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Power line risk to Cape (*Gyps coprotheres*) and White-backed (*G. africanus*) Vultures in southern Africa

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A dissertation submitted to the Faculty of Science,
University of Witwatersrand,
in fulfilment of the requirements for the degree of Master of Science
Johannesburg, South Africa

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Declaration

I declare that this dissertation is my own, unaided work. It is being submitted for the degree of Master of Science at the University of Witwatersrand, Johannesburg. It has not been submitted before any degree or examination at any other university.



Caroline G. Howes

31 May 2016

Supervisors:
Prof. Craig T. Symes
Dr. Lizanne Roxburgh

Abstract

This study examined the movements of white-backed (*Gyps africanus*) and Cape vultures (*G. coprotheres*) to assess their habitat preferences, measure seasonal changes in foraging behaviour, and examine where vultures are at risk of electrocution by and collision with power lines. White-backed and Cape vultures are two Old World vulture species found in southern Africa. They are listed as Critically Endangered and Endangered respectively, with massive population declines over the past three decades. These declines are due to poisoning, habitat loss, lack of food, use in traditional medicine, and electrical infrastructure mortality. Vultures provide key ecosystem services such as reducing disease transmission, cycling nutrients, and attracting tourists and therefore, a loss of vultures could cost the continent millions of US dollars.

Thirteen vultures (five white-backed and eight Cape vultures) were tracked using either DUCK-4A or BUBO-4A GPS-GSM trackers (Ecotone Telemetry, Sopot, Poland). Birds were tracked between April 2013 and October 2014. These data were used to examine the habitat suitability of both species using MaxEnt habitat suitability modelling. Key drivers of country-wide habitat suitability for white-backed vultures were mean temperature (30.9% contribution), precipitation seasonality (22.0% contribution), and biome (19.5% contribution), while key drivers for Cape vultures were distance to artificial feeding station (24.8% contribution), and precipitation seasonality (50.5% contribution). Anthropological variables (land use, cattle density, and population density) contributed very little to the models.

Using the same tracking data, seasonal changes in foraging movements were examined, particularly in relation to hypothetical food availability. Data were categorised by seasons (winter, spring, summer, and autumn) using weather data over the past decade. There was little evidence for seasonal movement in white-backed or Cape vultures which may be because food availability is not the limiting factor regardless of time of year.

Lastly, a model was constructed in MaxEnt using the Endangered Wildlife Trust's Wildlife and Energy Programme dataset of white-backed and Cape vulture electrocutions by and collisions with power lines. Voltage was a major contributor to risk in every model for both collision and electrocution. This is likely to be related to the type and height of the power line structures rather than actual voltage. Either land use or population density also contributed to all four models. Slope contributed to white-backed vulture models while

feeding station and elevation contributed to Cape vulture models. Each of these variables probably relates not only to the likelihood of vulture presence but also how vultures behave in the area (e.g. flying lower in natural or low population areas to forage more effectively therefore putting them at higher risk of collision).

This study suggests that management initiatives should include carefully placing vulture feeding stations to change foraging patterns and provide safe, uncontaminated carrion, and proactive retrofitting of high risk power lines to reduce the high unnatural mortality in white-backed and Cape vultures in South Africa. It is important to continue to improve these models using more tracking data from more populations of white-backed and Cape vultures, and more electrocution and collision data gathered from regular, randomly selected power line surveys.

Acknowledgements

I don’t think I quite understood what I was getting myself into when I moved to South Africa to begin my Masters of Science. Luckily through all of the work, I met friends and colleagues who could help me along the way. I, of course, would like to thank my two wonderful supervisors, Prof. Craig Symes and Dr. Lizanne Roxburgh, for their support and guidance throughout the process. I could not have done it without you. You have both taught me an immense amount about birds, writing, and just science in general.

I would also like to thank Constant Hoogstad and the Endangered Wildlife Trust for allowing me to use the vulture tracking data, South African Bird Atlas Project 2 for providing me with vulture occurrence data for model checking, and the South African Weather Service for providing me with the weather data for my seasonal analysis.

I have had so much support from those around me. My wonderful labmates, Elize Fourie and Stephanie Payne have kept me company and sane throughout this long process. I would not have made it without our numerous tea and coffee breaks, and rambling lab meetings. I am so lucky to have gotten to spend this time with you both.

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Preface

The purpose of this study was to examine how white-backed and Cape vultures move through their environment, and to assess how this may put them at risk of power line mortality. This thesis consists of five chapters, one introduction chapter (Chapter 1), three research chapters (Chapters 2, 3, and 4), and one conclusion chapter (Chapter 5). Chapter 1 gives an overview of white-backed and Cape vultures, as well as an introduction to vulture mortality due to power lines. Chapter 2 models the distributions of white-backed and Cape vultures using satellite-tracking data. Chapter 3 examines whether there are changes in movements seasonally in white-backed and Cape vultures using tracking data. Chapter 4 uses electrocution and collision data to examine which factors increase the risk of power lines on vultures and highlight the areas where vultures are at high risk of power line mortality in South Africa. Lastly, Chapter 5 is a conclusion chapter, examining how the research chapters connect and what it means for vulture conservation.

All chapters are written as standalone papers in a general journal format, so there is some repetition between the chapters.

Chapter 1: General Introduction

1.1: Background

Old world vultures are a diverse group of 16 species and nine genera of obligate scavenging birds (IUCN 2015). Vultures are the only true vertebrate obligate scavengers on the planet (Ruxton and Houston 2004, Dermody et al. 2011). Only large soaring birds can survive on carrion alone due to the stochastic and widespread nature of carrion distribution (Ruxton and Houston 2004). Flight allows vultures to cover vast areas in a relatively short period of time and soaring flight is highly economical, requiring little energy (Ruxton and Houston 2004). In addition to their soaring flight, vultures have also evolved a large body size, to better cope with long periods of little food, and a highly acidic stomach for bone digestion and to destroy the harmful bacteria, parasites, and other microorganisms found in carrion (Mundy et al. 1992, Ruxton and Houston 2004). To take advantage of carrion resources, vultures have lost traits needed to kill their own prey such as powerful talons, and wing shapes that allow for agility in the air (Ruxton and Houston 2004).

Gyps vultures, commonly known as griffons, are the largest group of Old World vultures and are found in Europe, Asia, and Africa (Mundy et al. 1992, IUCN 2015). All eight species have slightly downy heads, broad wings, and a ruff of feathers around their necks (Mundy et al. 1992, IUCN 2015). *Gyps* vultures rely on their keen eyesight to spot carrion while soaring (Martin et al. 2012). Of the eight *Gyps* species, one is Least Concern, one is Near Threatened, one is Endangered, and five are Critically Endangered (IUCN 2015). Threats include poisoning, electrocution and collision with power infrastructure (power lines, wind farms, etc.), habitat loss, lack of food, and declines in available food resources (Dean 2004, Verdoorn et al. 2004, Boshoff et al. 2011, Ogada et al. 2015).

Africa's vultures have experienced catastrophic declines over the past 30 years, particularly in East and West Africa (Ogada et al. 2015). The decline across the eight species of vultures found in Africa has been 62% over the past 30 years with seven of the species declining over 80% over the same period (Ogada et al. 2015). Poisoning was recorded as the number one threat to vultures followed by trade in traditional medicine (Ogada et al. 2015). Mortality due to electrical infrastructure was third, accounting for 9% of recorded vulture deaths across the continent (Ogada et al. 2015). White-backed (*Gyps africanus*) and Cape (*G.*

coprotheres) vultures are the two species of *Gyps* vulture regularly found in southern Africa and have followed the trends of vulture decline in Africa (IUCN 2015, Ogada et al. 2015).

1.1.2: Ecology of the white-backed vulture

The white-backed vulture is the smaller of the two southern African *Gyps* species (Figure 1.1, Table 1.1) (Mundy et al. 1992). They are a widespread species found throughout East and West Africa, as well as southern Africa (Mundy et al. 1992). In southern Africa, they are found in northern South Africa, Swaziland, eastern Namibia, Botswana, Zimbabwe, and parts of Mozambique (Mundy et al. 1992). White-backed vultures primarily forage in open wooded savannas, particularly those dominated by *Acacia species* (Mundy et al. 1992, Bamford et al. 2009, Pfeiffer et al. 2015). They avoid forested areas where carrion is difficult to locate, and they are more common at lower altitudes (Mundy et al. 1992, Simmons et al. 2007). White-backed vultures are gregarious feeders and can number up to 2000 birds at a large carcass such as an elephant (*Loxodonta africana*) (Mundy et al. 1992). In their preferred habitat, they usually outnumber all other vulture species at a carcass (Mundy et al. 1992).



Figure 1.2: A photo of an immature white-backed vulture at a carcass in the Kruger National Park near Skukuza camp. Photo by Melissa Whitecross.

Table 1.1: Comparison of the white-backed and Cape vultures in regards to size, range, and conservation status (Mundy et al. 1992).

	White-backed vulture	*Cape vulture*
Wingspan	2.2 m	2.5 m
Weight	4-7 kg	7-11 kg
Range	Southern, East, and West Africa	Southern Africa
IUCN status	Critically Endangered	Endangered

White-backed vultures nest in large stick nests in trees in loose colonies often along rivers (Mundy et al. 1992). They are a monogamous species and may occupy the same nest site for up to 15 years (Mundy et al. 1992). They lay one egg every one to two years and the parents care for and feed their fledged offspring for up to ten months (Mundy et al. 1992). Between 43% and 87% of eggs survive to the fledgling age of four months (Mundy et al. 1992). Mortality is high in young birds with around 15% mortality in second year birds in Mpumalanga province; this is most likely due to starvation (Mundy et al. 1992, Kendall and Virani 2012, Monadjem et al. 2012).

The total southern African population of white-backed vultures is unknown. In Kruger National Park, the largest population of white-backed vultures in southern Africa, a total of 900 pairs (or 2,000 individuals) were estimated from an aerial breeding survey (Murn et al. 2013). Populations have declined by 90% (or about 4.1% per year) over 30 years (Ogada et al. 2015). They are now listed as Critically Endangered by the International Union for Conservation of Nature (IUCN) (IUCN 2015).

1.1.2: Ecology of the Cape vulture

The Cape vulture is the larger of the two southern African *Gyps* species (Figure 1.2, Table 1.1) (Mundy et al. 1992). They are found in eastern South Africa (one small population in the Western Cape province), Lesotho, south-western Zimbabwe, and south-eastern Botswana with a remnant, non-breeding population in the Waterberg Plateau of Namibia (Mundy et al. 1992). They forage in a variety of habitats including savanna, grassland, fynbos, and alpine scrub (Mundy et al. 1992). Their altitudinal range is large, ranging from sea level to over 3000 metres (Mundy et al. 1992). Like all other *Gyps* species, the Cape vulture is a gregarious feeder and is often in the company of other vulture species at a carcass (Mundy et al. 1992). At a carcass, Cape vultures tend to be aggressive, staking out a portion of carrion (Mundy et al. 1992).

