, Packer et al. 2011). All three studies found lions to be more active during full moon than during darker moon phases. This is worth noting when determining environmental factors influencing lion movement but will not be investigated in this study. The effect of moonlight does not necessarily affect their occurrence but rather their movement activity.

2.3.4 Land Use

Namibia is the country with the largest surface area covered by National Parks after Botswana and Tanzania (Barnard et al. 1998). The land use within National Parks is conservation. Although lions are not relocated to communal conservancies in Namibia because of the human-wildlife conflict they cause, they disperse and naturally expand their range out of National Parks (Stander 2009).

From personal field observation in August 2011 where the author used a call up method to survey the density of lions in the Zambezi Region during the field season, it was noticed that lions did not respond outside of protected areas such as National Parks. Similar observations were made by Ogotu, Bhola & Reid (2005). They used a call up method (Ferreira & Funston 2010) to determine densities of various carnivores in their study area. A call up method is a surveying technique used whereby the sound of an animal in distress is played through loudspeakers to attract lions. The sound is played at several “calling stations” throughout the area being surveyed. Detailed descriptions of this method can be seen in in Ferreira & Funston (2010). Ogotu, Bhola & Reid (2005) noted that in protected areas lions responded to calls, but there was no response of lions in cattle ranch areas. They deduced from this that the conflict with humans is a factor causing a change in behaviour outside protected areas. An interpretation of this lack of response could be that trophy hunters bait and call during hunting; an activity also practiced by pastoralists, nomads raising livestock, when they experience human wildlife conflict.

2.4 HUMAN-WILDLIFE CONFLICT AND ANTHROPOGENIC INFLUENCES ON LIONS

Species such as lions in National Parks are exposed to being killed, deliberately or accidentally, by humans living or moving close to the borders of these National Parks (Bauer 2003, Woodroffe & Frank 2005). The edge effect of killing lions along protected area boundaries could cause extinction inside the protected areas. Therefore effective conservation is needed inside and out of protected areas (Woodroffe & Ginsberg 1998).

Conservation of large carnivores is difficult as they incur large socio-economic costs to people (Treves & Karanth 2003, Woodroffe, Thirgood & Rabinowitz 2005). Conflict with carnivores is the main cause of a decrease in large carnivore populations in some areas (Winterbach et al. 2013). In other areas, despite human-carnivore conflict, populations are on the increase (Stander 2010).

In the Zambezi Region, it is important to emphasise the value of wildlife and conservation to communal farmers, as they are the ones deciding on land use (O'Connell-Rodwell et al. 2000). The impact of humans on large carnivore populations can reach into protected areas, especially for species such as lions that range beyond the boundaries of protected areas (Woodroffe & Frank 2005). Valeix et al. (2012) found that prey abundance is the most likely factor driving lion ecology inside their studied protected area, but once entering the human dominated area outside the park, conflict with humans is the major factor influencing lion movement (Ogutu, Bhola & Reid 2005, Valeix et al. 2012). Their study did not consider whether lions avoided areas of historic human-carnivore conflict. Woodroffe & Frank (2005), however, did do a study on the effect of problem animal control on the movements of collared lions in their study area (Laikipia District, Northern Kenya), and found that the collared lions in their study area did not avoid areas where there was lion mortality due to retaliatory killing by farmers (Woodroffe & Frank 2005). Woodroffe & Frank (2005) collared lions outside protected areas. In their study area, the farmers shot and killed in retaliation to livestock attacks. The study focused on investigating selection against stock raiding behaviour. Known stock raiding lions did not avoid areas of human habitation, but they did have a lower reproductive success. Their finding is that the sustainable coexistence of lions and humans needs to develop an approach to livestock

husbandry that discourages predators (in this case lions) from stock raiding behaviour. In addition, lethal control is important to prevent the spread of stock killing behaviour.

2.5 HOME RANGE ANALYSIS METHODS

Before analysing the lion data together with the correlate data, we need to understand how the lion data are distributed across the study area. There are many different forms of home range analysis. Before explaining the ones I adopted for this study, it may be useful to describe what is meant by the term home range. Burt described a home range as "...the area traversed by the individual in its normal activities of food gathering, mating, and caring for young. Occasional sallies outside the area, perhaps exploratory in nature, should not be considered as in part of the home range." (Burt 1943).

Home range sizes of lions varied across studies, with arid regions revealing a larger home range and wetter regions revealing a smaller home range (Celesia et al. 2009). Celesia et al. (2009) found through their review of recent wide ranging factors that the population density of lions was the lowest in arid and semi-arid areas and higher in moist savannahs, especially in East Africa (Celesia et al. 2009). Equally, home ranges were found to be smallest in moist savannahs and larger in arid areas (Celesia et al. 2009, Stander 2009).

Davidson et al. (2011) did a study investigating the change in home range of lions before and during a hunting moratorium in Hwange National Park Zimbabwe. The study found home ranges to become smaller once hunting stopped (Davidson et al. 2011).

The size of home ranges is partially influenced by the density of water holes, with an increase of water availability in turn reducing home range size and increased population density (Loveridge et al. 2009). Loveridge et al. (2009) also showed that there is a change in home range size between times of prey abundance and scarcity; although lions do not actively migrate with their prey in rainy seasons, they do alter their diet in times of low prey densities. This in turn supports a study done in Makgadikgadi Pans National Park where lions remained resident in times of prey migration rather than taking the risk of losing their territories when migrating with the prey

(Valeix et al. 2012). Their home range increased or shifted slightly between seasons, but did not move completely.

Further studies found that lions change their prey preference in times of prey migration or scarcity rather than migrate with their prey (Bissett, Bernard & Parker 2012). This is typically a change from grazers to browsers, but in the case of Bissett, Bernard & Parker (2012) it was a change from Kudu to Warthog. In Suvuti, Botswana, lions prey on elephants in times of ungulate migrations (Power & Compion 2009).

Home ranges are calculated differently by different studies. Woodroffe & Frank (2005) used the 100% Minimum Convex Polygon (MCP) method for determining home range of lions. MCP can be calculated at different percentages; the lower the percentage the smaller the home range becomes (Bauer 2003). The use of 100% MCP includes outliers, consequently normal practice is to use a 95% MCP to exclude outlier points (Moorcroft 2008). MCPs are often used in combination with kernel density or harmonic means (Lehmann 2007, Stander 2007, van Rijssel 2008, Hayward et al. 2009) to calculate a more accurate home range.

Getz et al. (2007) expanded on the MCP method and found a more effective method to determine home ranges. They preferred the local convex hull (LoCoH) nonparametric kernel method, as it has the ability to identify obvious hard boundaries such as fences, cliff edges and rivers (Getz & Wilmers 2004, Ryan, Knechtel & Getz 2006, Getz et al. 2007). Similarly, Long & Nelson (2012) found a new way of estimating home ranges called Potential Path Area (Long & Nelson 2012).

The call up survey method described earlier was found to be a failure in The Zambezi Region as a census method due to the density of lions being low. To determine population size and density of the lion population in the Zambezi Region one needs to consider other methods. A method commonly used in sandy areas is spoor frequency (Stander 1998, Gusset & Burgener 2005, Funston et al. 2010). This method was used in 2004 by Stander and Hanssen along with sighting information to determine the density of large carnivores for the Carnivore Atlas (Hanssen & Stander 2004). Due to the high density of elephants in the Zambezi Region (O'Connell-Rodwell et al. 2000), spoors of other animals are often trampled before a transect is completed. Individual identification through camera trapping and sightings together with spoor frequency is a suitable method for this study site (Funston 2012, Pers comms).

Collar types have also advanced over the years. Very High Frequency (VHF) collars were used for many studies referenced in this literature review (Stander 1991, Bauer & De Iongh 2005) but collection of this data depends solely on the researcher. Global Positioning System (GPS) Collars have made data collection more standardised through regular recording of GPS positions (Valeix et al. 2010, Tambling et al. 2012). The main deciding factor for choice of collar type is often the cost, with VHF being the cheapest and GPS Satellite collars being the most expensive (Haupt 2012, Pers com).

Lehman used a grid system to analyse lion GPS positions (Lehmann 2007, Mosser & Packer 2009). Both studies calculated the frequency of occurrence of lion positions for each grid cell, and then did analyses depending on what their study focused on. This is the method this study aims to use to correlate frequency of occurrence to six factors.

Time Local Convex Hull method (tLoCoH) is similar to the Local Convex Hull method discussed previously but includes the factor of time, making it more than just a home range analysis method. It calculates the amount of time spent in an area and the visitation rates and duration of visits to areas within its home range. This is why the TLoCoH method is included in the geographical analysis of distribution data.

2.6 SPECIES DISTRIBUTION MODELLING

Calculating the home range gives a reasonably accurate estimation of the space used by the lions i.e. geographic distribution. There are then various other methods which can be used to find out how this information relates to a species' environment; how factors such as water, land cover, land use, and human activity influence lion occurrence.

Species distribution modelling is also known as ecological niche modelling. This concept can be defined as “associative models relating occurrence or abundance data at known locations of individual species (distribution data) to information on the environmental characteristics of those locations” (Elith & Leathwick 2009, Cassini 2011). This study uses two methods of species distribution modelling, one local regression model called geographically weighted regression

(GWR), and the other a predictive machine learning technique referred to as maximum entropy, shortened to MaxEnt. The literature makes reference to a number of techniques which have been used, such as generalised linear models (GLMs), general additive models (GAMs) and Genetic Algorithm for Rule-set Prediction (GARP) (Stockman, Beamer & Bond 2006). A comparison of GARP and MaxEnt can be seen in (Peterson, M. & Eaton 2007)

2.6.1 Geographically weighted regression

Ecological and geographical studies often use linear regressions assuming that variations remain constant throughout a study area i.e. assuming that one factor has the same influence in all instances within the study area. This appears to contradict Tobler's first law of geography which states "Everything is related to everything else, but near things are more related than distant things" (Tobler 1970). Therefore using a global regression model - such as an ordinary least squares (OLS) regression - assumes that there is no variability across the study area. This makes it difficult to interpret the results of such methods in a changing landscape (Shi et al. 2006). The author explores a method called geographically weighted regression (GWR) due to the impact of the environment not remaining homogenous. GWR is an analysis used where dependent and explanatory variables do not remain stationary over space (Brunsdon, Fotheringham & Charlton 1998).

GWR has been applied to a variety of research. In China, this method was used to understand the net primary production of forest ecosystems; GWR was proven to have a better model performance than OLS regression and spatial lag models (Wang, Jian & Tenhunen 2005). Similarly a study in Spain focussing on Calandra Larks highlighted the importance of understanding spatial autocorrelation and non-stationarity when modelling species distribution (Osborne, Foody & Suárez-Seoane 2007). Testing for autocorrelation and non-stationarity are two aspects which will be applied to the data in this study of lions in the Zambezi Region.

GWR is used across different disciplines as a method to understand the effect of explanatory variables on a dependent variable by using a local regression. For example in this study the dependent variable is lion occurrence and an explanatory variable would be distance to water. When using a local regression we need to understand how the choice of bandwidth for analysis affects the model output (bandwidth is the spatial extent of the regression). The effect of bandwidth can be seen in research done on fisheries in Newfoundland, Canada (Windle et al. 2010). Windle et al. 2010 show how to select the model by minimising the Akaike information criterion (AICc) to show the closest estimate to reality. This is a method which this lion study uses to determine the model which best fits the lion data. A more detailed explanation can be seen in (Fotheringham, Brunsdon & Charlton 2002). A detailed description of how the method is applied to this study can be seen in Chapter 3.

2.6.2 MaxEnt

The use of species distribution models is increasing in biogeography and ecology to understand the effects of environmental variables on species occurrence (Elith & Leathwick 2009, Smith, Duffy & Leathwick 2013). Often in these practices, we only have presence data for species, but not necessarily reliable absence data (Elith et al. 2011), i.e. we know where the animals are but we do not know where they are not. Many different techniques have tried to overcome the inaccuracies to deal with presence-only data. The species distribution modelling technique which was chosen for this study is MaxEnt. MaxEnt uses presence-only data or occurrence points of a species together with environmental variables to produce indices proportional to habitat suitability (Phillips, Anderson & Schapire 2006) which can be mapped.

The distribution maps have been used for a number of applications across studies ranging from invasive species modelling, predicting geographic range shifts caused by climate change (Hof et al. 2011), describing species richness, and mapping the distribution of species in their current range (Roxburgh & Buchanan 2010).

CHAPTER 3: RESEARCH DESIGN AND METHODOLOGY

This chapter provides an overview of the research methodology used in this study. It explores the research design and describes the data collection process. It describes how the data were prepared for analysis. Ethical clearance was obtained from the University of Stellenbosch for this study (see Addendum).

3.1 STUDY AREA

The Zambezi Region, formerly known as the Caprivi Region, is located in the north eastern part of Namibia (Siljander 2009). It shares borders with Angola, Zambia, Botswana and Zimbabwe, and lies between the Kavango River to the West and the Zambezi and Chobe rivers to the East (Chase & Griffin 2009), (see Figure 3.1). The rainfall for the region is between 600mm-700mm per annum (Mendelsohn & Roberts 1997) and is defined by three seasons: a hot dry season from August to October, a hot wet season from November to April, and a cool dry season from May to July. (Chase & Griffin 2009). Average maximum monthly temperatures range from 25 degrees Celsius (°C) in the winter to 35°C in the summer while monthly minimum temperatures range from 5°C to 20°C respectively (Mendelsohn & Roberts 1997). The topography of this area is relatively flat ranging from 930-1100 metres above sea level (Mendelsohn & Roberts 1997, Naidoo et al. 2012). The study area falls within three eco-regions; namely the Zambezi Baikiaea woodlands, the Zambezi and Mopane woodlands, and the Zambezi flooded grasslands eco-region. Its vegetation is characterised by *Baikiaea plurijuga* (Zambezi Teak) in the northern part of the study area and *Colophospermum mopane* (Mopane) in Mudumu National Park, with interspersed savannah grasslands and flooded grasslands along the rivers.

The study area includes three National Parks in the eastern and western Zambezi Region. The eastern Zambezi Region has two National Parks namely Nkasa Rupara National Park and Mudumu National Park. The western Zambezi Region has one National Park - Bwabwata National Park - which stretches across the Caprivi Strip and is broken up into core areas on either side. The eastern core area bordering the Kwando River forms part of the study site and will hereafter be referred to as the Kwando Core Area Bwabwata East National Park. All three parks are small relative to the size of other National Parks in Namibia: Nkasa Rupara National Park is

350 km², Mudumu 700 km², and Kwando Core Area Bwabwata East 450 km² (O'Connell-Rodwell et al. 2000).

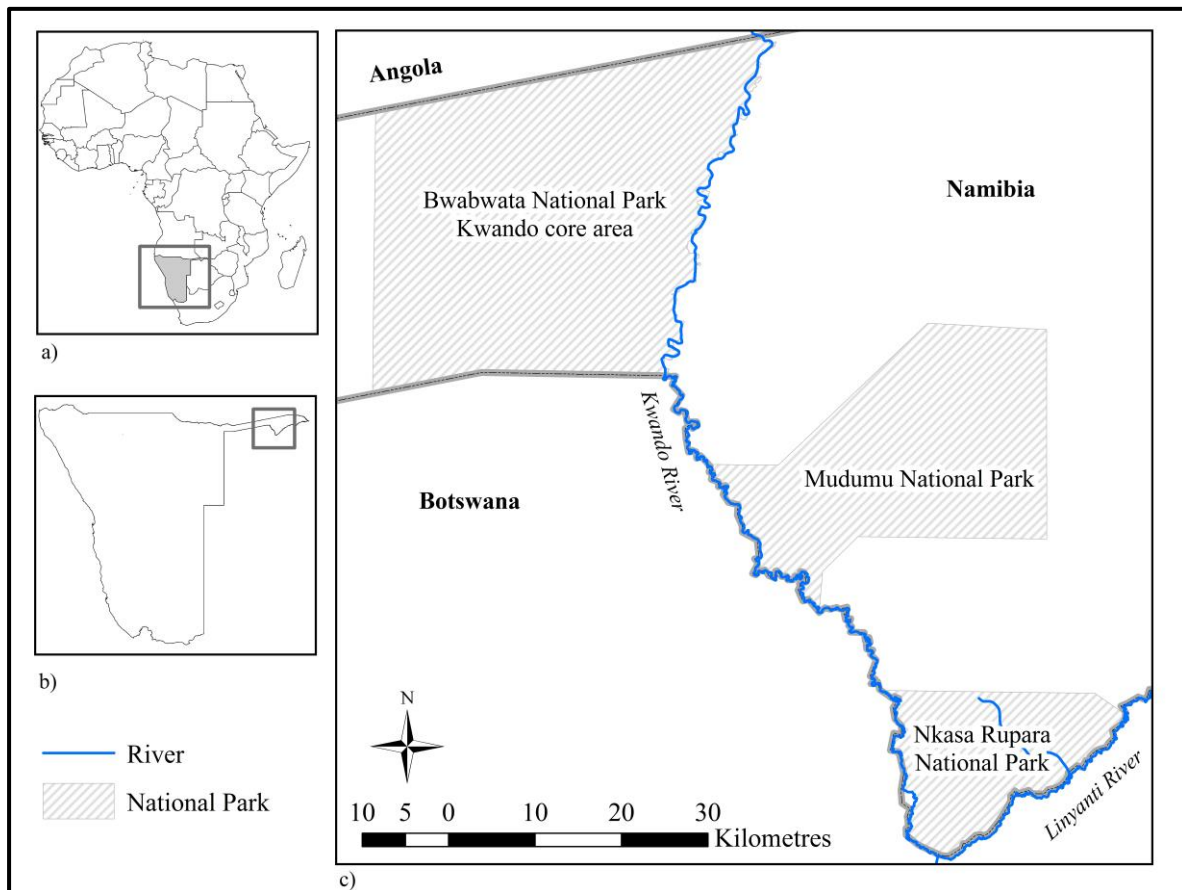


Figure 3.1 a) Placement of Namibia on the African Continent. b) Study area within Namibia. c) The three National parks with in the study area (labelled) and the two main rivers flowing in the study area. The rivers form part of the border between Namibia, Zambia, Angola and Botswana.

These National Parks are unique because their boundaries are not fenced; instead they are only defined by a graded cut-line (cleared two-track road). Seven Communal Conservancies border the National Parks, which are areas that have traditionally been used for livestock farming. The Communal Conservancies, assisted by NGOs and government, use the Community Based Natural Resource Management (CBNRM) approach to manage these areas (Naidoo et al. 2011). The CBNRM approach encourages wildlife tourism and sustainable trophy hunting for income (Naidoo et al. 2011). The Zambezi Region is the fifth most densely populated region in Namibia (6.1 people per km²) with a total population of 90,100 people (Agency 2011). Because of the extent of National Parks and Communal Conservancies in this relatively small region of Namibia (14,785 km²), there are areas where wildlife and people are in close proximity (Naidoo et al. 2012).

The Zambezi Region has many ex SADF (South African Defence Force) military stations dotting the National Parks, and the remnants of these can still be seen. Some were transformed into ranger stations for the Ministry of Environment and Tourism after the Angolan war. From 1969 to 1989, the Caprivi Strip was used as a base for the SADF to support the National Union for the Total Independence of Angola (UNITA) (Chase & Griffin 2009). Wildlife was decimated in Angola and Caprivi during this time, and it is speculated that this was for ivory and meat (Kumleben 1996). Wildlife populations have made a recent come-back, which is extraordinary considering the impact of the political history in this area.

The area is characterised by ancient river beds, known as omurambas. These run in a north-westerly to a south-easterly direction, perpendicular to the Kwando River.

3.2 DATA COLLECTION AND PROCESSING

3.2.1 Lion Data

Global Positioning System (GPS) satellite tracking devices (built by African Wildlife Tracking for the Namibian Ministry of Environment and Tourism) were used to collect lion locality and movement data from different individual lions in the study area. Each collar was manufactured with the intention that it should last two years, but this time-frame could not be guaranteed. The GPS unit on the collars has an accuracy of 2.5 meters (pers. comms. AWT, 2012). Collaring (or tagging) of the lions in the study area began in August 2011, with the last individual lion collared in April 2012.

Six lions were fitted with GPS satellite tracking devices in this time. Each tracking device took six GPS locations per day at four hourly intervals. In each case, only one animal in a pride or coalition was collared. In August 2011, one lioness was collared in each of Bwabwata National Park, Mudumu National Park and Nkasa Rupara National Park. One lion was collared in a previous study in 2010 in Bwabwata National Park, but later moved to Mudumu National Park. His collar was replaced for this study in December 2011 but he only lived one month after collaring. In April 2012, one lion was collared in each of Mudumu National Park and Nkasa

Rupara National Park. Details of these animals can be seen in Table 3.1. Lions were darted by a veterinarian from the Ministry of Environment and Tourism, Namibia, using standard veterinary and capture procedures.

All GPS collars had a very high frequency (VHF) backup mechanism. This was useful for tracking individual lions manually to retrieve the collars (in the case of mortality), or to find the lion (in case of collar failure). VHF collars were tracked from the ground using a telemetry receiver - a Telonics R-1000 model - with an H-type antenna. If animals could not be located using this method, they would be tracked from the air (Beaty & Tomkiewicz 1997). Aerial tracking was used in an extreme case and in conjunction with other projects to maximise the availability of flying time.

GPS locations from the collars could be retrieved from the Internet at any time during the study. The system provides the most recent position taken by the collar, as well as its historical data. A complete set of the data was downloaded on a monthly basis. Details are given below. A summarised version of this information is given in Table 3.1:

Bwabwata National Park (Kwando Core Area)

- SAT101: Lioness collared on 20 August 2011 at 18:00. She was alone at the time of collaring and was lactating, a sign of her having cubs. She was sighted in December 2011 with the rest of her pride and cubs, which confirmed this assumption.
- SAT00580025VTI92DA: Lion collared on 15 October 2010 at 13:00. This collar information does not fit the temporal extent of the study, but he is specifically noted because he migrated to Mudumu National Park (crossing the Kwando River) and is later collared and used for the study as SAT207 (see Mudumu National Park).

Mudumu National Park

- SAT102: Lioness collared on 25 August 2011 at 21:00. This was during a call up survey and she was with two other lionesses at the time. She was never sighted with cubs during field work but there was a reported sighting of her with two males.
- SAT207: The collar on this lion failed and he could not be tracked from the ground. The lion was located from the air and the collar removed. He was collared again on 17

December 2011 at 18:00 to replace his previous collar. He died one month later in January 2012, the cause of death unknown. The collar was still functioning and was fitted to a different male, see SAT2072 below.

- SAT2072: Lion collared on 21 April 2012 at 01:10. He was with another male lion at the time and both were caught on a camera trap shortly after collaring. This collar only lasted until April 2013. The other lion was fitted with a VHF radio collar so that he could be identified if he split from SAT207/2. The data from the VHF collar was not used as readings had to be taken manually. The collar was removed in a photographic concession in Botswana in April 2013, after which event the location and movements of this lion remain unknown.

Nkasa Rupara National Park (formerly Mamili National Park)

- SAT103: Lioness collared on 21 August 2011 at 14:00. She was mating with a lion at the time of collaring. In December 2011 a change of movement was noted from her collar and, after following up in the field, she was found with young cubs. This lioness was shot in April 2013 after a number of human-wildlife conflict incidents.
- SAT 272: Lion collared on 26 April 2012 at 02:20. He was de-collared and written out for trophy hunting in April 2013 due to human-wildlife conflict.

Table 3.1 Information about collared lions in the study area.

Collar Type	VHF Frequency	Animal ID	Sex	Location (latitude, longitude)	National Park	Date deployed	Time deployed (UTC+2)	Date collar removed or found to be malfunctioning	Interval between GPS readings	Number of locations
Satellite	148.170	SAT101	Female	-17.87714 23.30626	Bwabwata	20/08/2011	18:00	?	4 hours	4909
Satellite	149.240	SAT00580025VTI92DA (same as SAT2072)	Male	-17.92456 23.27833	Bwabwata	15/10/2010	13:00	17/12/2011	4 hours	unknown
Satellite	148.210	SAT102	Female	-18.03091 23.60104	Mudumu	25/08/2011	21:00	?	4 hours	4719
Satellite	149.130	SAT207	Male	-18.17468 23.45259	Mudumu	17/12/2011	18:00	14/01/2012	4 hours	141
Satellite	149.130	SAT2072	Male	-18.17467 23.45403	Mudumu	21/04/2012	01:10		4 hours	2006
Satellite	148.370	SAT103	Female	-18.38287 23.73858	Nkasa Rupara	21/08/2011	14:00	Shot April 2013	4 hours	3374
Satellite	150.110	SAT272	Male	-18.37179 23.70532	Nkasa Rupara	26/04/2012	02:20	Removed April 2013	4 hours	2005

The data collection of lion location points ran from August 2011 to August 2013. Once all the data was downloaded, it was then cleaned and all irregular outlying points filtered out. These irregular outlying points are sometimes caused by satellite or recording inaccuracies, for example, a GPS point suddenly showing as being in the ocean. Following recommendations given in literature, the first five days of GPS readings after capture were omitted from the analyses (Withey, Bloxton & Marzluff 2001). The resultant raw data collection can be seen Figure 3.2 below.

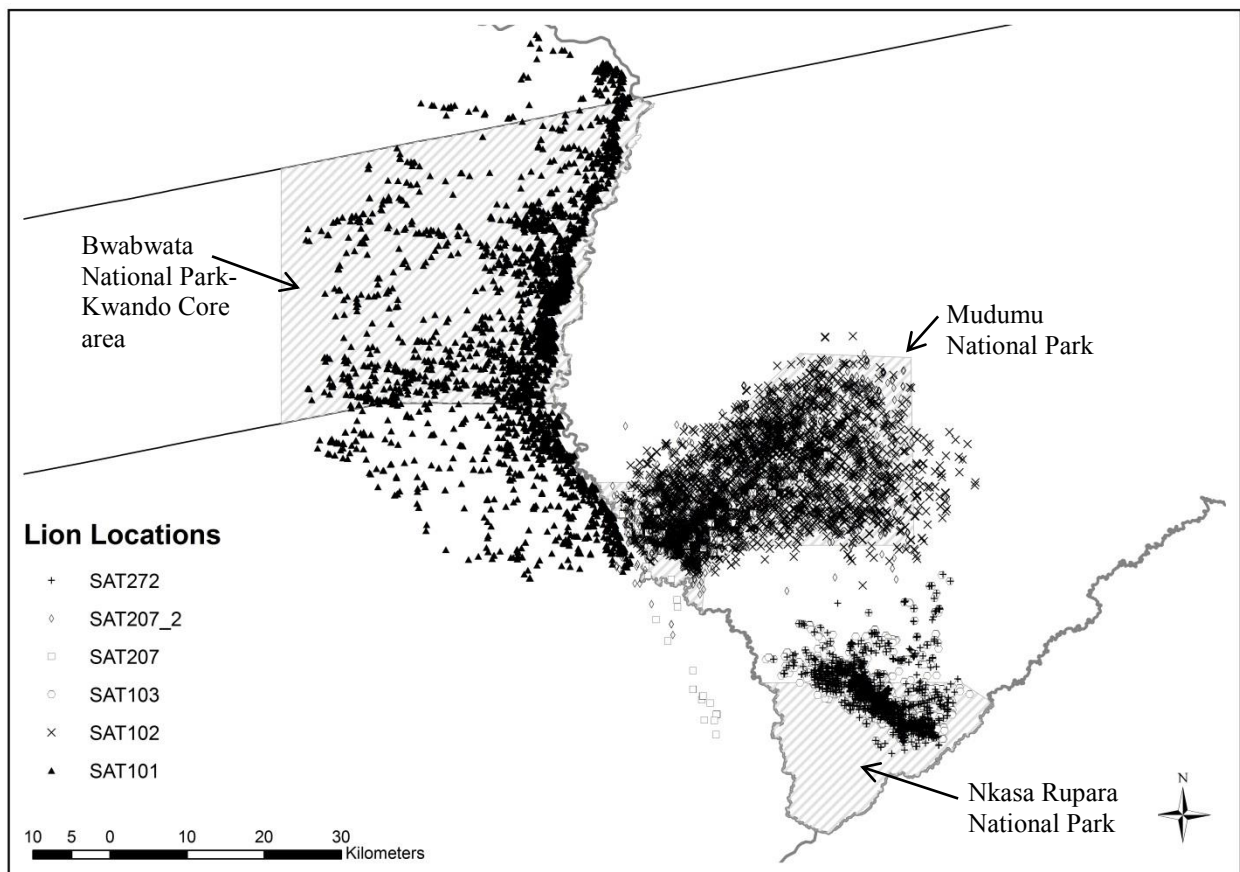


Figure 3.2 Raw data from lion collars.

A vector grid was created for the study area to encompass all points collected. This resulted in a grid spanning 106 x 113 grid cells of which each grid cell measures 1 km x 1 km creating a total of 11988 grid cells for the study area. This size was chosen on the base of the accuracy of the intrinsic and extrinsic correlate data to be analysed. The frequency of GPS locations was then calculated for each grid cell. This resulted in the mapping of data as displayed in Figure 3.3.

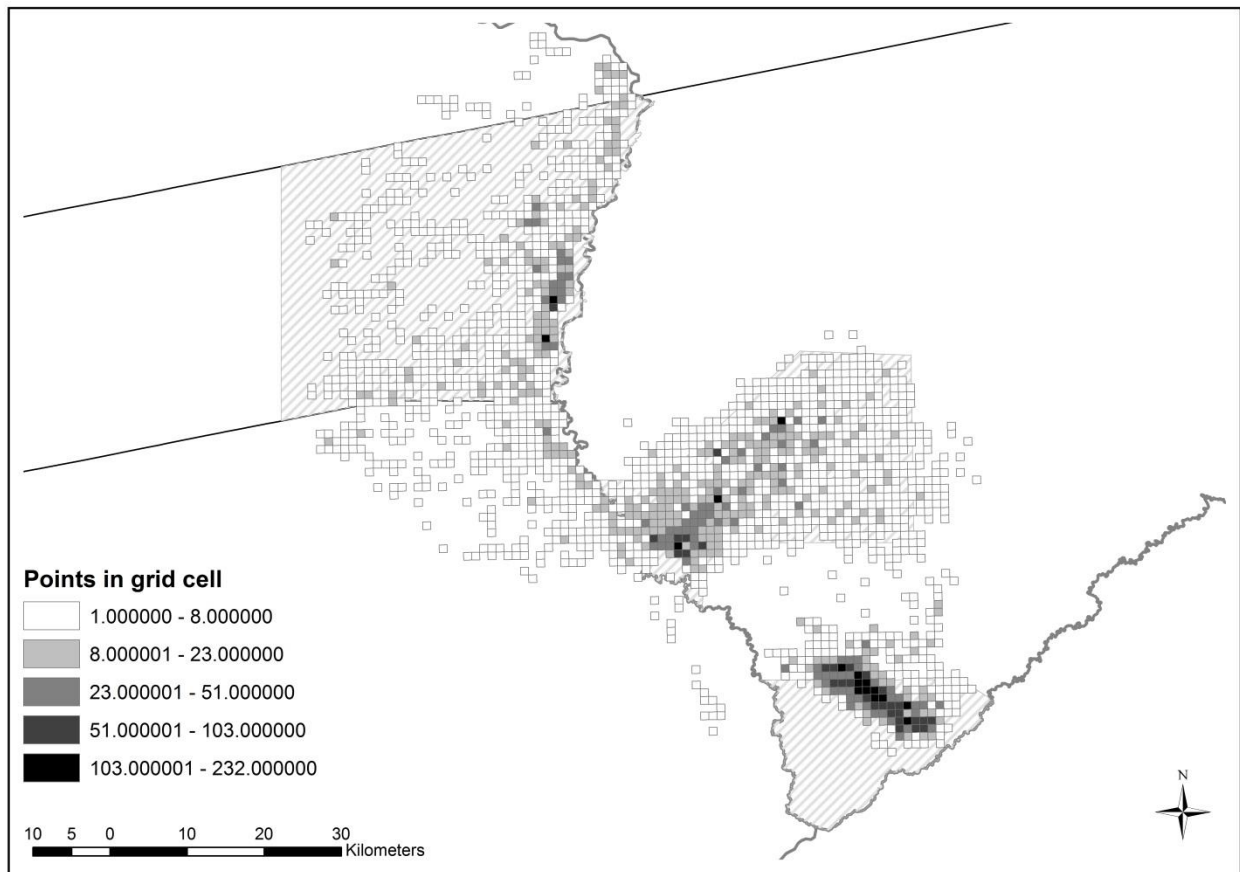


Figure 3.3 Lion data mapped using 1 km x 1 km grid cells. White shows low point frequency per grid cell and the darkest shade of grey shows highest point frequency per grid cell.

3.2.2 Environmental Factors

The study aims main to determine which environmental and human factors affect the spatial occurrence of lions. Environmental variables are defined as rivers, land cover and land use for the purpose of this study. Below is a brief explainanation of how each factor is thought to play a role in affecting lion occurrence as well as data collection methods for the study.

3.2.2.1 Rivers

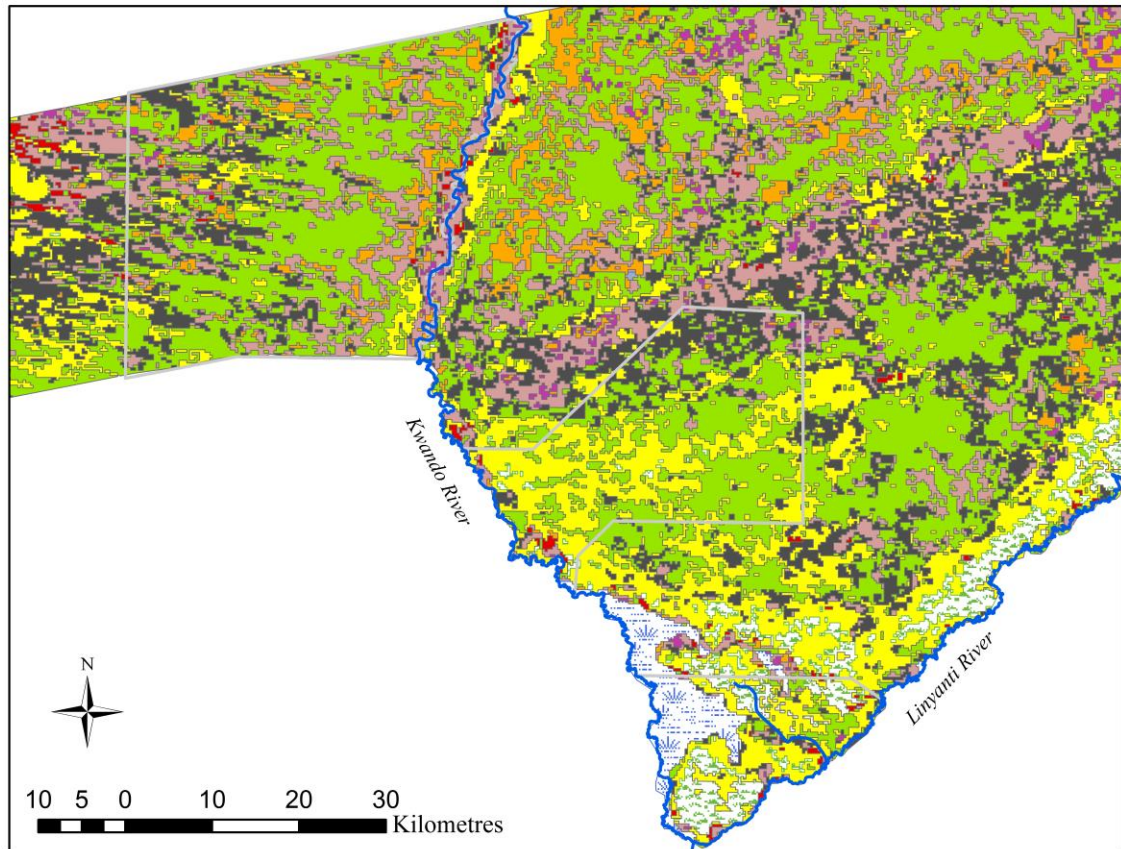
The study area has two main rivers flowing through it, namely the Kwando River (flowing north-south) bordering all three National Parks and the Linyanti River bordering the Nkasa Rupara National Park in the south-east. Rivers as a main permanent water source for wildlife are a unique factor in this study area, as the main source of permanent water for wildlife in other protected areas are often water points. Water points are classified as a human factor in this study

as these occur mainly in the form of cattle drinking troughs or for human consumption; as such they will be described in section 3.2.3. Other studies have only investigated the influence of waterholes (Valeix et al. 2012). If human-wildlife conflict is increased by the availability of water, then measuring the effect of water availability on lion occurrence and movement can be useful for the placement of future waterholes.

For the purpose of this study, permanent water is defined as permanent rivers. The spatial data were outdated at the time this study commenced, so GPS locations of each water point had to be collected. Permanent rivers are available as vector shape files. The vector shape files were then converted into a raster file with distances calculated, and these distances were then extracted into the existing grid made from the lion data. Distances were categorised into five classes: 0-2, 2-4, 3-6, 6-8 and >8 km as described by Valeix et al. (2010). An ordinary least squares (OLS) regression was then done for lion frequency and distance to the river, and the results showed the residuals to be spatially clustered.

3.2.2.2 Land Cover

Land cover affects lion hunting success and was discussed in Chapter 2 (Hayward & Kerley 2005). In the Zambezi Region there are different types of land cover which could have an effect on lion movement for this reason. Land cover data are available as a vector shape file and the classes which fall in the Zambezi Region can be seen in Figure 3.4 below. The data are in a vector format and are at a resolution of 300m. The temporal extent of the data is from 01 January 2005 to 31 December 2005. The land cover map is broken up into 46 classes for the whole of Namibia and was classified using the Food and Agricultural Organisation of the United Nations (FAO)/United Nations Environment Program (UNEP) Land Cover Classification System (LCCS) (Martucci & Latham 2005). Ten of these classes occur within the study area (Figure 3.4). Each class is given a value which was used for the species distribution modelling information. Later in the results one can see the effect each vegetation class has on the lion occurrence when assessing the MaxEnt results.



Vegetation of Study Area	
Label	
	Closed (>40%) broadleaved deciduous forest (>5m)
	Closed to open (>15%) (broadleaved or needleleaved, evergreen or deciduous) shrubland (<5m)
	Closed to open (>15%) grassland or woody vegetation on regularly flooded or waterlogged soil - Fresh, brackish or saline water
	Closed to open (>15%) herbaceous vegetation (grassland, savannas or lichens/mosses)
	Closed to open (>15%) mixed broadleaved and needleleaved forest (>5m)
	Mosaic forest or shrubland (50-70%) / grassland (20-50%)
	Mosaic grassland (50-70%) / forest or shrubland (20-50%)
	Mosaic vegetation (grassland/shrubland/forest) (50-70%) / cropland (20-50%)
	Open (15-40%) broadleaved deciduous forest/woodland (>5m)
	Open grassland
	Water bodies
	River
	National Park Boundary

Figure 3.4 Landcover map 2005 with vegetation classification values explained in Table 3.2 below.

3.2.2.3 Land Use

Land use differs from land cover in that it classifies how the land is used rather than what the land is covered by, i.e. vegetation. Land use will be considered when lions venture outside of the National Parks and a correlation is made to see whether there is any land use type they utilise more often than others (e.g. community forests rather than agricultural areas). Each Communal Conservancy has a zonation plan. Within these zonation plans the proposed and current land use of the conservancy is described, this varies from settlements, cattle grazing areas, cropping to wildlife exclusive areas.

As stated previously, the land use within National Parks is conservation. The National Parks are not fenced, making the reasons for lion movement less obvious than in protected areas with predator proof fences. Lions cross the National Parks' borders and come into contact with areas where the land use may be different to conservation. The aim of investigating this factor is to see whether lions prefer to stay in the National Parks rather than outside. This is done by classing the area into two land uses, namely conservation and non-conservation. As the zonation plans for the Communal Conservancies are currently still in the draft phase, the classification of land uses outside of the National Parks could not be categorised further within the time-frame of this study.

The grid covering the study area is classified into park (coding 1) or non-park (coding 0) to see if National Parks affects the occurrence of the lions in the study area.

3.2.3 Human Factors

Human-wildlife conflict situations usually increase closer to human settlements. Quite often the conflict results in lions being driven away or shot, and for this reason the distance to human settlement could be a factor influencing lion movement in this study area. Distance to the nearest human settlement will be calculated for each grid cell to see whether it influences the lions' movements.

Human settlement data were collected in the field for the seven conservancies surrounding the National Parks. Collected data can be seen in Figure 3.5. GPS locations of corrals were also collected and mapped (Figure 3.6). The distance to the nearest cattle post and human settlement was then calculated for each grid cell.

At the start of this study, there was no up to date human settlement data available for the Zambezi region. During the field work time, GPS locations of each corral, village and water point were collected by the author in all seven Communal Conservancies in the study area. This was done using a handheld GPS device (Garmin Oregon 450). Three readings were taken at five minute intervals for each location and were averaged to get a more accurate reading. This took approximately one week per conservancy so the total data collection lasted seven weeks. The date, time, name of feature and any other comments were all recorded for each location. This resulted in 1310 locations being collected, the benefits of which ranged beyond the confines of this study. The data is currently stored in the National database of information called ConInfo.

Accurate up to date maps were produced for each Communal Conservancy and better informed decision could be made for corridor planning. It was argued that satellite imagery could have been used to collect this data, instead of the laborious field work. However, satellite imagery was tested and, because the image was either out of date or abandoned infrastructures not removed, relocated villages or corrals were very easily mistaken as active from satellite imagery. Once this was realised, a firm commitment was made to collect accurate data in the field. The vector grid made from the lion locations was then coded for the distance to each nearest corral, village and water point. The factors were then tested for co-linearity using a cross plot and a multiple regression. When results showed the corral, village and water points to be >0.97 linearly related, it was decided to combine these three factors and call them "distance to nearest human activity".