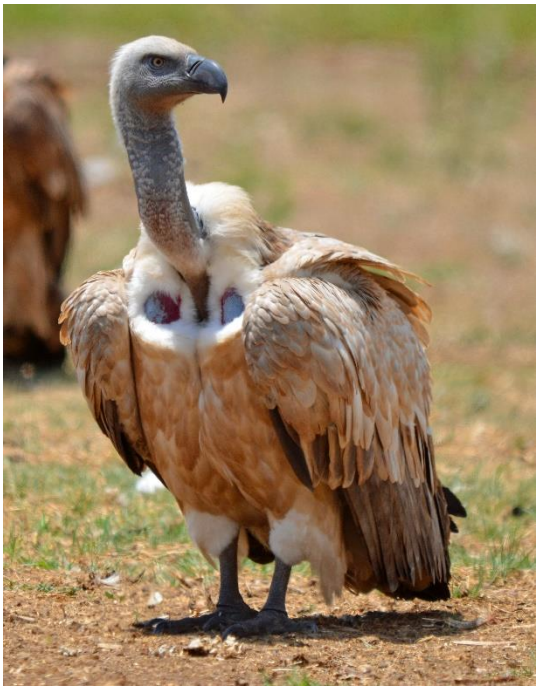


Figure 1.2: A photo of an adult Cape vulture at a vulture feeding station in North West province. Photo by Melissa Whitecross.

Unlike white-backed vultures, Cape vultures nest and roost colonially on large cliffs, and in river gorges (Mundy et al. 1992). Pairs of Cape vultures tend to be monogamous and will return to the same nest site year after year if breeding is successful (Mundy et al. 1992). They lay one egg every one to two years (generally every year), and care for the chick for over a year including a long post-fledging dependence period of up to a year (usually several months) (Mundy et al. 1992). Between 45% and 78% of eggs reach the fledgling stage (Mundy et al. 1992). However, the fledgling survival rate of Cape vultures can be very low (only 11% reach three years old) due to high competition for food and mortality due to human factors (Mundy et al. 1992, Piper et al. 1999).

The 2013 population of Cape vultures is believed to be around 4700 breeding pairs or 9400 mature individuals (IUCN 2015). Populations have decreased 92% (or 5.1% per year) over the past three decades, leading them to be listed as Endangered by the IUCN (IUCN 2015, Ogada et al. 2015). The causes of mortality for the species are similar to those of vultures worldwide (see above) (Ogada et al. 2015).

1.1.3: White-backed and Cape vulture movement

Both white-backed and Cape vulture have been tracked extensively in southern Africa over the past decade (Bamford et al. 2007, Simmons et al. 2007, Kendall et al. 2013, Phipps et al. 2013a, Phipps et al. 2013b, Spiegel et al. 2013, Pfeiffer et al. 2015). White-backed vultures have been tracked in South Africa (North West and Limpopo provinces), Namibia, and Kenya (Figure 1.3) (Kendall et al. 2013, Phipps et al. 2013a, Spiegel et al. 2013). There are currently no papers published with Minimum Convex Polygon (MCP) or kernels (methods that estimate home ranges) calculated for adult white-backed vultures. Immature white-backed vultures have been found to have a smaller MCP than immature Cape vultures (Table 1.2) (Phipps et al. 2013a). Phipps et al. 2013a found that the vultures spent only a small amount of time in protected areas, about 4.3% of their 99% kernels. In the Serengeti-Mara region in East Africa, white-backed vultures have been shown to spend the dry season following western white-bearded wildebeest (*Connochaetes taurinus*) herds, and in the wet season move elsewhere. This is thought to be because of the high rate of wildebeest mortality during the dry season providing a steady food source for the vultures (Kendall et al. 2013). There appear to be no tracking studies examining habitat use for white-backed vultures.

Table 1.2: The minimum convex polygon (MCP) values of adult and immature white-backed vultures[1] and Cape vultures[2] in four studies in southern Africa. Values represent mean ± standard deviations (where available).

Location	Adult MCP (km^2)	Immature MCP (km^2)	Study
North West, South Africa[1]	N/A	297,521 ± 189,581	Phipps *et al.* 2013
Waterberg Plateau, Namibia[2]	21,320	482,276	Bamford *et al.* 2007
North West, South Africa[2]	121,655 ± 90,845	492,300 ± 259,427	Phipps *et al.* 2013
Eastern Cape, South Africa[2]	breeding: 14,707 ± 2,155 non-breeding: 16,887 ± 366	N/A	Pfieffer *et al.* 2015

Cape vultures have been trapped and tracked in South Africa (Limpopo, Eastern Cape, and North West provinces) and Namibia (Bamford et al. 2007, Phipps et al. 2013b, Pfeiffer et al. 2015). All three of the currently published papers included MCP (Bamford et al. 2007, Phipps et al. 2013b, Pfeiffer et al. 2015). The adults in Namibia and the Eastern Cape province had much smaller ranges than those in North West province (Table 1.2) (Bamford et al. 2007, Phipps et al. 2013b, Pfeiffer et al. 2015). Immature birds had much larger home ranges than the adults (Bamford et al. 2007, Phipps et al. 2013b). Cape vultures

in the North West province had the largest known home range of any vulture species (Phipps et al. 2013b).



Figure 1.3: A map of southern Africa with key points, major cities and South African provinces labelled.

Seasonal differences in movement and habitat use have also been examined in Cape vultures (Bamford et al. 2007, Pfeiffer et al. 2015). Namibian Cape vultures spent significantly more time daily flying during the non-breeding season than during the breeding season, when birds flew greater distances on the days when they did leave the nest (Bamford et al. 2007). Home range did not change despite the greater distances flown; the birds rather intensified their search in the same area (Bamford et al. 2007). No significant differences in home range between the breeding and non-breeding seasons were found in the Eastern Cape province Cape vultures (similar to Namibia) (Pfeiffer et al. 2015). Birds there also disproportionately favoured subsistence farming and natural woody vegetation over all other land cover types (Pfeiffer et al., 2015).

1.1.4: Power lines and vultures in southern Africa

Power lines are often cited as one of the major mortality factors for vultures in southern Africa (Ledger 1981, van Rooyen and Ledger 1997, Boshoff et al. 2011, Martin et al. 2012, Phipps et al. 2013b). In South Africa, Eskom is the primary source of electricity producing around 95% of South Africa's power and 45% of power for Africa as a whole (van Rooyen and Ledger 1997). As of 1996, Eskom was responsible for 255,745 kilometres of power lines in South Africa (van Rooyen and Ledger 1997). Vulture electrocutions associated with power lines was first observed in 1972 in the North West province (Markus 1972). Now both electrocution and collision with lines are widely acknowledged throughout southern Africa, as well as Europe (Markus 1972, Sarrazin et al. 1994). Vultures are vulnerable to power line deaths in both collision and electrocution (Janns 2000, Rubolini et al. 2005). Vultures will perch and nest on power lines, especially in areas such as the Northern Cape province that are largely devoid of trees (Anderson and Hohne 2007). Although it is difficult to quantify the number of vulture deaths caused by power lines (as few as 2.6% of power line deaths may to be reported; Boshoff et al., 2011), white-backed and Cape vultures are particularly susceptible to power line deaths (Janns 2000, Jenkins et al. 2010, Shaw et al. 2010). In the similar Eurasian griffon vulture (*G. fulvus*), conflicts with power lines were the number one cause of death in a reintroduced population in France (Sarrazin et al. 1994). The Eastern Cape study that examined the power line deaths of vultures not only highlighted the high mortality rate but also how inaccurate the current bird strike database (the Central Incidence Register, or CIR, managed by Eskom and the Endangered Wildlife Trust in South Africa) may be (Boshoff et al. 2011). While the database estimated an average of 14 vulture deaths per year, the surveys indicated 80 birds, a 5.7 fold increase in mortality (Boshoff et al. 2011).

Collisions occur when a flying bird strikes a power line, usually the ground wire, and is either injured or killed by the impact (Janns 2000). Although vultures are less susceptible to this in comparison with electrocution, there are still many records of the birds being killed in this manner (Bevanger 1998, Jenkins et al. 2010, Shaw et al. 2010). In the Eastern Cape province, bird strike records indicated that 16% of vulture deaths on power lines were due to collision (Boshoff et al. 2011). This is particularly true when the birds are startled off a carcass into power lines, resulting in the death of more than one bird (Bevanger 1998). Vultures are susceptible to collisions due to their limited, forward facing vision (de Lucas et al. 2012, Martin et al. 2012). While foraging a *Gyps* vulture's vision is focused on the ground and the bird cannot see what is in front of it (Martin et al. 2012). Vultures also fall into a

group of birds known as the "thermal soarers", which means that they are heavy birds with a large wingspan (Janns 2000). This puts them at greater risk for collision because they have less control over their flight, particularly in windy conditions (Janns 2000)

Electrocution accounted for 84% of Cape vulture power line deaths in the Eastern Cape province according to the CIR, over five times more than collisions (Boshoff et al. 2011). Electrocution occurs when vultures span the gap between two conductors usually with their wings. Many factors affect whether or not the bird is electrocuted including weather, voltage, and other condition (Lehman et al. 2007) This may not only kill the vulture but often causes a disruption in electricity delivery, which makes workers more likely to record the bird mortality (Ledger 1981, van Rooyen and Ledger 1997). Large numbers of vultures will often perch on pylons where they move around and interact with each other, adding to the risk of electrocution (van Rooyen and Ledger 1997). Because of their extremely large wing span, vultures are often electrocuted when they take off from their perches. Based on the CIR, 26% of all bird electrocutions were Cape vultures and 6% were white-backed vultures (van Rooyen and Ledger 1997). Certain types of electricity pylons account for the majority of *Gyps* vulture deaths, largely due to the configuration of conductors, and if and where on the pylon perches are available (Ledger 1981, van Rooyen and Ledger 1997). If the distance between the conductors is narrow (less than the wingspan of an adult vulture), the birds are more likely to be electrocuted when taking off (van Rooyen and Ledger 1997). Perch location can affect how close the birds are to the conductors while roosting, taking off or landing (van Rooyen and Ledger 1997).

In South Africa, there has been a concerted effort by Eskom and EWT to reduce the risk of collision and electrocution for vultures and other large raptors (van Rooyen and Ledger 1997, Lehman et al. 2007). For collision risk, one commonly used tactic is to remove the ground wire because this appears to be the most deadly of the lines (Figure 1.2) (Bevanger 1998, Lehman et al. 2007, Jenkins et al. 2010). It's thinness and uppermost position on the power line configurations make the ground wire particularly risky, because of the birds' reduced ability to detect it and its location at a height where birds are most likely to be flying (Jenkins et al. 2010). Removal of the ground wire is fairly successful in reducing mortality (up to 80%) for many bird species (Jenkins et al. 2010). Marking the wire with shiny metal "flappers", bright spirals, or coloured "aviation balls" may make the line more visible to birds, allowing them to avoid colliding with it (Jenkins et al. 2010). These methods may result in a 42-82% reduction in bird mortality depending on the area and type of marker (Jenkins et al. 2010). To reduce electrocution risk, Eskom began by adding new perches on

pylons away from lines and conductors (van Rooyen and Ledger 1997). This was successful except in areas with high vulture density resulting in more vultures than available perches (van Rooyen and Ledger 1997). To alleviate this problem, Eskom fitted many of the conductors with PVC spirals to keep the vultures' flight feathers from touching live conductors. Spirals, spines, and other bird guards were attached onto favoured perches to discourage the birds from landing on pylons (van Rooyen and Ledger 1997). Eskom also stopped producing certain unsafe constructions such as kite structures (Figure 1.2) (van Rooyen and Ledger 1997). An additional option is the routing new power lines away from crucial vulture habitat (e.g. nesting colonies or artificial vulture feeding stations) (Jenkins et al. 2010).