A decision was made to focus on villages as these indicate an area of human activity where people live. Villages range in size from one or two courtyards to more than 20 courtyards in a village. Corrals, for keeping cattle together and safe at night, were also highlighted. Human-wildlife conflict history shows that lions often catch cattle at a corral. Water points were recorded, as these are mainly cattle drinking points or areas where people gathered to fill water.

A correlation was done between lion occurrence and the independent variables and due to autocorrelation among human factors these factors were grouped as mentioned previously. This initial analysis was done using an ordinary least squares regression and a Morans I test was done on the residuals to test for autocorrelation. The results show that, because the p value for Morans I is 0, the variables are significant but clustered. This makes geographically weighted regression an ideal candidate for this analysis.

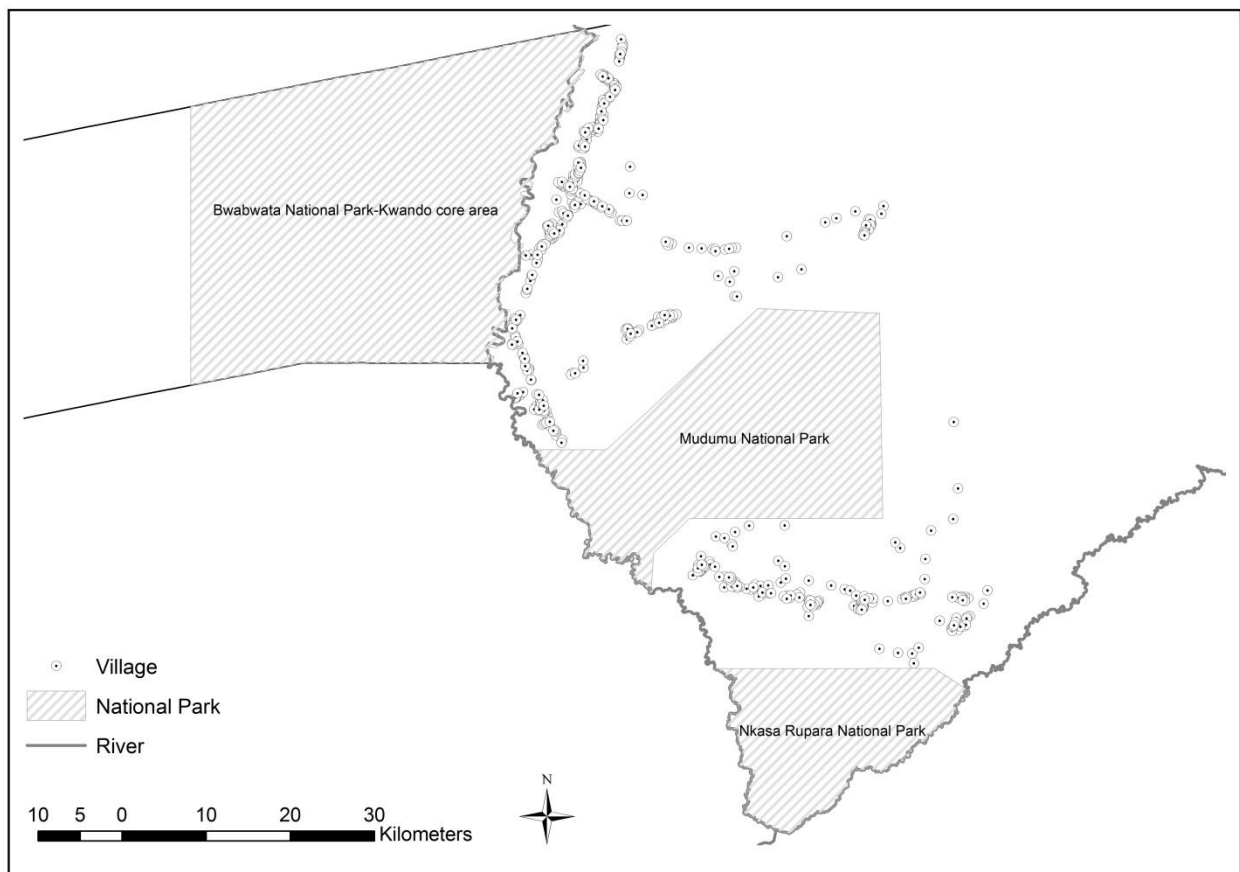


Figure 3.5 GPS locations of recorded villages.

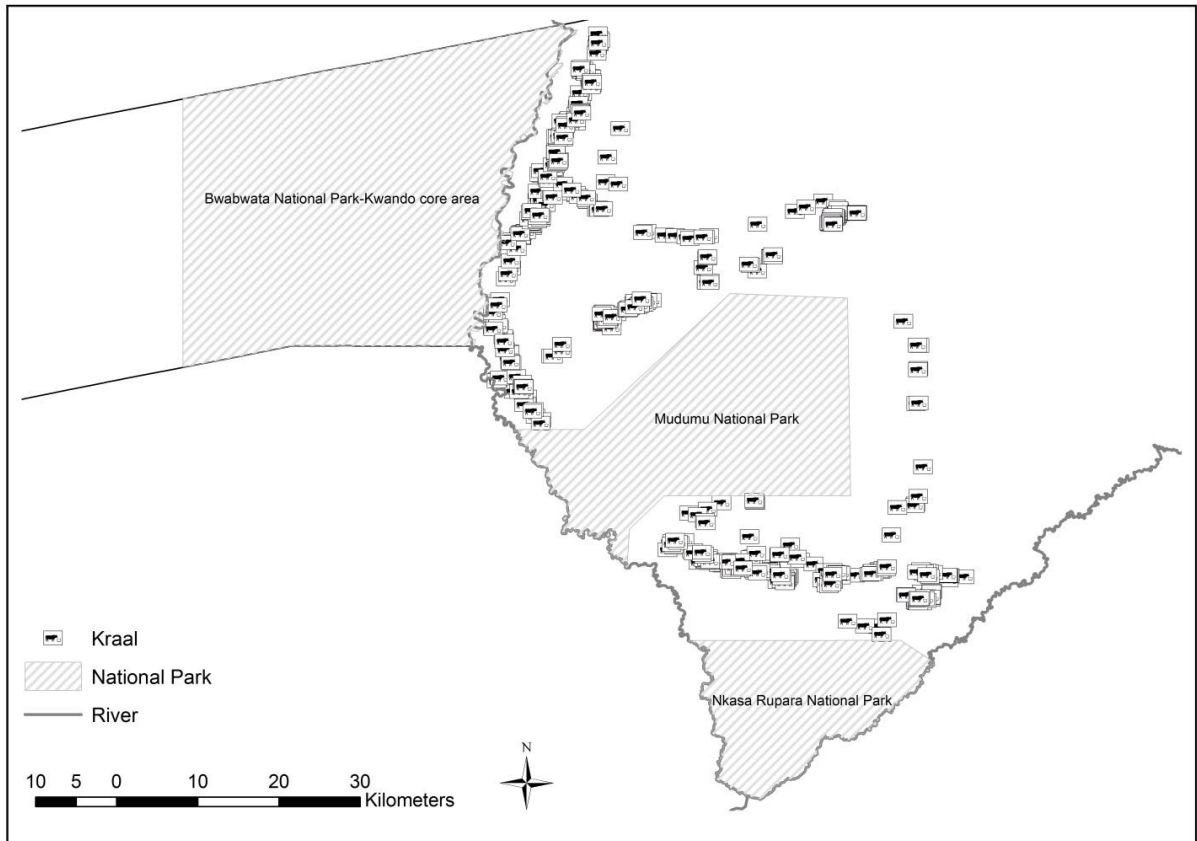


Figure 3.6 GPS locations of recorded corrals.

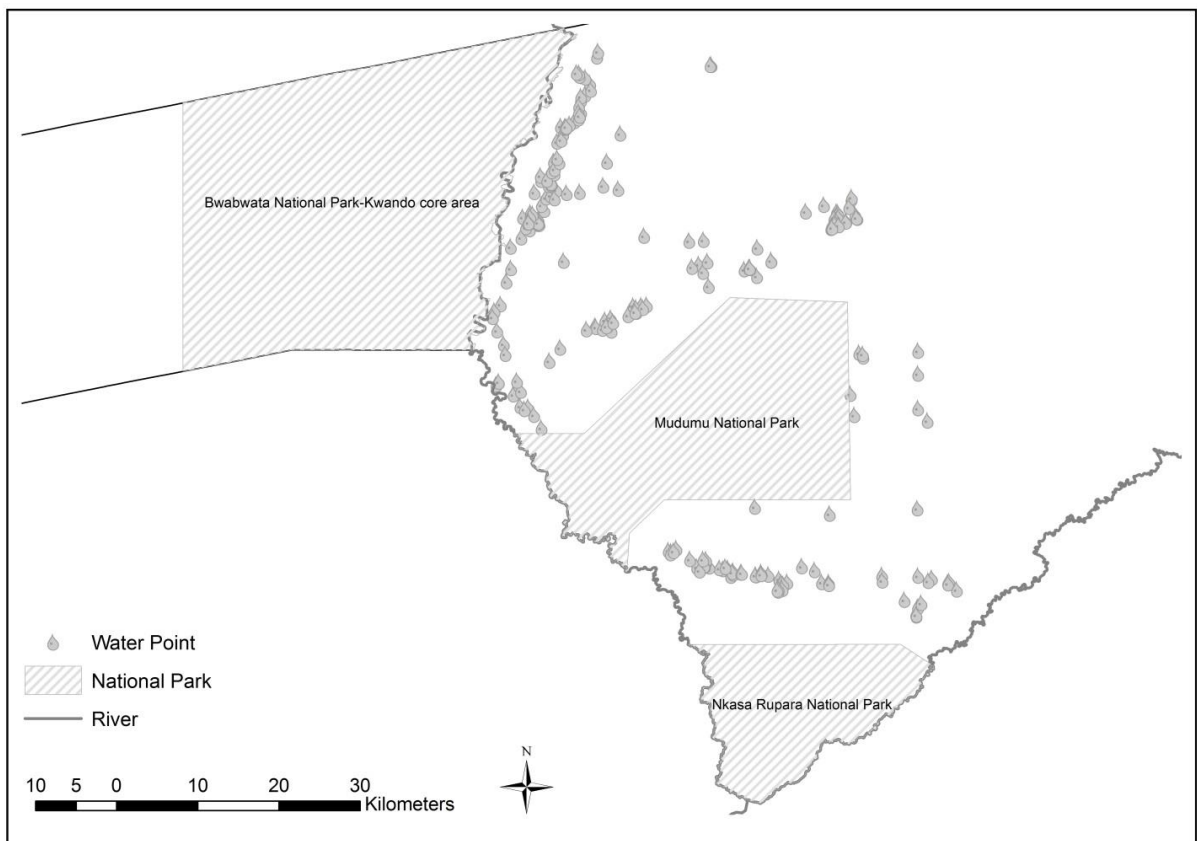


Figure 3.7 GPS locations of recorded water points.

3.2.4 Environmental and human data distribution and correlation

The first part of the environmental data analysis is to calculate the variables in relation to the lion data available. This was done using the “near” tool ArcMap 10.2. This calculated the distance to the nearest river, village, corral and waterpoint. An ordinary least squares regression was done for log-transformed lion data as dependent and distance to river, village, corral and water point as explanatory variable. From the results it was evident that the human factors (village, corral, waterpoint) were collinear. The distance to river, village, corral, land cover and land use was calculated for each grid cell showing. The distance to each factor was then plotted against the frequency of lions occurrence for each grid cell. This was a necessary step to do before running the species modelling (a geographically weighted regression and MaxEnt).

3.3 DATA ANALYSIS

3.3.1 Home Range Analysis

As discussed in the literature review, one of the oldest forms of home range estimation is called the Minimum Convex Polygon (MCP). This takes the outer points and connects them to create a polygon. A 100% MCP includes outliers in the data. To overcome this problem the estimation is usually made using a 95% MCP. This method usually estimates the maximum area an animal uses. It does not allow for mapping areas which are most often used or for areas which are seldom visited in the home range.

A second home range estimation method commonly used is the kernel density method (KDE). This home range estimator is based on the estimation of probability of an animal to occur in the home range (Reinecke et al. 2013). The KDE calculates and quantifies the intensity at which a space is used within a home range (Kie et al. 2010).

The downfall of both these methods is that they include areas which have not been traversed by the animals. It tells us the probability of the animal being there but not if it actually has been there. These areas may even include sections within the home-range which are physically not

accessible, for example steep cliffs, fences, large bodies of water or are possibly areas the animal naturally avoids (Reinecke et al. 2013). To overcome this problem a method called nearest-neighbour convex hull was developed (Getz & Wilmers 2004). This was later extended to the local convex hull (LoCoH) method (Getz et al. 2007). LoCoH is an extension of MCP which estimates a utilisation distribution by a non-parametric kernel function (Getz et al. 2007, Reinecke et al. 2013). Local hulls convex polygons - also referred to as hulls - are created for each point with a given number of neighbours, and an MCP is created for each of these points. The hulls are then categorised by size increasingly and a probability distribution of the overlapping hulls is calculated (Getz et al. 2007, Lyons, Turner & Getz 2013, Reinecke et al. 2013).

A further spatial temporal method has been developed recently called a time Local convex hull which is shortened to tLoCoH. This estimates the amount of time an animal spends within an area in its home range, which in turn shows us which areas are visited less often but for long periods of time (i.e. grazing) and which areas are often visited but only for short periods of time (i.e. waterholes) (Lyons, Turner & Getz 2013). It does this by selecting “parent points” for which hulls are created in time rather than the nearest neighbours in space. This can be seen in Figure 3.8. The “parent point” is the triangle and the circles indicate the 15 nearest neighbours in time. Although there are many other points which may be closer to the parent point, they might have temporally been months apart and therefore are not chosen to create the hull. This is a package in R and was used to calculate the home range as well as the temporal use of the lions in this study. The data need to be in a Universal Transverse Mercator (UTM) projection which is UTM34S for this study area. It is then cleaned from irregular bursts in the data. Then an appropriate nearest neighbour (k) is determined. The determined size for k in this study is $k=15$ (meaning 15 neighbours).

This is a very new technique allowing researchers to understand the home range of study animals in a different way. Results are shown from this study, but the interpretation of the results would justify further research. As lions do not have set dens (as hyenas or wild dogs do), areas which they spend a lot of time in may be because of a large kill. Areas that lions visit often may be for the purpose of make-shift dens that they create for their young, which they move every ten days within the first six weeks.

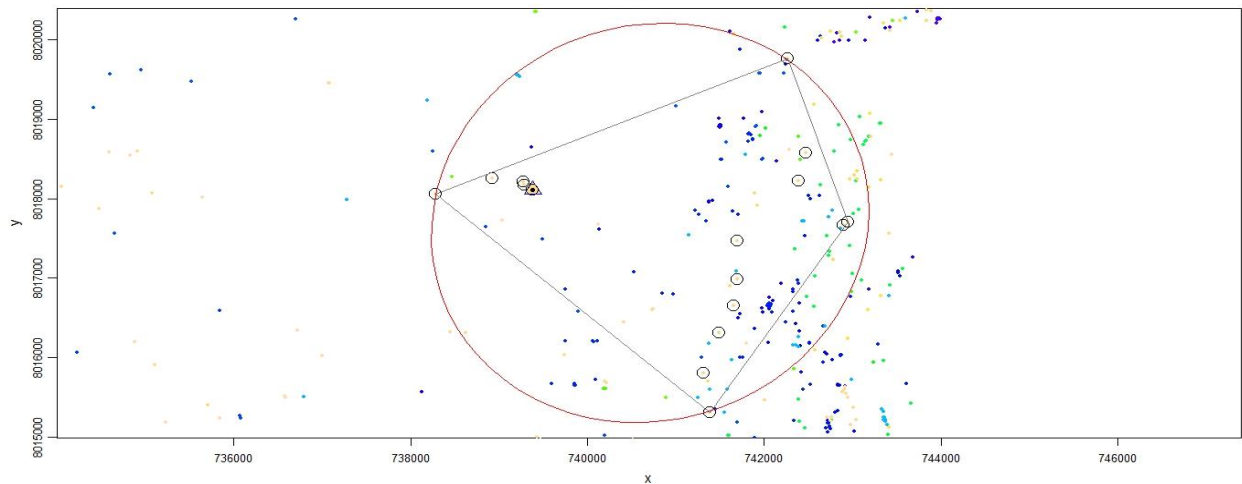


Figure 3.8 An example of how tLoCoH calculate the size of hulls using points nearest to the parent point in time. The parent point is shown by a triangle. Nearest neighbours used for hull construction are circled. The remaining points in different colours indicate GPS locations from collars used in this study. Data used for this example originates from this study.

3.3.2 Species Distribution Modelling Methods

3.3.2.1 Geographically weighted regression

Ordinary least squares (OLS) regression is a global regression model. Models such as these are usually applied globally and assume spatial stationary in the relationships among variables (Foody 2003). Wang, G Ni, J and Tenhunen J (2005) illustrate OLS and geographically weighted regression (GWR):

“A global regression model can be presented as:

$$\gamma = \beta_0 + \beta_1\chi_1 + \dots + \beta_p\chi_p + \varepsilon$$

where γ is the dependent variable, χ_1 to χ_p are independent variables, β_0 is the intercept, β_1 to β_p , are estimated coefficients, and ε is the error term.

GWR allows local rather than global parameters to be estimated and the above model is rewritten as:

$$\gamma = \beta_0(\mu, \nu) + \beta_1(\mu, \nu)\chi_1 + \dots + \beta_n(\mu, \nu)\chi_n + \varepsilon$$

where (μ, ν) denotes the coordinates of the samples in space” (Wang, Jian & Tenhunen 2005).

An initial analysis of the data in this study showed that the independent variables evidence heteroscedasticity and spatial clustering. Results of OLS regression and Morans I analysis can be seen in Appendix A. This called for a method which deals with the non-stationary nature of the data. The most appropriate method identified was GWR.

GWR was used as an analysis tool for this study as it is able to compute variables even when they are spatially non-stationary. This is called a local model because it can take into consideration the variability of factors within the study area. A global model, such as OLS regression, calculates one regression line across a whole study area. This often results in residuals being spatially auto-correlated. For this study GWR could reduce - and in some cases remove - the spatial autocorrelation of the residuals. To select the best model, we consider the Akaike information criterion (AICc) values from the ordinary least squares regression and the geographically weighted regression.

3.3.2.2 MaxEnt

As described in Chapter 2, MaxEnt is a technique used for species distribution modelling. The data need to be prepared for use in the user interface written for MaxEnt and are described in a number of tutorials. All environmental layers were converted to raster format with identical cell size for all the layers. This was done in Arc Map 10.2. Environmental variables used to understand the distance to a feature were converted into distance rasters. The variables were distance to river, distance to road and distance to human activity. Categorical variables were park/non-park and vegetation. A further continuous variable used was elevation. Elevation for the area was downloaded using the SRTM 90. The projection of all the layers was converted to Universal Transverse Mercator 36 so that response curves relate to distance. The layers were however defined as geographic projection World Geodetic System 1984 (WGS84). This was done to match the location points of the lions, which were in WGS84.

All models were run with 30 percent training data leaving 70 percent for test data. MaxEnt background samples were drawn as described in Phillips & Dudik (2008). A maximum of 10,000 background pixels was drawn and, because the study area has less than 10,000 pixels, it drew background samples from the whole study area. Background samples were drawn over the whole study area for pixels which included all environmental variables where species could occur. The

model compares this with where the species occurs from the data given. Merow, Smith & Silander suggest masking out areas where the species is expected not to occur (Merow, Smith & Silander 2013), but lions are expected to occur everywhere in the study area as there was no stratified sampling to determine areas where lions definitely not occur. The parks are not fenced so lions are not limited to the National Parks meaning they can occur anywhere in the study area even if the probabilities are low in some areas. Villages would be a deterrent but the lions could venture to the villages to catch cows if they wanted to. For this reason no areas are masked out for creating background pixels as lions could occur anywhere in the study area.

MaxEnt produces an output showing the explanatory power of each variable; the output also shows how well the model performs if a variable is omitted. For this reason various runs were done with the data. Ideally one would want to run a model with all available data. However, for the purposes of this study individual runs were made for each park, as well as for the wet and dry season data. The bottom red bar from the jackknife outputs shows the overall training gain of the model. The dark blue bar shows the explanatory power of a variable and the light blue bar shows the gain lost if the variable is omitted (see Figure 3.9).

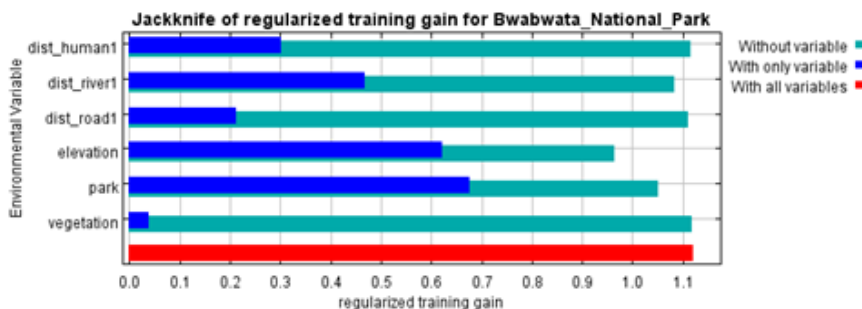


Figure 3.9 Example of Jackknife output from MaxEnt.

All MaxEnt models were run using the cross-validation method at 10 replications per run. All data were cleaned to remove the first five days of GPS readings. In addition, any major outliers due to satellite errors and all values with a horizontal dilution of precision (HDOP) values of more than 5 were removed.

Since GPS collars were used with data collected every four hours, the model did not require the running of a bias file. This data was not spatially biased; whereas data collection from a VHF

collar would require driving to a point to get a GPS reading, this is not necessary for GPS collars. GPS tracking has the added benefit of not being limited to where one can drive i.e. roads.

Seasonal data was partitioned between dry and wet season. The effect of the wet season is noticeable a month after the initial rains when vegetation starts to become green and prey species begin to change their movement. Bearing this in mind, the wet season data was taken from December to May and the dry season data from June to November.

Fourteen different models were run, as can be seen in Table 3.3. The AUC values are used to determine which models can be used for interpretation (Fielding & Bell 1997). The area under the receiver operating characteristic (ROC) function AUC is used as a primary index as it shows a measure of overall accuracy that is not dependant on a particular threshold (Deleo 1993). The ROC AUC values from Table 3.3 determined the following models to use for interpretation and explain what can be seen from their results: Model 8 and Model 8 without elevation and distance to roads for Bwabwata, Mudumu and Nkasa Rupara National Park; Model 13, 14, 15 showing dry and wet season results per park; Model 4 showing all lions; and Model 12 showing all lions for dry and wet season.

The MaxEnt results come in the format of jackknife tests, response curves, the Area Under the receiver characteristic Curve (AUC) and the probability of occurrence maps. The outputs from the MaxEnt models can be seen in Appendix D. These results are discussed in further detail in Chapter 5

Table 3.2 This table shows the outputs from the various MaxEnt models run. Dark grey indicates the two variables contributing the most to the model, the light grey shows the variables contributing less to the model and the white shows variables contributing the least to the model.

Model			Mean AUC	SD	Most gain	Gain loss	Human	Road	Park	River	Elevation	Vegetation
1	Panthera_leo	all	0.668	0.004	river	river	22.4	1.2	9.2	35.2	29	3
1	Panthera_leo	without_elevation	0.685		river	river	28.8	2.1	14.6	46.6		7.9
2	Panthera_leo	all	0.690	0.005	river	river	27.3	3.6	7.9	36.4	24	6
2	Panthera_leo	without_elevation	0.709		river	river	31.4	1.5	12.2	48.4		6.4
3	Panthera_leo	all	0.681	0.008	human	river	19.9	2	29.6	24.8	22.2	1.5
3	Panthera_leo	without_elevation	0.702		park	river	25.5	2.9	37.2	30		4.4
4	Panthera_leo	all	0.718	0.009	park	river	17.3	1.9	36.1	27.7	15.4	1.7
4	Panthera_leo	without_elevation	0.743		park	river	22.2	2.2	39.9	30.9		4.8
5	BNP	all bnp	0.825	0.006	elevation	river	18.4	1.4	0.2	39.6	40.4	0.1
		without_elevation	0.836		river	river	28.8	5.1	0.1	58.5		7.5
	MNP	all mnp	0.791	0.003	elevation	elevation	3.2	0	29	2.3	65.2	0.3
		without_elevation	0.806		park	human	24.6	3.5	57.7	8.1		6.1
	NRNP	all nrnp	0.835	0.003	river	river	6.3	3.9	0	44.1	54.1	0.6
		without_elevation	0.855		river	river	10	20.3	0.2	66.5		3
6	BNP	all bnp equal per park	0.843	0.006	elevation	river	18.5	1.7	0.2	42.6	36.9	0.1
		without_elevation	0.842		river	river	28.2	7.4	0	59.6		4.8
	MNP	all mnp equal per park	0.844	0.004	elevation	elevation	3.2	0.1	37.1	1.5	58.1	0.1
		without_elevation	0.848		park	human	24.3	3.9	56.5	9.3		6
	NRNP	all nrnp equal per park	0.864	0.003	river	river	6	4.7	0	49.9	38.6	0.8
		without_elevation	0.872		river	river	9.7	21.9	0.3	65.6		2.5
7	BNP	all bnp clipped to veg	0.871	0.007	park	elevation	1.1	1.1	55.1	13.4	29.2	0
		without_elevation	0.872		park	river	3.9	9.9	65.3	19		1.9
	MNP	all mnp clipped to veg	0.811	0.003	elevation	elevation	3.6	0.1	36.2	1.5	58.5	0.3
		without_elevation	0.816		park	human	22.7	3.4	61.7	7.4		4.7
	NRNP	all nrnp clipped to veg	0.852	0.003	river	river	6	4.6	0	48	40.5	0.8
		without_elevation	0.863		river	river	9.9	21.2	0.2	66.6		2.2
8	BNP	all bnp clipped to veg equal	0.870	0.004	park	elevation	1.2	0.8	56.1	11.3	30.4	0.1
		without_elevation	0.870		park	park	4.2	7.3	66.2	20.6		1.7
	MNP	all mnp clipped to veg equal	0.867	0.002	elevation	elevation	3.5	0.2	37.5	1.4	57.4	0.1
		without_elevation	0.870		park	human	23.7	3.7	57.6	9.2		5.8
	NRNP	all nrnp clipped to veg equal	0.889	0.003	river	river	6.2	6.4	0	48.9	37.7	0.8
		without_elevation	0.896		river	river	9.6	23.9	0.1	64.3		2.1
9	dry	done	0.752	0.003	river	river	27.4	2.2	3.5	30.3	33.7	2.9
	wet		0.748	0.003	river	river	17.3	0.6	21.1	31.8	23.9	5.2
10	dry	done	0.773	0.002	river	river	27	2.6	3.8	33.3	29.9	3.4
	wet		0.762	0.008	river	river	17.6	0.7	20.1	34.8	20.4	6.4
11	dry	done	0.766	0.003	human	river	21.2	3.1	24	19.6	30.1	2
	wet		0.762	0.005	park	river	12.2	1.7	40.3	23.6	19.2	2.9
12	dry	done	0.806	0.003	river	river	20.2	3.7	25.6	26.2	21.6	2.7
	wet		0.792	0.004	park	river	13.6	2	43	24.7	13.4	3.2
13	dry	done	0.893	0.007	elevation	river	14.7	6.4	0.1	39.5	39.2	0.1
	wet		0.891	0.004	elevation	river	22.7	2.2	1.4	37.2	36.2	0.2
14	dry	done	0.866	0.002	elevation	elevation	3.3	0.1	32.3	1.4	62.4	0.5
	wet		0.871	0.002	elevation	elevation	4.8	0.2	29.1	3	62.5	0.5
15	dry	done	0.907	0.002	river	river	7.4	13.4	0	53.1	25.6	0.6
	wet		0.907	0.001	elevation	river	8.1	4.3	0.3	40.1	45.8	1.4

CHAPTER 4: HOME RANGE AND UTILISATION DISTRIBUTION OF LIONS IN THE ZAMBEZI REGION

4.1 LION HOME RANGE SIZES IN THE ZAMBEZI REGION

This study is one of the first to document results for lions from a Time Local Convex Hull (tLoCoH) analysis in Southern Africa. As there are few studies to draw possible conclusions from, we can only present the results and speculate what these results might mean. Further studies are needed to fully understand the tLoCoH results presented.

Lion home range was calculated using the Time Local Convex Hull (tLoCoH) method, which was selected for its ability to incorporate the temporal extent of GPS collar data into construction of a home range (Lyons, Turner & Getz 2013). The script used for these analyses can be seen in Appendix B. The method was prepared according to Lyons (2013) (see section 3.3.1 for detail). The data need to be in a Universal Transverse Mercator (UTM) projection and the study area falls into UTM zone 34. This gives the home range size in square meters which was then converted to square kilometres in Table 4.1 below for ease of comparison between lion individuals. Isopleths are contour lines defining a subset of points based on probability of occurrence (Getz et al. 2007).

Table 4.1 tLoCoH results showing the home range size of each individual per National Park.

Isopleth level	SAT101 (km ²) Bwabwata Female	SAT102 (km ²) Mudumu Female	SAT103 (km ²) Nkasa Rupara Female	SAT2072 (km ²) Mudumu Male	SAT272 (km ²) Nkasa Rupara Male
0.95	840.13	599.64	98.63	661.23	124.03
0.75	287.57	342.03	50.13	264.70	45.57
0.5	94.84	127.34	21.84	92.29	19.94
0.25	19.51	36.20	5.32	18.30	7.02
0.1	1.53	2.23	0.31	7.05	1.08

The home range sizes vary from 90 km² (in Nkasa Rupara National Park) to 835 km² (in Bwabwata National Park) for the females, and 129 km² (in Nkasa Rupara National Park) to 606 km² (in Mudumu National Park) for the males. One of the potential driving factors in this large difference in home range sizes is the very small size of the southern park, Nkasa Rupara. The large difference in home range size is very unusual at first glance, given that the temporal extent of the data is the same and climatic conditions do not vary across the study area. Rainfall, which would usually impact on home range sizes, is similar across the three National Parks. This shows the importance of using other species distribution modelling analysis methods to understand the occurrence of the lion species in this area. Other studies have found climatic conditions to have the largest impact on home range size (Spong 2002, Loveridge et al. 2009, Davidson et al. 2013) but that does not necessarily apply to this study area. It can be seen from the home range maps in Figures 4.1 and 4.2 that the lions of Mudumu National Park remain largely within the park boundaries. Park boundaries would seem an obvious limiting factor to the extent of the home range, however, the parks in the study area are not fenced. This suggests that there might be an influence from the villages and human activity surrounding the National Park. The same applies to SAT103 and SAT272.

Home range size differs between males and females as well as between National Parks (Table 4.1, Figure 4.1 and Figure 4.2). SAT101 is a female lion in Bwabwata National Park and has the largest home range. Unfortunately there was no male lion collared with the same temporal extent as this female, but we can see that her home range is much larger than the other individuals in the other National Parks. The spatial extent of her home range did overlap with the male lion in Mudumu National Park. Where data exists, the home range size of the males is consistently larger than that of the females.

SAT101 was the most free-ranging of the lions. She remained on the western side of the Kwando River (see Figure 4.1) and never crossed over throughout the data collection period. We could only speculate as to why she remained on the western side; perhaps she did not feel comfortable crossing the river, or perhaps the human settlements on the other side of the river had an influence on her movements. During the study none of the female lions (SAT101, SAT102 and SAT103) crossed the Kwando River, which may be because lions generally avoid swimming. However, there have been recordings of lions crossing rivers in other studies (Cozzi et al. 2013). The female lions in this study did all have cubs at some stage during data collection, so it could be that they were wary to cross because of their young. The risk avoidance tendencies of lions

(Broekhuis et al. 2013) could include crossing a substantial river with cubs. This is something which could not be determined in the short temporal extent of this study, and is a reason for further research.

The males (SAT207, SAT2072 and SAT272) did all cross a river at some point during the study. Interestingly enough SAT207 and SAT2072 both crossed the Kwando River at the same location, but not at the same time. Although SAT207 was already dead when SAT2072 crossed the river and their collars do not span the same time, this river crossing may still have been learned behaviour in some form. It is possible that lions walk the length of this river until they find a suitable spot to cross, and that both these lions encountered this same spot at different times. The depth and velocity of rivers in lions' territories was not within the remit of this study; however, subsequent Internet searches for existing satellite images seem to suggest that this specific spot was the shallowest part of the river in their territory.

Male lions generally have a larger biological urge to wander and so they are more likely to cross rivers and rugged terrain in search of females to mate with. This trend towards larger male home ranges has been observed in another study in Hwange National Park, Zimbabwe (Benhamoua et al. 2014). Females, however, will remain in their home range and minimise possible risk (Broekhuis et al. 2013), for example avoiding crossing the river with cubs unnecessarily. If all the resource demands are met within their home range, the river will act as a barrier for movement across it. However, it was observed in this study in the field and in the satellite collar data, that lions do cross swampy areas and shallow channels, which can be seen in SAT103 (see Figure 4.1).

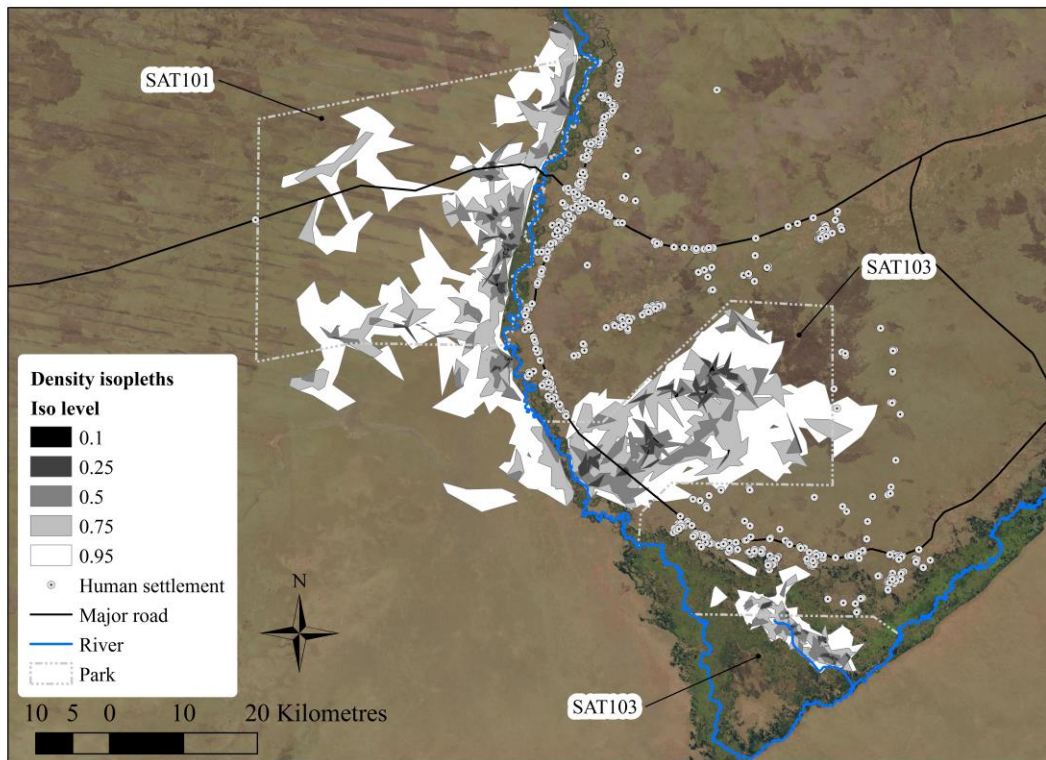


Figure 4.1 Home range estimation from a Time Local Convex Hull (tLoCoH) analysis on the female lions of the study. Isopleths show where the highest concentration of lion occurrence points are. Background satellite image is Landsat 8.

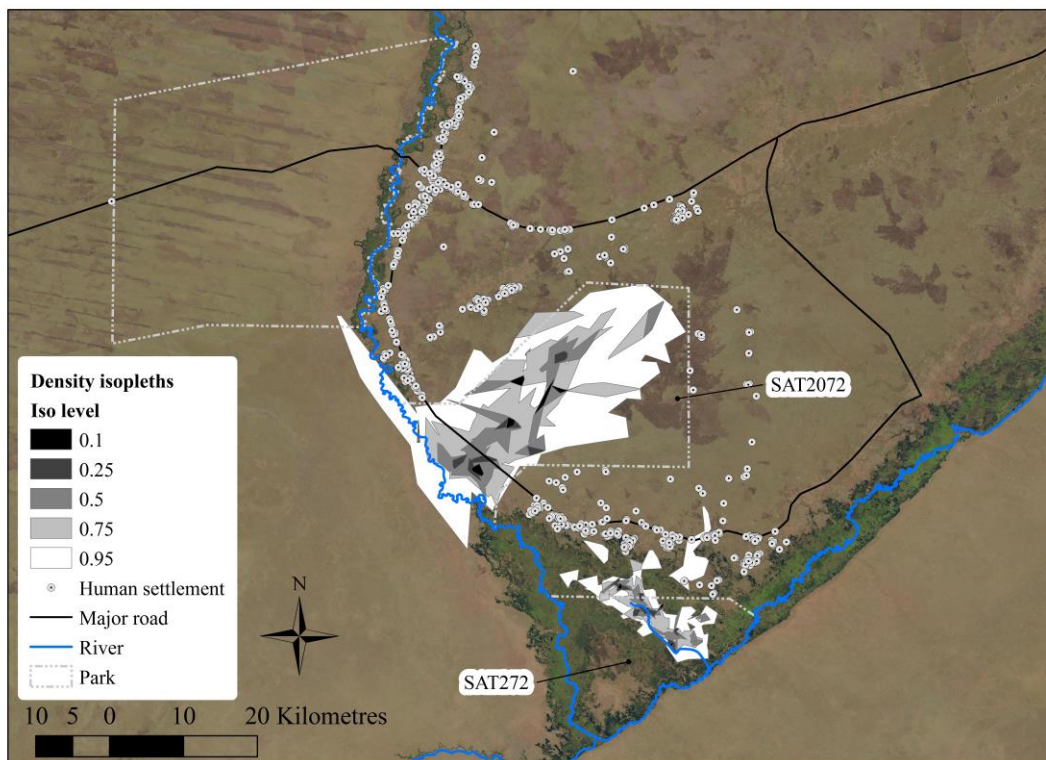


Figure 4.2 Home range estimation from a Time Local Convex Hull (tLoCoH) analysis on the male lions of the study. Background image is Landsat 8.

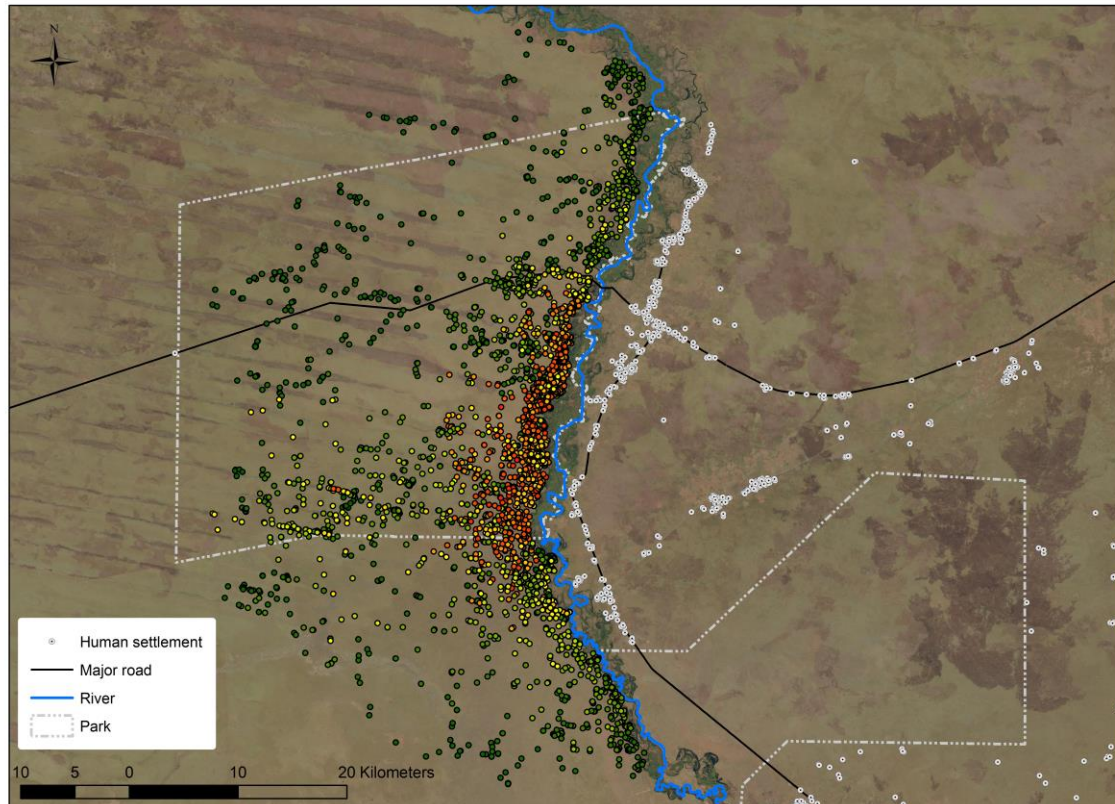
4.2 LION HOME RANGE UTILISATION IN TERMS OF TIME AND SPACE

Since the study spanned a reasonably short time-frame, it was not possible to reliably analyse seasonal shifts in home range. In general, no seasonal shifts were observed in the individuals collared in this study. Previous studies show that carnivores typically shift their home range or their prey preference from the dry to the wet season (Loveridge et al. 2009, Davidson et al. 2013, Tumenta et al. 2013, Laizer, Tarimo & Kisui 2014). The wet season in this study area runs from November to April and the dry season from May to October. The first big rains come from December onwards, but light rains can be expected from the beginning of November. The only possible seasonal shift in this study was observed in SAT103 and SAT272 from Nkasa Rupara National Park. These lions were collared for one wet season, and one dry season, and in the next wet season they sallied outside of the previous home range. This trip took them to the villages and corrals where they killed cattle and were thereafter shot. This conflict, and what drives the lions out of the park, is discussed in Chapter 5.

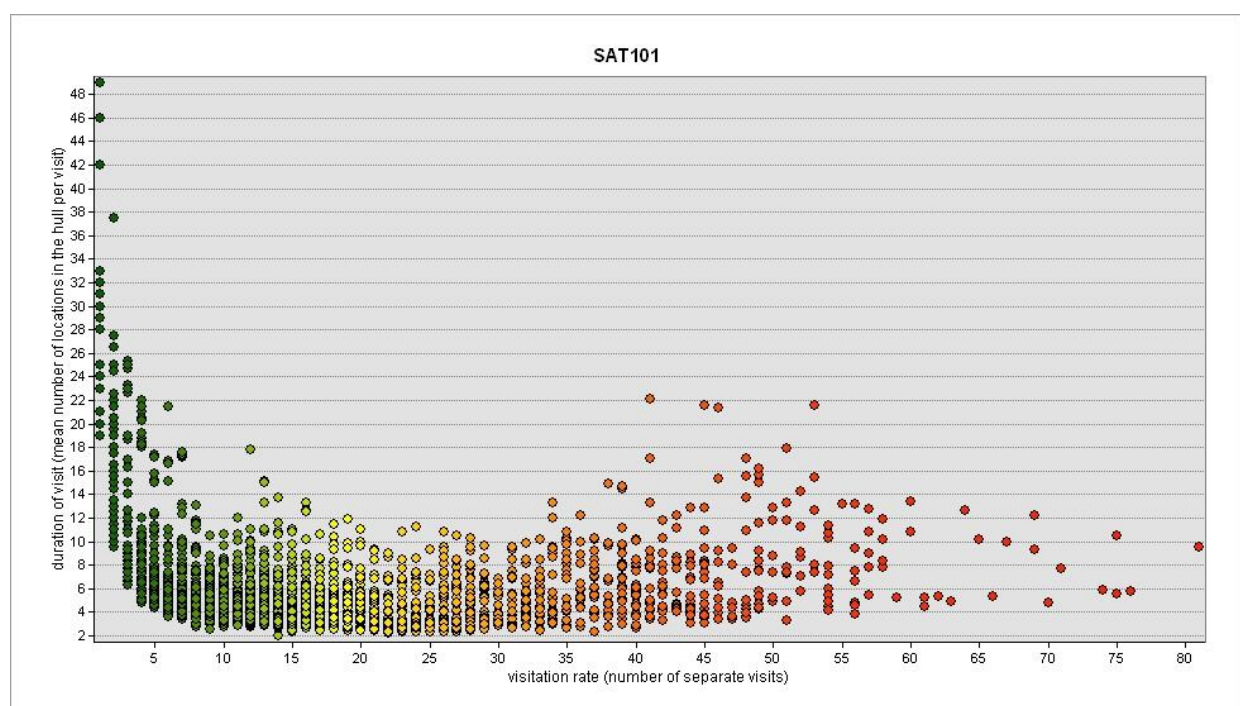
SAT272 was de-collared and declared a problem animal to be shot by trophy hunters. It is not known if he was ever hunted. Unfortunately SAT103 and her pride later became habitual stock raiders, catching cattle on at least three occasions. At this point the community could no longer financially sustain the losses and decided to kill her and one other lioness. These trips out of the park may have been the result of these lions searching for easier prey, as wildlife is known to disperse in the wet season making hunting challenging for the lions. Cattle are usually corralled at night and if the corral is not predator proof this makes the cattle easy prey. As indicated previously, it was not possible within the confines of this study to collate sufficient data to determine whether this slight shift in home range was typical wet season movement.

Below, results from the visitation rates and duration of visits of the individual lions using the tLoCoH analysis are presented. A general trend in the results is that all the individual lions had frequent visitations to the same location, and the duration of visits were mostly short. This will be discussed in detail below with the corresponding figures. Visitation rates are defined as the number of separate visits (NSV) to a hull and duration of visit is defined as the mean number of locations in the hull per visit (MNLV).

Figures 4.3 a) and b) show the visitation and duration of visits plotted against each other for lioness SAT101 in Bwabwata National Park. The green shades are areas which the lioness visited less frequently but for longer periods of time, and the orange to red shades show areas which were visited frequently but for short periods of time. From Figure 4.3 a) we can observe that when the lioness went to the outskirts of the home range she stayed there for longer periods of time. However, she did not return to these specific hulls within the time-frame of this study. Given knowledge accumulated in this area, the longer visits to the outskirts of the area may have been in search of prey. However, this speculation cannot be substantiated by the quantitative data collated in this study. The most frequently visited areas are along the river in the southern half of the Kwando core area of Bwabwata National Park.



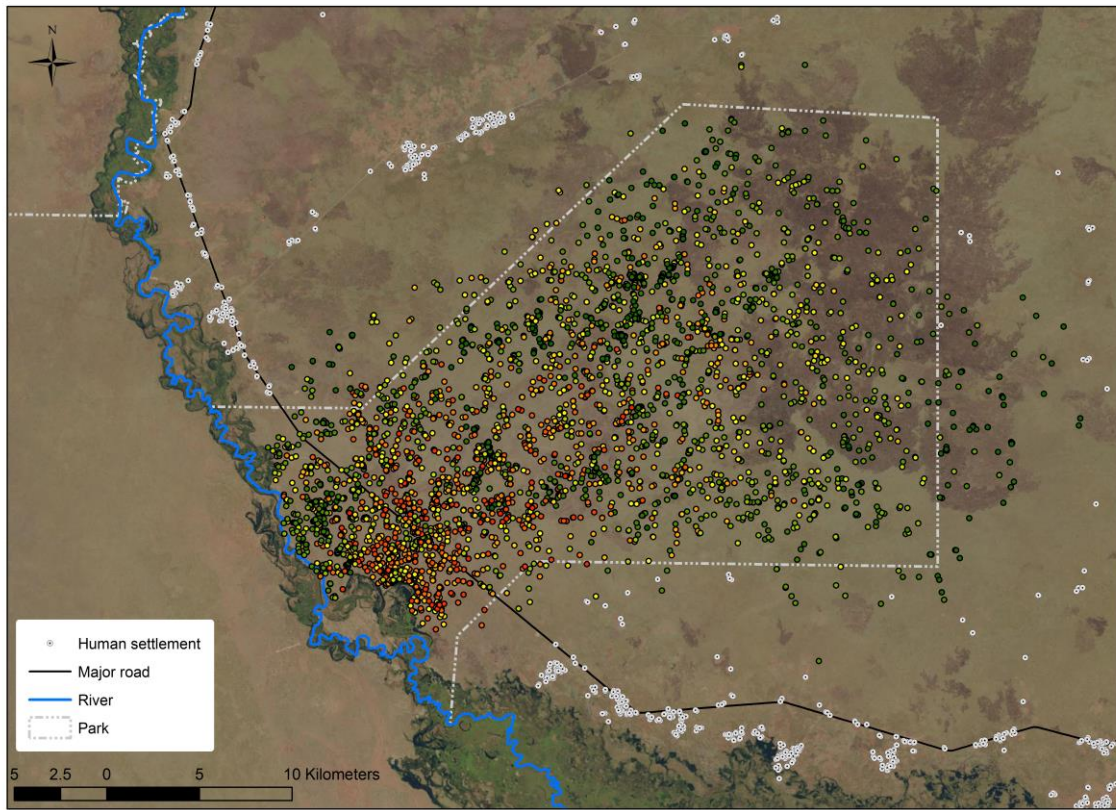
a)



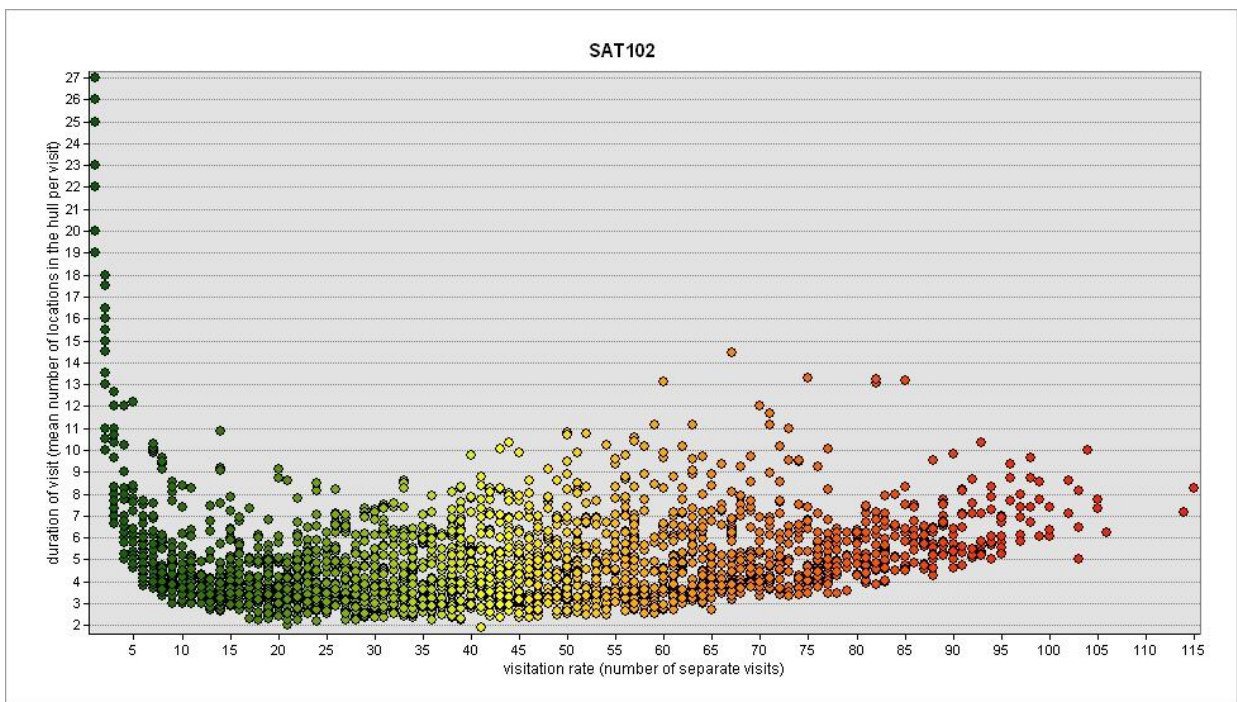
b)

Figure 4.3 a) SAT101 showing the parent points of hulls created using the Time Local Convex Hull analysis. The colour of points matches with those in b) to explain how the points relate to the landscape in the study area. b) Graph shows the duration of visits (MNLV) and visitation rate (NSV) of SAT101. The green dots are areas which the lioness visited less frequently but for longer periods of time, and the orange to red dots show areas which were visited frequently but for short periods of time

Figure 4.4 a) and b) show the time space utilisation of the home range of lioness SAT102 in Mudumu National Park. The colours in the figure 4.4 a) correspond to those in the graph in 4.4 b). We can see that the lioness spent longer periods of time in the outskirts of the park as well as inside the park (as indicated by green dots). Areas that were frequently visited but for shorter time periods are scattered inside the park. This is shown with greater clarity in Figure 4.4 b) below. The lioness frequently visited the river areas in the south eastern part of the park.



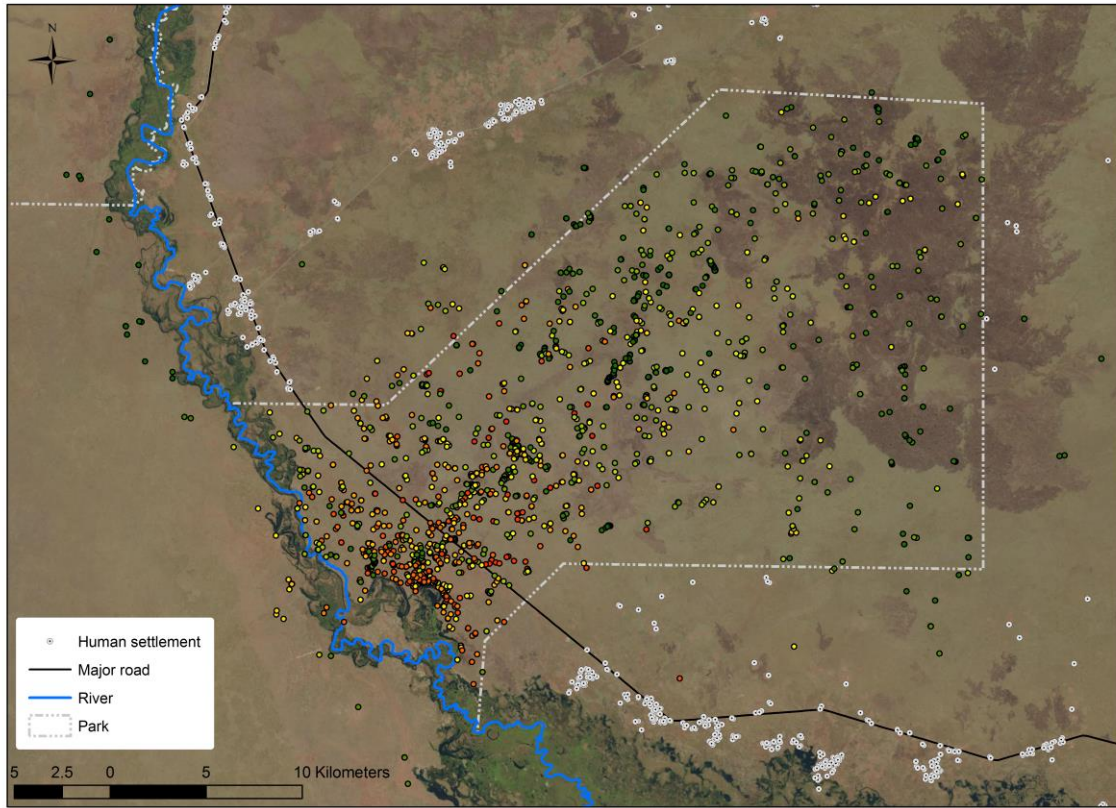
a)



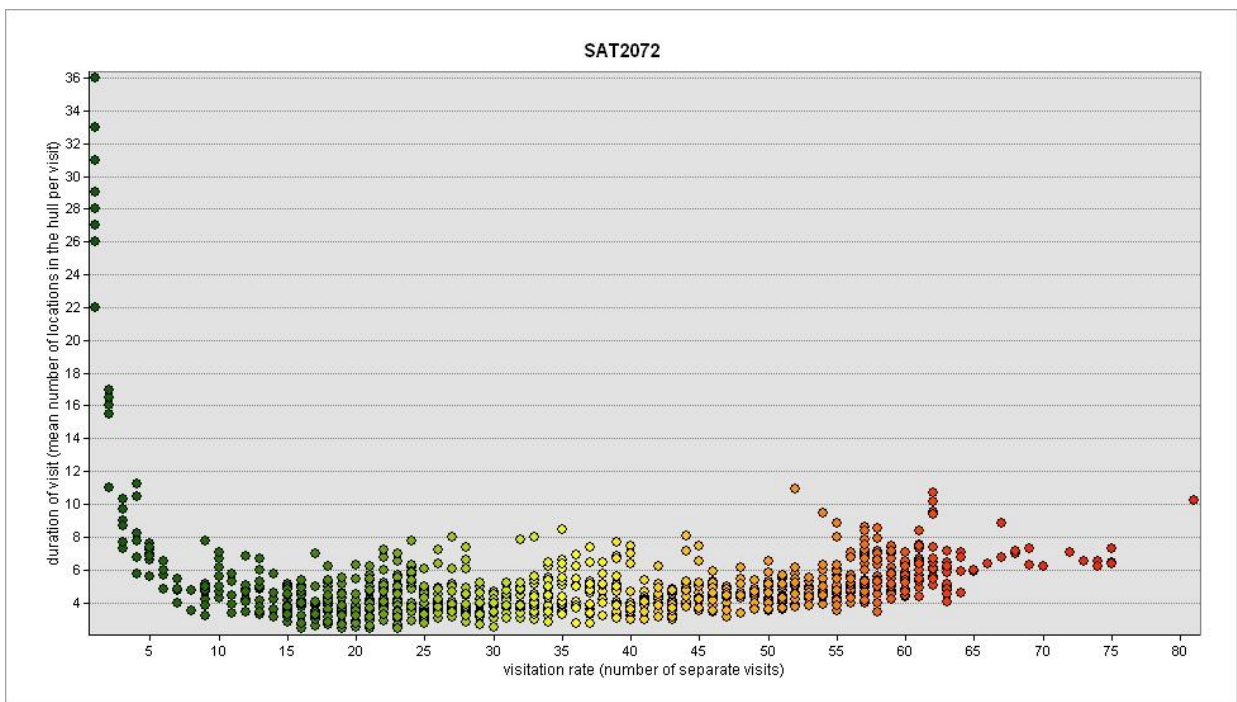
b)

Figure 4.4 a) Female SAT102 showing the parent points of hulls created using the time local convex hull analysis. The colour of points corresponds with those in b) to explain how the points relate to the landscape in the study area. b) Graph shows the duration of visits (MNLV) and visitation rate (NSV) of SAT102. For an explanation of colour refer back to Figure 4.3 or in text.

In Figure 4.5 a) and b) we can see the data from SAT2072 which is the male collared in Mudumu National Park. The time span of the data is only one year therefore it is difficult to compare to that of SAT102 (the female from the same park). However, for the available data we can see similar trends. SAT2072 frequently visited the same stretch of river in the south eastern part of the park and had longer, yet less frequent visits on the outskirts of the home range. Both SAT102 and SAT2072 spent a long period of time in the central part of the park. This could possibly have been elephant carcasses or poached elephants where they spent a longer period of time than normal feeding, but this was not confirmed in the field. A further contributing factor in this specific area may have been the proximity of a construction site located in the park at that time, where a road was being built and tarred. This could have been disturbing the female, resulting in the increased frequency and decreased time-span per visit as seen in the density of red points on the map.



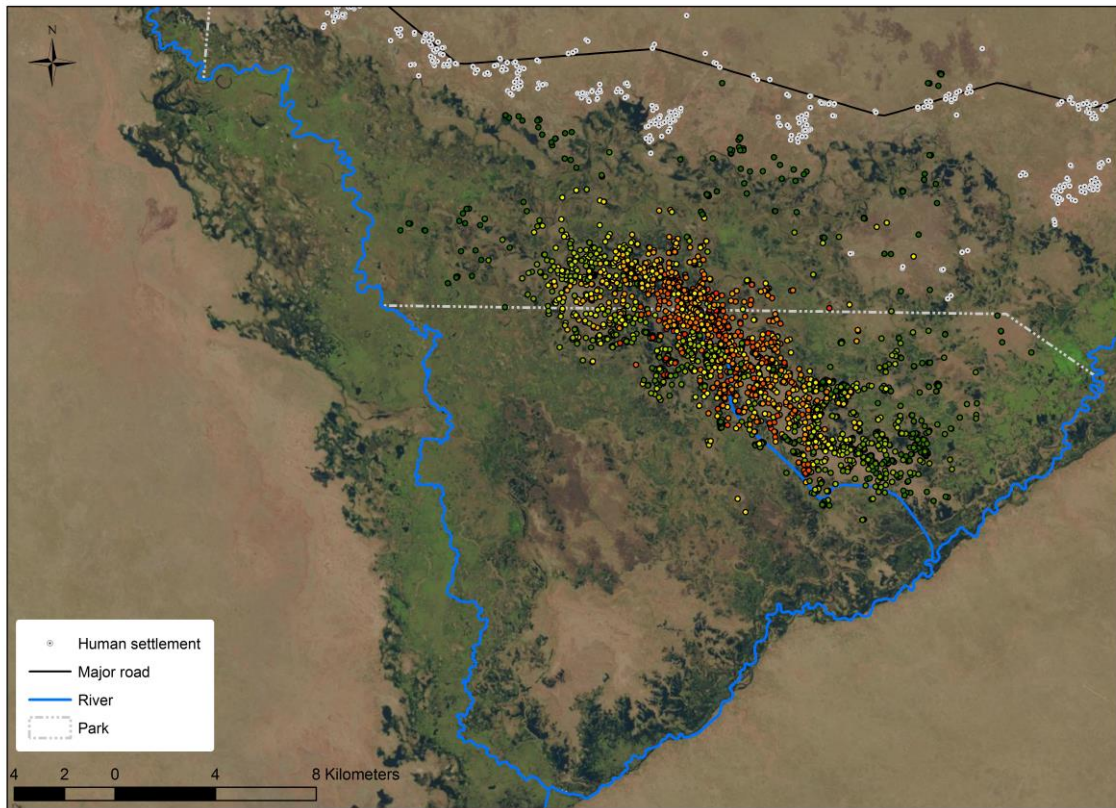
a)



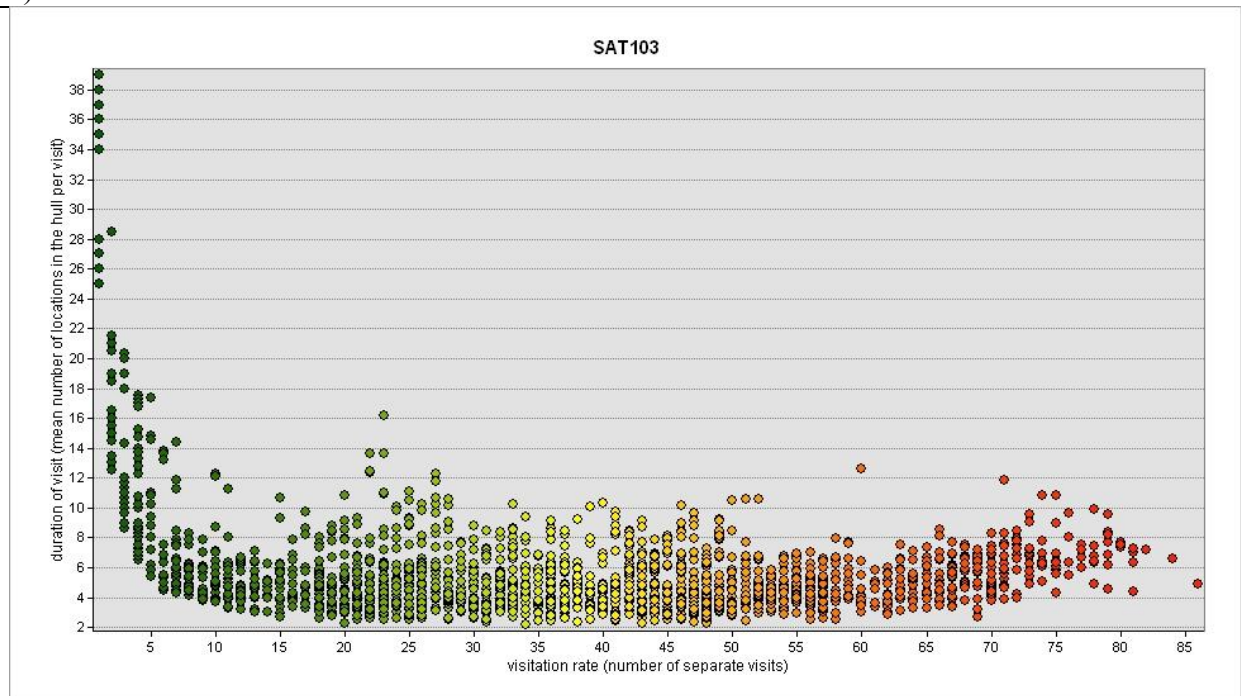
b)

Figure 4.5 a) Male lion SAT2072 showing the parent points of hulls created using the time local convex hull analysis. The colour of points corresponds with those in b) to explain how the points relate to the landscape in the study area. b) Graph shows the duration of visits (MNLV) and visitation rate (NSV) of SAT2072.

The results for lioness SAT103, the third female in the study, in Nkasa Rupara National Park are presented in Figure 4.6. Within the park there is a dry area of land surrounded by a swampy area of land which is known locally as Rupara Island. Given the density of dots indicating locations, it is not possible to see the dry area (Rupara Island) in the image below. Figure 4.6 shows the movement of SAT103 spending less frequent yet long time spans on the outskirts of the island and in close proximity of villages. This can also be observed in SAT272, the male collared in Nkasa Rupara National Park (see Figures 4.7). It is likely that this was due to the lions looking for easier prey to catch (cattle), as mentioned in the second paragraph of this section 4.2. Most of the frequent visits of SAT103 were on the north western part of the island, which extends beyond the park boundary.



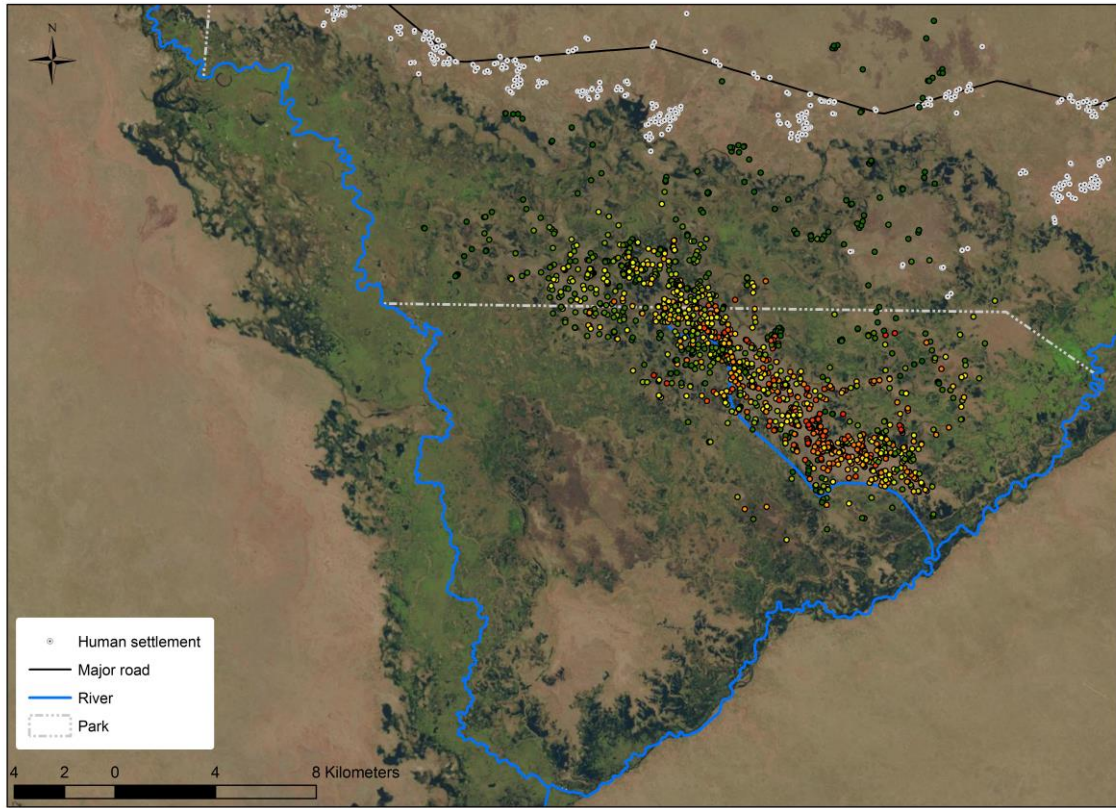
a)



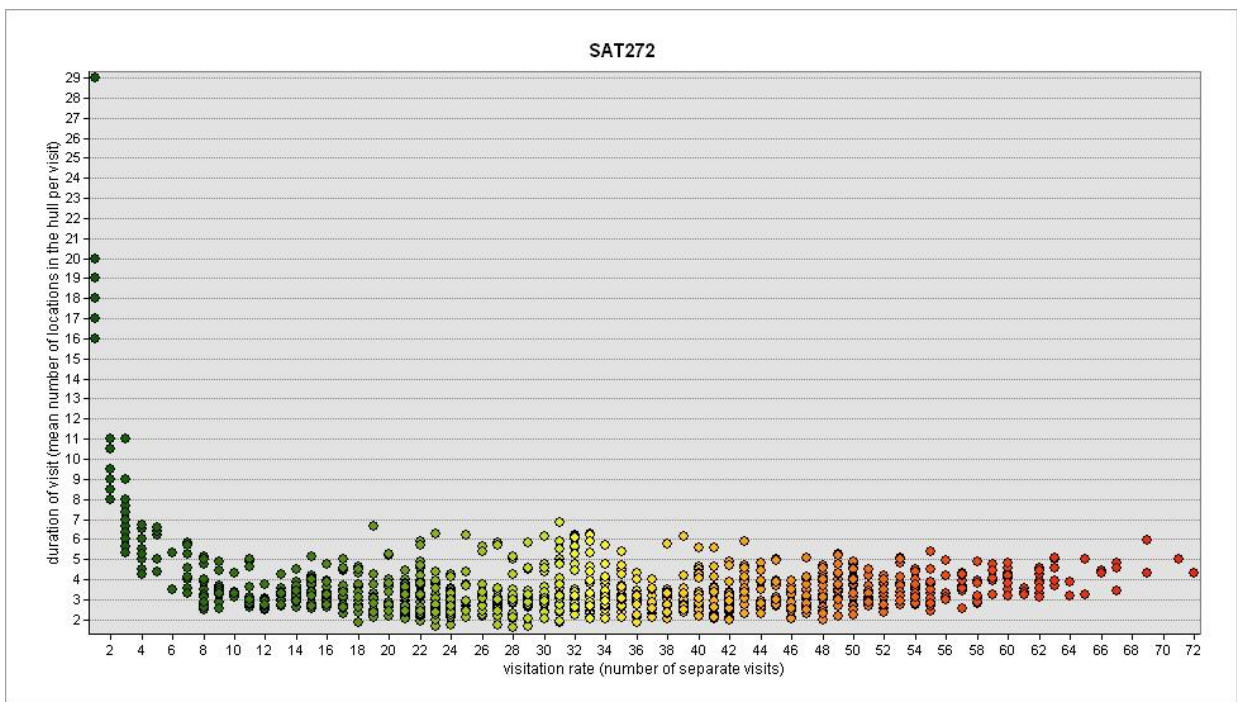
b)

Figure 4.6 a) Female SAT103 showing the parent points of hulls created using the time local convex hull analysis. The colour of points corresponds with those in b) to explain how the points relate to the landscape in the study area. b) Graph showing duration of visits (MNLV) and visitation rate (NSV) of SAT103

Patterns similar to SAT103 can be observed in the male, SAT272 also in Nkasa Rupara National Park. However, he frequents the south eastern part of the island which can be seen in the density of red dots in Figure 4.7 a) below. Trips outside of the more frequented part of the home ranges could be showing where the lions went to kill prey which may have been larger, and therefore spent longer periods of time there. In Figure 4.7 longer periods of time during an individual visit are indicated by green dots. There has been a perceived increase in wildlife poaching in the Zambezi Region since 2011 (Kahler, Roloff & Gore 2012), which could have influenced the movement of the lions, as the resultant carcasses would provide easy food to access.



a)



b)

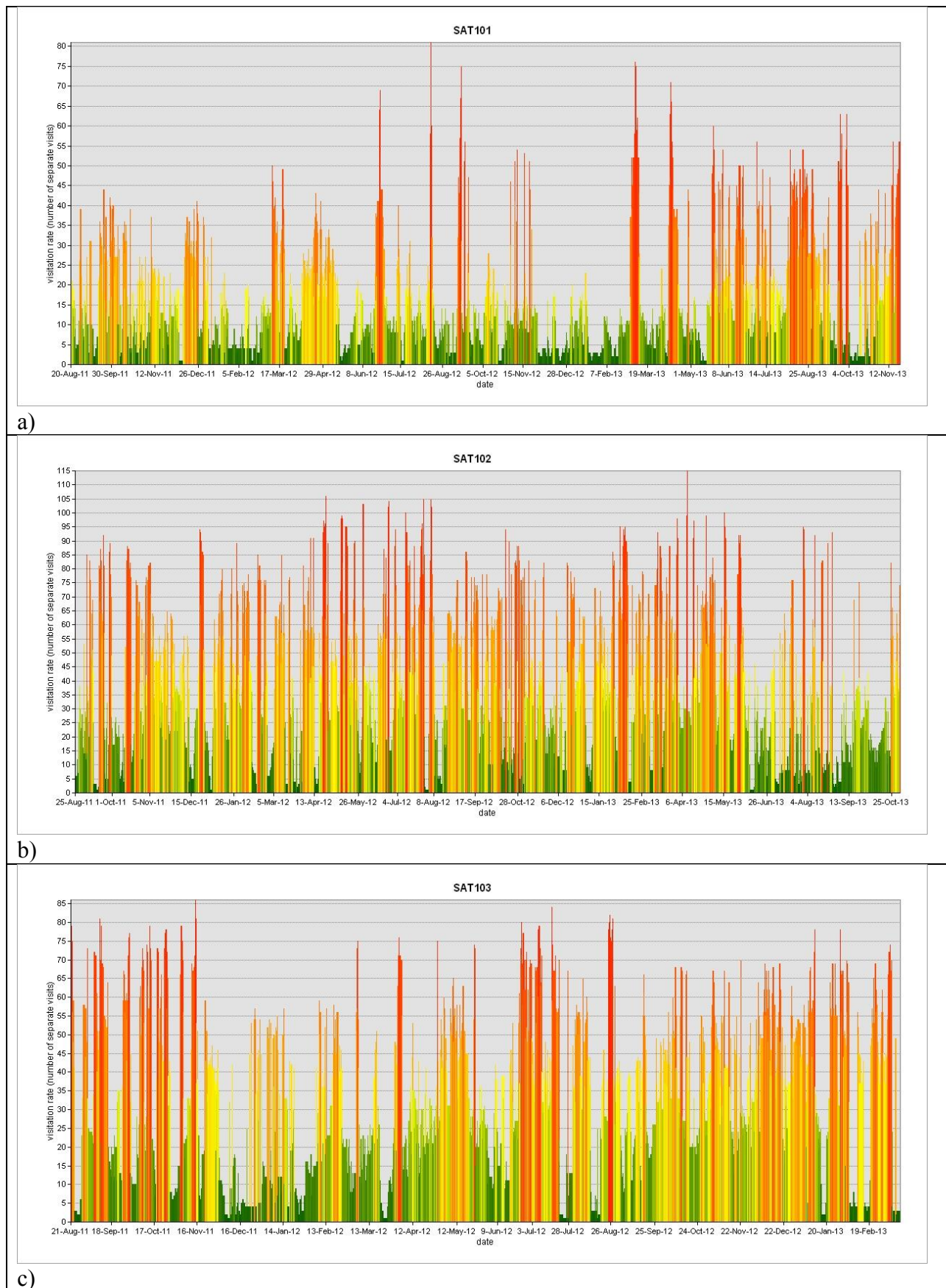
Figure 4.7 a) Male lion SAT272 showing the parent points of hulls created using the time local convex hull analysis. The colour of points corresponds with those in b) to explain how the points relate to the landscape in the study area. b) Graph shows the duration of visits (MNLV) and visitation rate (NSV) of SAT272.

4.3 VISITATION RATES AND DURATION OF VISITS IN DETAIL

The use of home range by individual lions can be demonstrated in greater detail when using graphs derived from the Time Local Convex Hull (tLoCoH) analysis. From the graphs below we can see how the duration of visits and visitation rates change over time among the different individuals.

Figure 4.8 below shows the three females' visitation rates over time for comparison. All three lions displayed a similar pattern of a period of frequent short visits, interspersed with a period of longer visits at one location. While in many occasions reasons for durations of visits could be derived from concurrent field observations, in other cases, where only GPS data were available, this was not possible. This is a reason to broaden future research so that tLoCoH results can be interpreted in greater detail for lions.

SAT101 shows a more stable pattern in 4.8 a) whereas SAT102 in 4.8 b) shows more erratic movement. This could be because Mudumu National Park is surrounded by humans; personal observation in the field revealed this lioness to have a nervous and skittish nature which might explain the frequent short visits. SAT101 was from a larger pride with males, whereas SAT102 was part of a pride of three females at the time of collaring. She was in the same location as the male SAT2072 much later in the study and had cubs in June 2013. SAT103 in Nkasa Rupara National Park shows similar movement to that of SAT102. The visitation patterns of SAT103 falls somewhere between those of SAT101 and SAT102. It is also slightly erratic but has more instances of longer yet infrequent visits, see figure 4.8 c).



c)

Figure 4.8 Visitation rate for females lionesses a) SAT101 in Bwabwata National Park b) SAT102 in Mudumu National Park and c) SAT103 in Nkasa Rupara National Park. The colour of the bars in the figures below matches the detail in the figures displayed in 4.2; shades of green are areas which were less frequently visited but for longer periods of time, shades of red are areas which were visited frequently but for short periods of time, a yellow indicating a range between green and red.

SAT2072 and SAT272 provided sufficient data to analyse their movements using tLoCoH, unlike the data extracted for SAT207 which only spanned two months. Figure 4.9 a) and b) show the visitation rates of the male lions, SAT2072 in Mudumu National Park and SAT272 in Nkasa Rupara National Park. SAT2072 shows a pattern of frequent short visits (indicated in red) interspersed with periods of longer visits at one location (indicated in green). A similar pattern is observed in SAT272.

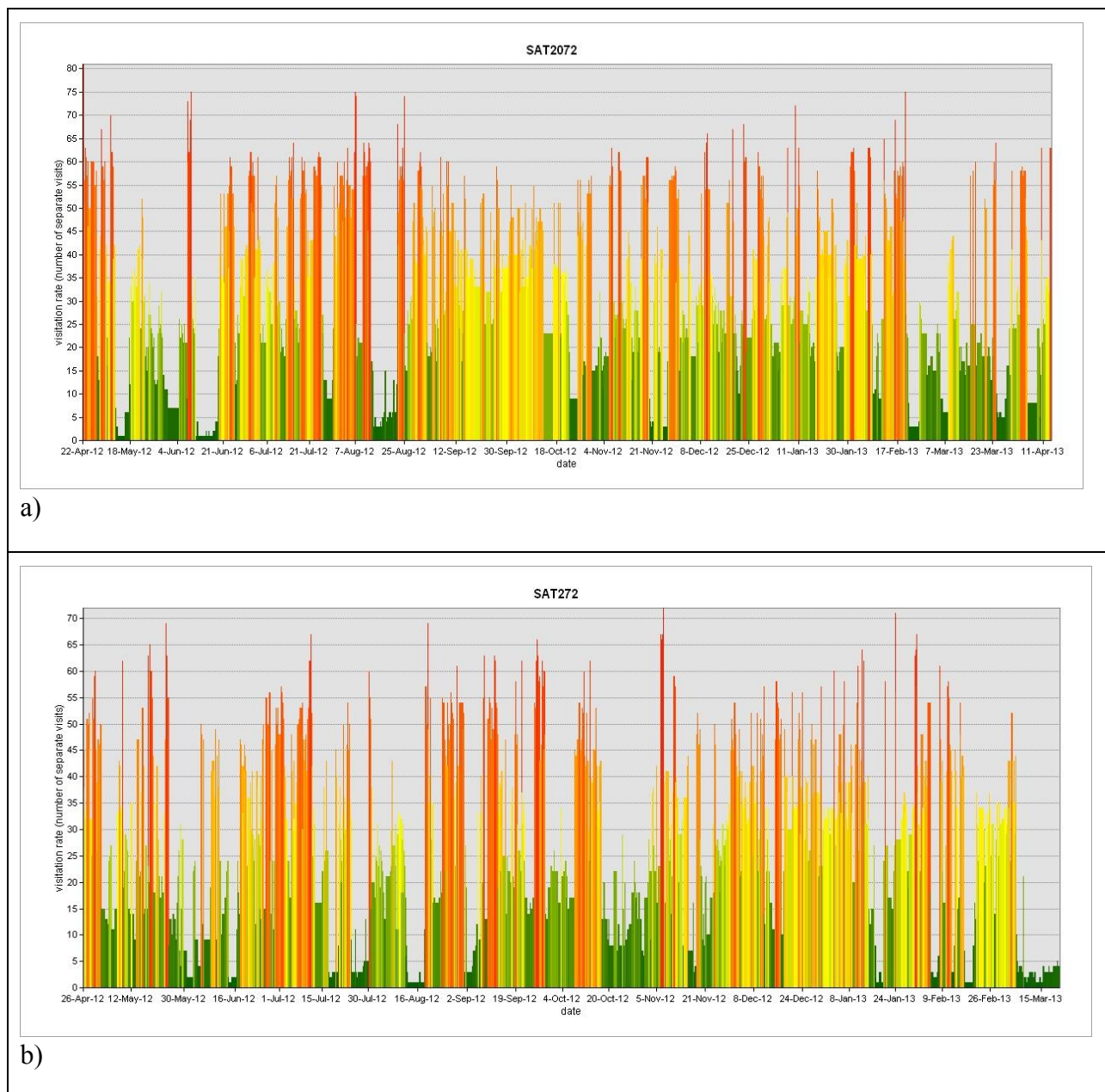
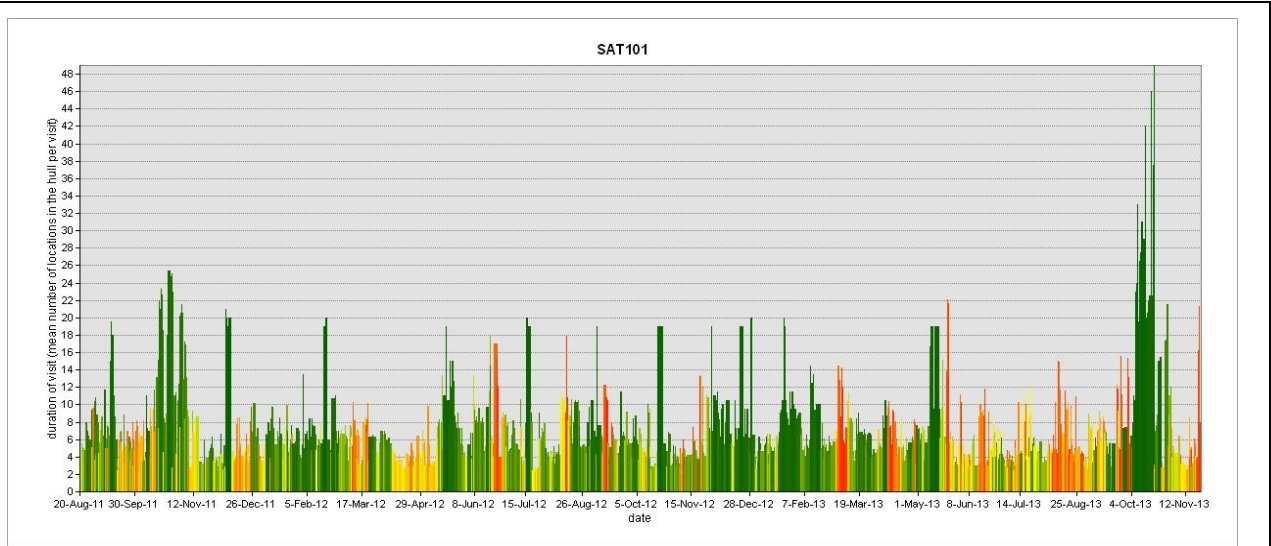


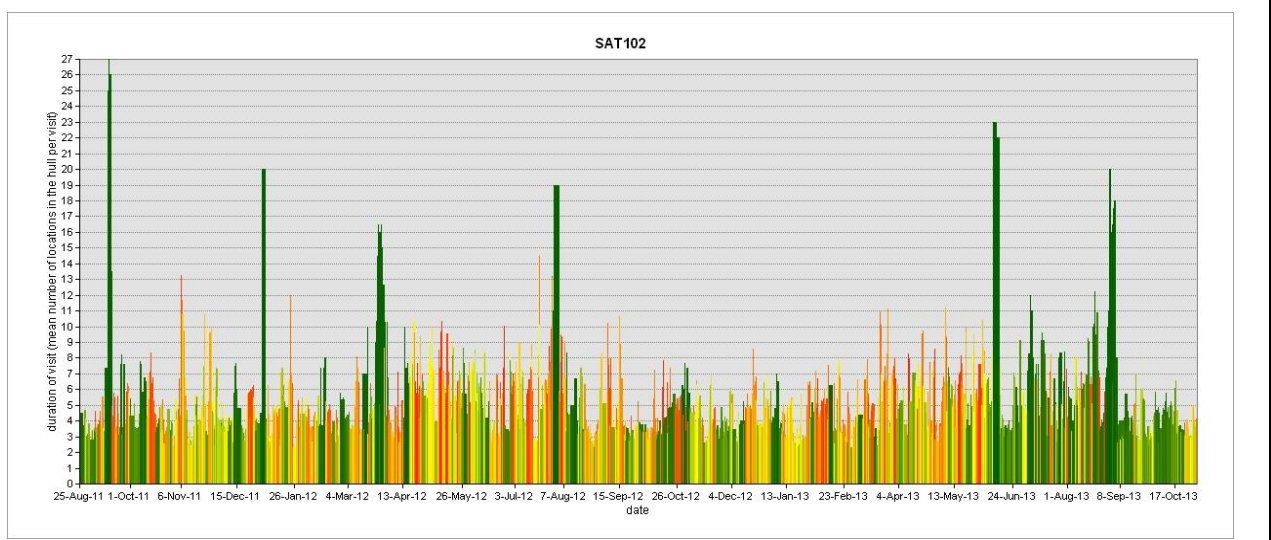
Figure 4.9 Visitation rate for the male lions in a) Mudumu National Park, SAT2072 and b) Nkasa Rupara National Park, SAT272.