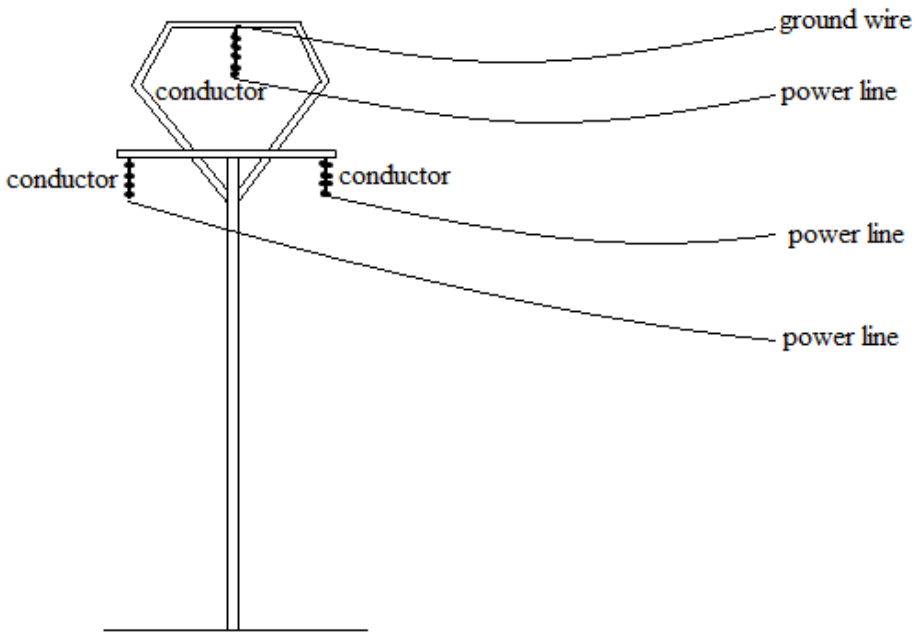


Figure 1.4: A diagram of a typical kite structure with a ground wire, three lines, and three conductors.

1.2: Rationale

The focus of this research was to better understand the movement patterns of white-backed and Cape vultures relative to the current power line networks. White-backed and Cape vultures (and all other African vulture species) have experienced catastrophic declines over the past three decades (Ogada et al. 2015). Declines in vulture populations affect human

health costs, and mammalian disease transmission (Markandya et al. 2008, Ogada et al. 2011, Ogada et al. 2012). These declines have focused researchers on better understanding the ecological importance of these birds, as well as finding ways to reduce human-caused mortality.

Both white-backed and Cape vultures are far-ranging species that cross international borders, using a large variety of private and public lands (Phipps et al. 2013a, Phipps et al. 2013b). There is currently little understanding of these species movements beyond home range, and some foraging patterns. I examined seasonal movements and habitat use for both white-backed and Cape vultures to inform conservation personnel about when feeding stations are the most effective, and where land conservation can best support these species. Power lines were found to be responsible for 9% of human-caused mortality of vultures in Africa over the past three decades (Ogada et al. 2015). In addition, power lines in the Eastern Cape province appear to be killing Cape vultures at a rate above the reproductive rate of the species (Boshoff et al. 2011). This makes power lines a top priority for vulture research. There have been no predictive studies of vulture mortality on power lines. By understanding what landscape factors make a power line dangerous to vultures, not only can current lines be prioritised for vulture-safe retrofitting based on risk, but planned new lines can be assessed before they are built (Benson 1982, Lehman et al. 2007)

1.3: Aims and Objectives

The aim of this study was to use tracking data to evaluate seasonal movements and habitat suitability for white-backed and Cape vultures, and to integrate this knowledge with an understanding of factors affecting power line mortality of both species.

The first objective of this study (Chapter 2) was to create a habitat suitability map of South Africa for white-backed and Cape vultures and to understand what landscape factors affect this suitability.

The second objective of this study (Chapter 3) was to examine whether white-backed and Cape vultures changed their foraging movements seasonally, particularly in relation to food availability and vulture feeding stations.

The third objective of this study (Chapter 4) was to create a map of power line mortality risk for white-backed and Cape vultures for South Africa, and to understand what landscape factors affect this risk.

1.4: References

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Chapter 2: Modelling habitat suitability of two threatened vulture species using tracking data

2.1: Abstract

White-backed and Cape vultures are threatened and declining rapidly across their ranges. Poisoning, electrocution and collision with power lines, lack of food, and habitat loss are all drivers of their decline. Predicting habitat suitability may help prioritise areas for conservation efforts. Using tracking data from both species and MaxEnt distribution modelling, habitat suitability models were created for both white-backed and Cape vultures. Four models were created for each species, two with climate variables and two without climate variables. Two models were for the whole of South Africa while two were for the northern provinces (Limpopo, Mpumalanga, North West, Free State, and Gauteng) of South Africa where the majority of the birds were tracked. Predicted ranges (for each species) remained similar regardless of the model. The most important variables for white-backed vultures using the country-wide models were mean temperature (30.9% contribution), precipitation seasonality (22.0% contribution), and biome (19.5% contribution). The most important variables for Cape vultures for the country-wide models were distance to feeding station (24.8% contribution), and precipitation seasonality (50.5% contribution). The models also showed that anthropological development variables, such as population density, land use, and cattle density, had little impact on the model. These models will allow conservationists to prioritise conservation efforts such as building feeding stations, educating people about poisoning and traditional medicine, and retrofitting power lines to be vulture-safe.

2.2: Introduction

During the past decade methods for tracking mammals and birds have improved dramatically, allowing researchers to follow daily and long term movement patterns of many terrestrial and aquatic species (Seegar et al. 1996, Bridge et al. 2011). Tracking data are used to study home range, migration routes, and foraging patterns (Cadahia et al. 2005, Guilford et al. 2006, Bridge et al. 2011, Gschweng et al. 2012). There are now many large tracking point datasets

of many different species across the globe (Cadahia et al. 2005, Guilford et al. 2006, Bridge et al. 2011, Gschweng et al. 2012). Recently, there has been a focus on using the data to assess habitat suitability, and species' ranges (Elith et al. 2011).

Generally a model uses environmental variables, and species presence and absence data have been used to create a predictive models (Elith et al. 2011). Because both presence and absence data were required, tracking data were considered inappropriate for this purpose (Elith et al. 2011). New modelling techniques, such as MaxEnt and others, require only presence data information, making tracking data more useful in creating these models (Elith et al. 2011). These habitat suitability modelling programs effectively use presence points, like tracking points, to define the limits of different species' variables. These limits are then extrapolated across larger areas of interest. Tracking data are also superior to ground-based sampling as they are unbiased by inaccessibility and varying sampling intensity (Gschweng et al. 2012), however, it is necessary to account for spatial autocorrelation and for biases from using a small number of animals (Endren et al. 2010). Tracking data, combined with new statistical methods for creating habitat suitability models and novel sources of environmental variables, are powerful tools for identification of appropriate habitat for many species (Endren et al. 2010, Gschweng et al. 2012).

Vultures are declining worldwide and the 16 Old World vulture species in particular are decreasing at an alarming rate (IUCN 2015). Eleven out of 16 species of Old World vulture are listed as Endangered or Critically Endangered by the International Union of Conservation of Nature (IUCN). The threats to vultures are varied and include accidental and targeted poisoning, harm caused by electrical infrastructure, lack of food, and habitat loss and disturbance (Verdoorn et al. 2004, Boshoff et al. 2011, IUCN 2015). The decline in vulture populations in Asia and Africa are particularly severe (Green et al. 2004, IUCN 2015, Ogada et al. 2015). Their decline has been linked to an increased likelihood of disease transmission between mammals, a higher human healthcare cost, and an increase in certain mammals such as feral dogs (*Canis lupus familiaris*) and rats (*Rattus* sp.) (Markandya et al. 2008, Ogada et al. 2012).

White-backed (*Gyps africanus*) and Cape (*G. coprotheres*) vultures are two African vulture species that are declining (Ogada et al. 2015). The white-backed vulture is a tree-nesting species found throughout sub-Saharan Africa and listed as Critically Endangered (Mundy et al. 1992, IUCN 2015). It is believed that they have decreased by 90% over three decades or 4.1% per annum (Ogada et al. 2015). The Cape vulture is a large, cliff-nesting southern African endemic species, currently listed as Endangered (Mundy et al. 1992, IUCN

2015). Recent evidence has indicated that populations have shrunk at a startling rate of 92% over three decades or 5.1% per annum (Ogada et al. 2015). Both species are in urgent need of protection in Africa especially from poisoning which has often been linked to their decline (Ogada et al. 2015).

Cape vultures are largely concentrated in the Drakensberg Mountains around Lesotho and into the Eastern Cape province, in harsh climates where snowfall is annual and temperatures are often below 0ºC, and in the north east of South Africa into southern Botswana and southern Zimbabwe where temperatures rarely fall below freezing (Mundy et al. 1992). There is also a remnant population in the Western Cape province, east of Cape Agulhas (Mundy et al. 1992). They have been reported as vagrants throughout southern Africa (Mundy et al. 1992). They are often found near nesting or roosting cliffs but in a variety of savanna and grassland habitats (Mundy et al. 1992). They appear to have adapted well to foraging in farmlands in many areas (Mundy et al. 1992, Pfeiffer et al. 2015).

White-backed vultures are found throughout southern Africa are the region's most abundant vulture species (Mundy et al. 1992). In South Africa, they are found in north-eastern KwaZulu-Natal (Zululand) province and the northern South African provinces (Limpopo, Northwest, Mpumalanga, and Northern Cape) from the border with Mozambique in the east to the Kgalagadi National Park in the west (Mundy et al. 1992). They occur in savannas, particularly those dominated by *Acacia* species, where they often nest in tall *Acacia* trees (Mundy et al. 1992). They prefer foraging in more open savannas (rather than those with a closed canopy) at an altitude below 1500 metres, and generally avoid human settlement (Mundy et al. 1992, Simmons et al. 2007).

South Africa is experiencing rapid human population growth, about 1.3% per year, with the associated expansion of infrastructure such as power lines and roads, and land transformation (Perkins et al. 2005, StatsSA 2015). This growth potentially threatens vultures, in particular the expansion of electrical infrastructure which Ogada et al. (2015) suggest was responsible for 9% of vulture deaths across Africa. By understanding where white-backed and Cape vultures occur or are likely to occur, geographically-focused conservation plans can be drafted to protect these species.

This study attempted to create habitat suitability maps (for the current conditions) for white-backed and Cape vultures in South Africa using satellite tracking data. It aimed to understand and define the variables that drive vulture distribution in South Africa. This understanding can lead to direct, responsible infrastructure expansion and anti-poisoning education efforts. The model was also checked by using the extensive datasets of the

Southern African Bird Atlas Project 2 to assess whether it accurately predicts the presence and absence of vultures in South Africa.