Figure 4.10 shows the duration of visits from the tLoCoH analyses for the three females for comparison. Figure 4.10 c) gives a noticeable indication that in December 2011 SAT103 visited single locations in close proximity for extended periods of time. It is assumed that this is because she gave birth to a litter of cubs at the beginning of December 2011. When she was collared late in August 2011 she was together with a male mating at the time. The gestation period of lions is 4 months which meant the estimation of birth in December 2011 is likely to be correct. She was then observed in the middle of December 2011 with cubs. This noticeable change in the behaviour of duration of visits using tLoCoH results together with biological factors (such as giving birth and the initial four weeks of rearing cubs) was not found in existing literature at the time of writing.

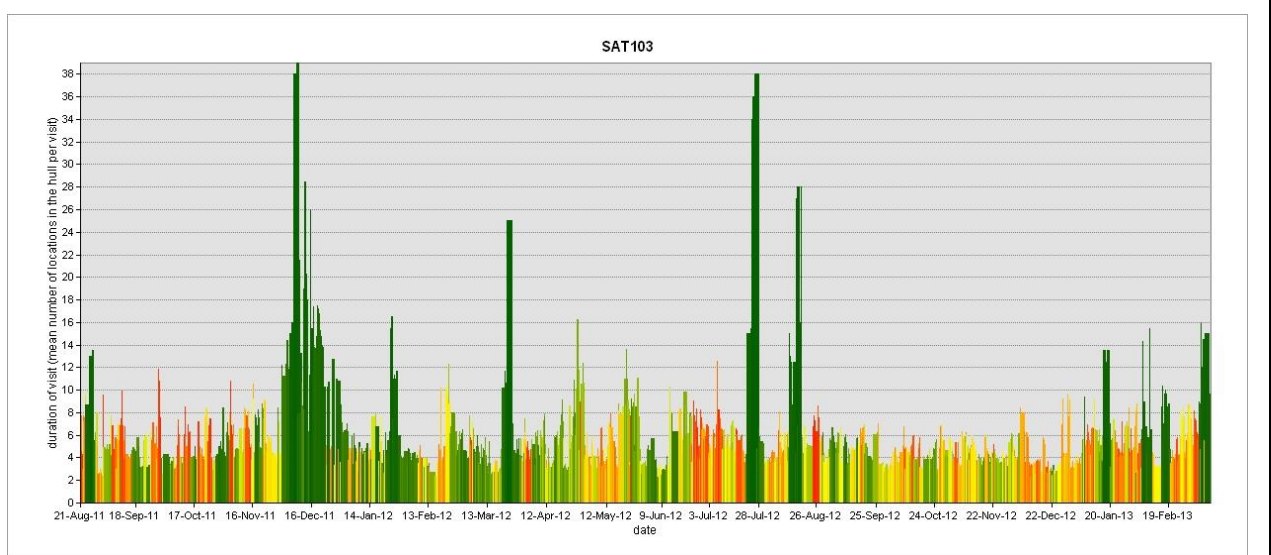
SAT102 was also sighted with cubs in July 2013 and in this time displays a similar pattern of visits as SAT103, albeit not as remarkable - see figure 4.10 b). SAT101 was observed with small cubs at the time of darting and collaring. It is unclear whether her initial movements immediately after collaring are due to the effect of collaring, or due to the cubs. It is possible that SAT101's long duration of visit in October 2013 – see figure 4.10 a) - indicates that she had cubs, if we extend the deduction from SAT103 as explained in the previous paragraph. However, there are no confirmed sightings and SAT101 has not been sighted again.



a)



b)



c)

Figure 4.10 Duration of visit for the female lionesses a) SAT101, Bwabwata National Park, b) SAT102, Mudumu National Park, c) SAT103, Nkasa Rupara National Park.

Figure 4.11 below shows the duration of visits over time for the two male lions SAT2072 in Mudumu National Park and SAT272 in Nkasa Rupara National Park. In 4.11 a) we can see that SAT2072 in Mudumu National Park had two main periods of long visits in May and June 2012, but most of his visits were shorter. SAT272 in Nkasa Rupara National Park shows similar patterns. Further research would need to be done to understand the meaning of longer duration of visits for male lions.

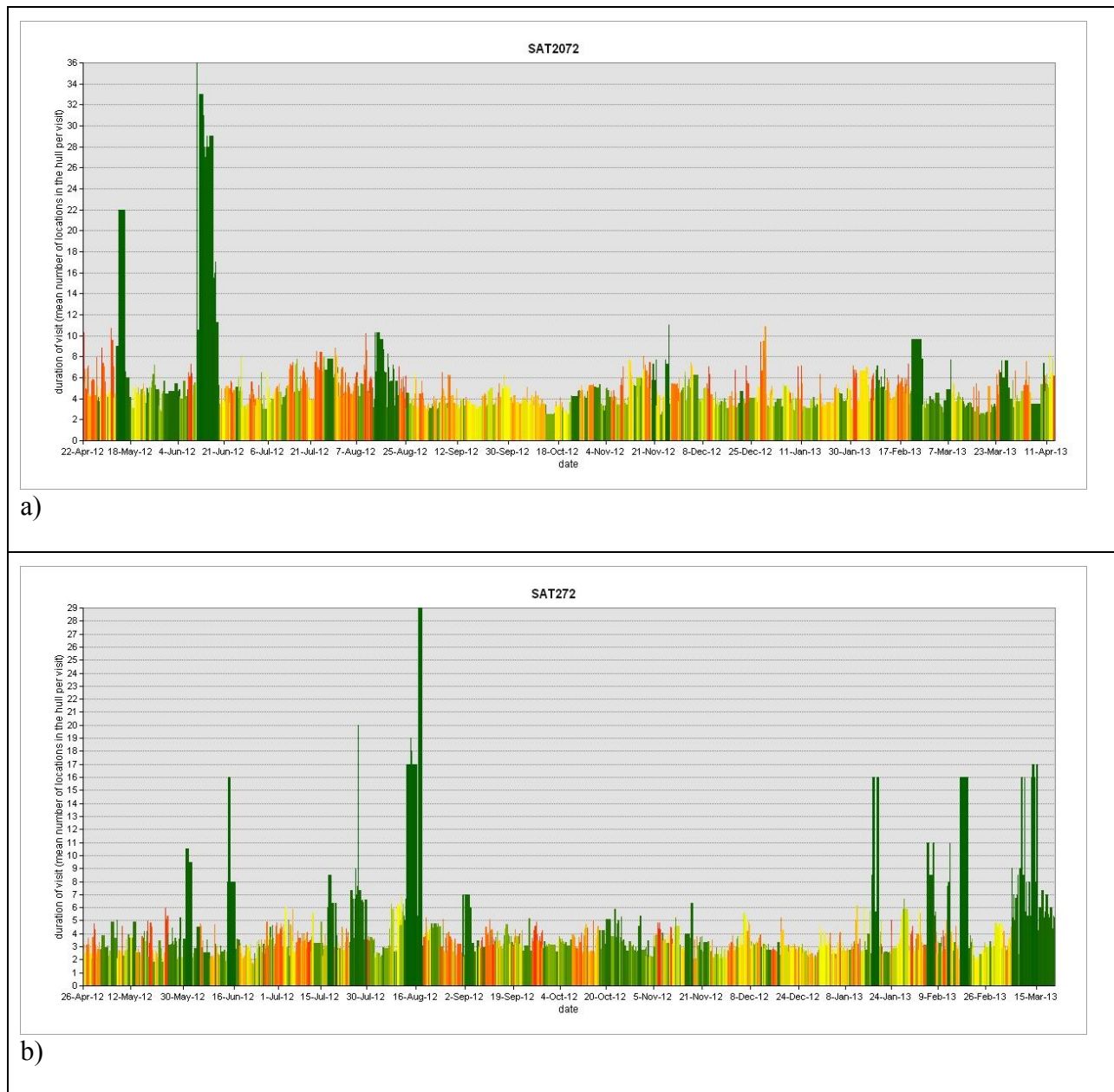


Figure 4.11 Duration of visit for the male lions a) SAT2072, Mudumu National Park, b) SAT272, Nkasa Rupara National Park.

In conclusion, it seems that lionesses have patterns of movement distinguishable from male lions. However, even within these two sub-categories the data show unique and diverse visitation rates. There appears to be no overwhelming pattern identifiable by tLoCoH analyses within the time-frame of this study, neither in the sex of the lion nor within the individual parks. Using the time-use metrics from tLoCoH we can qualitatively begin to understand the difference in home range use and adaptations to the heterogeneous landscape (Lyons, Turner & Getz 2013). However, this research is only the beginning of understanding how lions use their home range in terms of time. Factors such as kills, frequent drinking sites, resting sites and reproduction of the species may influence visitation rates and duration of visits and are expected to have done so in this study, although more field observations would need to be undertaken to verify how these factors relate to tLoCoH results.

4.4 STEP LENGTH

Other data extracted in relation to lions' movements was their average step length. Readings between points were separated by four hours. As such it was not possible to determine detailed movements within this four hour time-frame, however, the distance measured between two consecutive readings gives an accurate indication of minimum distance covered. Step length, i.e. the distance moved between four-hourly satellite fixes, confirms that lions move more at night (see Table 4.2) and most individuals show night step lengths of more than double the day step lengths. Only SAT103 deviated from this.

Interestingly, no difference in step length is noticeable between seasons. It was thought that lions might have a larger step length in the wet season. This derived from the fact that prey tend not to congregate along permanent water sources in the wet season, but scatter widely throughout available habitat (Valeix et al. 2010). In the dry season prey is concentrated along permanent water sources such as rivers. This thought was challenged as i.e. step length averages remained the same in the wet and the dry seasons with an average of ± 1000 metres between readings (see Table 4.2 and Appendix C).

Table 4.2 The mean (and standard deviation) of the step lengths of each individual lion in metres.

	SAT101 Bwabwata Female	SAT102 Mudumu Female	SAT103 Nkasa Rupara Female	SAT2072 Mudumu Male	SAT272 Nkasa Rupara Male	Overall Mean
Dry	1191.29 (1684.439)	1520.14 (1952.559)	713.89 (930.081)	1915.95 (2485.957)	1192.22 (1640.37)	1306.70
Wet	1047.71 (1530.371)	1390 (1673.885)	701.55 (934.605)	1952.54 (2719.393)	1086.72 (1448.85)	1235.70
Day	578.51 (906.968)	514.78 (883.944)	622.3 (775.598)	293.95 (1117.228)	503.92 (788.934)	502.69
Night	1391.15 (1807.823)	1890.99 (1983.245)	750.34 (1000.285)	2619.65 (2743.45)	1441.4 (1723.666)	1348.92

CHAPTER 5: DRIVERS OF LION OCCURRENCE IN THE ZAMBEZI REGION

5.1 USING GEOGRAPHICALLY WEIGHTED REGRESSION AS A TOOL FOR LOCAL REGRESSION ANALYSIS

Geographically weighted regression (GWR) was used for the analysis of lion occurrence and factors influencing occurrence (Brunsdon, Fotheringham & Charlton 1996, Brunsdon, Fotheringham & Charlton 1998, Fotheringham, Brunsdon & Charlton 2002, Charlton & Fotheringham 2009). The lion count data needed to be log transformed which improved the skewness and kurtosis values from 13.59 and 260.55 to 3.43 and 15.244 respectively, and normalised the data. Figure 5.1 below shows the grid which was used for the geographically weighted regression analysis which was limited to the extent of the smallest extent of the input variables. The grid is made up of 11988 grid cells.

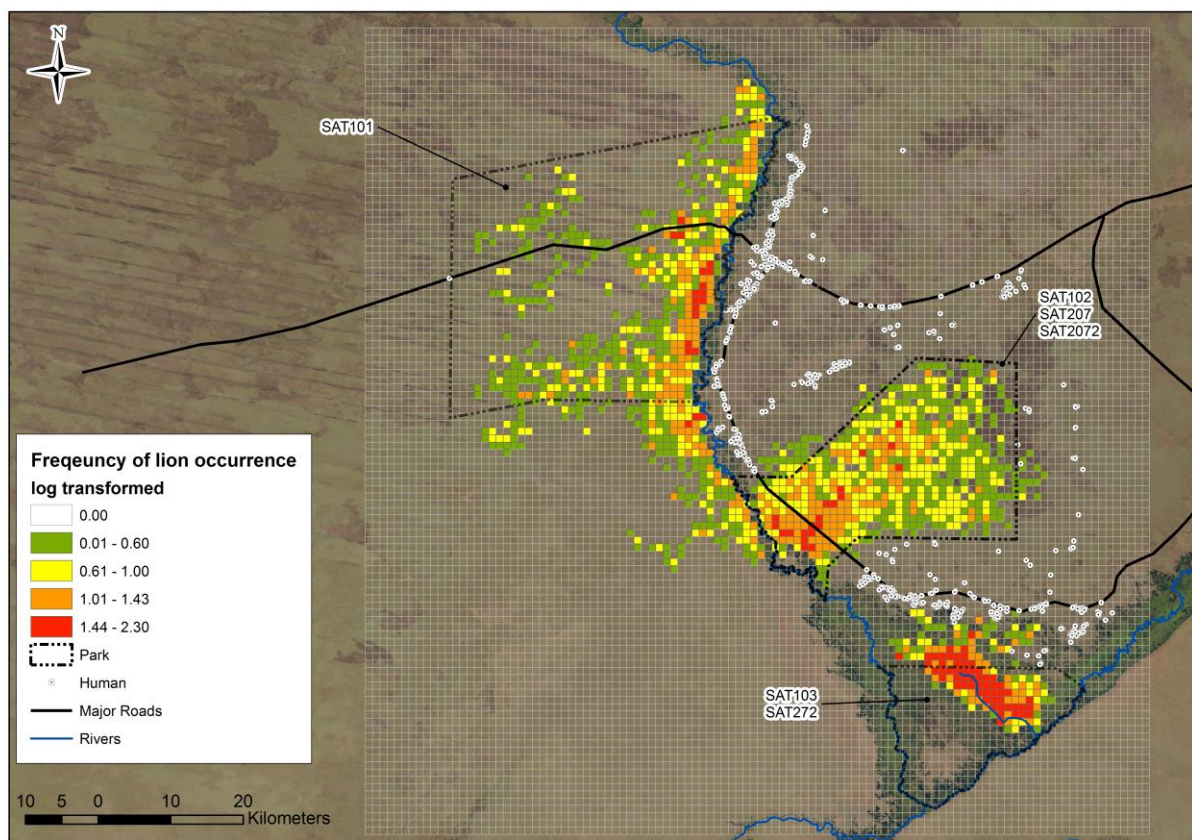


Figure 5.1 Log transformed lion occurrence data and grid used for GWR analysis.

An ordinary least squares (OLS) regression was done for each model as well as a GWR to compare the Akaike Information Criterion (AICc) values and the R^2 values. The AICc, as mentioned in Chapter 2, is a way to determine how well the model performs compared to previous runs of the model (Burnham & Anderson 2004). AICc values are only relevant if the dependent variable remains the same. The log transformed data performed consistently better than the non-transformed data, therefore it was decided to only present the log transformed data in the results.

Once the dependent variable was transformed, it was then correlated with the different variables individually using an OLS regression (see Appendix A for full results). The residuals of the OLS regression showed spatial autocorrelation in all cases (z-score from Moran's I ranged from 40.149 to 119.500, Appendix A). Consequently, GWR was used to run the same analysis. This method was used as it deals specifically with spatially auto-correlated independent variables (see Chapter 3 section 3.3.2 for more description), and this improved the spatial autocorrelation in the residuals. Distance to human and road were closely related, demonstrated by the variance inflation factor (VIF) values; and were above 7.5 for these two factors when all the grid cells were taken into consideration. This made sense as many of the villages are situated along a major road. However, when the regression was done on the grid cells which have lion count only there was no longer autocorrelation.

The independent variables which are tested are distance to river, distance to human activity, distance to park boundary and distance to road. These were shortened to river, human, park and road. To define location in relation to park boundaries, values showing distance to the boundary inside the park were classified as positive and values outside as negative. The results show that GWR performed consistently better than the OLS regression. This can be seen in Table 5.1 below; model 15 b) the AICc value for the OLS regression is 104.661 and for model 15 d) the AICc value for GWR is 73.43. The R^2 values were higher in the OLS regression but, because the GWR has a better AICc value, we consider the R^2 value from the GWR model as residuals are autocorrelated such that the AICc values from OLS are essentially invalid (see Appendix A for detailed results). This shows that GWR the better fit tool for the data and the variation in the data. The model which achieved the lowest AICc values using the GWR included river, human, road and park (model 15). Model 15 d) had the lowest AICc value (73.43), although it explained slightly less of the variability in the data than model 15 b) using the OLS regression (overall R^2

(model 15 OLS) = 0.704 versus overall R^2 (model 15 GWR) = 0.60). GWR was able to account for the majority of the variability in the data.

AICc values for GWR done on individual independent variables were much higher than when the bandwidth was set to 125 neighbours. For this analysis, the bandwidth estimator was set to 'adaptive parameter' for AICc. This parameter chooses 'nearest neighbours', prioritising AICc values. The results can be seen in Table 5.1 below.

Table 5.1 Geographically weighted regression and Ordinary least squares value outputs. Dependent variable was consistently lion count log transformed.

Model	Independent Variables	Method		AICc	adjusted R^2	Neighbours
1. a)	River	OLS	All	3815.948	0.048	
b)			Lion_only	1238.756	0.143	
c)		GWR	All	-4488.752	0.525	562
d)			Lion_only	604.634	0.461	83
2. a)	Human	OLS	All	3910.576	0.04	
b)			Lion_only	1407.144	0.039	
c)		GWR	All	-5644.964	0.57	414
d)			Lion_only	540.015	0.491	67
3. a)	Park	OLS	All	3044.533	0.107	
b)			Lion_only	1466.401	-0.0005	
c)		GWR	All	-5821.31	0.576	382
d)			Lion_only	477.11	0.523	44
4. a)	Road	OLS	All	3945.473	0.037	
b)			Lion_only	1423.926	0.028	
c)		GWR	All	-5684.475	0.571	421
d)			Lion_only	628.672	0.451	97
5. a)	River, Human	OLS	All	3600.436	0.065	
b)			Lion_only	1232.659	0.148	
c)		GWR	All	-1749.503	0.749	125
d)			Lion_only	512.247	0.495	125

Continued overleaf

Table 5.1 continued

Model	Independent Variables	Method		AICc	adjusted R ²	Neighbours
6. a)	River, Park	OLS	All	2959.894	0.113	
b)			Lion_only	1197.066	0.168	
c)		GWR	All	-836.867	0.705	125
d)			Lion_only	514.829	0.48	125
7. a)	River, Road	OLS	All	3568.164	0.678	
b)			Lion_only	1233.006	0.147	
c)		GWR	All	-763.61	0.702	125
d)			Lion_only	497.736	0.488	125
8. a)	Human, Park	OLS	All	3013.946	0.109	
b)			Lion_only	1402.491	0.042	
c)		GWR	All	-2479.644	0.0699	125
d)			Lion_only	561.089	0.481	125
9. a)	Human, Road	OLS	All	3907.83	0.041	
b)			Lion_only	1393.612	0.048	
c)		GWR	All	-2473.471	0.695	125
d)			Lion_only	563.764	0.461	125
10. a)	Park, Road	OLS	All	3003.213	0.11	
b)			Lion_only	1425.691	0.027	
c)		GWR	All	-2238.772	0.699	125
d)			Lion_only	446.481	0.441	125
11. a)	River, Human, Park	OLS	All	2921.771	0.116	
b)			Lion_only	1183.069	0.177	
c)		GWR	All	401.08	0.76	125
d)			Lion_only	320.171	0.567	125
12. a)	River, Human, Road	OLS	All	3570.071	0.067	
b)			Lion_only	1222.099	0.154	
c)		GWR	All	-344.103	0.75	125
d)			Lion_only	291.153	0.589	125
13. a)	River, Park, Road	OLS	All	2927.289	0.116	
b)			Lion_only	1176.241	0.18	
c)		GWR	All	226.853	0.721	125
d)			Lion_only	137.88	0.534	125
14. a)	Human, Park, Road	OLS	All	3005.189	0.11	
b)			Lion_only	1390.731	0.05	
c)		GWR	All	-847.726	0.748	125
d)			Lion_only	226.123	0.5	125
15. a)	River, Human, Park, Road	OLS	All	2923.11	0.116	
b)			Lion_only	1146.301	0.198	
c)		GWR	All	104.661	0.704	125
d)			Lion_only	73.43	0.6	125

Adaptive bandwidth parameter with combined factors failed, so the bandwidth had to be manually set. Bandwidths were tested for 25, 50, 75, 100, 125 and 150 nearest neighbours. 125 nearest neighbours seemed to have the widest range to be able to have enough data to run the regression across the study area without leaving gaps in the data. This bandwidth also meant residuals were less autocorrelated and random when all four factors were used for analysis (see Appendix A). 125 nearest neighbours is about marginally more than 5 km.

Results from river, park, and road can explain as much as 70% of the variation in the data (Table 5.1, Model 13 c)). However, GWR could not distinguish how much each factor contributed or the order of importance of the independent variables. From GWR it is difficult to see which factors have the strongest influence. Although it is a local regression model (as opposed to a global model such as OLS), more detailed investigations need to be undertaken to determine which factors influence the lion occurrence per park and the interplay among the factors. This calls for an analysis method which is more reliable with presence-only data, and more robust in predicting the probability of occurrence of the lions in the Zambezi Region. The Maximum Entropy method is used in section 5.2 and examines in further detail which factors affect lion occurrence in the study area.

5.2 MAXENT AS A TOOL FOR MODELLING SPECIES OCCURRENCE AND UNDERSTANDING DRIVERS

Maximum entropy (MaxEnt) is a machine learning technique (Phillips & Dudík 2008, Elith et al. 2011) as described in Chapters 2 and 3. It predicts probability of occurrence in the study area and can also deal with categorical data, which was a shortfall of geographically weighted regression. The factors used for analysis were distance to river, distance to human activity, distance to roads, vegetation, land use (inside and outside of parks) and elevation.

The response curves and results from the jackknife tests, as well as the probability maps from the outputs above, can be found in Appendix D. Each output shows two response curves, one for the response of an individual factor in isolation, and one for the response to the combination of other factors. To understand the interplay among factors, the latter of the two response curves (i.e. factors in combination) was chosen for interpretation. Each MaxEnt output produces a

probability of occurrence map; a prediction of probability can only be taken into account above the significance level of 0.5. The jackknife test shows which variable contributes the most gain to the model, and which variable contributes the most gain loss.

When a variable is used in isolation, it has the most gain. The highest gain loss means that the model loses predictive power if that variable is not present in the model.

The MaxEnt outputs give us a clearer idea about what may be occurring with lions in the Zambezi Region. From the outputs evident in the response curves, we can see at which distance from a river or human activity lions are most likely to occur and if they are expected to occur more outside of parks than inside parks (detailed response curves in Appendix D). In addition, with the vegetation layer, we can ascertain in which vegetation type they are most likely to be found. When considering the effect of humans we need to understand the response curves of the different parks to understand how the overall combined response curve in a MaxEnt model can be explained.

5.2.1 Drivers of lions in Bwabwata National Park

Model 8 was used as it shows the best AUC value of 0.87 (Table 6.1 in Appendix D). The most gain came from park and most gain lost came from elevation. The model was also run without elevation; in this instance the most gain came from and was lost through park as a categorical factor. The reason for park's influential nature could be because the data was clipped to fit the vegetation layer, which restricts the data to the park essentially. This could be the reason why the park is playing such a big role, because all the points used are inside the park.

The model was also run using dry and wet season data. From the seasonal data (model 13) we can deduce from the outputs that most gain comes from elevation and most gain is lost from river across both seasons. From the images in Appendix D we can see that the highest probability of occurrence is along rivers with omurambas (ephemeral river beds) also being shown slightly in yellow (see image of model 8 in Appendix D). However, this is relative as probability does not exceed 0.6

The probability of lion occurrence is the highest close to the river, as shown by the response curves across all iterations (see Appendix D). From response curves one can see that lions are most probable at 970m altitude but it is generally flat landscape and the results for elevation can better be interpreted from the probability maps. The probability of occurrence for lions along rivers is highest (0.6) at 2 km and tapers off from there. The 2 km could be because when the river floods the floodplain is quite broad so it is difficult to reach the river.

The movements of the female lion collared in Bwabwata National Park (SAT101) could be explained by the prey which is most evident along the river and along the omurambas when there is standing water in them. This ties in with findings discussed in Chapter 4 concerning home ranges, i.e. that lions are likely to be found in close proximity to rivers.

As rivers are the most important source of permanent water inside the National Parks, this is where the prey is expected to congregate particularly in the dry season. This is important as lions need areas of high prey availability to hunt easily as well as proximity to drinking water. As the vegetation is most lush along the river we would expect prey to frequent the river banks more than the interior of the National Parks. Permanent surface water availability decreases with distance from the rivers – and therefore vegetation density, which is the source of food for the prey. The combination of less available surface water and prey has found to affect lions in Katavi National Park, Tanzania (Kiffner et al. 2009). In the wet season the omurambas fill with water in certain places and, depending on the rainfall, this water can sometimes last long into the following dry season (Thomas et al. 2000, Gaughan & Waylen 2012). We can see that in the wet season the Bwabwata lion data shows movement along these omurambas (see Appendix D, Figure D.10). It is expected that prey species spend time at these omurambas as they are seasonally predictable water sources, where there is water and grazing which disappear later in the dry season when the water dries up. From the Figure D.10 in Appendix D we can see that lions are more likely to occur along omurambas in the wet season than in the dry season.

Since lions require both prey and water to survive, they tend to frequent areas where these resources are easily found (Lehmann et al. 2008, Valeix et al. 2010, Davidson et al. 2013). In Hwange National Park lions were found to be opportunistic in their prey selection, sometimes towards the end of the dry season catching juvenile elephants which would not keep up with their herd (Davidson et al. 2013).

From the individual response curves we can see that the probability of lion occurrence peaks at 0.5 at 5 km from human activity and does not exceed 0.5 after that (see Appendix D). This is a representation of what is expected, as lions are not expected to occur at villages frequently. However, because the Bwabwata animals tend to remain along the western part of the river, and the villages line the eastern banks of the river, they appear to always occur at a certain distance from humans. So their distance is not “by choice” but due to physical inaccessibility with the river as barrier.

In Bwabwata National Park the lions are concentrated along the river for access to prey and water. Humans are also concentrated along the river, on the opposite bank. As mentioned previously, SAT101 never crossed the river in the study period. It is not known whether the lions do not cross the river along these areas because of the humans on the other side, or whether they do not have the need to expand their home range across the river. Consequently in Bwabwata, the peak in lion probability of occurrence around 5 km from humans might simply be due to the fact that there is a distance of 5 km on average between the river and the villages on the opposite side of the river to the lion. In Bwabwata, the response curve drops slightly and shows lions to be most probable again at 28 km (see Appendix D, Table D.1), even more so than at 5 km. This shows us that lions prefer to avoid villages.

Roads do not contribute significantly to the models for Bwabwata National Park but one can see from the response curves that the highest probability of occurrence is further away from the major roads (see Appendix D for details). There is a national road (B8) traversing this park, and lion mortality due to collision with a car was recently recorded on this road. This information was gained from personal communication. (pers. comms. Hanssen 2014).

Overall in Bwabwata National Park, lions are most likely to occur in vegetation category 6 which is “open (15-40%) broadleaved deciduous forest/woodland (>5m)”. Vegetation only slightly influences the model but from it we can see that they are most likely to occur in “mosaic vegetation (grassland/shrubland/forest) (50-70%) / cropland (20-50%)” in the dry season and in “open (15-40%) broadleaved deciduous forest/woodland (>5m)” in the wet season. These results suggest that in general lions prefer more open habitat.

5.2.2 Drivers of lions in Mudumu National Park

From model 8 we can see that elevation is cause for the most gain and most gain loss. However, because the lions are most likely to occur in a very narrow elevation band with the highest probability at 959m dropping down to 0 metres on either side of this range, elevation can be omitted for this park as it is comparatively flat. When the model is run without elevation the most gain comes from park and the most gain lost comes from humans.

The highest probability for lions to occur is 10 km away from humans, and drops to 0 probability at 13 km away from humans (see Appendix D). This is because there is no point which is further than 13 km from human activity in this park. Outside of protected areas, villages in the Zambezi Region are mostly found along rivers (O'Connell-Rodwell et al. 2000, Gaughan & Waylen 2012) However, such expectations change when two or more variables co-occur. For example, although there is easy prey in the form of livestock close to villages and corrals and water points, the lions are often driven away and sometimes shot at when they are in closer proximity to humans. Cattle owners generally have a herdsman with the cattle and mostly corral their cattle at night; meaning if lions want to catch cattle, it is easiest to do so at the village where the cattle are corralled at night, and when everyone is sleeping. The chance of lion catching cattle in the bush is generally low because of this good animal husbandry practice. Therefore, if lions did want to catch cattle they would have to go close to humans. The communities surrounding the National Parks are all conservancies and they only give compensation for human-wildlife conflict if the cattle or crop owner can prove that measures were taken to mitigate the conflict (i.e. through corraling cattle at night and sending a herdsman with them during the day). So the incentive for farmers is high to maintain this good practice. When lions do go close to villages and are more than one time offenders in terms of catching cattle in the corral, they have been up until now declared problem animals and then shot by government officials or by a hunter if there is one available at the time. This persecution over time has made lions wary of moving permanently close to villages. Similar patterns have been observed in other study areas such as the Masai Mara National Reserve (Ogutu & Dublin 2004). In the southern part of the Masai Mara, it was found that lions and humans coexist as lions tend to stay in protected areas as human density increases (Schuette, Creel & Christianson 2013).

Lion probability inside versus outside a National Park was another striking result. The response curves for park show that the lions are more likely to occur inside (0.55) of the parks than outside (0.03). The National Parks in the study area have no permanent human occupation beyond the odd rangers' house or tourist facility, and are exclusive wildlife areas. They are, however, not fenced such that lions cannot easily move out. The fact that the model results show a clear preference for lions to be within the parks is notable. Lions could venture further afield outside the park boundaries, but they cannot necessarily do so with much success as the parks are surrounded by villages and corrals. From the maps in Appendix D we can conclude that the lions are most likely to occur inside the parks and this is because as soon as the lions leave they are faced with humans which one can see from the maps in there is a very low probability of them occur around human settlement because of possible persecution. Lions are mostly not tolerated close to villages. Even in areas where there have been efforts to mitigate human-wildlife conflict with lions, communities at most tolerate lions but do not live in harmony together with lions - lions that are seen are chased away.

Lions are most likely to occur up to 20 km away from the river. This large range could be because of waterholes which are placed on the park boundaries in the conservancies through which lions have access to drinking water. These waterholes are however not exclusive to wildlife and have been classified as "human" as they are used for cattle to drink. In both the dry and wet season the lions can occur from 2 to 35 km away from the river. In the wet season this makes sense as there is a lot of surface water which can persist long into the dry season. That could be why there is not much variation seen between seasons.

The road does not play a big role but one can see from the data that the lions are most likely to occur further away from the road with the highest probability being between 15 and 20 km away from the road. In both seasons lions are most likely to occur 20-30 km away from the main road which runs through the park parallel to the river. As mentioned in Chapter 4, there was a road under construction in Mudumu National Park at the time of this study.

The vegetation they are most likely to occur in is value 140 which is "closed to open (>15%) herbaceous vegetation (grassland, savannas or lichens/mosses)". In both seasons lions are likely to occur in all three of the following categories "mosaic vegetation (grassland/shrubland/forest)

(50-70%) / cropland (20-50%)”, “mosaic grassland (50-70%) / forest or shrubland (20-50%)” and “closed to open (>15%) herbaceous vegetation (grassland, savannahs or lichens/mosses)”

5.2.3 Drivers of lion in Nkasa Rupara National Park

In this park river accounts for the most gain and gain lost both with and without elevation as can be seen in the results for model 8 in Appendix D (Table D.1). In the dry and the wet season river shows the same pattern except in the wet season where elevation is the cause for most gain. The response curves for rivers show the lions to occur mostly at the river, dropping to a probability of zero, 10 km away from the river. This is because the Rupara Island is not very wide and is surrounded by swampy grassland.

Lions also occur in a very narrow elevation range with the highest probability being at 947 metres dropping to 0 probability on either side of the peak. Again this should be read with caution as the park is very flat and there is only a 100 metre difference across the whole study area.

The lions are most likely to occur 10 km away from a main road. This should be interpreted with caution as there is no road going through the park and this is more or less the distance the park is from the main road.

From the response curves we can see that lions are most likely to occur within 5 to 10 km away from humans. This is not to say that they cannot persist beyond this distance but they cannot reach further than this because ecologically they are on the Rupara Island which is surrounded by channels. These channels are close to humans, and therefore the lions cannot get further away than 10 km from humans.

Lions pose a perceived threat to humans in the study area. As many children walk to school through the bush, the community does not feel safe if they know that there are lions moving in the area. SAT103 was killed, together with three other female lions in her pride, as they killed cattle in five villages over a three month period. The financial loss to the farmers was too high to

sustain and it was decided to shoot these animals. SAT272 was then also declared a problem animal to be shot for trophy. This was an adult male in his prime with a full mane, which could bring a high trophy fee. It is not known whether this lion was shot, because the collar was removed and he could no longer be monitored. Although farmers are compensated from the communal conservancy for cattle losses, the money is not enough to buy another cow. Compensation is usually N\$1500 and cattle prices can vary anything from N\$2000 to N\$5000. Therefore value of the cattle is greater than the compensation for loss from lions. Studies in Kenya highlighted the complex perceptions on human-lion conflict, showing that wildlife is often killed outside of protected areas if no compensation is given for livestock losses (Hazzah, Mulder & Frank 2009). Because of this conflict that occurs when lions venture close to villages, they have learnt over time to generally avoid human activity where possible in the study area, which is similar to what studies have found in East Africa. However, avoidance is not always possible if prey disperses in the wet season as standing water is available along the rivers as well as in the bush. So lions are almost forced to turn to easier prey in terms of cattle if they cannot find sufficient resources in their home range to feed their entire pride.

Only the Nkasa Rupara National Park data deviate from the strong preference for remaining inside parks, where lions have a higher probability to be outside the park than inside in the dry season. This could be because there are ecological factors, which span across the park boundaries that drive lion occurrence. There may be insufficient prey on the Rupara Island within the park which forces them to move outside the park in search of food. The areas surrounding Nkasa Rupara National Park are Communal Conservancies but the areas immediately bordering the park are defined as wildlife exclusive areas - used exclusively for hunting and tourism. This is unique for the areas surrounding a National Park, and is something that conservancies surrounding other National Parks strive for. This in a way acts as a source-sink relationship for some species, with the park being the source and the surrounding areas being sinks where the animals are hunted (Woodroffe & Ginsberg 1998). Revisiting the response curves of the Nkasa Rupara National Park lions, they have a buffer outside the park where they feel safe, given that they are not hunted. That is why we see there being a higher probability of the lions occurring outside the National Park than is seen in Bwabwata and Mudumu National Parks.

The vegetation layer used is from 2005 which was in the middle of a particularly dry spell in the Zambezi Region. It was so dry that you could drive to the southern tip of the Nkasa Rupara National Park to where the Kwando and Linyanti Rivers meet and look across the border into

Botswana. This has not been possible since at least 2009 due to a permanently flowing river over much of southern Nkasa Rupara National Park, which had been classified as grassland in the vegetation layer. The channels in this area have filled up and remain high throughout the dry season. The lions never once crossed the large river channel defining the north-eastern part of the park from the south-western part of the park from the collar data which is available. Lions are known to persist on the south-western part of the park, as was identified in previous unpublished studies done by the Ministry of Environment and Tourism by Lou Scheepers. So either the large channel was a sufficient barrier for the lions - especially considering the female SAT103 which had cubs - or there is another pride dominating the south-western island of the park which deters the lions from moving across. MaxEnt also predicts there to be lions in this part of the park, so it is not unlikely that there are other lions in this area. Unfortunately lions could not be collared in that area as the channels were too deep to cross, making the area inaccessible for this study.

Another factor which the vegetation layer does not take into consideration is the fact that much of the previously open grassland is now waterlogged; these are areas which lions could traverse but would not do so unnecessarily.

5.2.4 Overall drivers of lions across all three National Parks

Model 4 was used for interpretation as it had the most suitable AUC value (0.71). These data contain all lion data clipped to the vegetation layer with equal numbers of points per park. The most gain came from park, meaning this variable when used in isolation has the most information by itself. The most gain loss came from distance to river; this variable has the most information in it which is not present in other variables for this model.

Response curves regarding distance to humans are interesting, particularly when considering the different models and park information. Lions have a low probability of occurring within the first 5 km from human activity across all models (see Appendix D). Over the whole study area we can see from the response curves show that lions do not occur at villages or kraals and probability only reaches 0.5 at 3 km away from human activity. The probability reaches 0.6 at 5 km and peaks to its highest at 20 km away from human activity. Essentially this means that lions are more likely to occur further away from humans. A similar curve is shown when the model is

run without elevation. Seasonally we can see that distance to human reaches a probability of 0.5 at about 4 km and peaks to a probability of 0.7 at 20 km away from human activity. It then drops to 0.4 and remains there until 35 km away from humans. In the wet season probability is the highest at 5 km away from humans and decreases to a probability of below 0.5 as of 13 km away from human activity.

Lions are likely to occur at the rivers and within 10 km from a river. From there the response curve decreases to a probability of 0, 35 km away from rivers. In the dry season we can see that the probability for lions to occur is highest (0.7) at the river and decreases linearly to a probability of 0.2, 30 km away from the river. In the wet season the probability of lions at the river is 0.5 and increases to 0.59 at about 1 km from the river, but probability does not exceed 0.59. The probability then decreases to 0.4 at 25 km away from the river, and to a probability of 0 at 35 km from rivers.