2.3: Methods

2.3.1: Satellite tracking

GSM-GPS (Global Systems for Mobile communications and Global Positioning System) tracking devices, either DUCK-4A or BUBO-4A (Ecotone Telemetry, Sopot, Poland; www.ecotone-telemetry.com), were fitted on five white-backed (three female, and two male) and eight Cape (two female, five male, and one unknown) by the Endangered Wildlife Trust (EWT) under a ToPs (Threaten or Protected Species) permit for the Limpopo Vulture Project (Table 2.1). All the birds were adult except for one sub-adult white-backed vulture. Birds were either trapped at Moholoholo Rehabilitation Centre (S24.5134º, E30.9048º) or Mockford Farm (S24.0628º, E29.2992º) feeding stations in Limpopo province, South Africa (Figure 2.1). Birds were caught in walk-in traps. Each individual was patagial tagged (a plastic cattle ear tag with a number attached to both wings) and ringed, and blood was taken for sexing (Hewitt and Austin-Smith 1966, Kendall and Virani 2012). Tracking points were collected hourly from 5:00 until 17:00 daily from April 2013 to October 2014.

2.3.2: Data filtering

To maximise data quality from the original tracking dataset, several criteria were applied. First, any point that was less than one kilometre from the previous tracking point was excluded from the analysis (Kassara et al. 2014). This reduces the chances of spatial autocorrelation (Endren et al. 2010, Kassara et al. 2014). This reduced the dataset to 6,595 points from 19,391 points for white-backed vulture and to 8,840 points from 26,097 points for Cape vulture. Next, all data outside of South Africa were excluded which reduced the datasets to 6,328 points for white-backed vulture and 8,162 points for Cape vulture.

Table 2.1: Vulture tracking data including the age and sex of each individual and the length of tracking period. Tracking start dates were all in 2013 and tracking end dates were all in 2014.

ID	Species	Age	Sex	Number of Points	Tracking Start Date	Tracking End Date
VULT05	White-backed vulture	Adult	Male	4,662	11 April	19 October
VULT09	White-backed vulture	Adult	Male	3,406	11 April	9 March
VULT07	White-backed vulture	Adult	Female	6,065	10 April	14 October
VULT16	White-backed vulture	Adult	Female	1,753	21 November	28 May
VULT10	White-backed vulture	Sub-adult	Female	3,505	11 April	9 September
VULT01	Cape vulture	Adult	Male	1,802	21 November	27 May
VULT23	Cape vulture	Adult	Male	4,237	12 April	19 October
VULT24	Cape vulture	Adult	Male	5,522	12 April	30 August
VULT25	Cape vulture	Adult	Male	5,681	12 April	19 October
VULT21	Cape vulture	Unknown	Male	1,482	12 August	16 January
VULT15	Cape vulture	Adult	Female	817	22 November	8 August
VULT17	Cape vulture	Adult	Female	1,934	22 November	18 June
VULT22	Cape vulture	Unknown	Unknown	4,622	8 August	19 October

To avoid unequal contributions by each bird due to different numbers of tracking points, a random set was selected from each dataset using the XLStat (Addinsoft SARL, 2015, vers. 2015.1) random data selection function. The quantity of points was determined by the smallest number of tracking points for an individual bird. Each bird contributed 350 points to the model. Three Cape vultures produced fewer than 350 points (295, 210 and 283 points). This resulted in a total of 1,750 points for the white-backed vulture and 2,887 points for the Cape vultures (Figure 2.2).

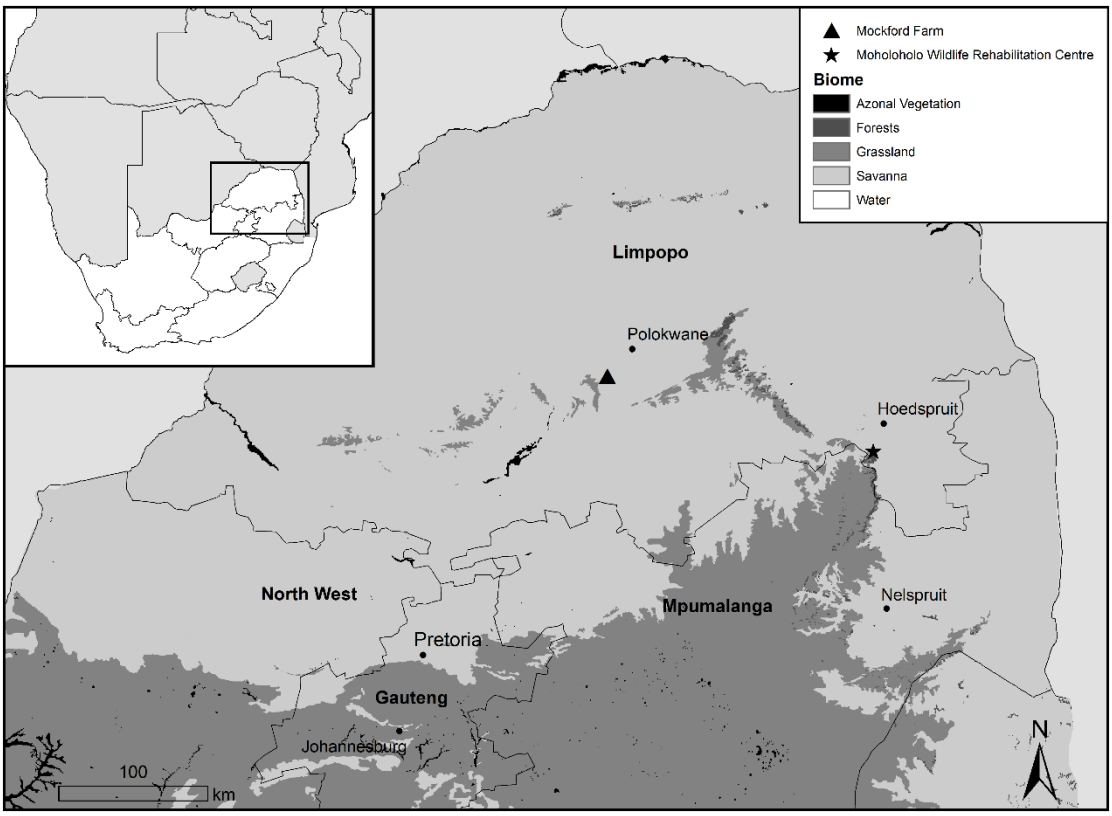


Figure 2.1: Map of north-east South Africa with biomes and capture point locations illustrated.

For the provincial models, the five provinces with the largest number of tracking points were included (Limpopo, Mpumalanga, Gauteng, North West and Free State) (Figure 2.2). The dataset began with the points more than one kilometre from the previous tracking point. When the datasets were reduced to only points contained in these provinces, white-backed vulture had 6,137 points and Cape vulture had 7,906 points. When points were randomly selected (as above) to account for different number of points from each birds, white-backed had 998 points and Cape had 1,747 points. Each individual of both species contributed 210 points to the model. One white-backed vulture produced fewer than 210 points (158) and a Cape vulture contributed fewer than 210 points to the model (67).

2.3.3: Climate and no-climate models

Four models were created for each species, two for the five provinces and two for the entirety of South Africa. The province model was created to assess whether the models were stronger

in the areas where the majority of the tracking points were located. To test the effect of climate on the ranges of the vultures, two models included climatic variables (e.g. mean temperature, annual rainfall, and all other environmental variables) and two excluded them.

2.3.4: Environmental variables

The following variables were used to create all the models. All rasters datasets had a resolution of 400m.

2.3.4.1: Topography

Two topographic variables were used: elevation and slope. Cape vultures are often observed in mountainous areas (where they breed and roost) whereas white-backed vultures are less likely to be (Mundy et al. 1992). This is likely to reflect in their use of different elevations and slopes. Elevation was a 90m DEM model from BioClim and slope was derived in ArcGIS 10.2 (ESRI Inc., 2015, vers. 10.2.0.3348) from the elevation (Hijmans et al. 2005).

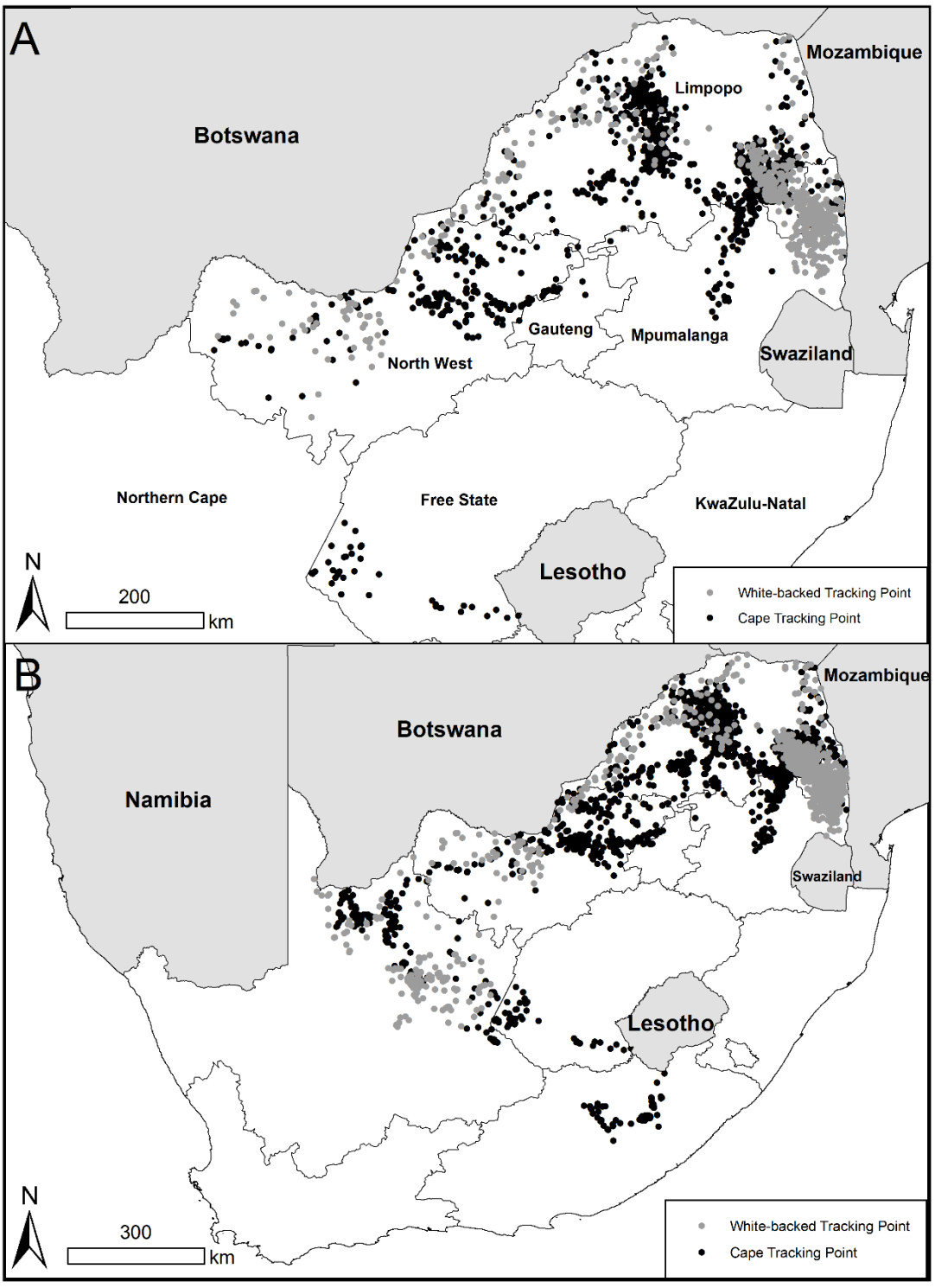


Figure 2.2: Map of A) selected provinces and B) South Africa with the samples of white-backed and Cape vulture tracking points.