From the response curves for roads we can see that lions are likely to occur at a probability of 0.53 at major roads with the probability increasing to 0.6, 15 km away from the roads. At 21 km there is a probability of 0 that lions are likely to occur. In the dry season the probability of lions at the road is 0.4 which increases to 0.65 at 8 km away from the road. This then decreases sharply to a probability of 0.13, 22 km away from roads. In the wet season the probability is 0.5 at the road which increases to 0.56 at 5 km and then drops to 0.17 at 22 km away from the road.

As the area is very flat, elevation should be interpreted with caution. However, we can see that lions are likely to occur from 950 metres to 990 metres over the whole study area. Elevation shows that in the dry season probability of lion occurrence is highest (0.67) at 955 metres and decreases to a probability of 0.25 at 1018 metres. The probability then increases again sharply at 1019 metres to 0.5 (this may be indicating occurrence points in the omurambas). In the wet season the probability of lion presence is highest (0.69) at 950 metres and decreases gradually to 0.17 at 1000 metres, where it then remains. There is no sharp increase later as observed in the dry season data.

Overall lions have a probability of nearly 0.6 occurring in parks versus a probability of 0.4 that lions will occur outside of parks. The probability of lion presence in the National Parks is 0.64 where the probability of presence outside of the National Parks is 0.47 in the dry season. In the

wet season the probability of presence is 0.52 in the parks and 0.29 outside of parks. There is a higher probability difference between these two categories in the wet season (0.23) than in the dry season (0.15).

From these response curves for National Parks we can conclude that lions are restricted largely to the National Parks and even if they did want to roam wider they cannot because of the human pressures from outside. From this we can say that there is a high chance that lions only persist in the study area because there are National Parks. If it were not for the National Parks there would not necessarily be lions occurring in the study area, given the data we have on lion occurrence. There are no resident prides known to inhabit areas outside of the National Parks. This also shows that fencing is not necessarily needed around these National Parks as the animals have already learnt over time where it is safe for them to forage and breed without encountering danger. Wildlife areas are partially safe for wildlife, with the only danger being that they might be hunted if there is a quota set for a given species.

Hunting quotas in areas surrounding National Parks have been found to play a role in other areas of Africa. A study in Katavi National Park in Tanzania found that lions inside the National Park were below carrying capacity because of hunting outside of the National Park (Kiffner et al. 2009). None of the lions involved in this study were hunted for trophy animals (at least not while they were collared). Only animals which were declared problem animals were shot, and this was closer to villages, which are areas outside of the wildlife core areas defined by the conservancies. In the wildlife core areas surrounding the National Parks there were no lions hunted. Trophy hunting has shown to affect the population dynamics of lions inside National Parks (Sogbohossou et al. 2014). Studies from Hwange National Park in Zimbabwe show that over a five year time period the proportion of male cubs increased as older males were being hunted (Loveridge et al. 2007).

If we take the response curves of the vegetation layer we have, it shows lion occurrence to be most probable in open grassland or semi open grassland areas (see LCCS 0 in the response curves in Appendix D). Some studies have found lions to prefer medium to high grassland for hunting (Funston, Mills & Biggs 2001) where others have found woodland areas to be of preference for hunting and resting (Loarie, Tambling & Asner 2013). The vegetation layer is at a 300 metre resolution which will not necessarily pick up small tree islands where lions were

observed to rest during the day. This might just be a small group of ten bushes where they rest, but is largely surrounded by grassland and might have generally been classified as open grassland with the current classification.

One of the major interpretative challenges for the data collated in this study is the lack of accurate vegetation data for the study area. This could unfortunately not be overcome during the relevant time frame, and the study had to use what unrefined vegetation data was available. There were also no accurate flooding maps for the area, so the effect of the annual flooding from the rivers could not be observed during the study. It would be interesting to see whether lions avoid waterlogged areas when the Kwando and Linyanti Rivers come down in flood. This could also be a reason why in some response curves lions are not most likely to occur right at the rivers but a few hundred meters away; when the rivers flood there is a buffer around the areas which become waterlogged and backwaters are filled.

Even though the distance to humans is often listed as the primary factor in lion occurrence, this is not always the strongest driving force. We can see from the results that in Bwabwata National Park lions are mostly influenced by the park and elevation. In Mudumu National Park lions are mostly influenced by park and humans. Elevation has the highest influence when included in the model but the factor is not relevant to this park as it is in a very specific elevation range and flat. Investigating elevation over the whole study reveals that the lions only occur in a very specific elevation range. In Nkasa Rupara National Park we can see that the river has the most effect on the lions' probability of occurrence.

Across all three National Parks, park protected status and river seem to have the biggest influence. Although park and humans are not correlated factors, the lions tend to stay mostly in parks because they are surrounded by villages and other human infrastructure. The avoidance of humans can be seen by the near 0 probability surrounding the villages and human activities in all of the figures.

CHAPTER 6: SUMMARY AND RECOMMENDATIONS FOR FURTHER RESEARCH

As mentioned in Chapter 1, an impetus for this study was the Kavango Zambezi Trans Frontier Conservation Area's need to identify trans-boundary movement. From data collated and analysed, it is clear that in the overwhelming majority of cases lions tend to stay within National Parks. Typically, National Parks in southern Africa are fenced. Since the National Parks in the Zambezi Region are not fenced, it became increasingly relevant to investigate other factors as well. This study further focused on factors such as permanent water sources, human activity, roads, vegetation and seasonal changes.

Analyses presented in this thesis show it is important to conserve protected areas and create buffers for wildlife, such as the wildlife core areas in communal conservancies as explored in Chapter 5.2.3. This is especially relevant to carnivores; this study clearly identified that the existence of parks contributes substantially to the persistence of lions in the Zambezi Region.

This study shows that humans impact lions. More data specifically on human-wildlife conflict situations need to be collected and refined in order to determine its influence on the movements of lions. Current human-wildlife conflict data, although useful, proved too coarse for the original purposes of this study. More persistent and systematic recordings of human-wildlife conflict would present a greater level of accuracy from which hotspots of conflict could be pinpointed. Mitigation methods could then be implemented in priority areas. Essentially needed are records of the GPS locations of individual instances of human-wildlife conflict.

Currently there is no accurate estimate of the lion population in the Zambezi Region. It was therefore not possible to calculate sample size. By extension, it was not possible to extrapolate probability of occurrence very accurately. This is because calculations could not be made as to whether the data collected was statistically relevant. Ideally a survey needs to be done, either by a spoor-based occupancy survey (Midlane et al. 2014) or identification by physical sightings of individual lions. From such information a minimum estimate for lions in the Zambezi Region can be made.

Although a large number of species were collared, clearly this study focused on lions. This collaboration facilitated the collaring of lions in all three National Parks, however, a data gap existed for collar data of male lions in Bwabwata National Park. If future studies of this kind are undertaken in the Zambezi Region, data from male lions in the Bwabwata National Park should be included. In addition, individual lions can be lost through various causes as lions are a conflict prone species. Provision should be made for this by increasing the number of individuals collared in each pride.

Following on from the above, widening the temporal range could enable more robust research and a better understanding of lion movement. For example, this would allow analyses of factors such as the impact that seasonal shifts may have on lion occurrence. Regional management of the species would benefit from research into the reasons why male lions tend to cross rivers where females do not.

Little seasonal difference was observed in the data, but this is probably due to the short temporal extent of the study and the small number of collared individuals compared to other studies. As with all species, lions need to adapt to the ecological changes in their habitat - in particular, vegetation and the effects of dry periods, as well as flooding. Technology in the form of remotely sensed images now exists, which could enable more accurate vegetation and flooding maps. These maps could be used to accurately predict the effects of flooding and vegetation on lion occurrence in the Zambezi Region. For example, these factors may drive lions closer to human activity at certain times. If this could be foreseen, it could assist in preventing human-wildlife conflict.

A longitudinal study is needed to capture the location and time of fires using remote sensing techniques. Such time-series data could then be combined with data reflecting lion presence and movements within the same time period. The suggestion is to analyse the relationship between animal movement and environmental factors such as fire.

Simplistically speaking, if you know what lions eat you are likely to know where to find them. More reliable data regarding patterns of lion movement in relation to their prey would be beneficial to understand predator-prey dynamics. To put this in context, local perception in the Zambezi Region is that lions are likely to be present when buffalo are sighted grazing in the area.

If this could be proven (or disproven) by solid data, more could be done to support attempts to minimise human-wildlife conflict. This was outside the realm of this study but should be incorporated into future studies.

To supplement the suggested greater level of detail in quantitative data, qualitative fixed data collection would introduce a more dynamic angle to the research. In this study various personal observations and personal communications are referred to. In future studies, a more rigorous approach to the collection of qualitative data might well prove the impact of factors such as poaching and road construction.

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PERSONAL COMMUNICATIONS

Funston P.J. 2012. Department of Nature Conservation Tshwane University of Technology.

Email on 16 March about suitable censusing methods for Caprivi Lion Population.

Haupt S. Haupt M. 2012. Owners of African Wildlife Tracking. Email on 20 November 2011

about enquiry of different Collar cost..

APPENDICES

- Appendix A Ordinary least squares (OLS) regression and geographically weighted regression (GWR) results
- Appendix B R Script for Time Local Convex Hull analysis
- Appendix C Step length histograms
- Appendix D MaxEnt results

APPENDIX A

Ordinary least squares (OLS) regression and geographically weighted regression (GWR) results

Model	Independent Variables	Method		AICc	multiple R2	Neighbours	Moran's Index	Expected Index	Variance	z-score	p-value	Clustered
1	River	OLS	All	3815.948	0.048		0.771744	-0.000083	0.000042	119.038516	0	Clustered
			Lion_only	1238.756	0.144		0.398382	-0.000685	0.000053	55.022312	0	Clustered
		GWR	All	-4488.752	0.529	562	0.540719	0.000083	0.000042	83.408962	0	Clustered
			Lion_only	604.634	0.491	83	0.036648	-0.000685	0.000053	5.147993	0	Clustered
2	Human	OLS	All	3910.576	0.04		0.774117	-0.000083	0.000042	119.407767	0	Clustered
			Lion_only	1407.144	0.039		0.467095	-0.000685	0.000053	64.498883	0	Clustered
		GWR	All	-5644.964	0.575	414	0.491992	-0.000083	0.000042	75.901742	0	Clustered
			Lion_only	540.015	0.529	67	0.021708	-0.000685	0.000053	3.087624	0.002018	Clustered
3	Park	OLS	All	3044.533	0.107		0.756563	-0.000083	0.000042	116.698389	0	Clustered
			Lion_only	1466.401	0.0001		0.48813	-0.000685	0.000053	67.399992	0	Clustered
		GWR	All	-5821.31	0.581	382	0.485377	-0.000083	0.000042	74.876442	0	Clustered
			Lion_only	477.11	0.576	44	-0.015065	-0.000685	0.000053	-1.982652	0.047406	Dispersed
4	Road	OLS	All	3945.473	0.038		0.774715	-0.000083	0.000042	119.500587	0	Clustered
			Lion_only	1423.926	0.028		0.464454	-0.000685	0.000053	64.13985	0	Clustered
		GWR	All	-5684.475	0.576	421	0.492697	-0.000083	0.000042	76.008407	0	Clustered
			Lion_only	628.672	0.478	97	0.057395	-0.000685	0.000053	8.008262	0	Clustered
5	River, Human	OLS	All	3600.436	0.065		0.767684	-0.000083	0.000042	118.411835	0	Clustered
			Lion_only	1232.659	0.149		0.396757	-0.000685	0.000053	54.798661	0	Clustered
		GWR	All	-1749.503	0.761	125	0.265504	-0.000083	0.000042	40.965758	0	Clustered
			Lion_only	512.247	0.521	125	0.043514	-0.000685	0.000053	6.094621	0	Clustered
6	River, Park	OLS	All	2959.894	0.114		0.754617	-0.000083	0.000042	116.396182	0	Clustered
			Lion_only	1197.066	0.169		0.37688	-0.000685	0.000053	52.058294	0	Clustered
		GWR	All	-836.867	0.718	125	0.275937	-0.000086	0.000043	41.961874	0	Clustered
			Lion_only	514.829	0.505	125	0.035721	-0.000685	0.000053	5.02039	0.000001	Clustered
7	River, Road	OLS	All	3568.164	0.679		0.767089	-0.000083	0.000042	118.320084	0	Clustered
			Lion_only	1233.006	0.149		0.39122	-0.000685	0.000053	54.033355	0	Clustered
		GWR	All	-763.61	0.716	125	0.265395	-0.000084	0.000042	40.807867	0	Clustered
			Lion_only	497.736	0.514	125	0.056311	-0.000685	0.000053	7.858969	0	Clustered
8	Human, Park	OLS	All	3013.946	0.11		0.755965	-0.000083	0.000042	116.606505	0	Clustered

			Lion_only	1402.491	0.044		0.467278	-0.000685	0.000053	64.52431	0	Clustered
		GWR	All	-2479.644	0.712	125	0.281958	-0.000083	0.000042	43.502757	0	Clustered
			Lion_only	561.089	0.509	125	0.045984	-0.000685	0.000053	6.435107	0	Clustered
9	Human, Road	OLS	All	3907.83	0.041		0.774007	-0.000083	0.000042	119.390816	0	Clustered
			Lion_only	1393.612	0.05		0.456398	-0.000685	0.000053	63.026654	0	Clustered
		GWR	All	-2473.471	0.709	125	0.292389	-0.000084	0.000042	44.935074	0	Clustered
			Lion_only	563.764	0.489	125	0.047919	-0.000685	0.000053	6.702044	0	Clustered
10	Park, Road	OLS	All	3003.213	0.11		0.755642	-0.000083	0.000042	116.55663	0	Clustered
			Lion_only	1425.691	0.028		0.46425	-0.000685	0.000053	64.111882	0	Clustered
		GWR	All	-2238.772	0.712	125	0.28496	-0.000083	0.000042	43.94094	0	Clustered
			Lion_only	446.481	0.47	125	0.051853	-0.000685	0.000053	7.244403	0	Clustered
11	River, Human, Park	OLS	All	2921.771	0.117		0.753829	-0.000083	0.000042	116.274899	0	Clustered
			Lion_only	1183.069	0.178		0.372553	-0.000685	0.000053	51.46191	0	Clustered
		GWR	All	401.08	0.77	125	0.233723	-0.00009	0.000046	34.565193	0	Clustered
			Lion_only	320.171	0.595	125	0.018133	-0.000685	0.000053	2.594902	0.009462	Clustered
12	River, Human, Road	OLS	All	3570.071	0.067		0.767086	-0.000083	0.000042	118.319615	0	Clustered
			Lion_only	1222.099	0.156		0.387266	-0.000685	0.000053	53.488259	0	Clustered
		GWR	All	-344.103	0.766	125	0.231956	-0.000092	0.000047	34.013359	0	Clustered
			Lion_only	291.153	0.616	125	0.026163	-0.000685	0.000053	3.702061	0.000214	Clustered
13	River, Park, Road	OLS	All	2927.289	0.116		0.753839	-0.000083	0.000042	116.276377	0	Clustered
			Lion_only	1176.241	0.182		0.36328	-0.000685	0.000053	50.181312	0	Clustered
		GWR	All	226.853	0.738	125	0.234019	-0.000091	0.000047	34.3269	0	Clustered
			Lion_only	137.88	0.565	125	0.018833	-0.000685	0.000053	2.691282	0.007118	Clustered
14	Human, Park, Road	OLS	All	3005.189	0.11		0.755647	-0.000083	0.000042	116.557365	0	Clustered
			Lion_only	1390.731	0.05		0.455323	-0.000685	0.000053	62.878388	0	Clustered
		GWR	All	-847.726	0.764	125	0.197434	-0.000092	0.000024	40.149605	0	Clustered
			Lion_only	226.123	0.534	125	0.028725	-0.000685	0.000053	4.055364	0.00005	Clustered
15	River, Human, Park, Road	OLS	All	2923.11	0.117		0.753789	-0.000083	0.000042	116.26878	0	Clustered
			Lion_only	1146.301	0.2		0.35404	-0.000685	0.000053	48.907197	0	Clustered
		GWR	All	104.661	0.728	125	0.118194	-0.000108	0.00002	26.308392	0	Clustered
			Lion_only	73.43	0.63	125	0.005474	-0.000685	0.000053	0.849254	0.39574	Random

APPENDIX B

R Script for TLoCoH

```
require(tlocoh)

class(sat101)

head(sat101)

plot(sat101[, c("long","lat")], pch=20)

require(sp)

require(rgdal)

sat101.sp.latlong <- SpatialPoints(sat101[, c("long","lat")], proj4string=CRS("+proj=longlat
+ellps=WGS84"))

sat101.sp.utm <- spTransform(sat101.sp.latlong, CRS("+proj=utm +south +zone=34
+ellps=WGS84"))

sat101.mat.utm <- coordinates(sat101.sp.utm)

head(sat101.mat.utm)

colnames(sat101.mat.utm) <- c("x","y")

head(sat101.mat.utm)

class(sat101$timestamp.utc)

head(as.character(sat101$timestamp.utc))

sat101.gmt <- as.POSIXct(sat101$timestamp.utc, tz="UTC")

sat101.gmt[1:3]

local.tz <- "Africa/Johannesburg"

sat101.localtime <- as.POSIXct(format(sat101.gmt, tz=local.tz), tz=local.tz)

sat101.localtime[1:3]

sat101.lxy <- xyt.lxy(xy=sat101.mat.utm, dt=sat101.localtime, id="sat101",
proj4string=CRS("+proj=utm +south +zone=34 +ellps=WGS84"))

summary(sat101.lxy)

plot(sat101.lxy)
```

```
hist(sat101.lxy)

lxy.plot.freq(sat101.lxy, deltat.by.date=T)

lxy.plot.freq(sat101.lxy, cp=T)

sat101.lxy <- lxy.thin.bursts(sat101.lxy, thresh=0.6)

sat101.lxy <- lxy.ptsh.add(sat101.lxy)

lxy.plot.sfinder(sat101.lxy)

lxy.plot.sfinder(sat101.lxy, delta.t=3600*c(12,24,36,48,54,60))

sat101.lxy <- lxy.nn.add(sat101.lxy, s=0.003, k=25)

summary(sat101.lxy)

sat101.lxy <- lxy.nn.add(sat101.lxy, s=c(0.0003, 0.003, 0.03, 0.3), k=25)

lxy.plot.mtdr(sat101.lxy, k=10)

lxy.plot.tspan(sat101.lxy, k=10)

lxy.save(sat101.lxy, dir=".")

sat101.lhs <- lxy.lhs(sat101.lxy, k=3*2:8, s=0.003)

summary(sat101.lhs, compact=T)

sat101.lhs <- lhs.iso.add(sat101.lhs)

plot(sat101.lhs, iso=T, record=T, ufipt=F)

plot(sat101.lhs, iso=T, k=18, allpts=T, cex.allpts=0.1, col.allpts="gray30", ufipt=F)

lhs.plot.isoarea(sat101.lhs)

lhs.plot.isoear(sat101.lhs)

sat101.lhs.k18 <- lhs.select(sat101.lhs, k=18)

sat101.lxy <- lxy.nn.add(sat101.lxy, s=0.003, a=auto.a(nnn=15, ptp=0.98))

summary(sat101.lxy)

sat101.lxy <- lxy.nn.add(sat101.lxy, s=0.003, a=15000)

sat101.lhs.amixed <- lxy.lhs(sat101.lxy, s=0.003, a=4:15*1000, iso.add=T)

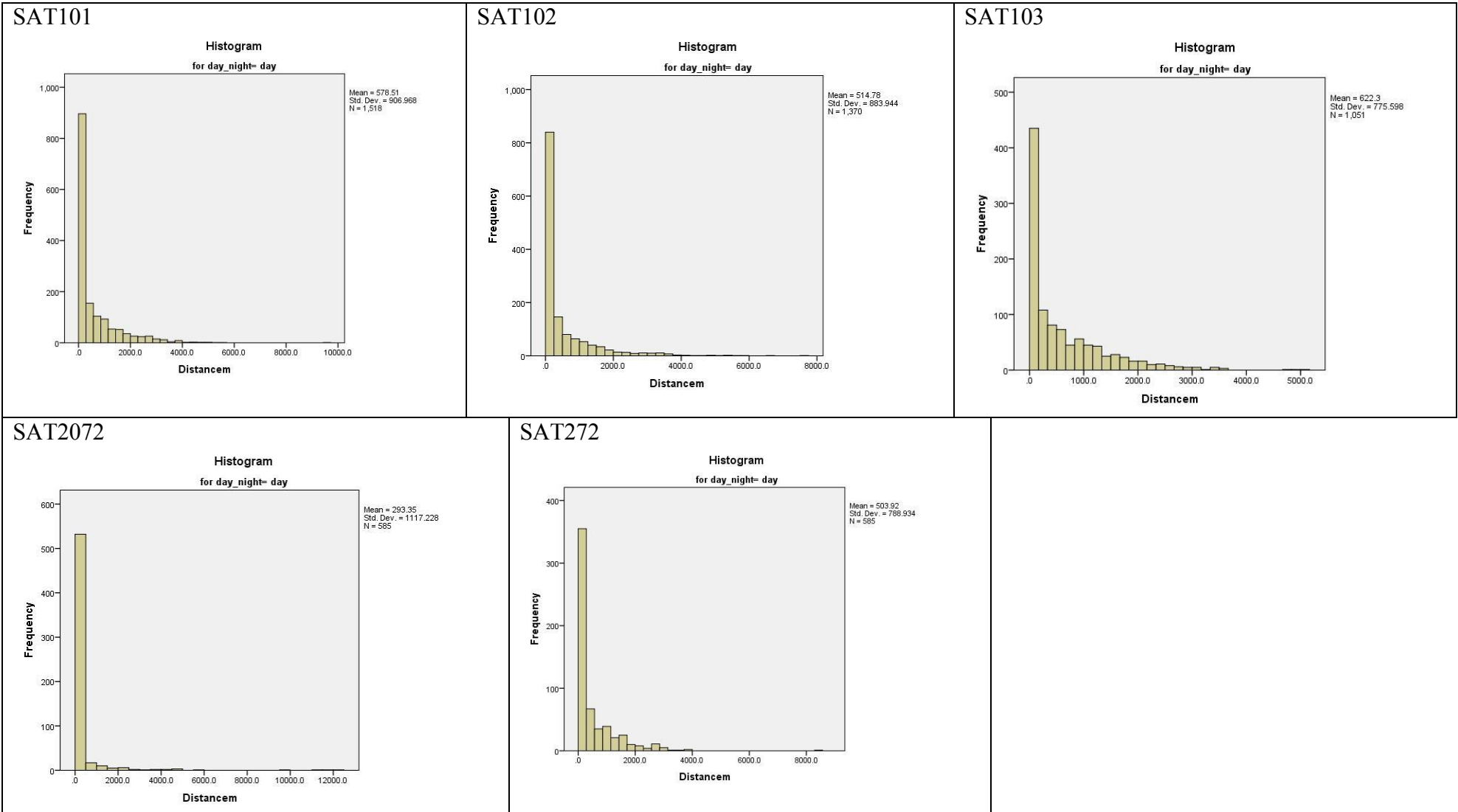
lhs.plot.isoarea(sat101.lhs.amixed)

lhs.plot.isoear(sat101.lhs.amixed)
```

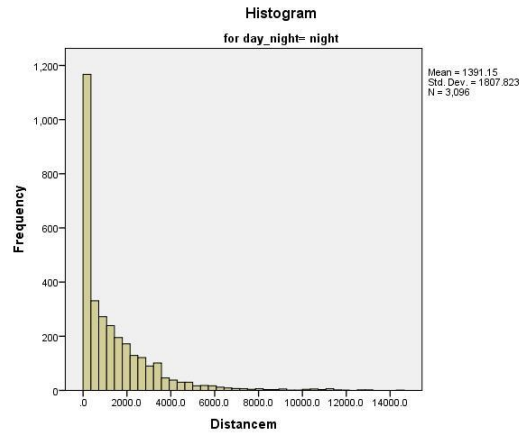
```
sat101.lhs.k18 <- lhs.ellipses.add(sat101.lhs.k18)
summary(sat101.lhs.k18)
plot(sat101.lhs.k18, hulls=T, ellipses=T, allpts=T, nn=T, ptid="auto")
sat101.lhs.k18 <- lhs.visit.add(sat101.lhs.k18, ivg=3600*12)
summary(sat101.lhs.k18)
lhs.save(sat101.lhs.k18)
sat101.lhs.k18 <- lhs.iso.add(sat101.lhs.k18, sort.metric="ecc")
plot(sat101.lhs.k18, iso=T, iso.sort.metric="ecc")
hist(sat101.lhs.k18, metric="nsv")
plot(sat101.lhs.k18, hpp=T, hpp.classify="nsv", ivg=3600*12, col.ramp="rainbow")
sat101.aoi <- aoi() lxy
plot(sat101.lhs.k18, hpp=T, hpp.classify="nsv", col.ramp="rainbow", aoi=sat101.aoi)
hist(sat101.lhs.k18, metric="mnlv", ivg=3600*12)
plot(sat101.lhs.k18, hpp=T, hpp.classify="mnlv", col.ramp="rainbow")
hsp <- lhs.plot.scatter(sat101.lhs.k18, x="nsv", y="mnlv", col="spiral", bg="black")
plot(sat101.lhs.k18, hpp=T, hsp=hsp, hpp.classify="hsp")
```

APPENDIX C

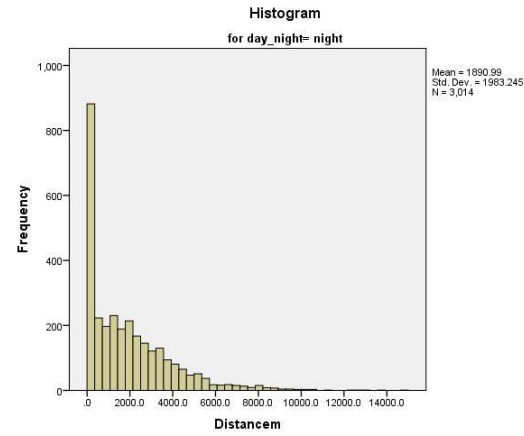
Step length histograms



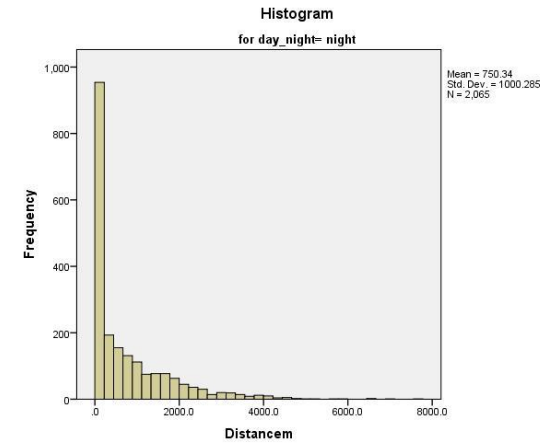
SAT101



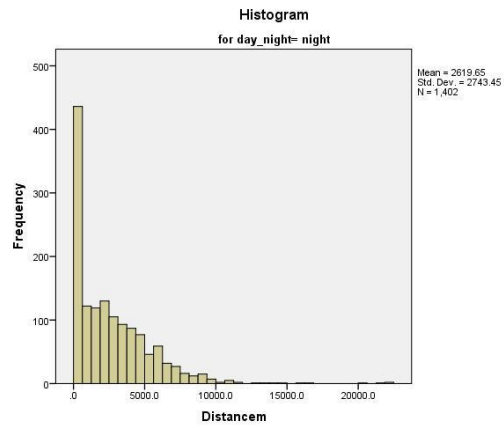
SAT102



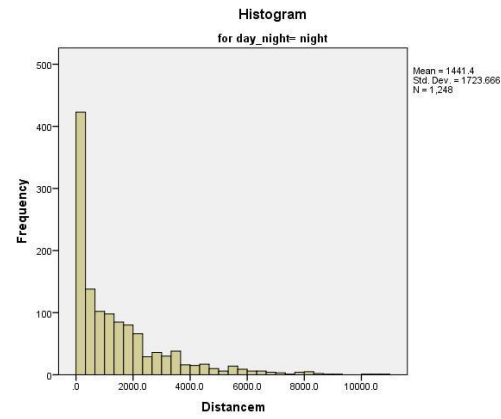
SAT103

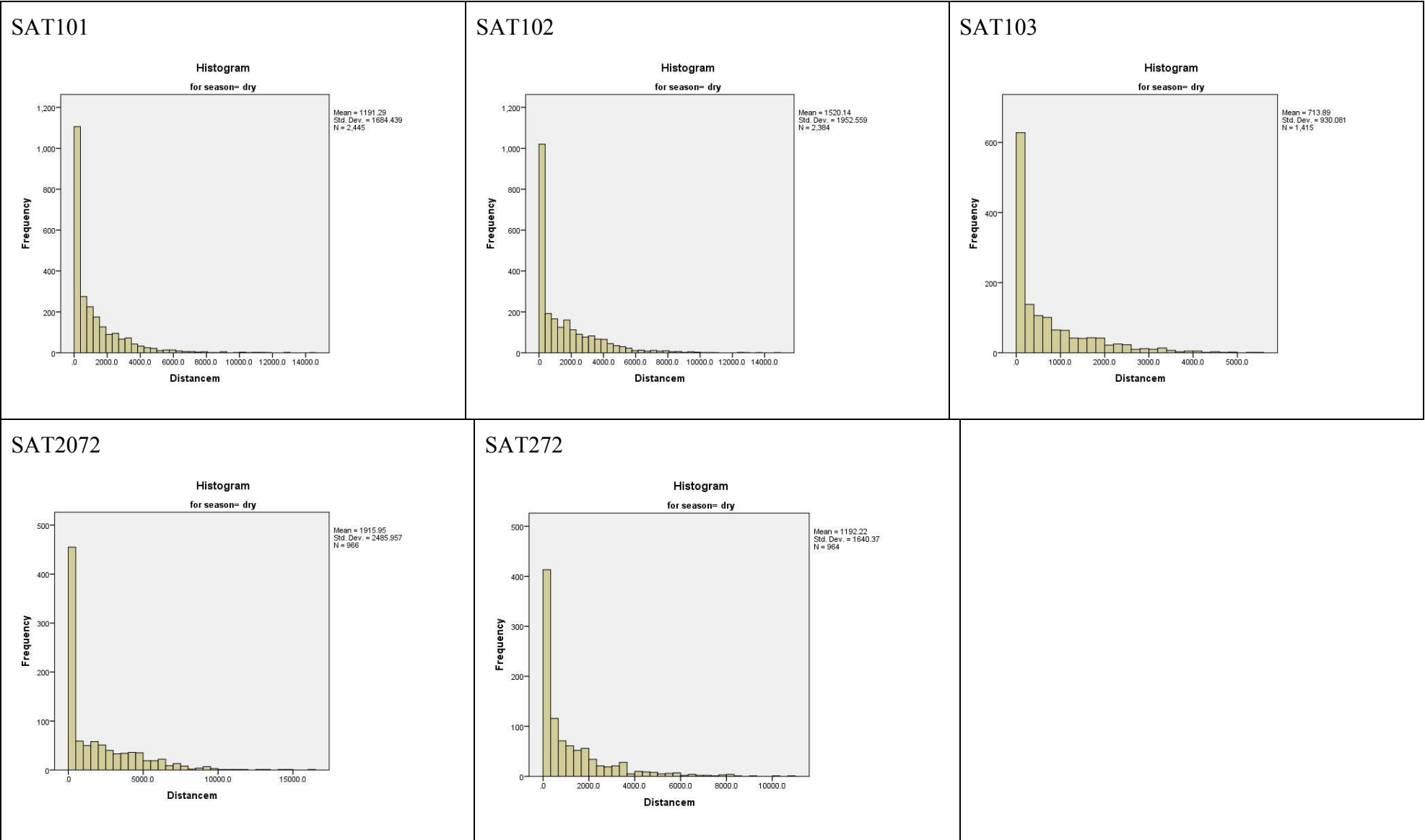


SAT2072

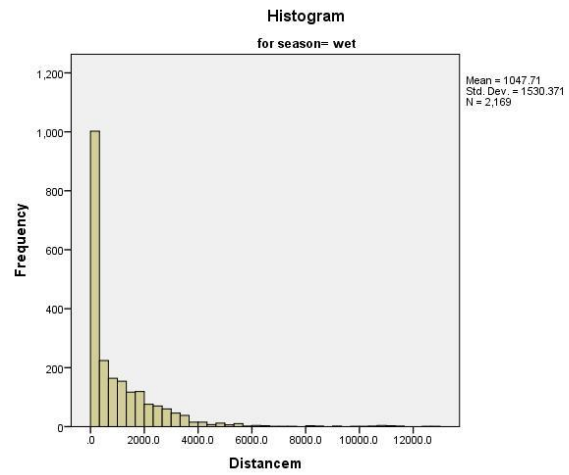


SAT272

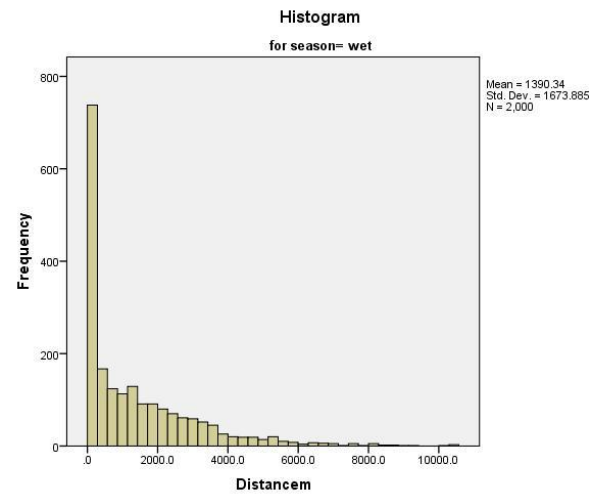




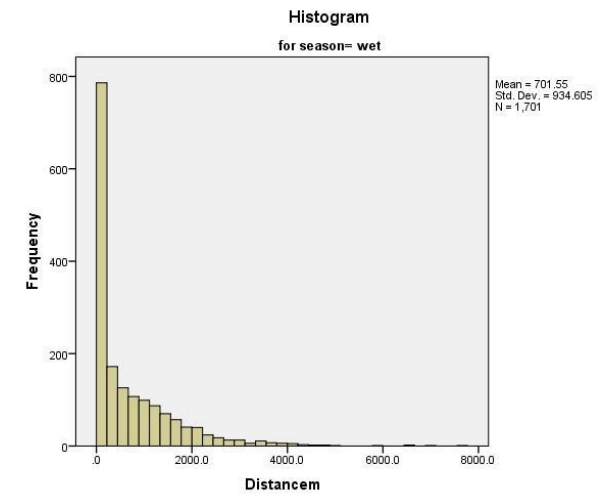
SAT101



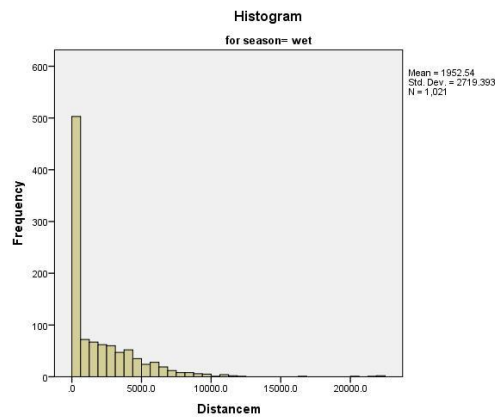
SAT102



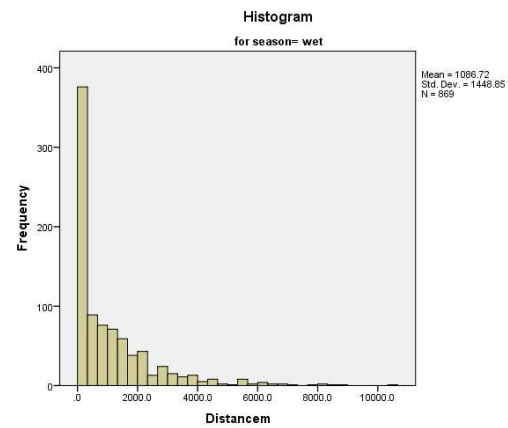
SAT103



SAT2072



SAT272



APPENDIX D

MaxEnt results

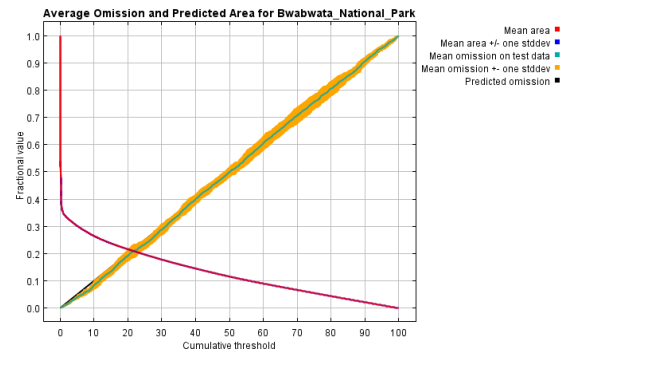
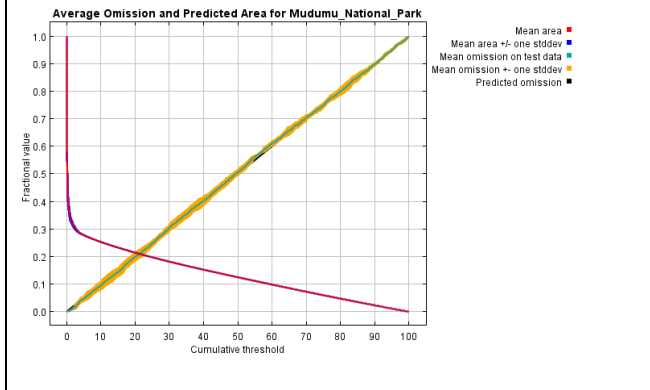
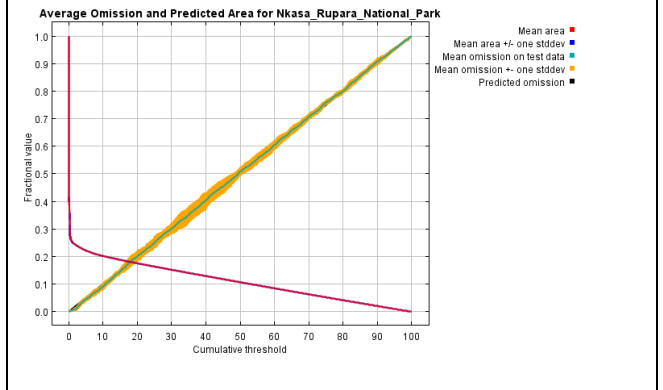
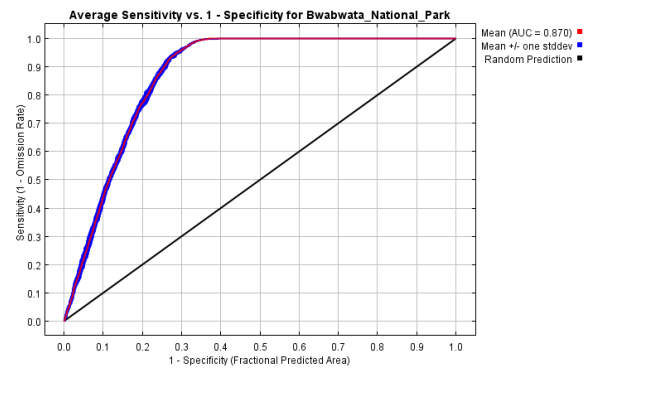
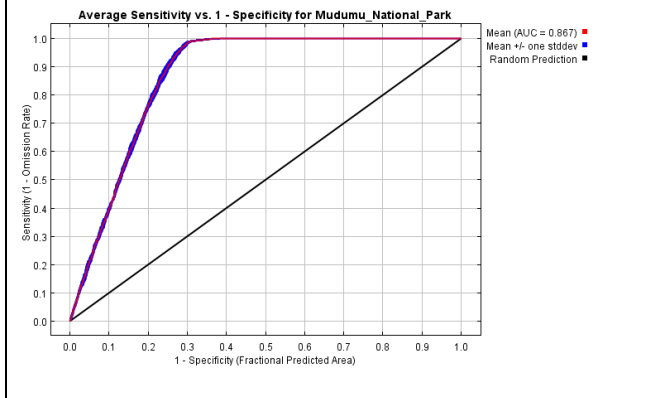
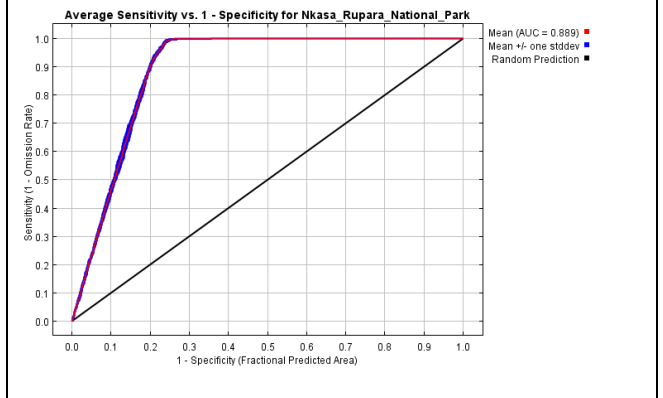
List of Tables