2.3.4.2: Distance to resources

Distance to, i) fresh water, ii) vulture feeding stations, and iii) protected areas were used. Vultures use water for bathing and drinking. In South Africa, this could be a limiting resource. Feeding stations, where carcasses are provided to vultures by people, food is highly variable. At some feeding stations food is provided daily, at others only sporadically. In some areas these feeding stations are a major source of vulture food in South Africa, and birds are likely to stay near them. Protected areas provide key nesting areas with little human disturbance. Distance to water was calculated using the South African National Biodiversity Institute (SANBI) rivers layer and the South African vegetation map which plots lakes, dams, and other large water bodies (SANBI 2009, 2011). From this dataset, a Euclidean distance raster was created. Feeding station GPS points were mapped from the EWT dataset and a Euclidean distance raster was created. The SANBI protected area layer was used to create a Euclidean distance raster. Both formal and informal protected areas were included (SANBI 2010).

2.3.4.3: Cattle density

Both species utilise domestic livestock as a food source (Benson 2004). Cattle make up the largest livestock biomass in South Africa (DAFF 2013). There were 13.9 million head of cattle in South Africa in 2012 (DAFF 2013). The dataset was obtained from the Food and Agriculture Organization's (FAO) Animal Production and Health department (FAO 2005). The cattle density layer is a model using various environmental variables and livestock counts.

2.3.4.4: Population density

Human population is likely to be a disturbance to both vulture species. Population data were obtained from the Council for Scientific and Industrial Research (CSIR) Geospatial Analysis Platform (Naude et al. 2007). Population counts for individual mesozones were converted into a population density raster.

2.3.4.5: Land use

Land use is also likely to be related to disturbance for vultures (similar to population density). Land use data were obtained from the SANBI Land Cover map from 2009 (SANBI 2009). It includes seven categories: i) natural, ii) cultivated, iii) urban, iv) degraded, v) water, vi) plantation, and vii) mines. These categories were defined using provincial governments on land use data, and information from the Agricultural Research Council, Eskom, and the Department of Water Affairs and Forestry.

2.3.4.6: Biome

Vultures are more successful when foraging in open habitats (Mundy et al. 1992). Biome data suggest how open a habitat is, with grassland, Nama-karoo, succulent karoo, desert, and fynbos being nearly devoid of trees while forest, Indian Ocean coastal belt, and Albany thicket being mostly covered in trees. Savanna and azonal vegetation areas are variable in their tree cover. Biome data were obtained from the SANBI vegetation map and included eleven categories: i) savanna, ii) grassland, iii) Albany thicket, iv) azonal vegetation, v) desert, vi) forest, vii) fynbos, viii) Indian Ocean coastal belt, ix) Nama-karoo, x) succulent karoo, and xi) water (Mucina and Rutherford 2010).

2.3.4.7: Climate

Climate variables were used in two models for each species. Temperature and rainfall often affect the distribution of organisms and the type of biome found in an area. These variables can affect resource availability for species. Species can also be limited by temperature and water due to their physiology. Climate data were obtained from BioClim (Hijmans et al. 2005). A total of eight variables were used: i) annual precipitation, ii) minimum monthly precipitation, iii) maximum monthly precipitation, iv) seasonality of precipitation, v) mean temperature, vi) minimum temperature, vii) maximum temperature, and viii) seasonality of temperature.

2.3.5: Species distribution modelling

MaxEnt (2015, vers. 3.3.3k) was used to create habitat models with presence-only data on variable scales (Phillips and Dudik 2008, Elith et al. 2011). MaxEnt is highly compatible for use with tracking data (Endren et al. 2010, Elith et al. 2011). It allows presence-only data, is robust to overfitting in the case of correlated environmental variables, and can perform well with even small numbers of points (Phillips and Dudik 2008, Elith et al. 2011). MaxEnt uses a maximum likelihood approach. It maximises the entropy between two probability densities, the presence-only data and the landscape data. It then plots likelihood value responses for each variable in the model. Categorical variables (e.g. biome or land use) are given likelihood values for each category. For these models, the standard settings of MaxEnt were used. For the climate models, 17 variables were used and nine for the no-climate models. Values above 0.5 were considered suitable habitat and those above 0.75 very suitable habitat (Liminana et al. 2012, Liminana et al. 2014).

2.3.6: Testing the models

To test the models, Southern African Bird Atlas Project 2 (SABAP2) data were used (SABAP2 2015). SABAP2 is a citizen science project within southern Africa that involves surveying bird diversity in pentads (approximately 9 kilometre by 9 kilometre squares) (Harebottle et al. 2007). More than 130,000 pentad survey cards have been submitted in the eight years (July 2007 to October 2015) of the project. Data for white-backed and Cape vultures were extracted on October 10th, 2015. Pentads were either categorised as each species present (any full protocol, ad hoc protocol, or incidental record) or absent (which included pentads that had no data) (SABAP2 2015). For the province area (covering 455,135 km^2), there were 588 pentads (or 10.3% of the total area) with white-backed vultures present and 753 pentads (or 13.4% of the total area) with Cape vultures present (Figure 2.3). For South Africa (with a total area of 1,220,341 km^2) there were 1,124 pentads (or 7.5% of the total area) with white-backed vultures present and 1,068 pentads (or 7.1% of the total area) with Cape vultures present (Figure 2.4). An equal number of pentads without vultures was chosen randomly for all groups by assigning individual numbers to pentads and using R (The R Foundation for Statistical Computing Platform, 2015, vers. 3.2.2) to randomly select the correct number of pentads. The maximum and mean values of the MaxEnt models were

calculated for each pentad using Geospatial Modelling Environment (Spatial Ecology LLC, 2014, vers. 0.7.4.0) as the pentads were much larger than the resolution of the MaxEnt model (Beyer 2012). The maximum values were compared between pentads with each species present or absent for all models. The maximum was used as it was assumed that even a small amount of suitable environment could have a vulture present regardless of the surrounding habitat. All data are presented as a mean with ± standard deviation.

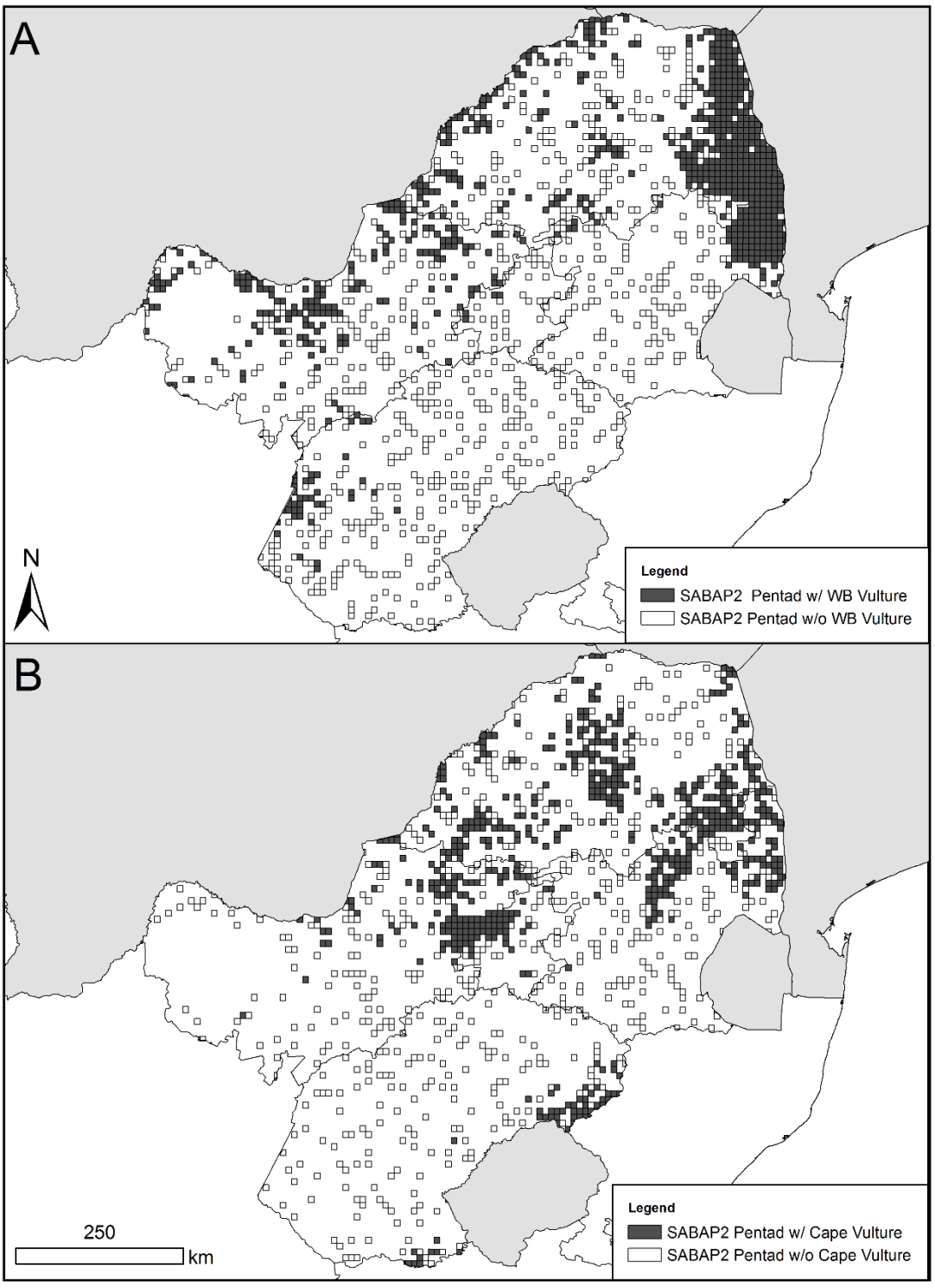


Figure 2.3: SABAP2 pentads within Limpopo, Mpumalanga, North-west, Free State and Gauteng with and without A) white-backed vultures and B) Cape vultures.

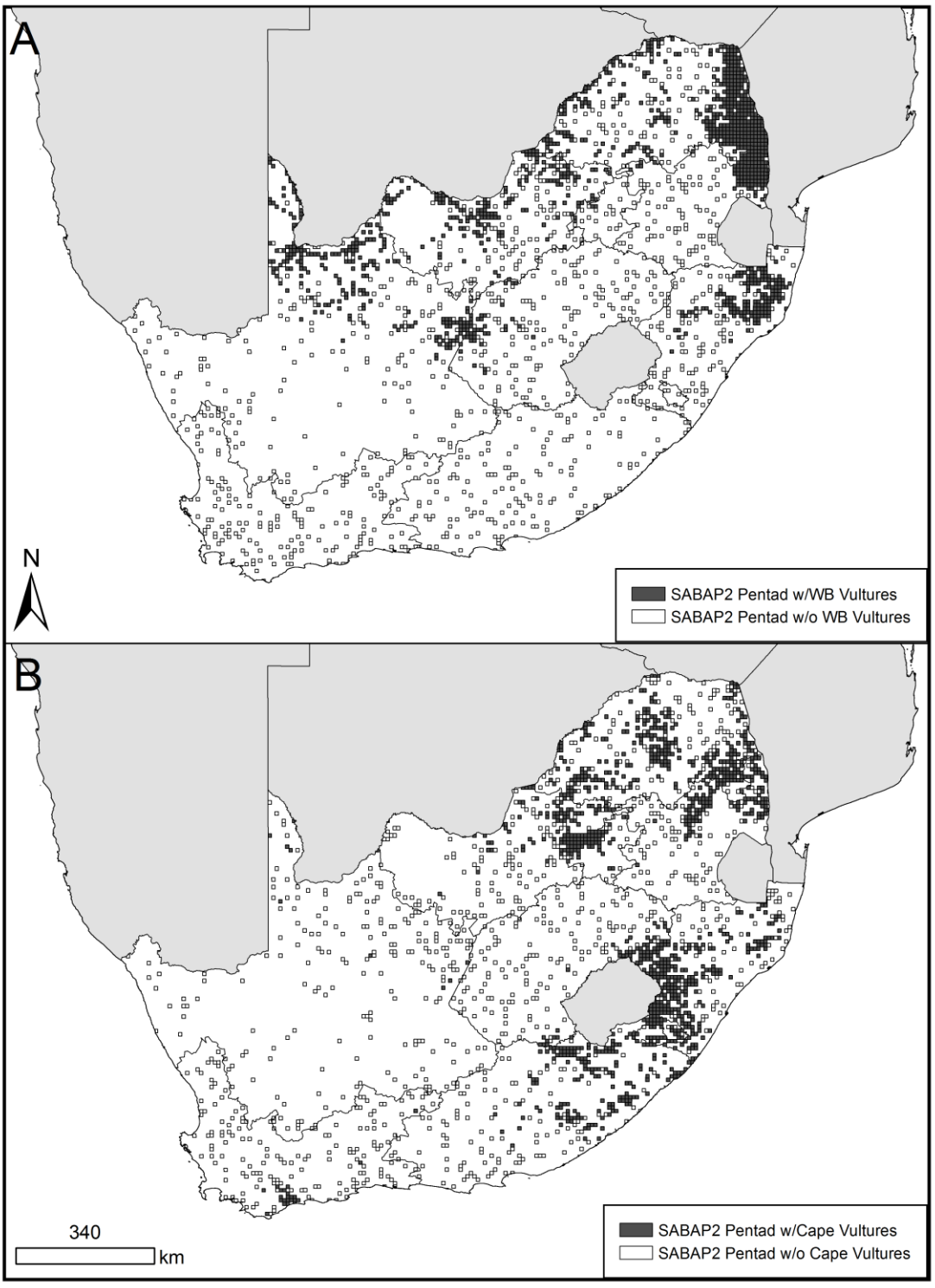


Figure 2.4: SABAP2 pentads with and without A) white-backed vultures and B) Cape vultures in South Africa.

2.4: Results

2.4.1: Province models

Four models were produced for the five provinces, two for white-backed vultures and two for Cape vultures (Figure 2.5). The white-backed vulture model with climate had an area under the curve (AUC) of 0.93, indicating the model had high discriminatory power. The likelihood of occurrence values ranged from 0.00 to 0.81. The total area of suitable habitat (values above 0.5) was 11,222 km^2 (2.5% of the total area of the provinces). Habitat was largely restricted to the far north of Limpopo and North West provinces (very arid areas) and Kruger National Park in the east. Mean temperature, minimum temperature, and distance to protected area each contributed over 10% to the model (Table 2.2).

The white-backed vulture model without climate data had an AUC of 0.91, meaning it had less discriminatory power than the model with climate data. The likelihood of occurrence values ranged from 0.00 to 0.88. The total area of suitable habitat was 15,680 km^2 (3.4% of the total area of the provinces). Suitable habitat was more widely spread across Limpopo province than in the previous model. Elevation, distance to protected area, and biome each contributed over 10% to the model. Savanna was the most preferred biome followed by grassland according the likelihood values. All other biomes were equally preferred.

The Cape vulture model with climate data had an AUC of 0.87. The likelihood of occurrence values ranged from 0.00 to 0.85. The total area of suitable habitat was 23,580 km^2 (5.2% of the total area of the provinces). Suitable habitat covered a large portion of Limpopo province and portions of North West province. Only a small portion of Kruger National Park was included. Distance to feeding station, temperature seasonality, and minimum temperature each contributed over 10% to the model.

The Cape vulture model without climate data had an AUC of 0.83. This was the lowest value of the four models. The total area of suitable habitat was 35,760 km^2 (7.9% of the total area of the provinces). The likelihood of occurrence values ranged from 0.00 to 0.89. Suitable habitat covered most of Limpopo province and parts of North West province. Distance to feeding station, and distance to protected area each contributed more than 10%.

Table 2.2: Percent contribution of individual variables to four provincial MaxEnt models. Values in bold contributed over 10% to the model. The signs next to the percent indicate how the likelihood response lines for each continuous variable were shaped. "-" indicates negative. "+" indicates positive. "-/+" indicates an initial decrease followed by an increase. "+/-" indicates an initial increase followed by a decrease. "n" indicates no clear pattern.

Variable	White-backed w/Climate		White-backed w/o Climate		Cape w/Climate		Cape w/o Climate	
Elevation	3.3	-	**50.3**	-	0.6	+	4.1	+/-
Slope	1.7	-	2.2	-	0.3	+	1.7	+
Distance to Water	0.3	n	0.3	n	0.3	n	0.8	n
Distance to Feeding station	1.7	-	4.3	-	**31.0**	-	**66.1**	-
Distance to Protected Area	**17.6**	-	**25.2**	-	0.8	-	**15.2**	-
Cattle Density	0.4	-	2.1	-	1.3	n	3.3	-/+
Population Density	1.6	-	3.0	-	1.4	-	2.0	-
Land Use	0.9		1.8		0.9		2.0	
Biome	8.7		**10.8**		0.8		4.7	
Mean Temperature	**39.0**	+/-	-		0.6	+	-	
Maximum Temperature	0.4	-	-		1.4	-	-	
Minimum Temperature	**18.2**	+	-		**16.8**	+/-	-	
Temperature Seasonality	3.2	n	-		**25.5**	-	-	
Annual Precipitation	1.3	-	-		5.4	-	-	
Maximum Precipitation	0.8	+/-	-		3.0	-	-	
Minimum Precipitation	0.3	+/-	-		0.9	-	-	
Precipitation Seasonality	0.6	+	-		9.1	n	-	

2.4.2: Testing the province models

Pentads with white-backed vultures present had significantly higher maximum habitat suitability (HSI) values from the model with climate variables than pentads without (Mann-Whitney U = 491,232, $n_p = 588$, $n_a = 589$, $p < 0.001$) (Figure 2.6). The mean maximum HSI values for pentads with white-backed vultures present was 0.34 ± 0.23 and for pentads where birds were absent was 0.07 ± 0.12. Pentads with white-backed vultures present also had significantly higher maximum HSI values in the model without climate variables (Mann-Whitney U = 502,444, $n_p = 588$, $n_a = 589$, $p < 0.001$). The mean maximum HSI values for pentads with white-backed vultures was 0.41 ± 0.24 and for pentads without was 0.10 ± 0.13. More pentads with white-backed vultures present had suitable habitat within them with the no-climate model than with the climate model (Table 2.3).

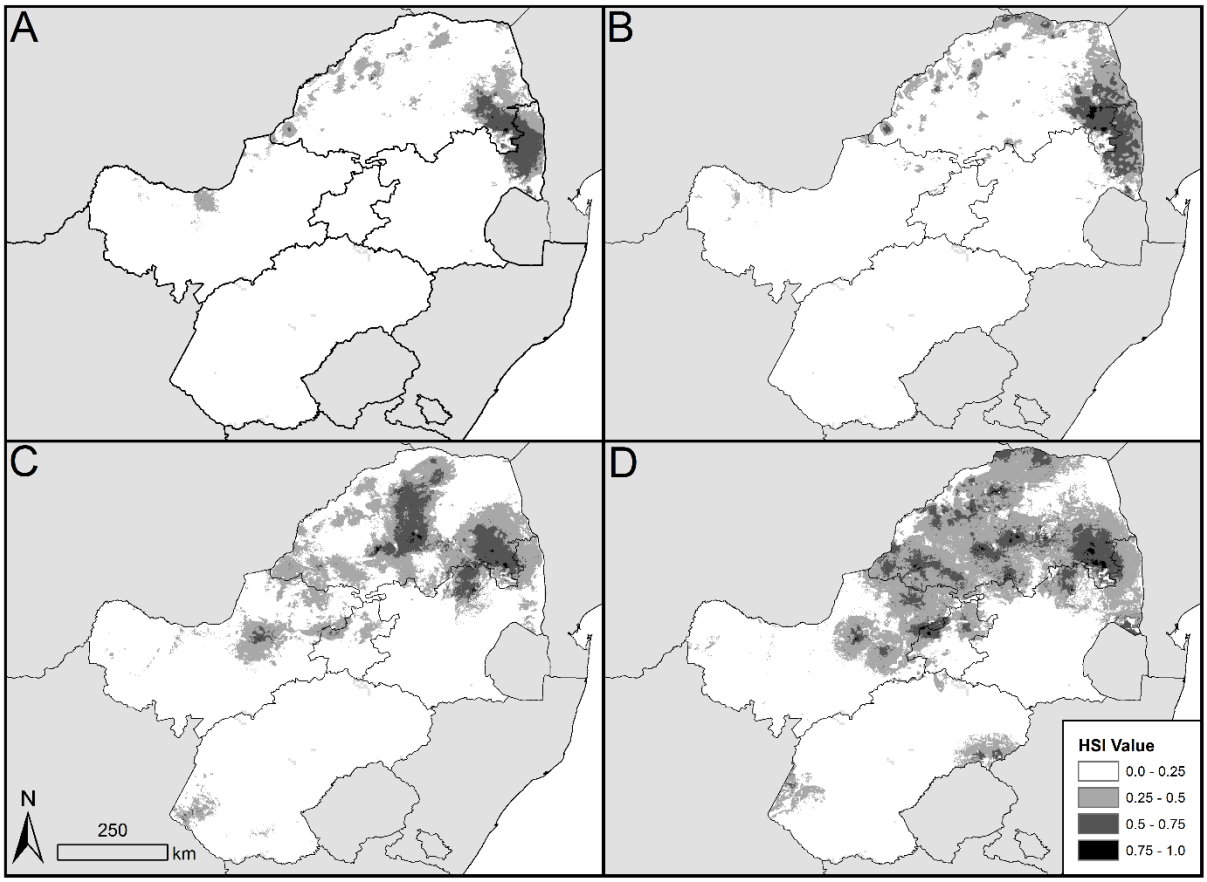


Figure 2.5: MaxEnt models for north-eastern provinces. A) white-backed vulture with climate data, B) white-backed vulture without climate data, C) Cape vulture with climate data, and D) Cape vulture without climate data.

Pentads with Cape vultures present had significantly higher maximum habitat suitability values from the model with climate variables than pentads without (Mann-Whitney U = 274,182.5, $n_p = n_a$ =753, $p < 0.001$) (Figure 2.7). The mean maximum HSI values for pentads with Cape vultures was 0.43 ± 0.22 and for those without was 0.20 ± 0.19. Pentads with Cape vultures present had significantly higher maximum HSI values from the model without climate variables than pentads without the birds (Mann-Whitney U = 277,720, $n_p = n_a$ =753, $p < 0.001$). The mean maximum HSI value for pentads with Cape vultures was 0.52 ± 0.19 and for pentads without was 0.28 ± 0.20. More pentads with Cape vultures present had suitable habitat within them with the no-climate model than with the climate model (Table 2.3).