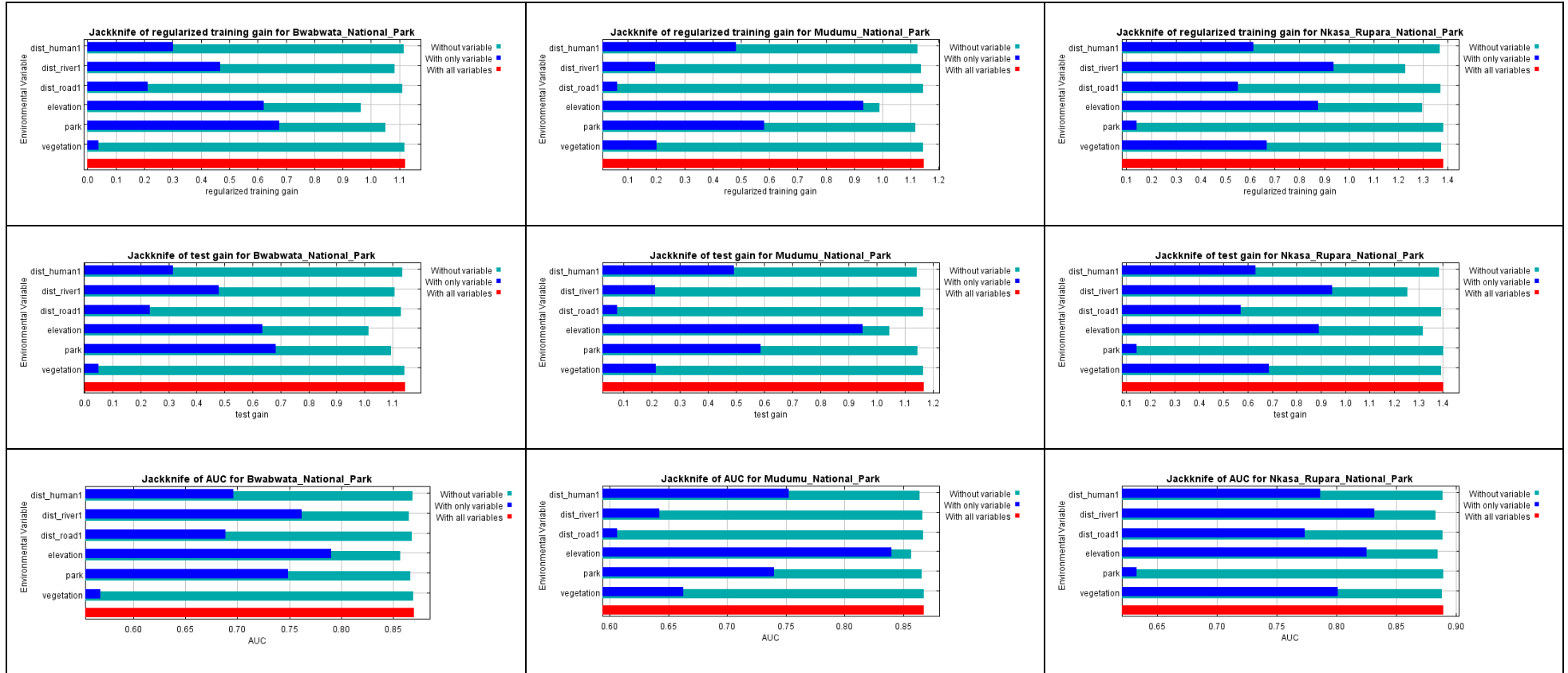
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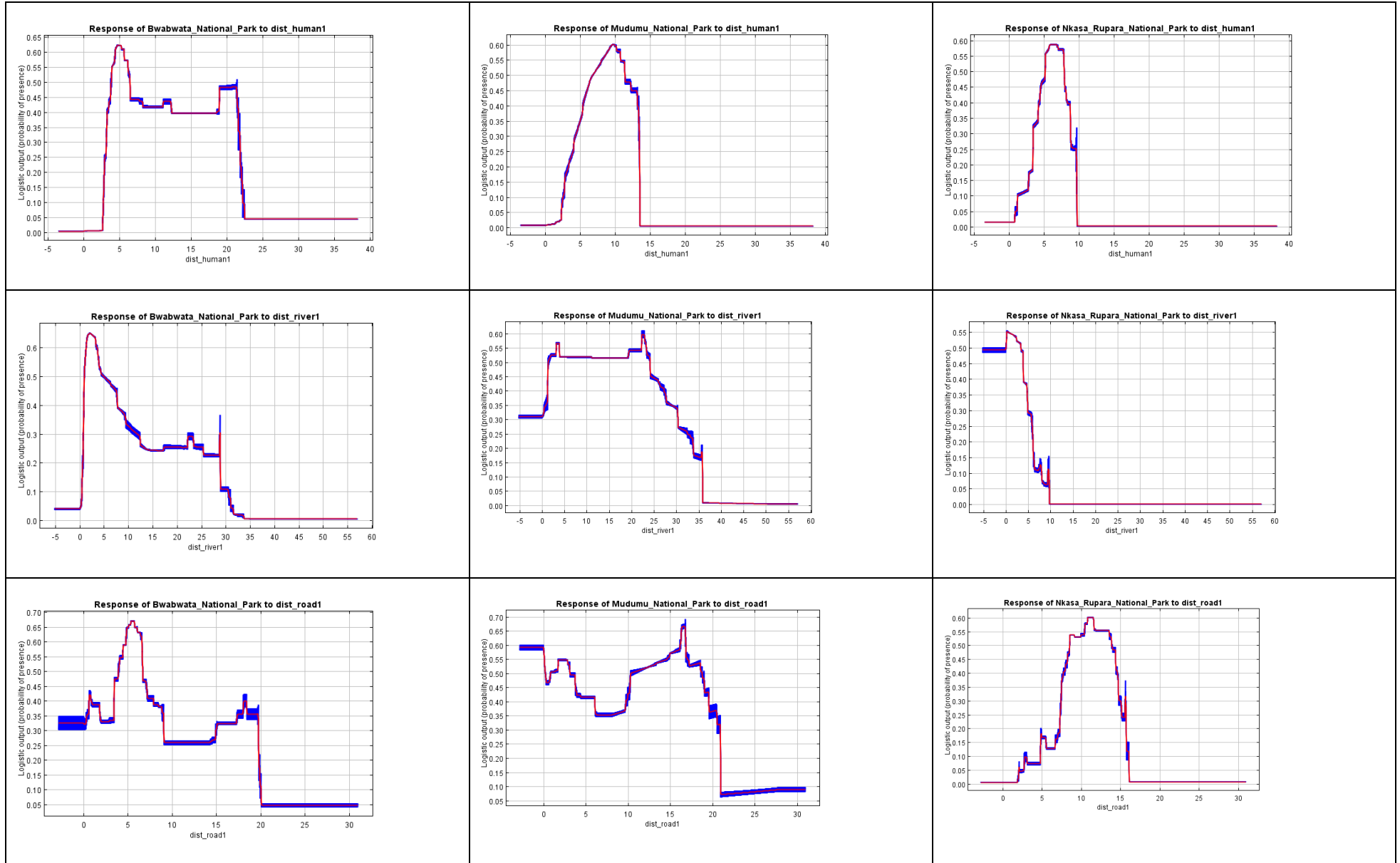
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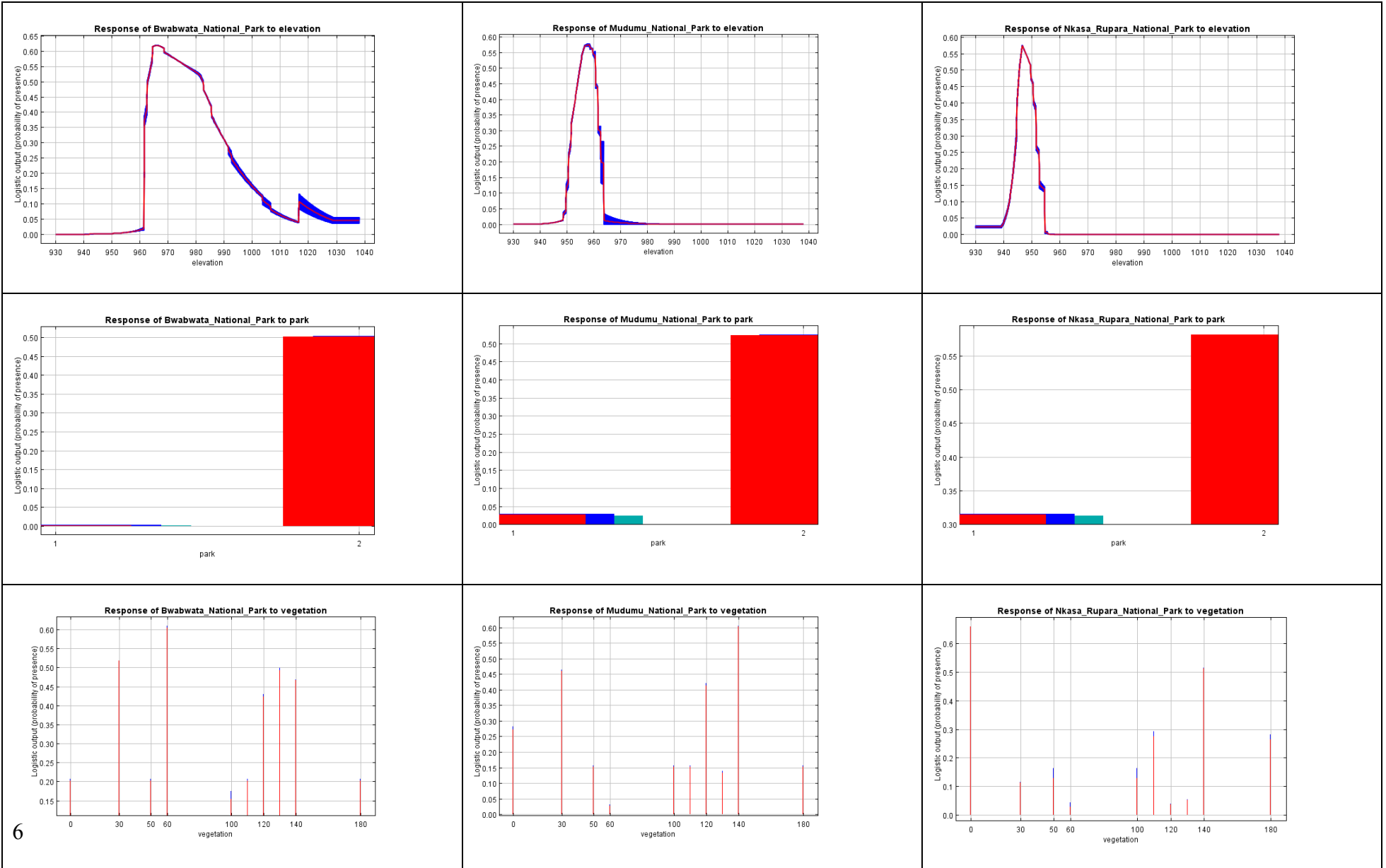
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Table D.1 Model 8 Showing output from MaxEnt for BNP, MPN and NRNP

Model 8 – Bwabwata National Park	Model 8 – Mudumu National Park	Model 8 – Nkasa Rupara National Park
<p>Omission Curve</p> 	<p>Omission Curve</p> 	<p>Omission Curve</p> 
<p>Roc AUC</p> 	<p>Roc AUC</p> 	<p>Roc AUC</p> 







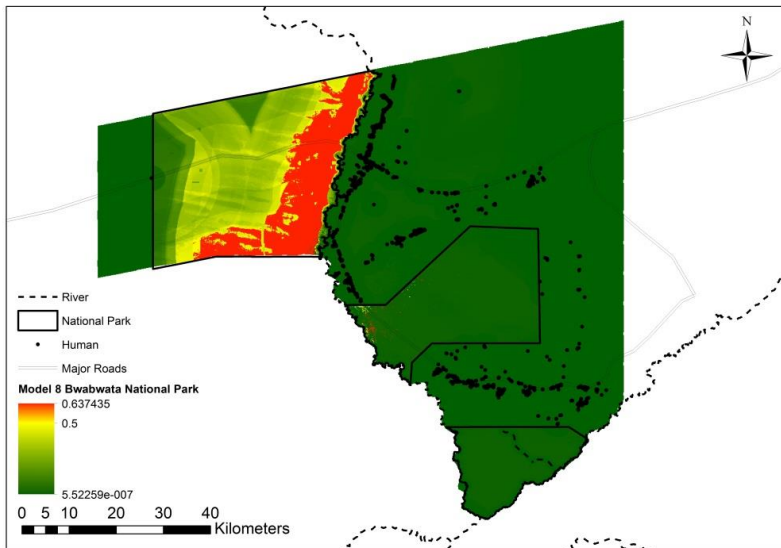


Figure D.1 Model 8 MaxEnt results from Bwabwata National Park

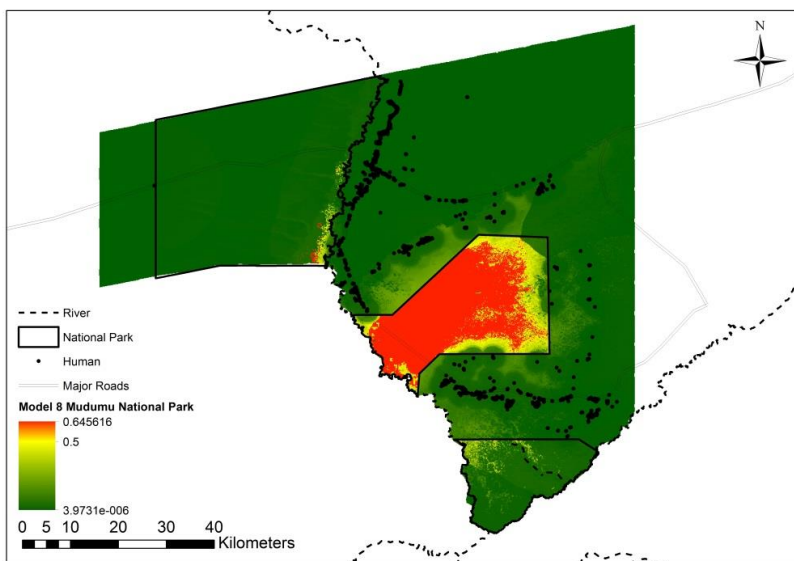


Figure D.2 Model 8 MaxEnt results from Mudumu National Park

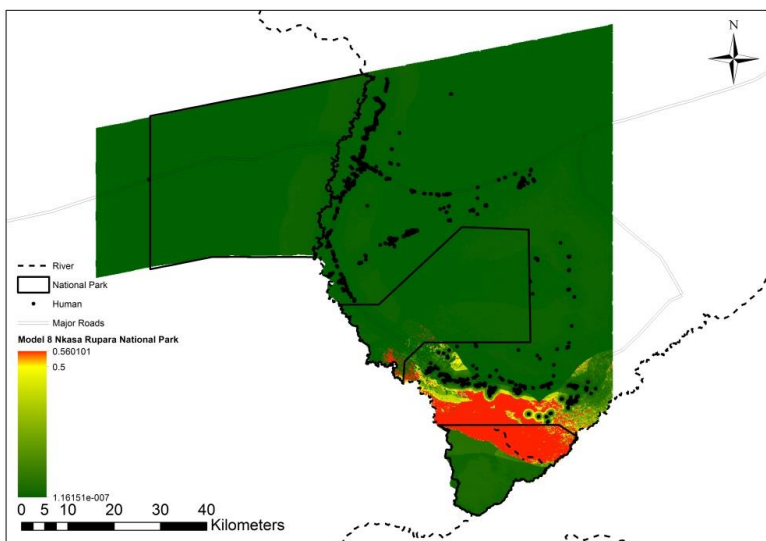
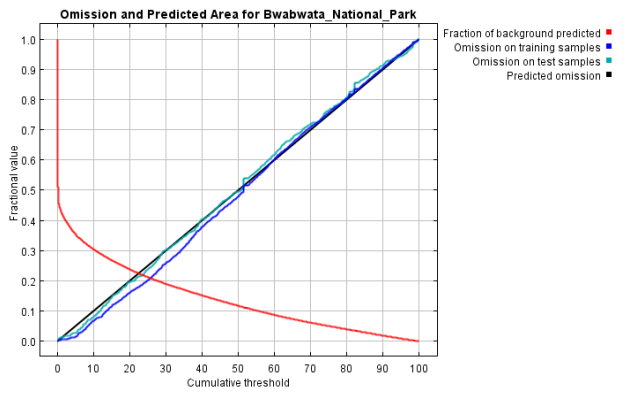
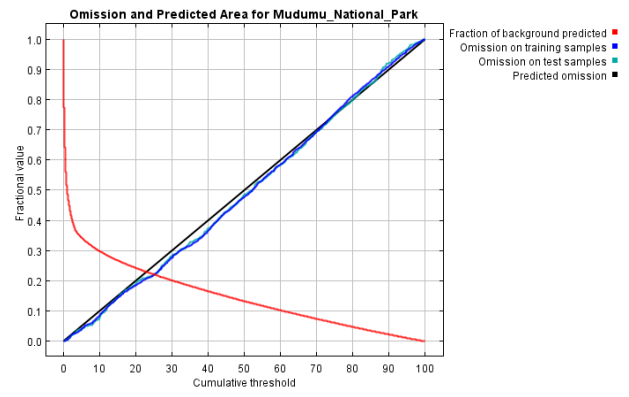
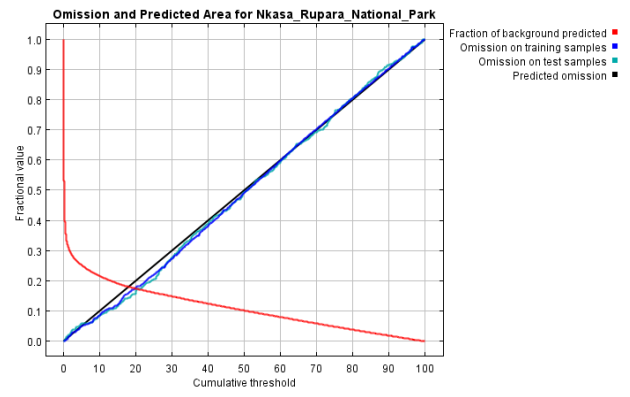
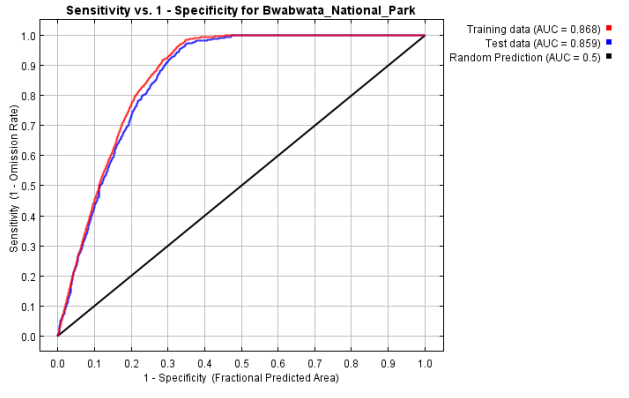
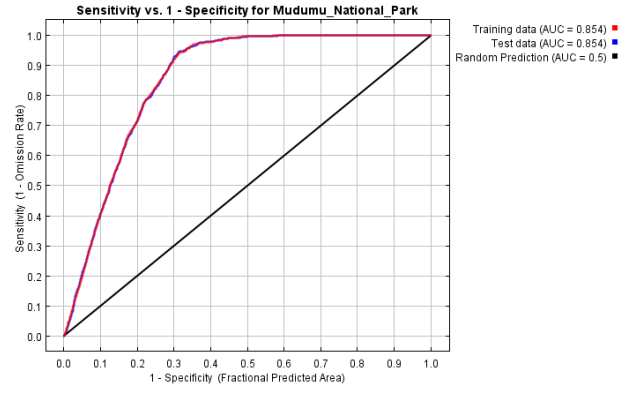
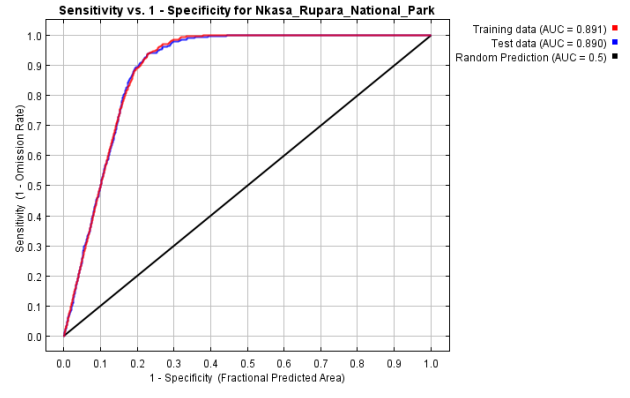
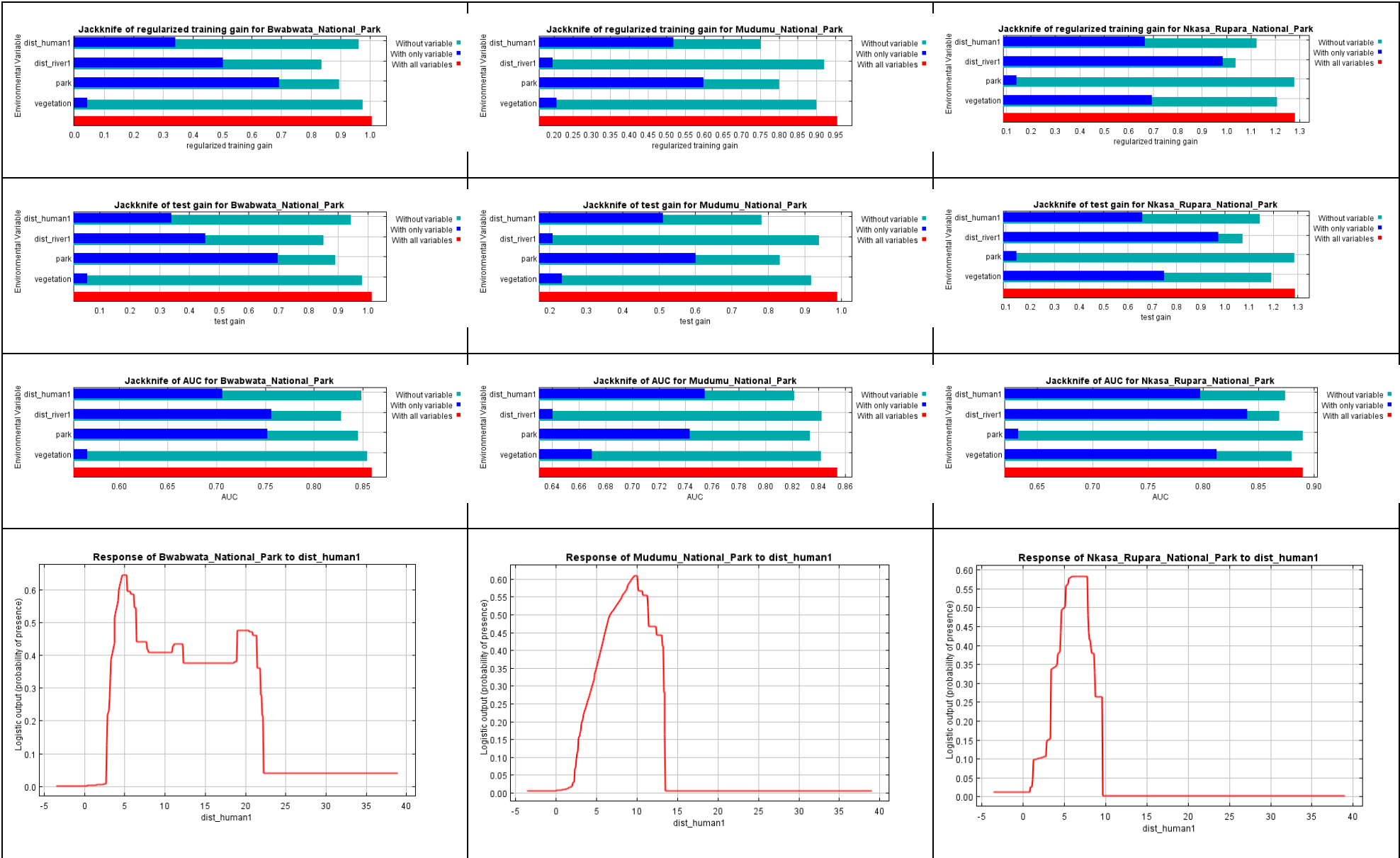
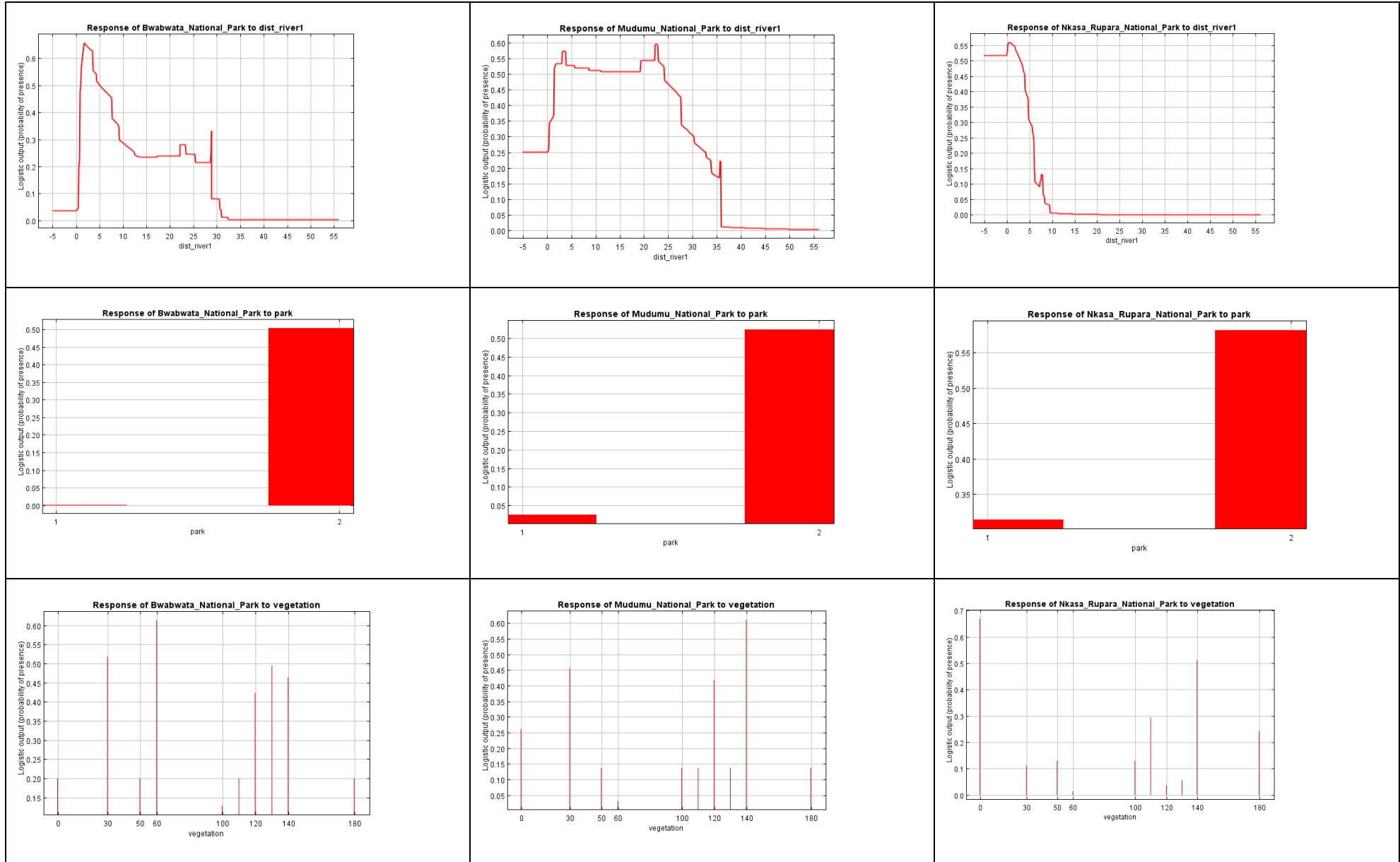


Figure D.3 Model 8 MaxEnt results from Nkasa Rupara National Park

Table D.2 Model 8 without elevation and distance to roads

Model 8 – Bwabwata National Park	Model 8 – Mudumu National Park	Model 8 – Nkasa Rupara National Park
<p>Omission</p>  <p>Omission and Predicted Area for Bwabwata National Park</p> <ul style="list-style-type: none"> Fraction of background predicted Omission on training samples Omission on test samples Predicted omission 	<p>Omission</p>  <p>Omission and Predicted Area for Mudumu National Park</p> <ul style="list-style-type: none"> Fraction of background predicted Omission on training samples Omission on test samples Predicted omission 	<p>Omission</p>  <p>Omission and Predicted Area for Nkasa Rupara National Park</p> <ul style="list-style-type: none"> Fraction of background predicted Omission on training samples Omission on test samples Predicted omission
<p>ROC AUC</p>  <p>Sensitivity vs. 1 - Specificity for Bwabwata National Park</p> <ul style="list-style-type: none"> Training data (AUC = 0.868) Test data (AUC = 0.859) Random Prediction (AUC = 0.5) 	<p>ROC AUC</p>  <p>Sensitivity vs. 1 - Specificity for Mudumu National Park</p> <ul style="list-style-type: none"> Training data (AUC = 0.854) Test data (AUC = 0.854) Random Prediction (AUC = 0.5) 	<p>ROC AUC</p>  <p>Sensitivity vs. 1 - Specificity for Nkasa Rupara National Park</p> <ul style="list-style-type: none"> Training data (AUC = 0.891) Test data (AUC = 0.890) Random Prediction (AUC = 0.5)





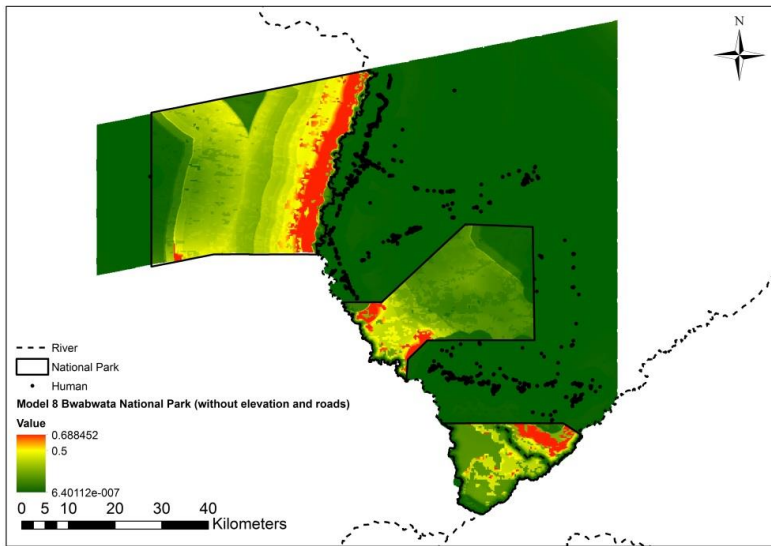


Figure D.4 Model 8 without elevation and distance to roads MaxEnt results from Bwabwata National Park.

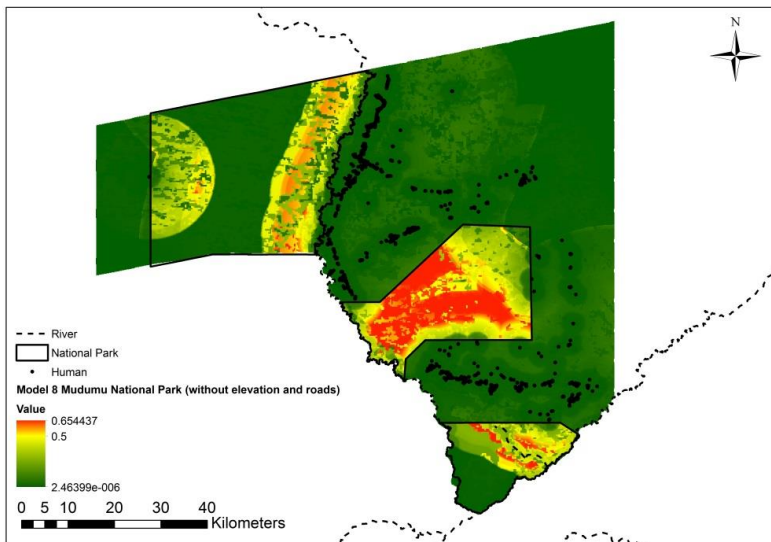


Figure D.5 Model 8 without elevation and distance to roads MaxEnt results from Mudumu National Park.

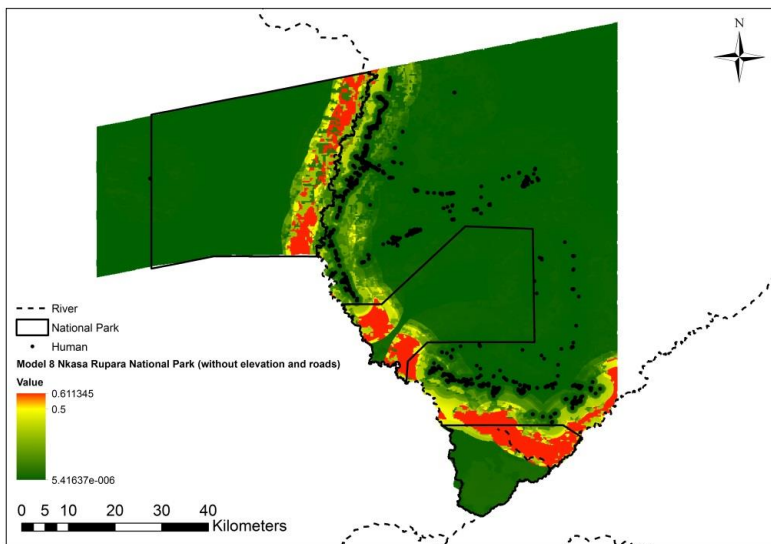
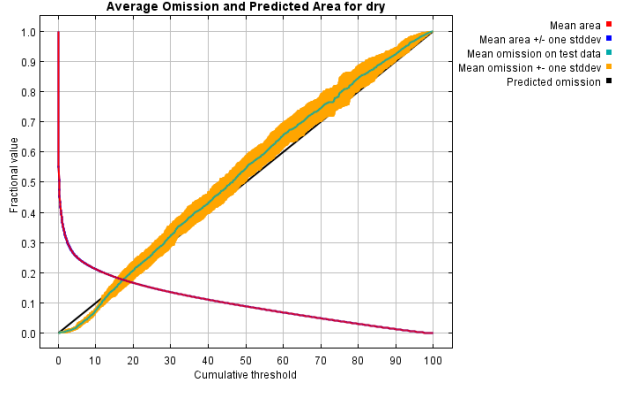
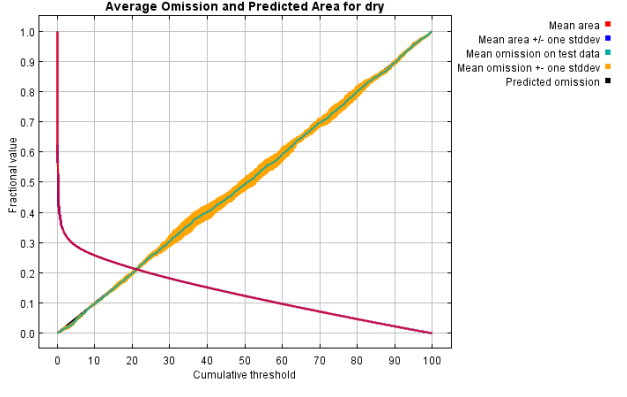
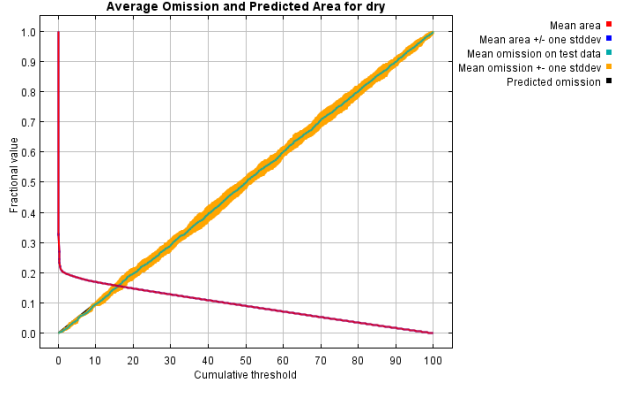
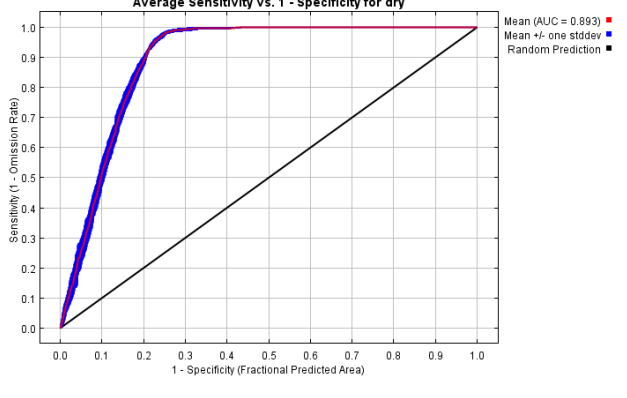
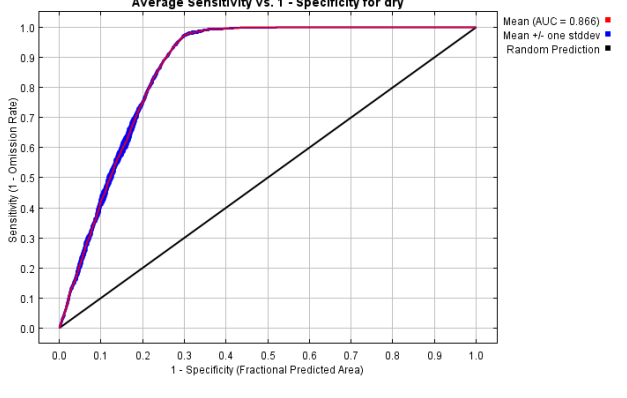
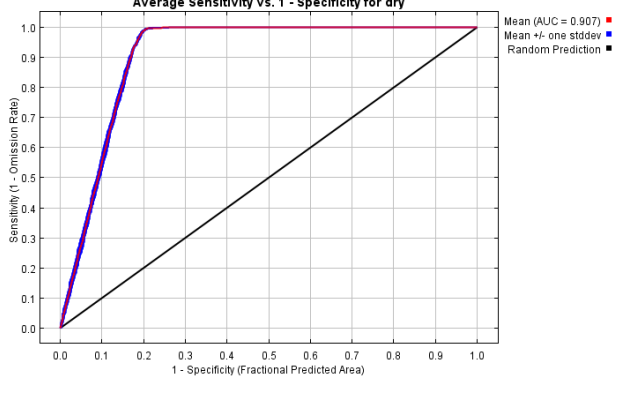
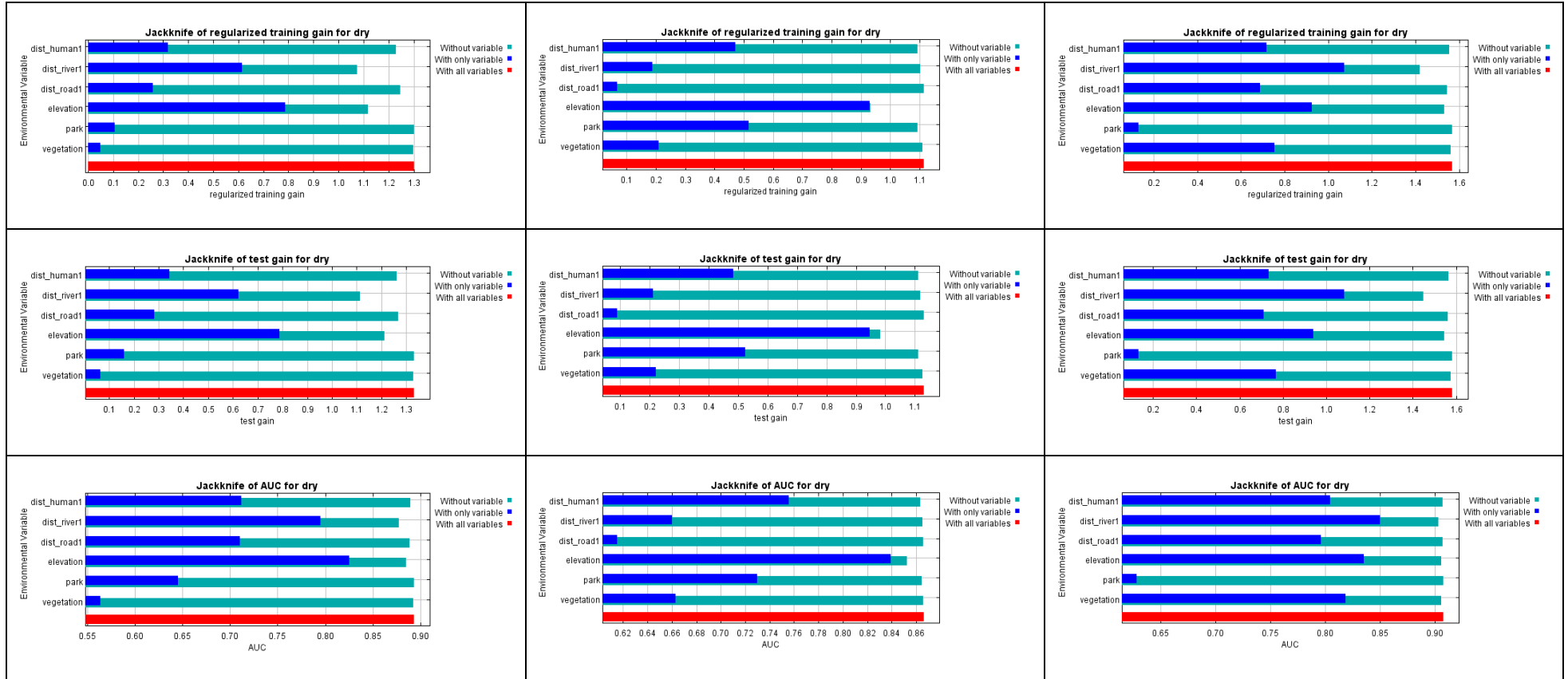
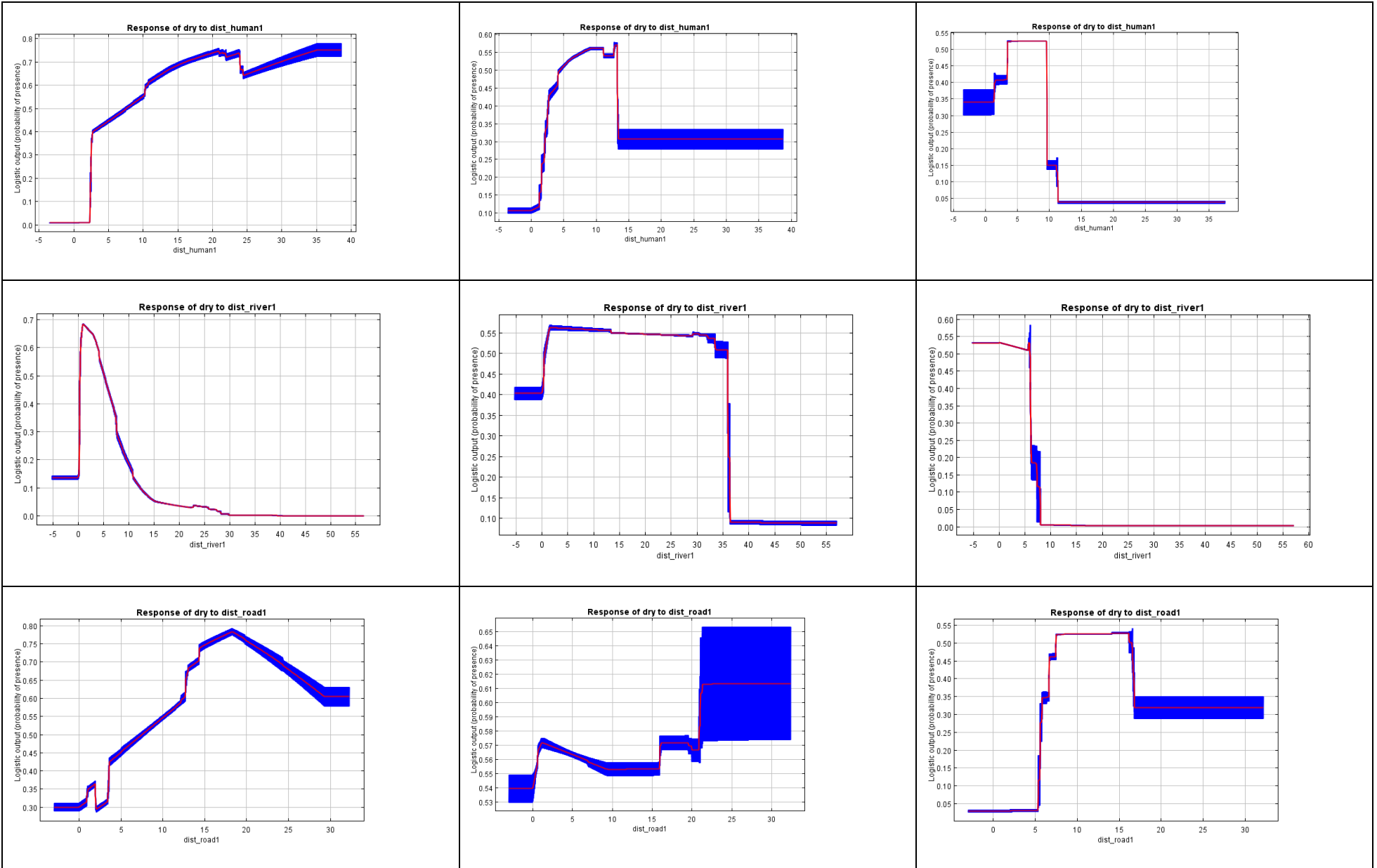


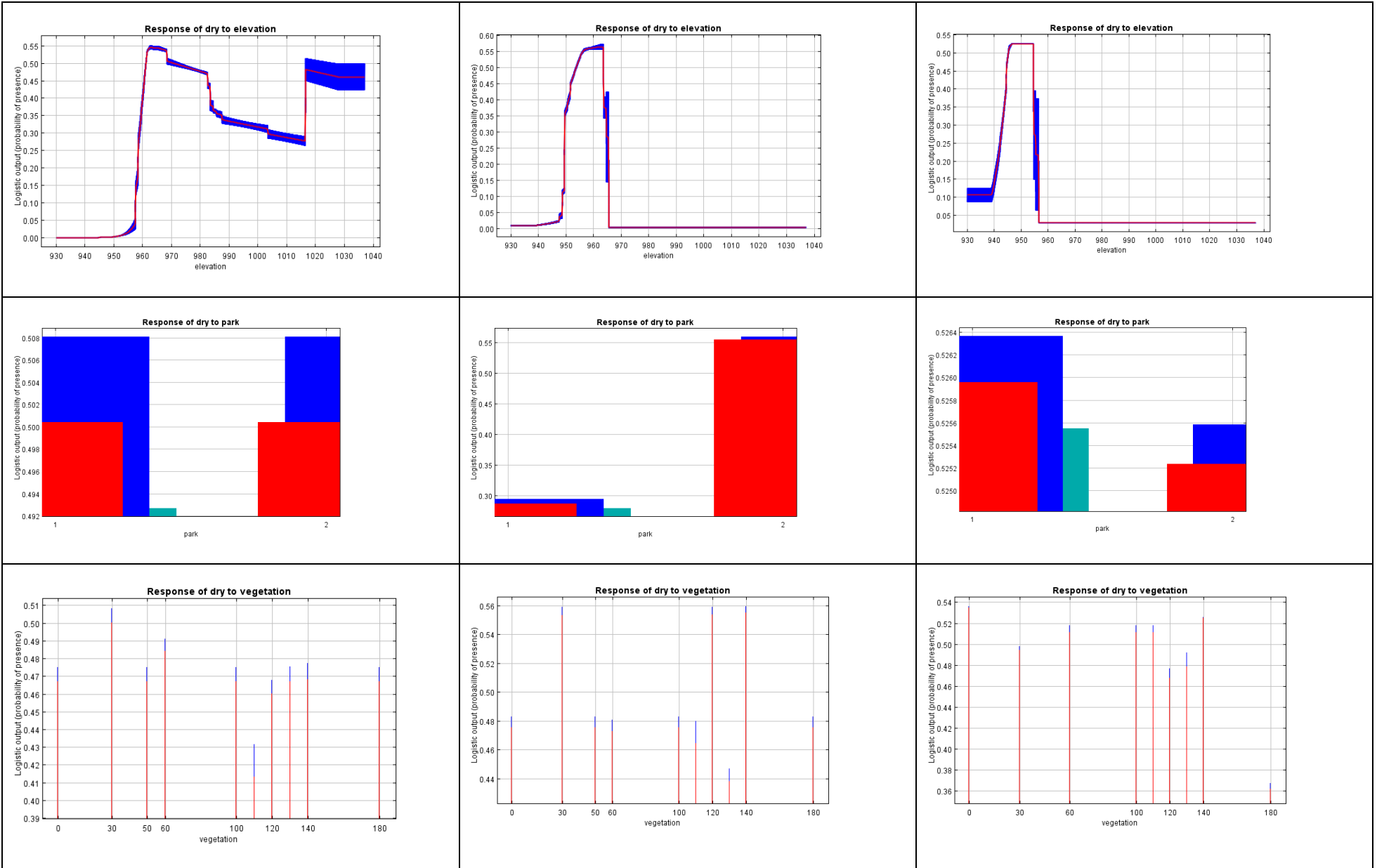
Figure D.6 Model 8 without elevation and distance to roads MaxEnt results from Nkasa Rupara National Park.

Table D.3 Model 13, 14 and 15 showing dry season results per park

Model 13 – Bwabwata National Park	Model 14 – Mudumu National Park	Model 15 – Nkasa Rupara National Park
<p>Omission</p>  <p>Average Omission and Predicted Area for dry</p> <ul style="list-style-type: none"> Mean area Mean area +/- one stdev Mean omission on test data Mean omission +/- one stdev Predicted omission 	<p>Omission</p>  <p>Average Omission and Predicted Area for dry</p> <ul style="list-style-type: none"> Mean area Mean area +/- one stdev Mean omission on test data Mean omission +/- one stdev Predicted omission 	<p>Omission.</p>  <p>Average Omission and Predicted Area for dry</p> <ul style="list-style-type: none"> Mean area Mean area +/- one stdev Mean omission on test data Mean omission +/- one stdev Predicted omission
<p>ROC AUC</p>  <p>Average Sensitivity vs. 1 - Specificity for dry</p> <ul style="list-style-type: none"> Mean (AUC = 0.893) Mean +/- one stdev Random Prediction 	<p>ROC AUC</p>  <p>Average Sensitivity vs. 1 - Specificity for dry</p> <ul style="list-style-type: none"> Mean (AUC = 0.866) Mean +/- one stdev Random Prediction 	<p>ROC AUC</p>  <p>Average Sensitivity vs. 1 - Specificity for dry</p> <ul style="list-style-type: none"> Mean (AUC = 0.907) Mean +/- one stdev Random Prediction







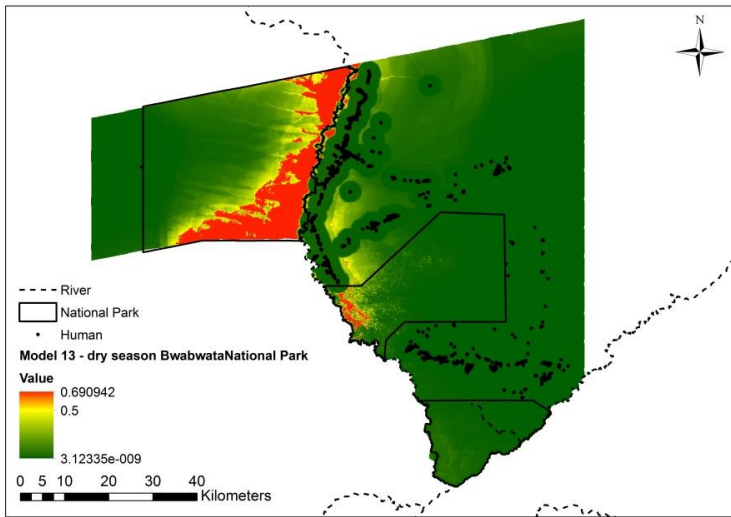


Figure D.7 Model 13 showing the dry season results for Bwabwata National Park

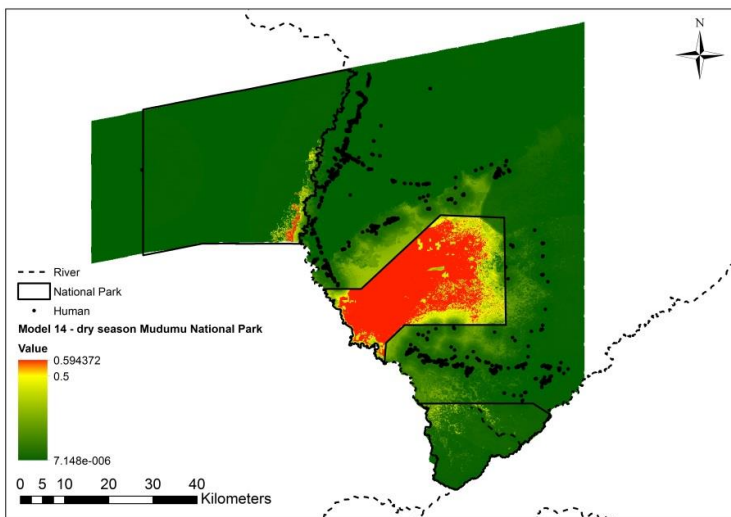


Figure D.8 Model 14 showing the dry season results for Mudumu National Park

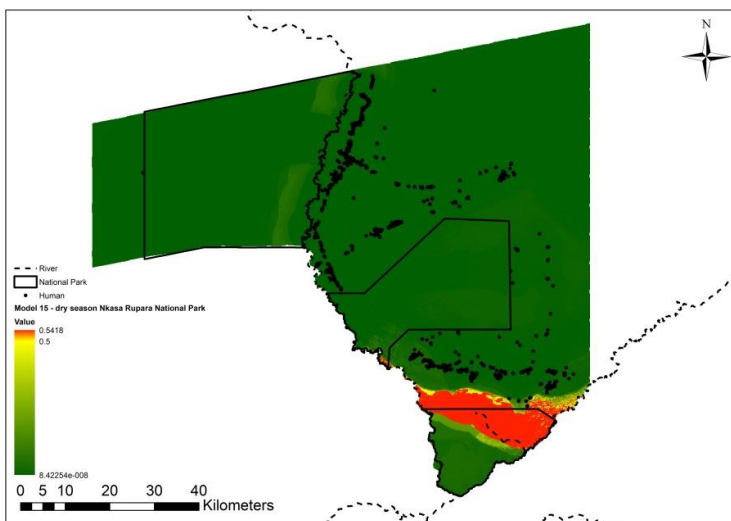
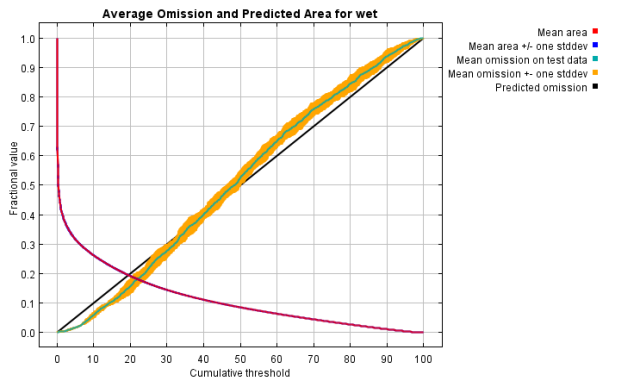
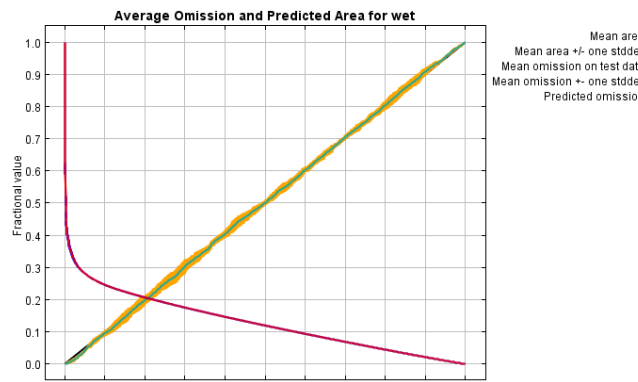
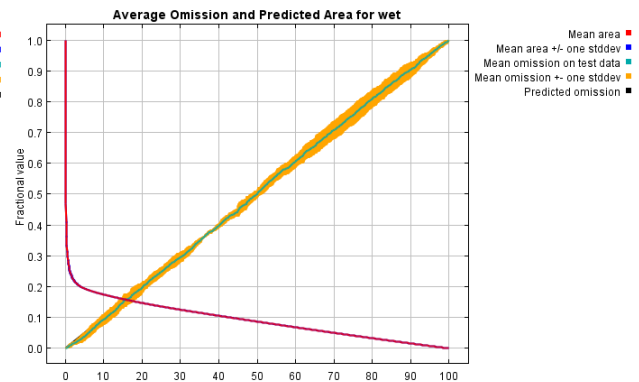
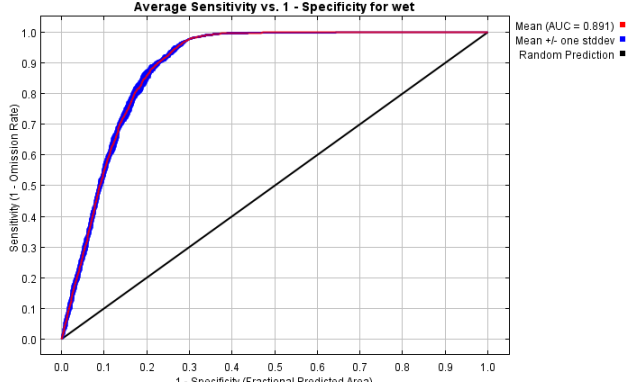
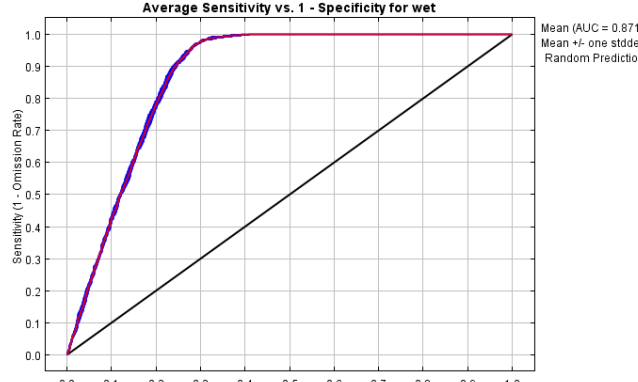
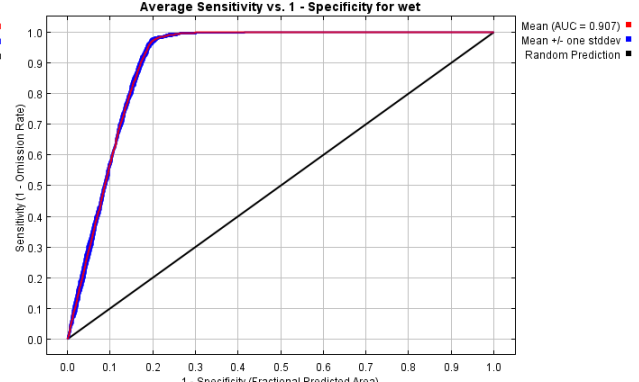
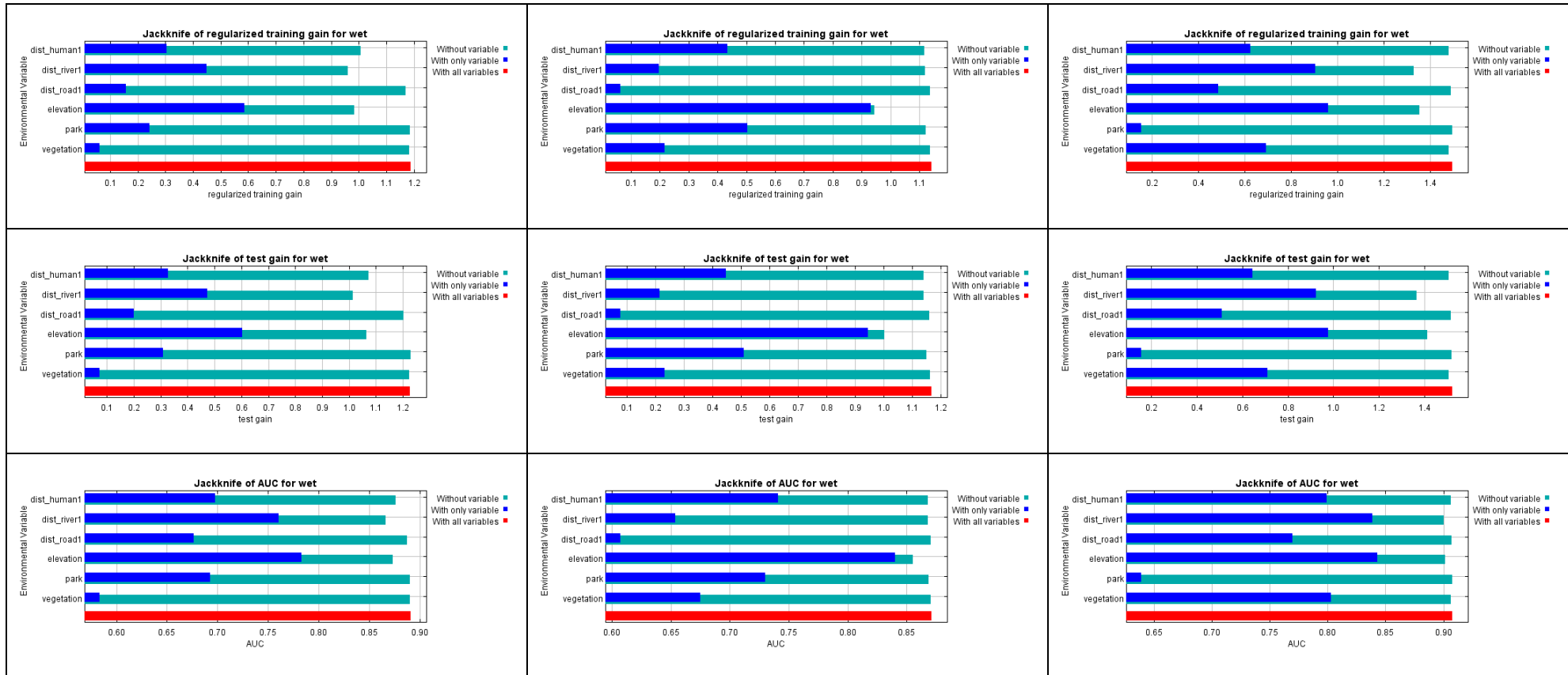
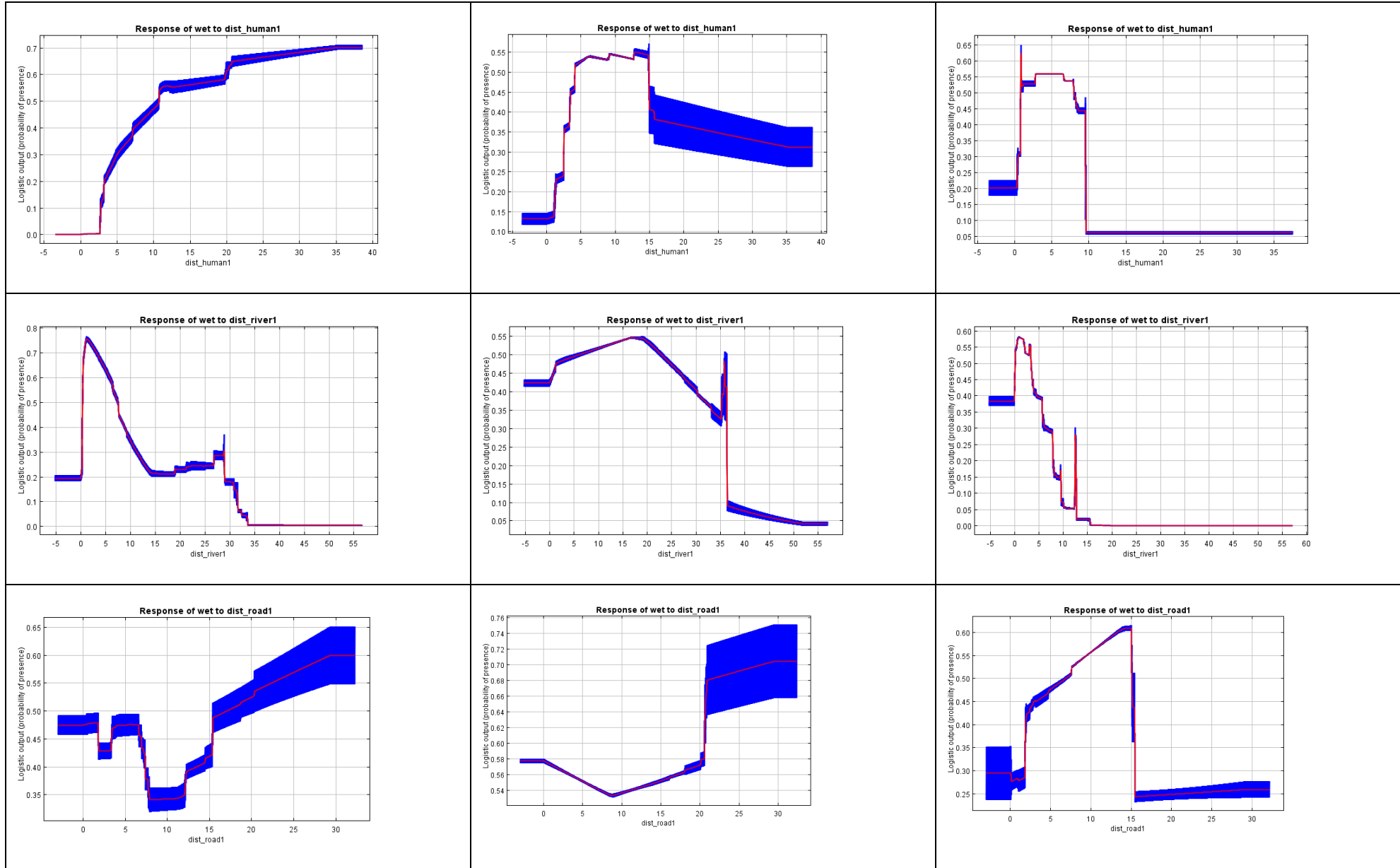


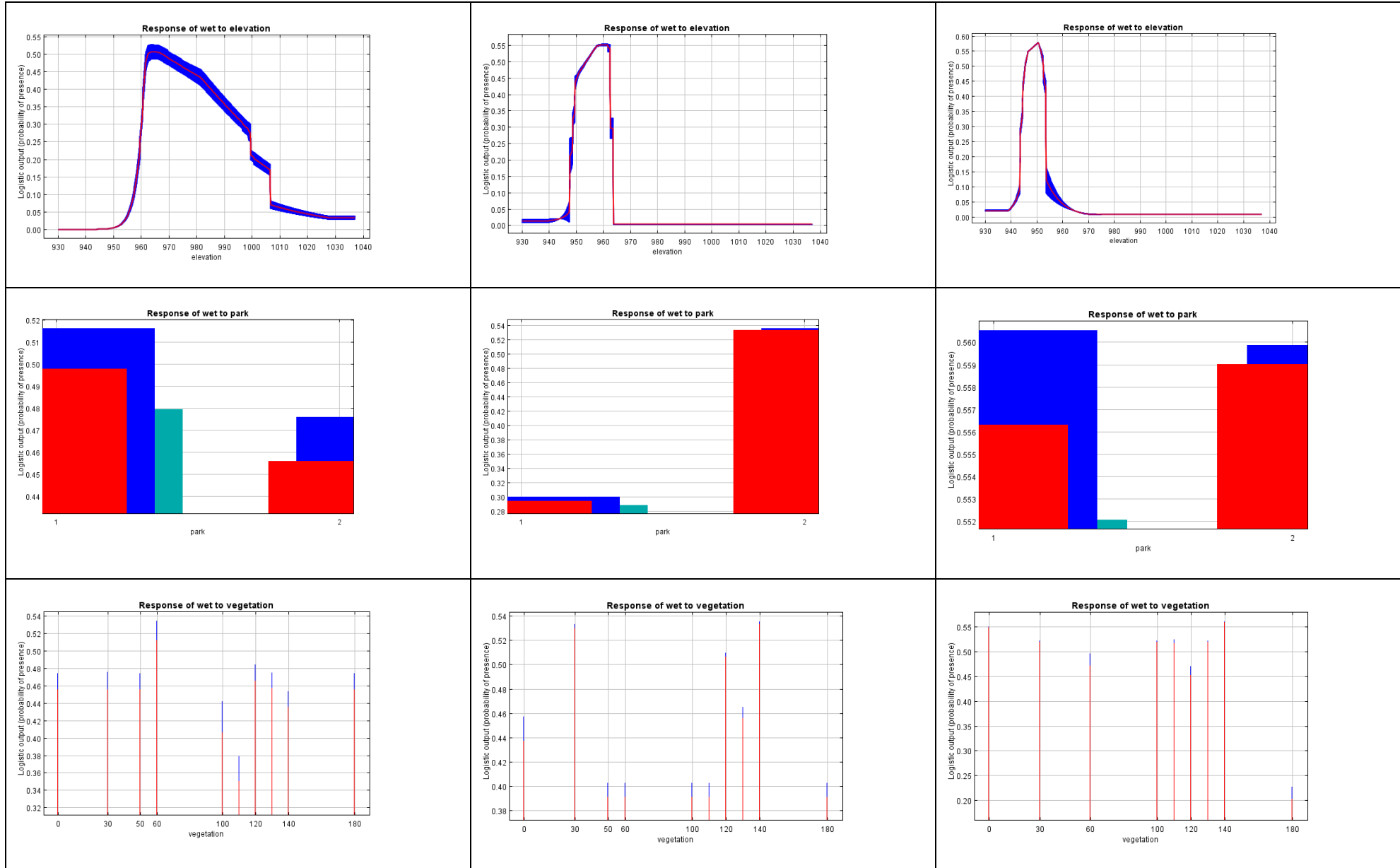
Figure D.9 Model 15 showing the dry season results for Nkasa Rupara National Park

Table D.4 Model 13, 14 and 15 showing wet season results per park

Model 13 – Bwabwata National Park	Model 14 – Mudumu National Park	Model 15 – Nkasa Rupara National Park
<p>Omission</p>  <p>Average Omission and Predicted Area for wet</p> <ul style="list-style-type: none"> Mean area Mean area +/- one stddv Mean omission on test data Mean omission +/- one stddv Predicted omission 	<p>Omission</p>  <p>Average Omission and Predicted Area for wet</p> <ul style="list-style-type: none"> Mean area Mean area +/- one stddv Mean omission on test data Mean omission +/- one stddv Predicted omission 	<p>Omission</p>  <p>Average Omission and Predicted Area for wet</p> <ul style="list-style-type: none"> Mean area Mean area +/- one stddv Mean omission on test data Mean omission +/- one stddv Predicted omission
<p>ROC AUC</p>  <p>Average Sensitivity vs. 1 - Specificity for wet</p> <ul style="list-style-type: none"> Mean (AUC = 0.891) Mean +/- one stddv Random Prediction 	<p>ROC AUC</p>  <p>Average Sensitivity vs. 1 - Specificity for wet</p> <ul style="list-style-type: none"> Mean (AUC = 0.871) Mean +/- one stddv Random Prediction 	<p>ROC AUC</p>  <p>Average Sensitivity vs. 1 - Specificity for wet</p> <ul style="list-style-type: none"> Mean (AUC = 0.907) Mean +/- one stddv Random Prediction







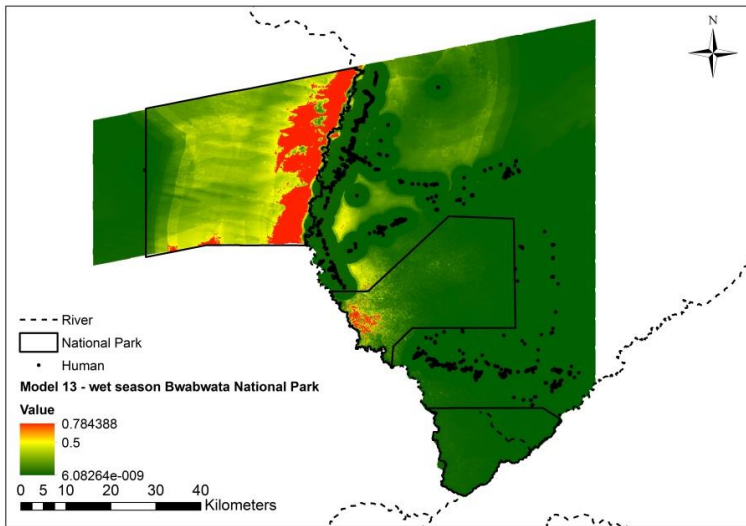


Figure D.10 Model 13 showing the wet season results for Bwabwata National Park

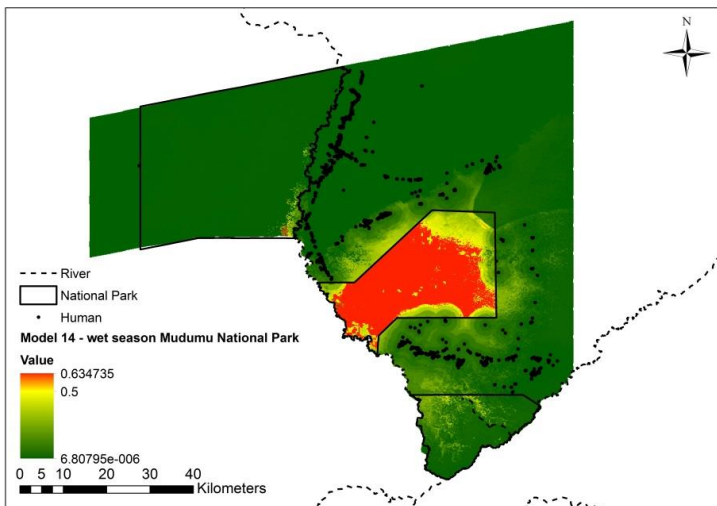


Figure D.11 Model 14 showing the wet season results for Bwabwata National Park

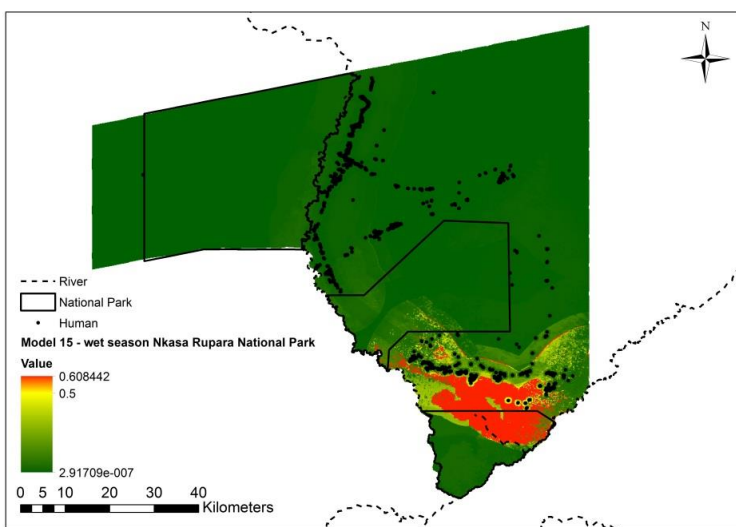
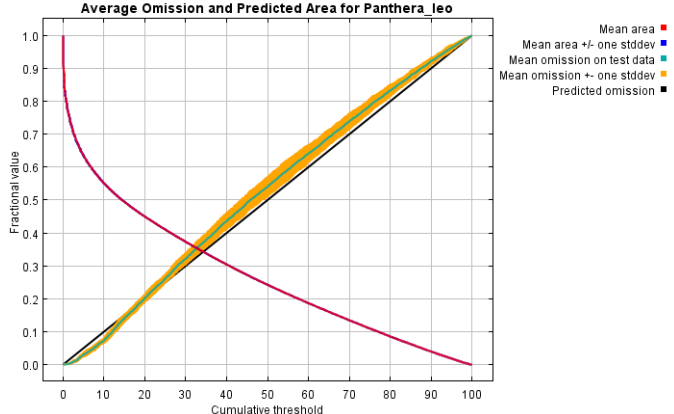
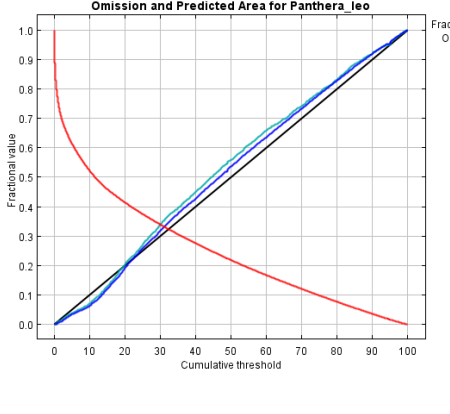
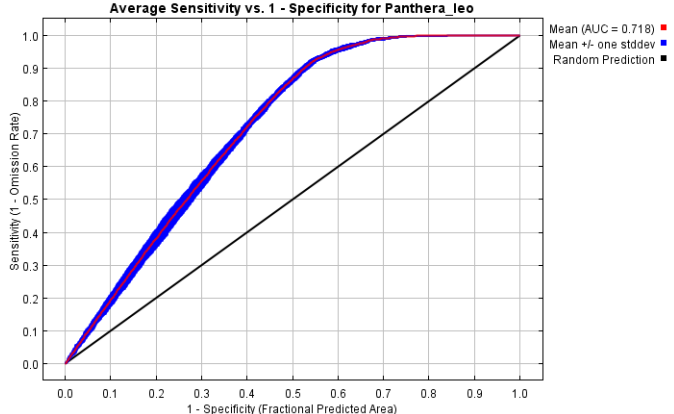
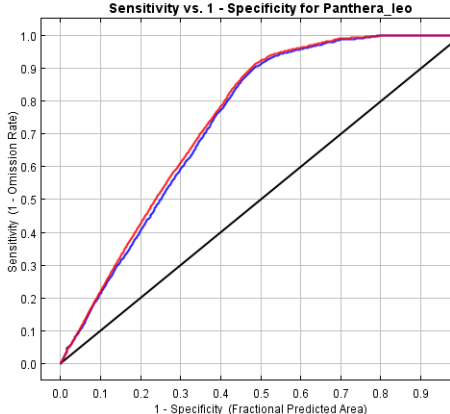
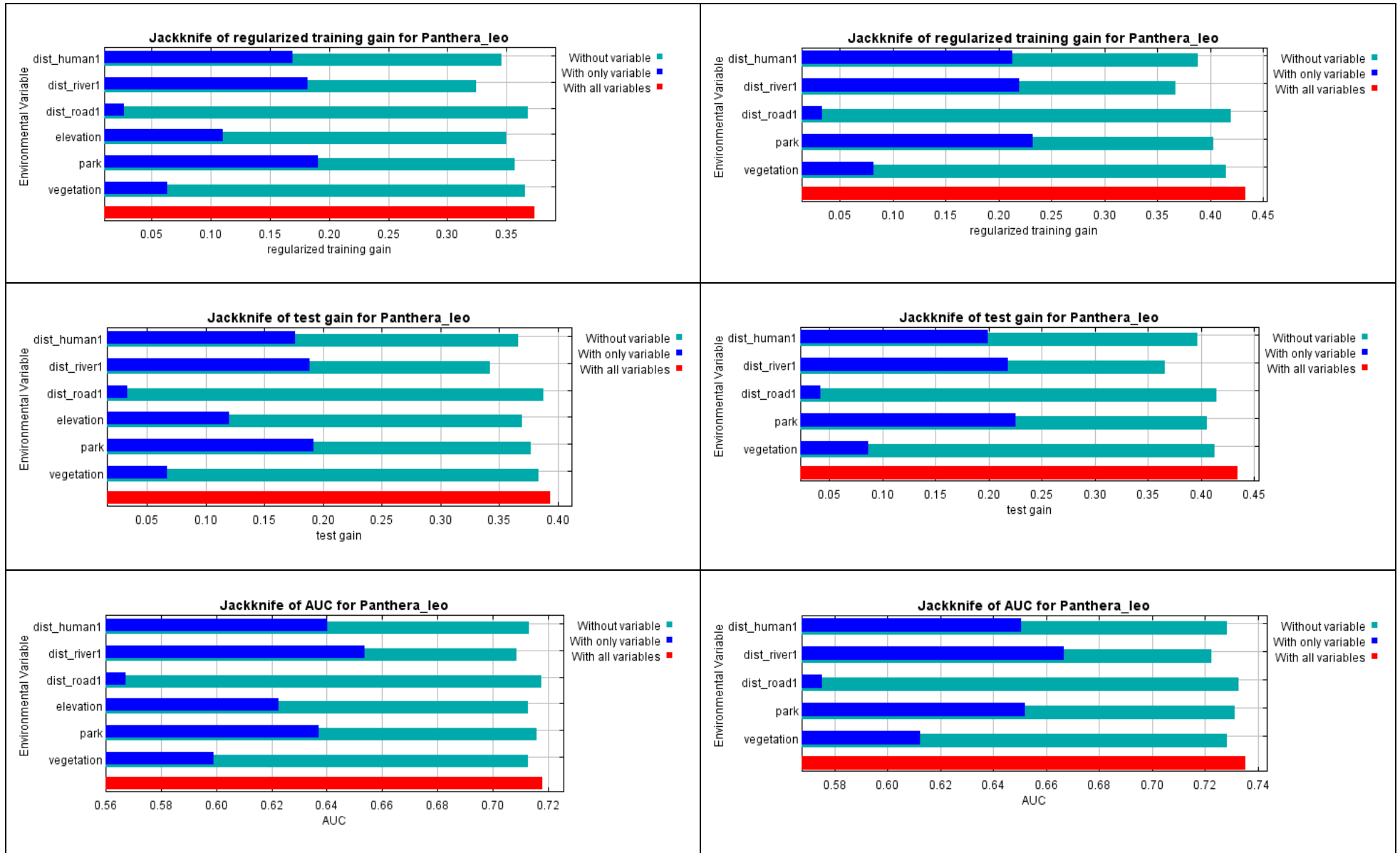
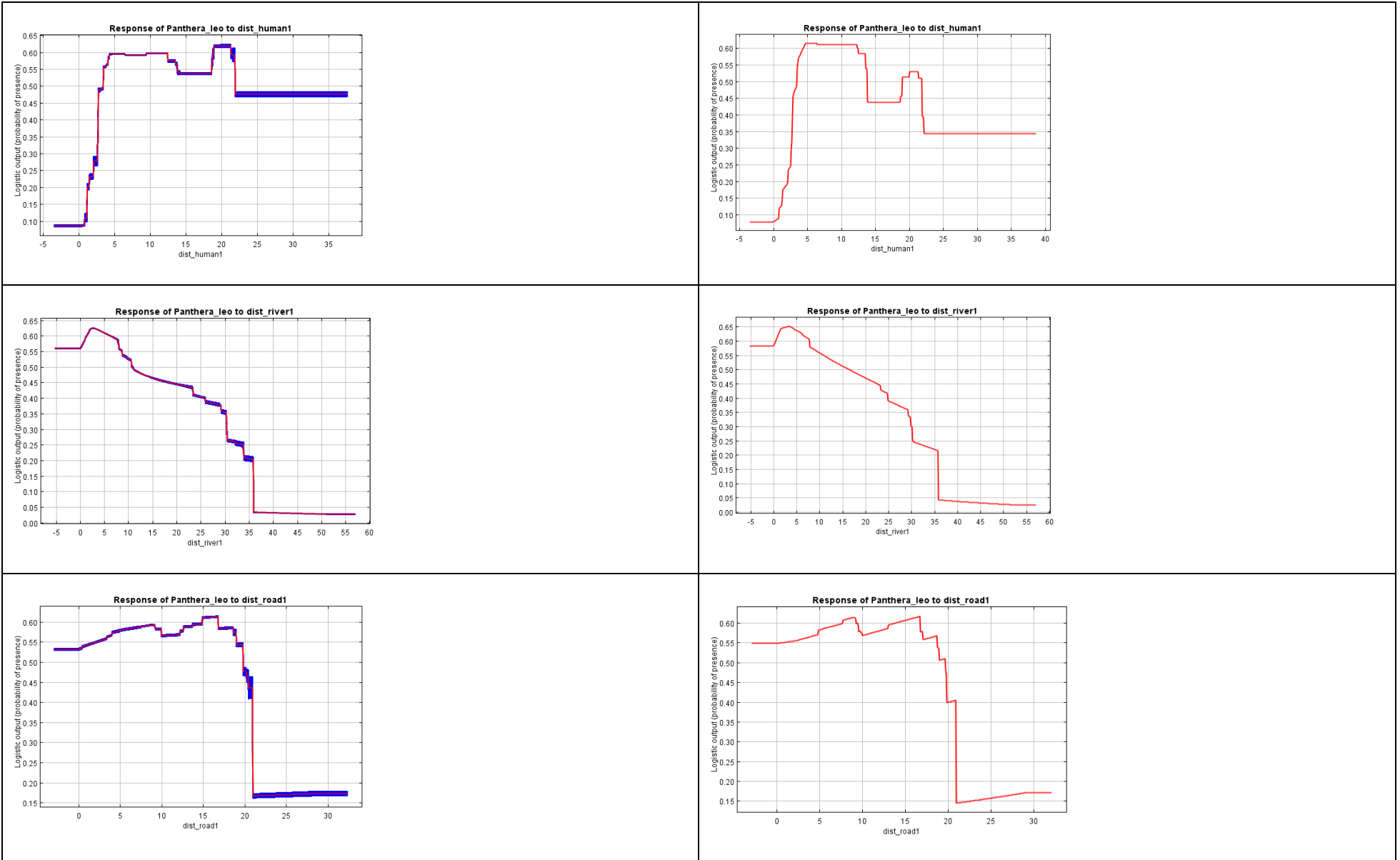