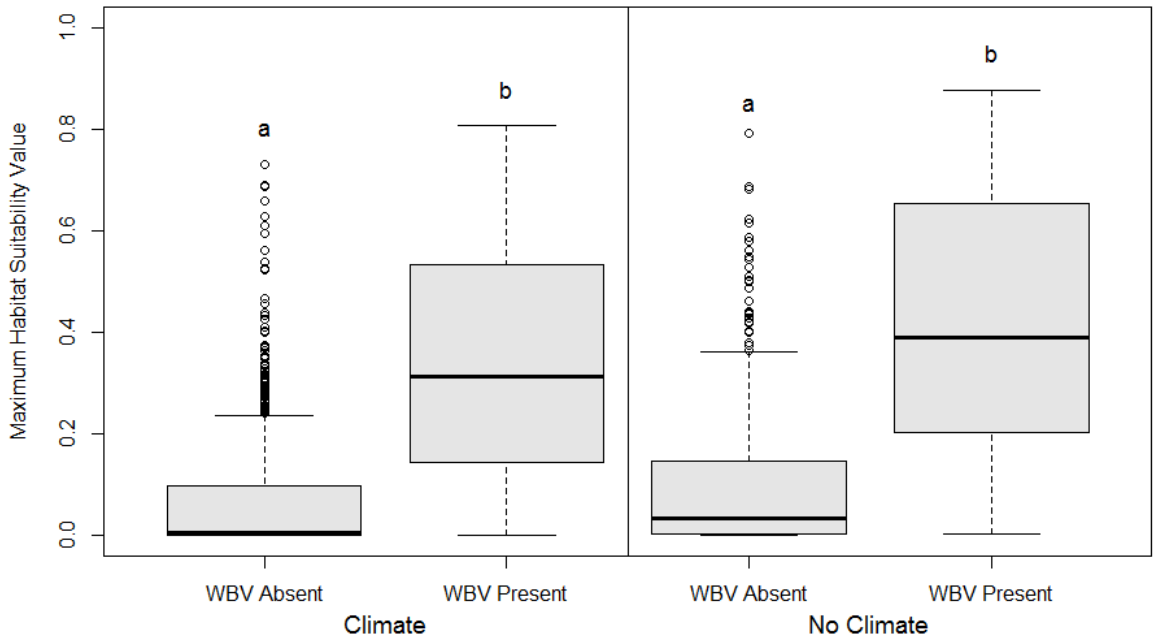


Figure 2.6: Box plots displaying the maximum habitat suitability values of pentads with and without white-backed vultures (WBV) for the two models of the five provinces. The letters represent significant differences within not between the models. The boxes represent the 25% and 75% quantiles. The line across the box represents the mean. The open circles are outliers.

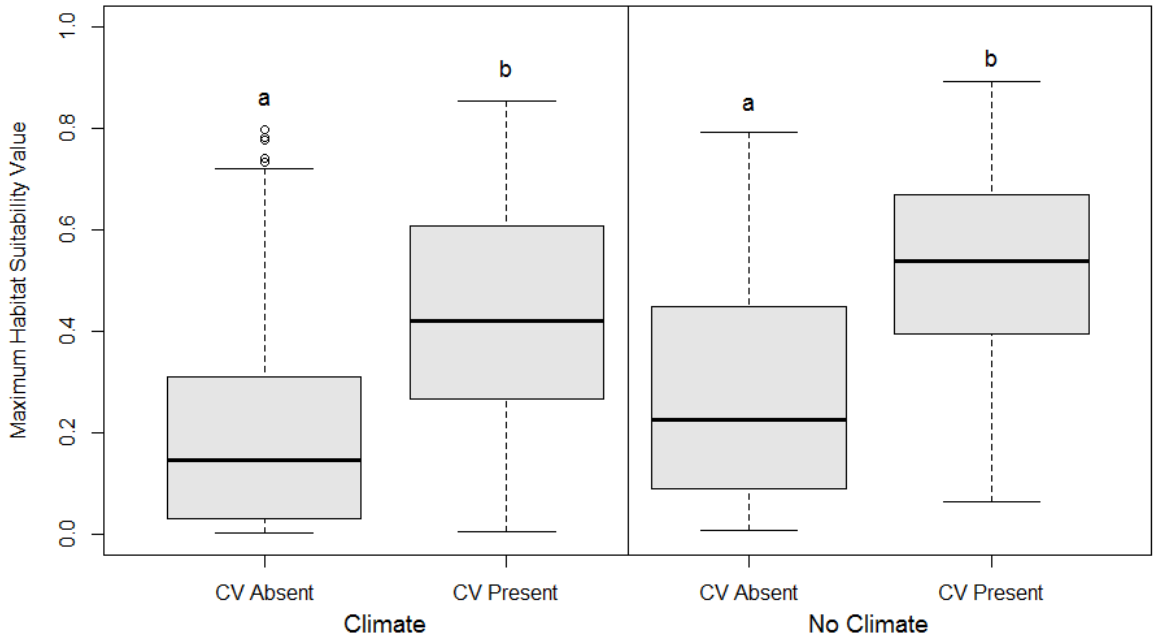


Figure 2.7: Box plots displaying the maximum habitat suitability values of pentads with and without Cape vultures (CV) for the two models of the five provinces. The letters represent significant differences within not between the models. The boxes represent the 25% and 75% quantiles. The line across the box represents the mean. The open circles are outliers.

Table 2.3: The percent of pentads (and the number of pentads out of the total) with vultures present that had suitable habitat according to the four province models.

	White-backed vulture	Cape vulture
Climate	27.9% (211/757)	38.1% (225/591)
No-climate	39.4% (298/757)	57.4% (339/591)

2.4.3: Country models

Four models were produced for South Africa, two for white-backed vultures and two for Cape vultures (Figure 2.8). The white-backed vulture model with climate variables had an AUC of 0.92. The likelihood of occurrence values ranged from 0.00 to 0.83. The total area of suitable habitat was 17,820 km^2 (1.5% of the total area of the country). The model indicated that much of Limpopo province was suitable habitat, the whole of Kruger National Park and parts of the Northern Cape and North West provinces. The model did not predict suitable habitat in KwaZulu-Natal province. Mean temperature, precipitation seasonality, biome, and minimum temperature all contributed over 10% to the model (Table 2.4). Savanna was the preferred biome while grassland was the least preferred. All other biomes were equally preferred.

The white-backed vulture model without climate variables had an AUC of 0.90. The likelihood of occurrence values ranged from 0 to 0.87. The total area of suitable habitat was 25,406 km^2 (2.1% of the total area of the country). The model, once again, predicted suitable habitat in Limpopo, Northern Cape, and North West provinces, and in the Kruger National Park. It also showed some suitable habitat in northern KwaZulu-Natal province. Biome and elevation contributed over 10% to the model. Savanna was the most preferred biome followed by Nama-karoo, azonal vegetation (e.g. marshes, riverine habitat, etc.), and grassland. All other biomes were equally preferred.

The Cape vulture model with climate variables had an AUC of 0.87. The likelihood of occurrence values ranged from 0 to 0.93. The total area of suitable habitat was 45,075 km^2 (3.7% of the total area of the country). The model covered Limpopo province and part of the Highveld in Gauteng and North West provinces. It also had suitable habitat in parts of the Eastern Cape province. There was very little suitable habitat in KwaZulu-Natal province. Precipitation seasonality and distance to feeding station contributed over 10% to the model.

The Cape vulture model without climate variables had an AUC of 0.84. The likelihood of occurrence values ranged from 0 to 0.84. The total area of suitable habitat was 87,558 km^2 (7.2% of the total area of the country). It covered the same areas as the model without climate variables but also included much larger portions of the Eastern Cape and KwaZulu-Natal provinces especially in the Drakensberg region. Distance to feeding station and biome contributed over 10% to the model. Nama-karoo, savanna, grassland, and forests were preferred over all other biomes.

Table 2.4: Percent contribution of individual variable to four South Africa MaxEnt models. Values in bold contributed over 10% to the model. The signs next to the percent indicate how the likelihood response lines for each continuous variable were shaped. "-" indicates negative. "+" indicates positive. "-/+" indicates an initial decrease followed by an increase. "+/-" indicates an initial increase followed by a decrease.

Variable	White-backed w/Climate		White-backed w/o Climate		Cape w/Climate		Cape w/o Climate	
Elevation	0.6	-	**13.7**	-	1.4	+	4.4	+/-
Slope	1.2	-	5.4	-	0.2	+	1.4	+
Distance to Water	<0.1	+/-	<0.1	+	0.2	+	1.0	+
Distance to Feeding station	2.5	-	4.1	-	**24.8**	-	**68.4**	-
Distance to Protected Area	2.5	-	1.8	-	0.8	-/+	4.4	-/+
Cattle Density	0.2	-	0.5	-	0.1	-	2.2	-/+
Population Density	0.8	-	1.8	-	1.0	-	1.5	-
Land Use	0.8		0.6		0.6		1.2	
Biome	**19.5**		**51.5**		0.9		**15.5**	
Mean Temperature	**30.9**	+/-	-		0.5	-/+	-	
Maximum Temperature	0.9	+/-	-		1.3	+/-	-	
Minimum Temperature	**15.0**	+	-		3.6	+/-	-	
Temperature Seasonality	1.5	+	-		9.4	-/+	-	
Annual Precipitation	0.3	+/-	-		1.6	+/-	-	
Maximum Precipitation	1.1	+/-	-		1.8	+/-	-	
Minimum Precipitation	0.3	+	-		1.2	-/+	-	
Precipitation Seasonality	**22.0**	+/-	-		**50.5**	+	-	

2.4.4: Testing the country models

For the white-backed vulture model with climate variables, pentads with vultures present had significantly higher maximum habitat suitability values than pentads with where the birds were absent (Mann-Whitney U = 1,067,802.2, n_p = 1,124, n_a =1,130, $p < 0.001$) (Figure 2.9).

The mean for maximum HSI values for pentads with white-backed vultures was 0.30 ± 0.23 while for those without birds was 0.07 ± 0.12. There was also a significant difference between pentads in the model without climate variables (Mann-Whitney U = 1,125,959, n_p = 1,124, n_a =1,130, $p < 0.001$). The mean for maximum HIS values for pentads with white-backed vultures was 0.42 ± 0.20 while the mean for pentads without vultures was 0.11 ± 0.14. More pentads with white-backed vultures present had suitable habitat within them with the no-climate model than with the climate model (Table 2.5).