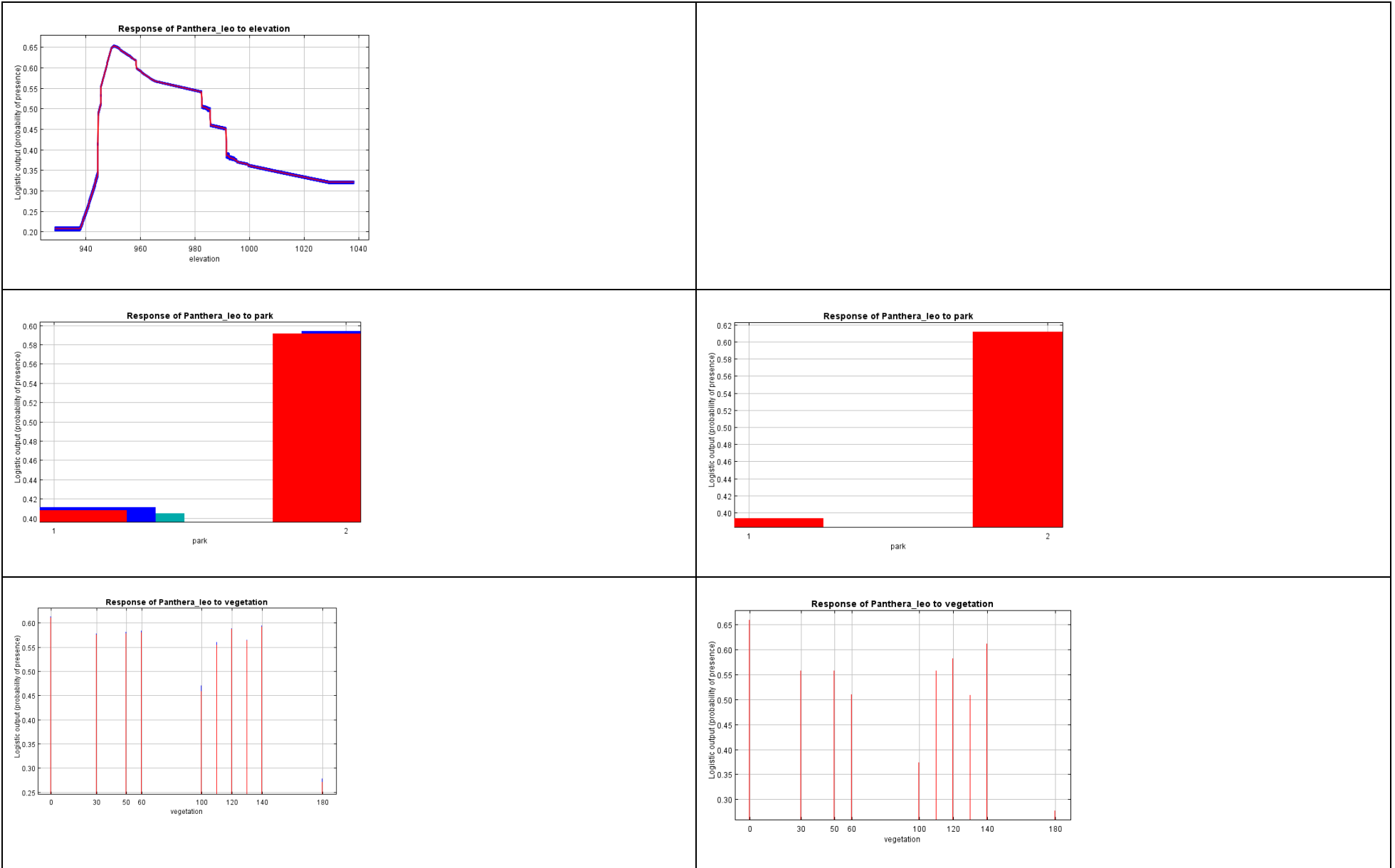
Figure D.12 Model 15 showing the wet season results for Bwabwata National Park

Table D.5 Model 4 - All *Panthera leo* with equal number of points clipped to the vegetation layer

Model 4 – All Panthera leo clipped to veg equal	Model 4 – All Panthera leo without elevation
<p>Omission</p>  <p>Average Omission and Predicted Area for Panthera_leo</p> <ul style="list-style-type: none"> Mean area Mean area +/- one stddv Mean omission on test data Mean omission +/- one stddv Predicted omission 	<p>Omission</p>  <p>Omission and Predicted Area for Panthera_leo</p> <ul style="list-style-type: none"> Fraction of background predicted Omission on training samples Omission on test samples Predicted omission
<p>ROC AUC</p>  <p>Average Sensitivity vs. 1 - Specificity for Panthera_leo</p> <ul style="list-style-type: none"> Mean (AUC = 0.718) Mean +/- one stddv Random Prediction 	<p>ROC AUC</p>  <p>Sensitivity vs. 1 - Specificity for Panthera_leo</p> <ul style="list-style-type: none"> Training data (AUC = 0.743) Test data (AUC = 0.735) Random Prediction (AUC = 0.5)







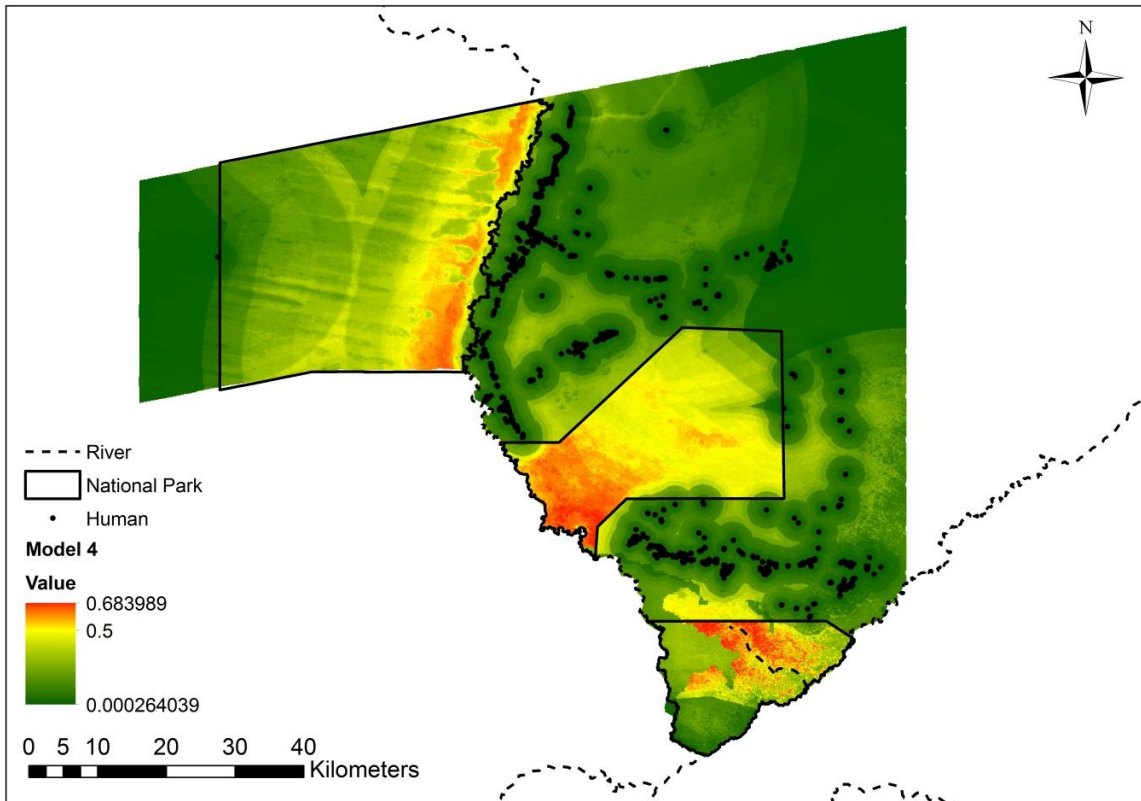


Figure D.13 Maxent results for all lion for model 4.

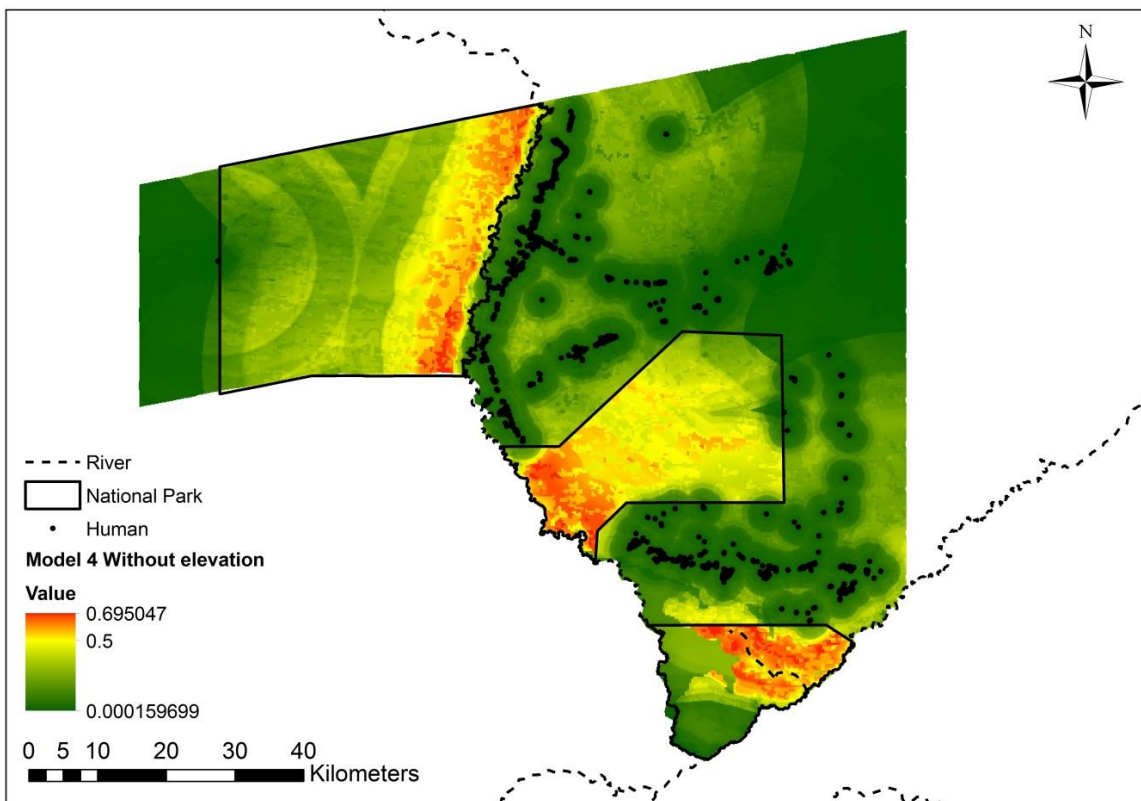
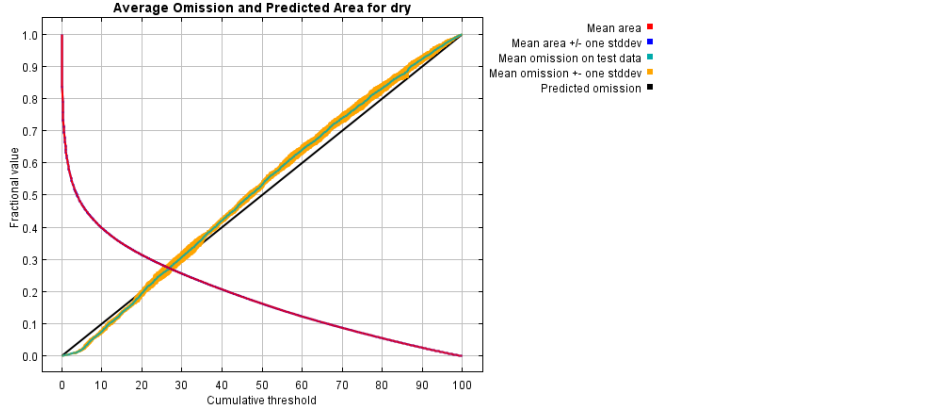
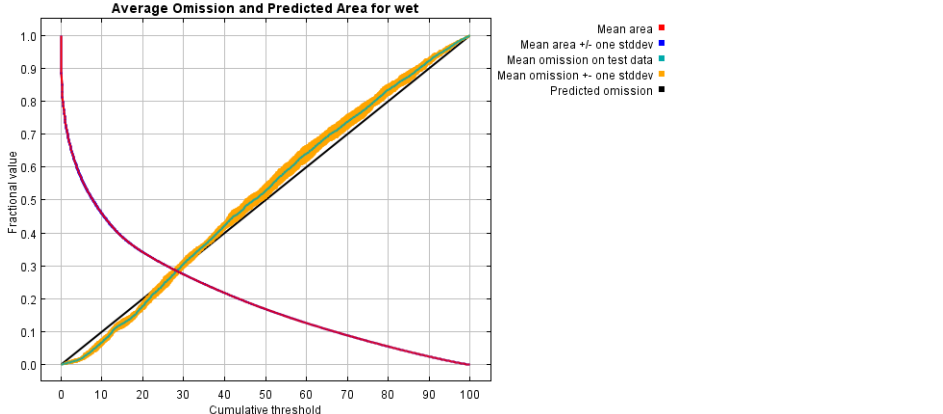
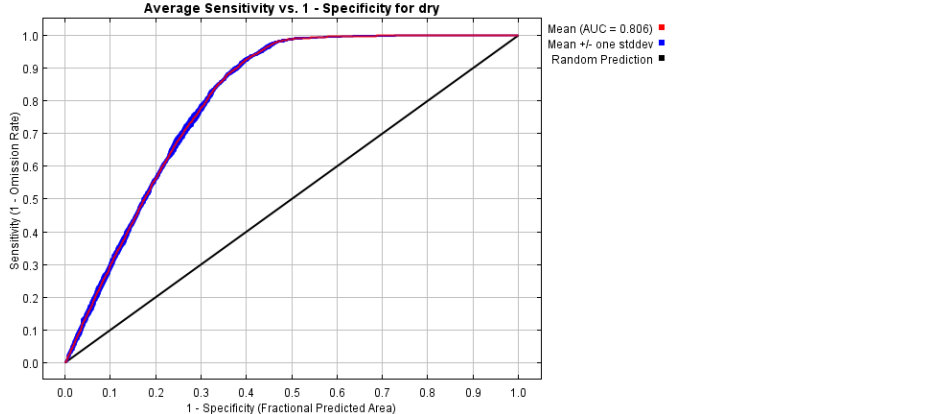
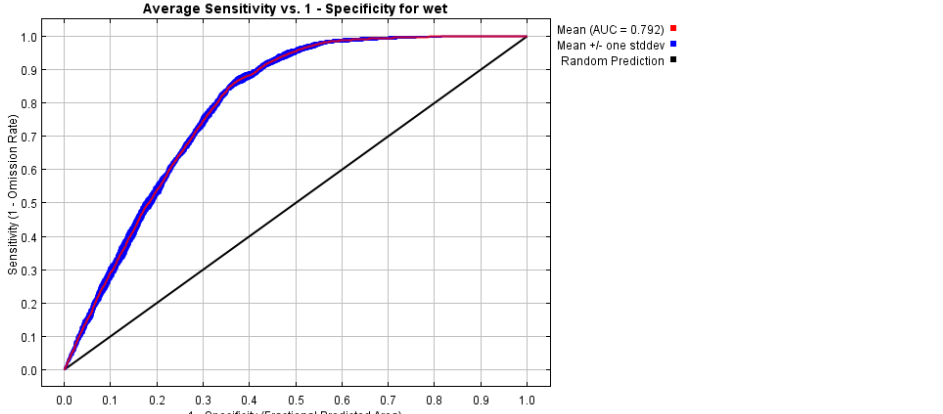
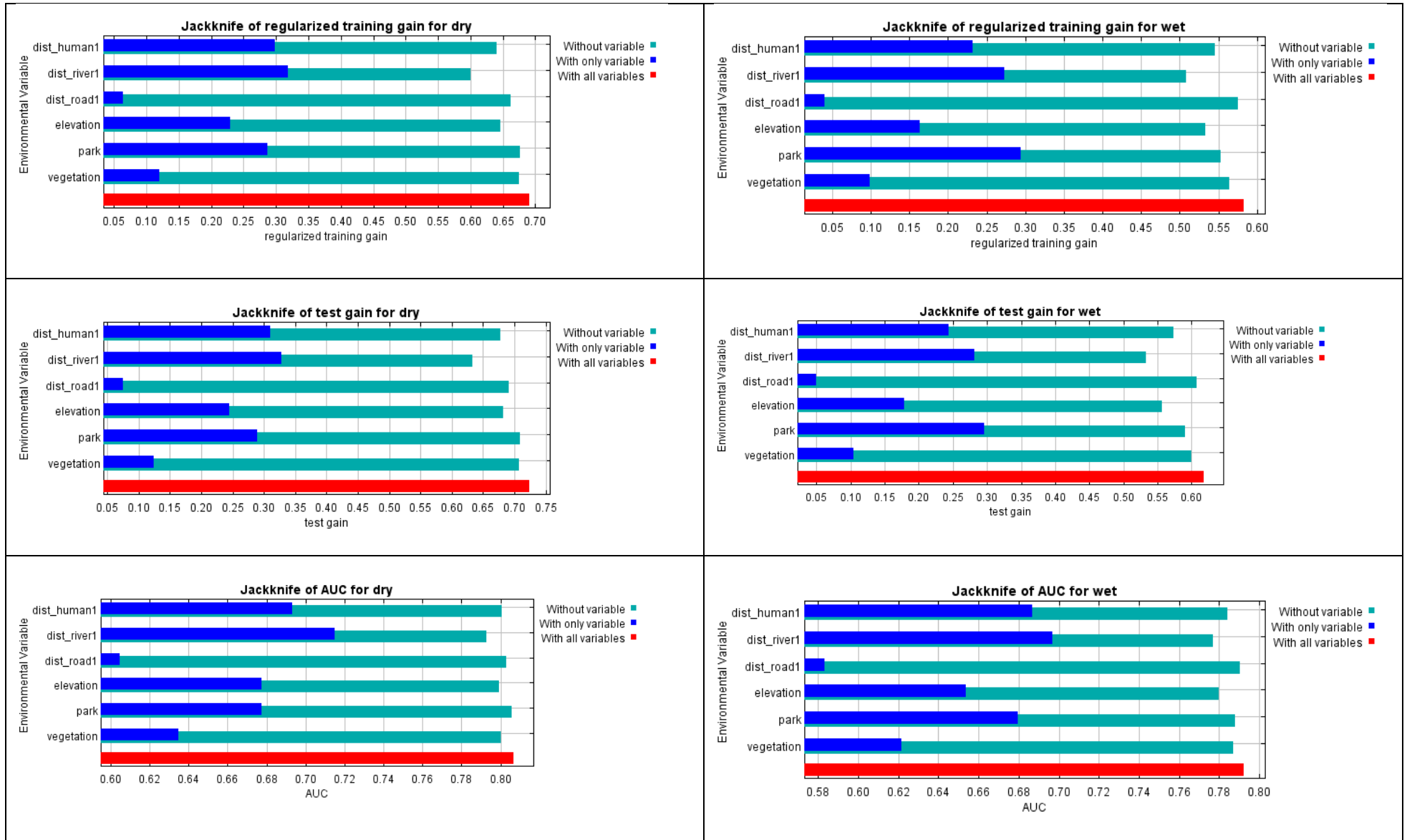
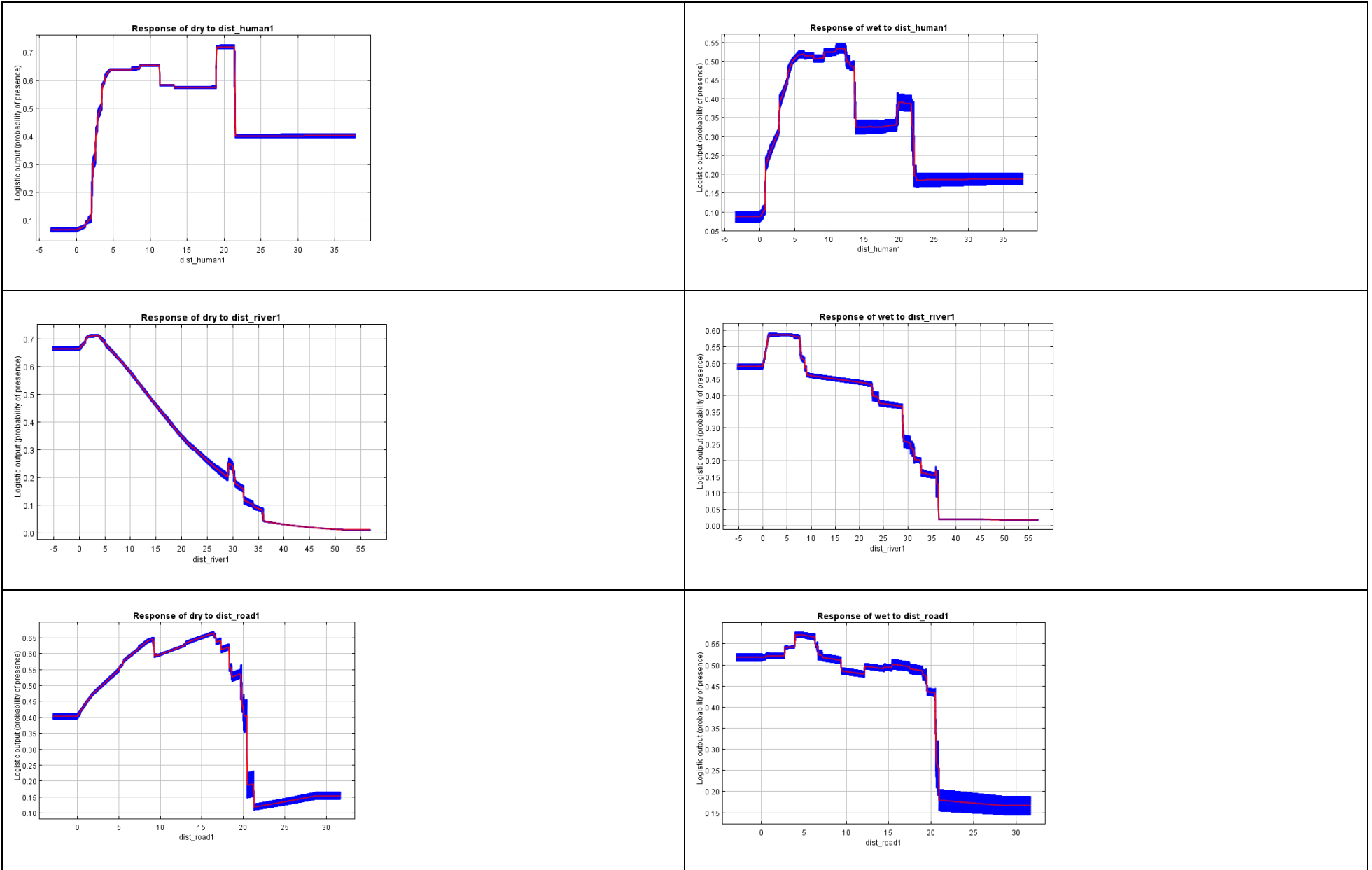


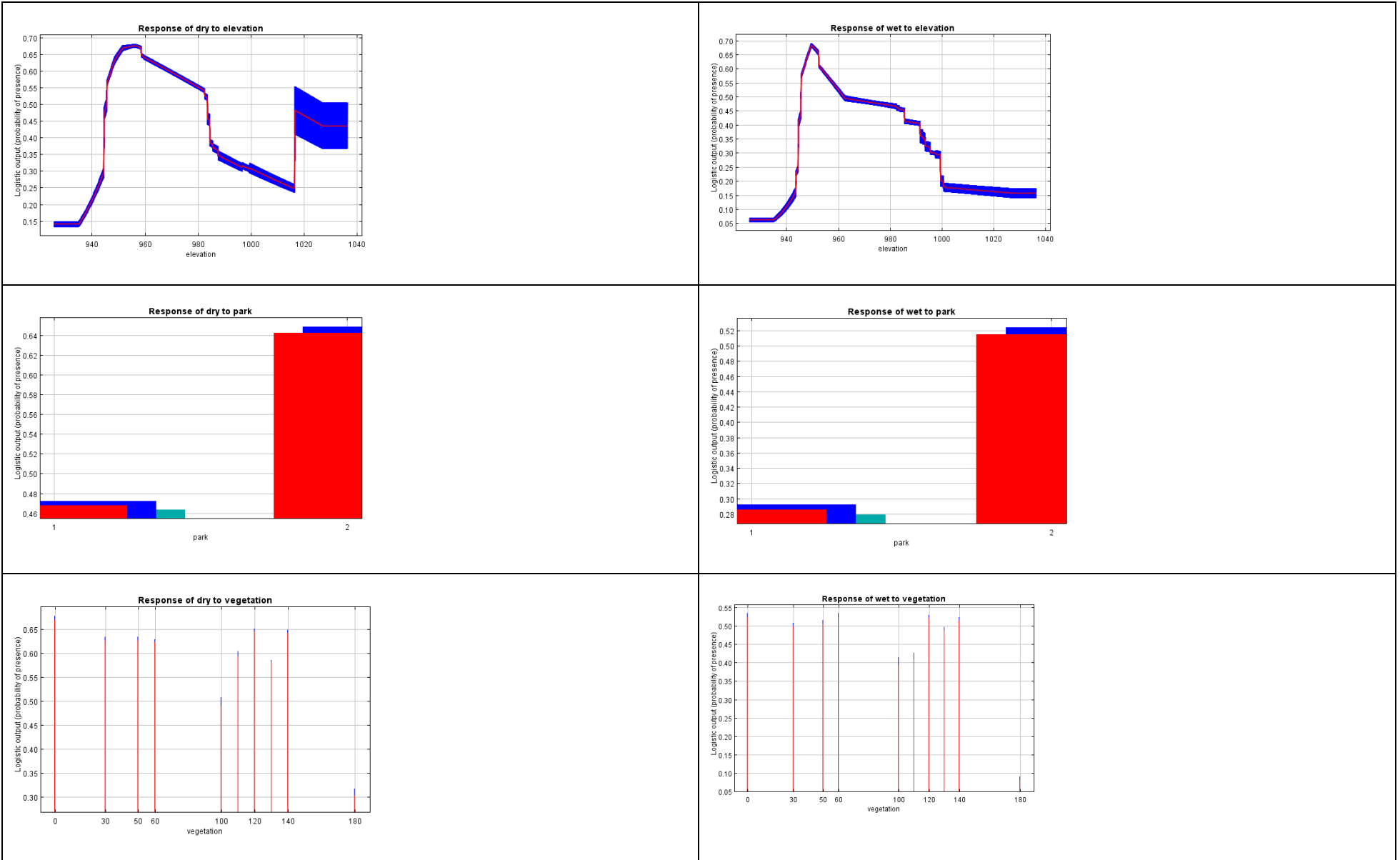
Figure D.14 Maxent results for all lion for model 4 without elevation.

Table D.6 Model 12 – All *Panthera leo* clipped to the vegetation layer for dry and wet season.

Model 12 – All <i>Panthera leo</i> clipped to veg equal dry season	Model 12 – All <i>Panthera leo</i> clipped to veg equal wet season
<p>Omission</p>  <p>Average Omission and Predicted Area for dry</p> <ul style="list-style-type: none"> Mean area Mean area +/- one stddv Mean omission on test data Mean omission +/- one stddv Predicted omission 	<p>Omission</p>  <p>Average Omission and Predicted Area for wet</p> <ul style="list-style-type: none"> Mean area Mean area +/- one stddv Mean omission on test data Mean omission +/- one stddv Predicted omission
<p>ROC AUC</p>  <p>Average Sensitivity vs. 1 - Specificity for dry</p> <ul style="list-style-type: none"> Mean (AUC = 0.806) Mean +/- one stddv Random Prediction 	<p>ROC AUC</p>  <p>Average Sensitivity vs. 1 - Specificity for wet</p> <ul style="list-style-type: none"> Mean (AUC = 0.792) Mean +/- one stddv Random Prediction







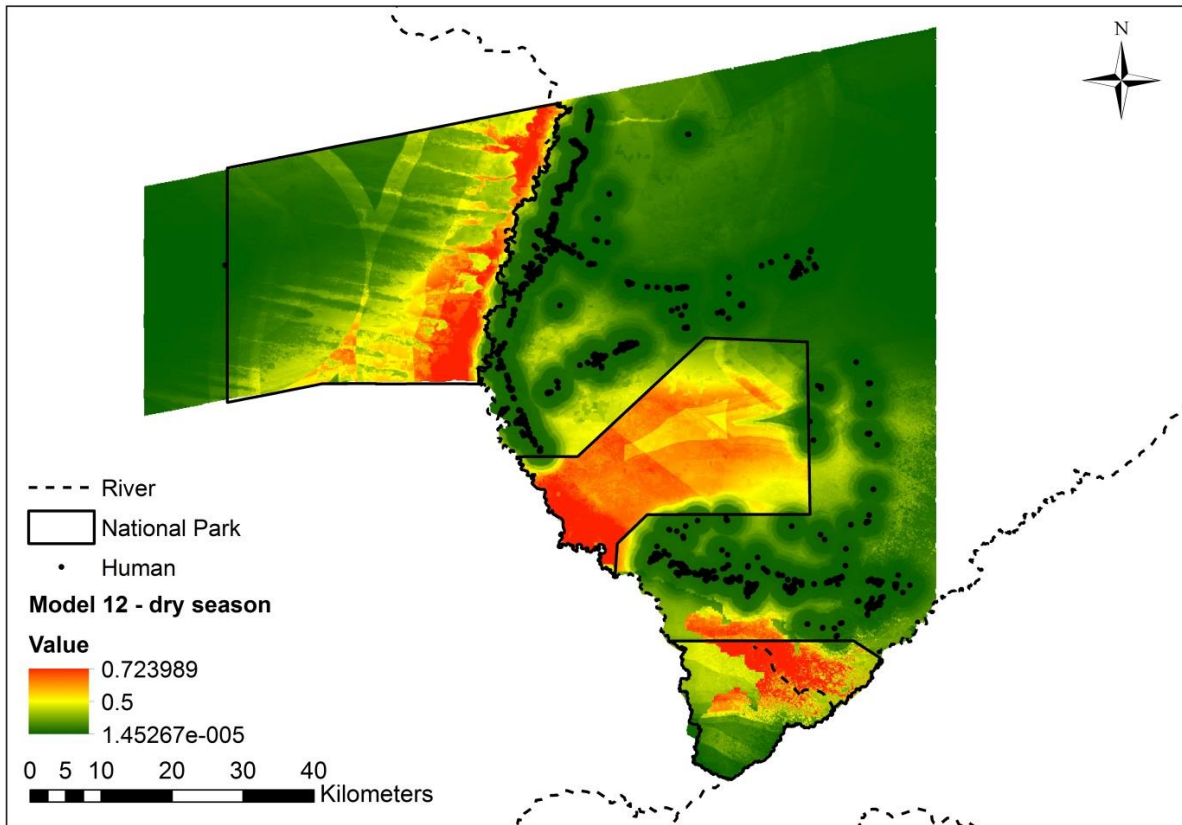


Figure D.15 Model 12 showing all lions data for dry season.

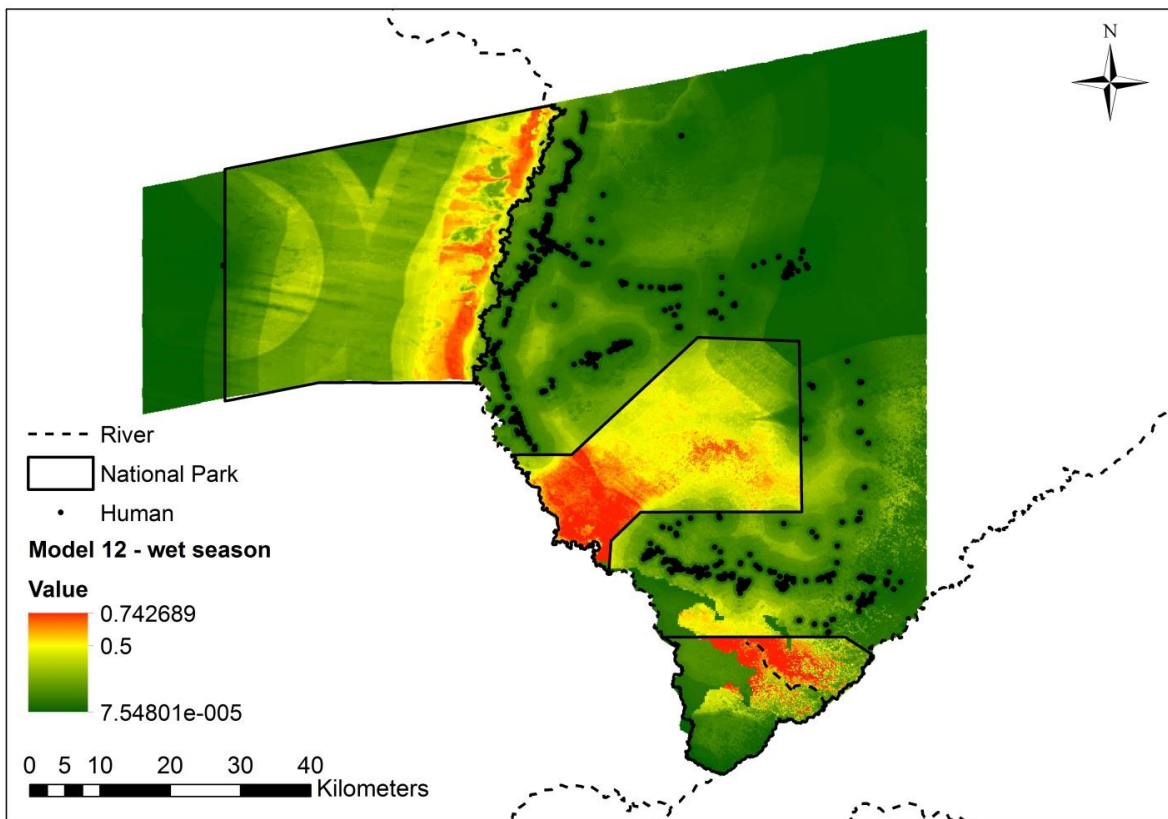


Figure D.16 Model 12 showing all lions data for wet season.

ADDENDUM



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Approval Notice New Application

14-May-2014
Kastern, Michelle M

Proposal #: DESC/Kastern/May2014/8

Title: Factors influencing Lion (Panthera leo) Spatial Selection in Caprivi, Namibia.

Dear Ms Michelle Kastern,

Your **New Application** received on **08-May-2014**, was reviewed
Please note the following information about your approved research proposal:

Proposal Approval Period: **13-May-2014 -12-May-2015**

Please take note of the general Investigator Responsibilities attached to this letter. You may commence with your research after complying fully with these guidelines.

Please remember to use your **proposal number (DESC/Kastern/May2014/8)** on any documents or correspondence with the REC concerning your research proposal.

Please note that the REC has the prerogative and authority to ask further questions, seek additional information, require further modifications, or monitor the conduct of your research and the consent process.

Also note that a progress report should be submitted to the Committee before the approval period has expired if a continuation is required. The Committee will then consider the continuation of the project for a further year (if necessary).

This committee abides by the ethical norms and principles for research, established by the Declaration of Helsinki and the Guidelines for Ethical Research: Principles Structures and Processes 2004 (Department of Health). Annually a number of projects may be selected randomly for an external audit.

National Health Research Ethics Committee (NHREC) registration number REC-050411-032.

We wish you the best as you conduct your research.

If you have any questions or need further help, please contact the REC office at 0218089183.

Included Documents:

Research proposal
DESC application

Sincerely,

Clarissa GRAHAM
REC Coordinator
Research Ethics Committee: Human Research (Humanities)

Investigator Responsibilities

Protection of Human Research Participants

Some of the general responsibilities investigators have when conducting research involving human participants are listed below:

1. Conducting the Research. You are responsible for making sure that the research is conducted according to the REC approved research protocol. You are also responsible for the actions of all your co-investigators and research staff involved with this research. You must also ensure that the research is conducted within the standards of your field of research.

2. Participant Enrollment. You may not recruit or enroll participants prior to the REC approval date or after the expiration date of REC approval. All recruitment materials for any form of media must be approved by the REC prior to their use. If you need to recruit more participants than was noted in your REC approval letter, you must submit an amendment requesting an increase in the number of participants.

3. Informed Consent. You are responsible for obtaining and documenting effective informed consent using **only** the REC-approved consent documents, and for ensuring that no human participants are involved in research prior to obtaining their informed consent. Please give all participants copies of the signed informed consent documents. Keep the originals in your secured research files for at least five (5) years.

4. Continuing Review. The REC must review and approve all REC-approved research proposals at intervals appropriate to the degree of risk but not less than once per year. There is **no grace period**. Prior to the date on which the REC approval of the research expires, **it is your responsibility to submit the continuing review report in a timely fashion to ensure a lapse in REC approval does not occur**. If REC approval of your research lapses, you must stop new participant enrollment, and contact the REC office immediately.

5. Amendments and Changes. If you wish to amend or change any aspect of your research (such as research design, interventions or procedures, number of participants, participant population, informed consent document, instruments, surveys or recruiting material), you must submit the amendment to the REC for review using the current Amendment Form. You **may not initiate** any amendments or changes to your research without first obtaining written REC review and approval. The **only exception** is when it is necessary to eliminate apparent immediate hazards to participants and the REC should be immediately informed of this necessity.

6. Adverse or Unanticipated Events. Any serious adverse events, participant complaints, and all unanticipated problems that involve risks to participants or others, as well as any research related injuries, occurring at this institution or at other performance sites must be reported to Malene Fouch within **five (5) days** of discovery of the incident. You must also report any instances of serious or continuing problems, or non-compliance with the REC's requirements for protecting human research participants. The only exception to this policy is that the death of a research participant must be reported in accordance with the Stellenbosch University Research Ethics Committee Standard Operating Procedures. All reportable events should be submitted to the REC using the Serious Adverse Event Report Form.

7. Research Record Keeping. You must keep the following research related records, at a minimum, in a secure location for a minimum of five years: the REC approved research proposal and all amendments; all informed consent documents; recruiting materials; continuing review reports; adverse or unanticipated events; and all correspondence from the REC

8. Provision of Counselling or emergency support. When a dedicated counsellor or psychologist provides support to a participant without prior REC review and approval, to the extent permitted by law, such activities will not be recognised as research nor the data used in support of research. Such cases should be indicated in the progress report or final report.

9. Final reports. When you have completed (no further participant enrollment, interactions, interventions or data analysis) or stopped work on your research, you must submit a Final Report to the REC.

10. On-Site Evaluations, Inspections, or Audits. If you are notified that your research will be reviewed or audited by the sponsor or any other external agency or any internal group, you must inform the REC immediately of the impending audit/evaluation.