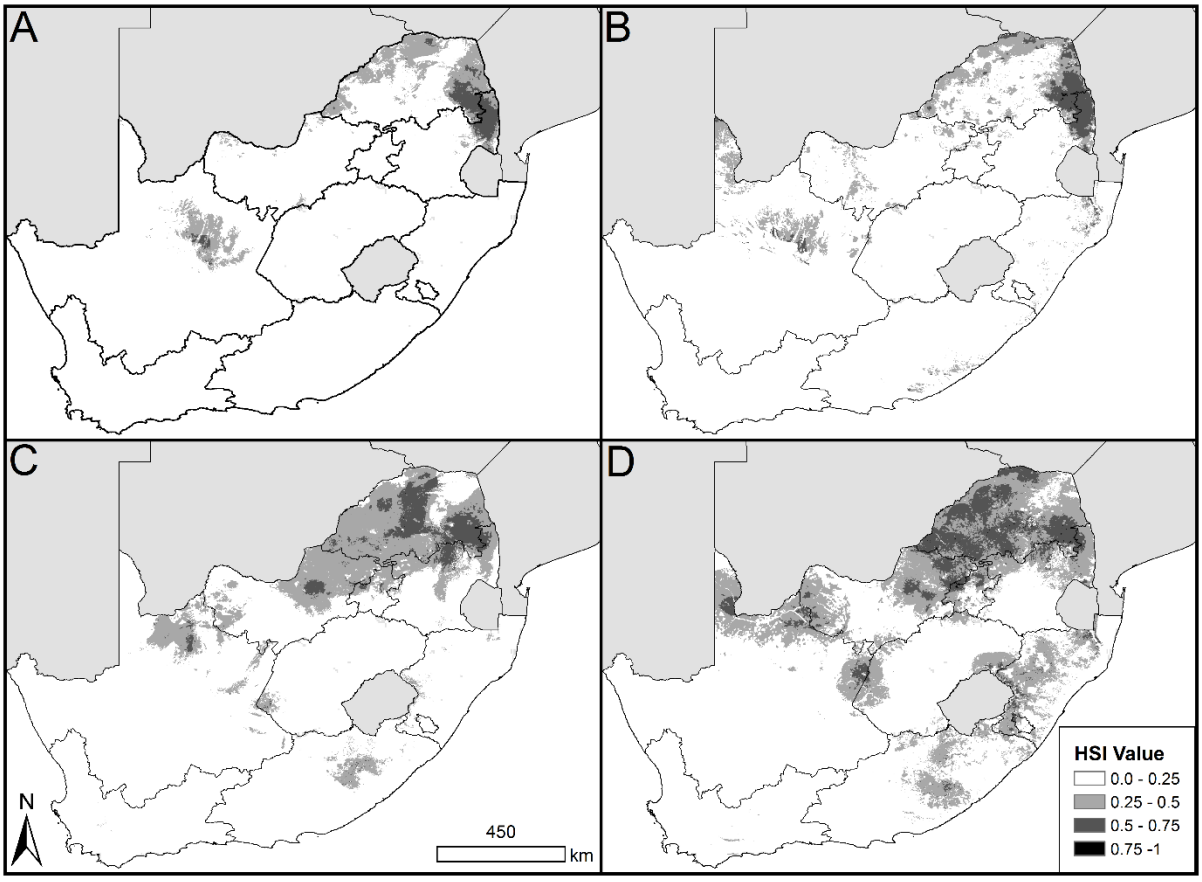


Figure 2.8: MaxEnt models for South Africa. A) white-backed vulture with climate data, B) white-backed vulture without climate data, C) Cape vulture with climate data, and D) Cape vulture without climate data.

For the Cape vulture model with climate variables there was a significant difference in maximum HSI values between pentads with vultures present and where absent (Mann-Whitney U = 861,528.5, n_p = 1,068, n_a =1,060, $p < 0.001$) (Figure 2.10). The mean value for pentads with Cape vultures present was 0.36 ± 0.22 where they were absent was 0.17 ± 0.19.

For the model without climate variables, there were also significant differences between pentads with and without Cape vultures (Mann-Whitney U = 924,419, n_p = 1,068, n_a =1,060, $p < 0.001$). The mean value for pentads with vultures was 0.51 ± 0.17 while for pentads without birds was 0.26 ± 0.21.

Table 2.5: The percent of pentads (and the number of pentads out of the South African total) with vultures present that had suitable habitat according to the four national models.

	White-backed vulture	Cape vulture
Climate	24.0% (278/1156)	32.4% (352/1087)
No-climate	39.2% (453/1156)	57.4% (624/1087)

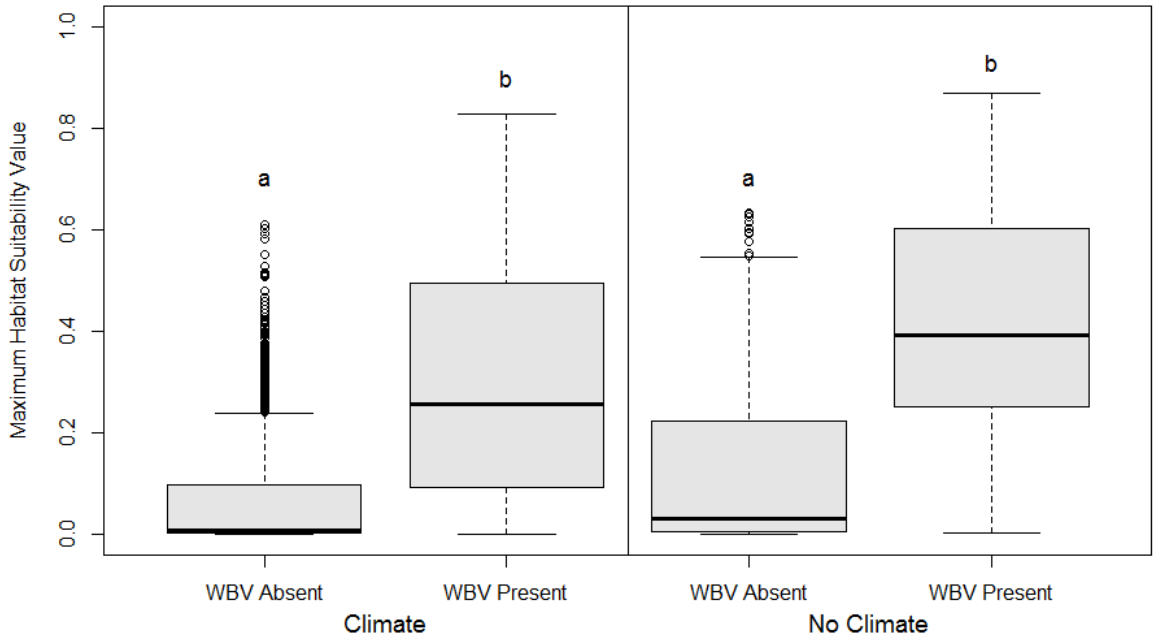


Figure 2.9: Box plots displaying the maximum habitat suitability values of pentads with and without white-backed vultures (WBV) for the two models of South Africa. The letters represent significant differences within not between the models. The boxes represent the 25% and 75% quantiles. The line across the box represents the mean. The open circles are outliers.

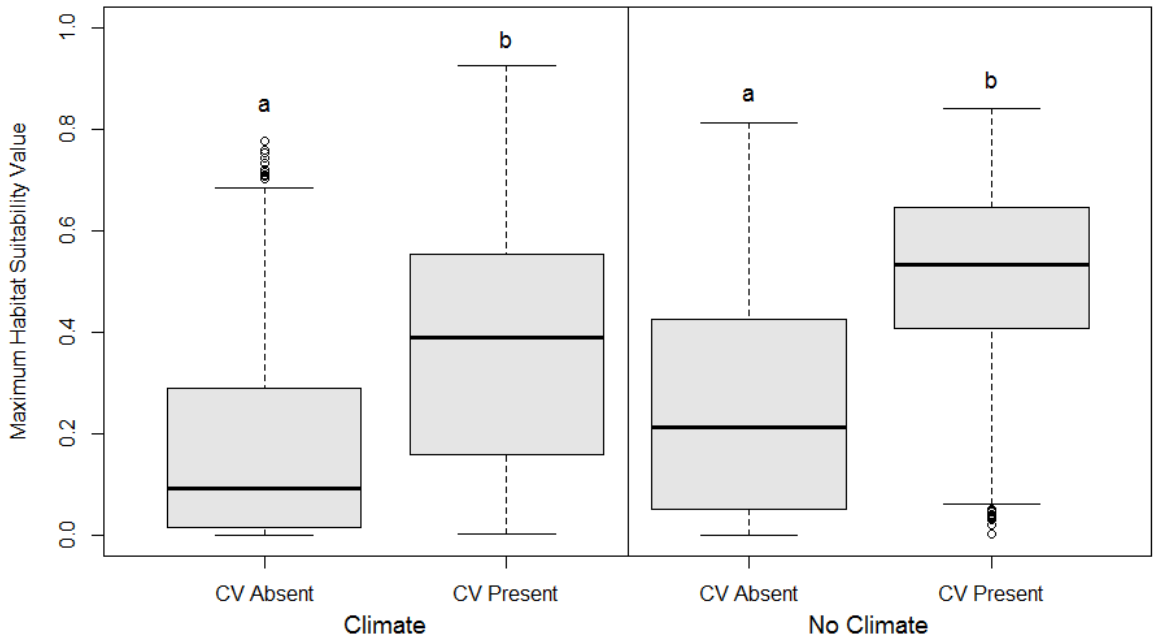


Figure 2.10: Box plots displaying the maximum habitat suitability values of pentads with and without Cape vultures (CV) for the two models of South Africa. The letters represent significant differences within not between the models. The boxes represent the 25% and 75% quantiles. The line across the box represents the mean. The open circles are outliers.

2.5: Discussion

2.5.1: White-backed vulture model

All white-backed vulture models had a high AUC value and showed similar results in terms of both areas where the birds were likely to be found, and which variables were important in determining suitable habitat. The habitat models predicted small areas of appropriate habitat. This included the Kruger National Park, northern parts of North West and Limpopo provinces, and in the national models, parts of the Northern Cape province and Zululand (northern KwaZulu-Natal province). These are locations with a number of protected areas and relatively low human population density which could help the vultures to remain safe from poisoning and the traditional medicine trade. The models did miss parts of the white-backed vultures' range including large swathes of northern Zululand, North West province, and eastern Northern Cape province (Mundy et al. 1992). This is likely due to the fact that the

vultures tracked were caught in Limpopo province and were mostly from the greater Kruger population, which implies that there may be sub-populations in different regions or site fidelity among the birds (Mundy et al. 1992). Adding data collected from birds across the country (including KwaZulu-Natal province population and the population further to the west of South Africa) may help correct this.

The variables that were important were similar between all the models and largely support what is known about white-backed vultures. Biome contributed over 10% to three of the models and, in all, savanna was the most preferred type. This was followed by grassland, Nama-karoo, and azonal vegetation. White-backed vultures are largely a savanna species although they do move through other biomes including grassland, and karoo vegetation, particularly in the Northern Cape province (Mundy et al. 1992). The azonal vegetation may be explained by their reliance on riverine habitat for large trees to nest in (Bamford et al. 2009). Elevation played a role in both models without climate. The birds were more common at lower elevations, as expected. Elevation may also be serving as a proxy for many of the climactic variables (in the models without climatic data). The last non-climatic variable that was important for the provincial models is distance to protected area. Protected areas are important nesting areas for white-backed vultures and also have large game populations with natural mortality (Monadjem and Garcelon 2005). Protected areas were only important in the provincial models which may indicate a case of scale, suggesting that on the local level, protected areas may be extremely important (especially for breeding birds) while on a national level they may be less important. This is supported by evidence from another tracking study indicating that vultures (particularly young birds) spend very little of their time in protected areas (Phipps et al. 2013b).

Three climatic variables contributed over 10% to at least one of the models: i) minimum temperature, ii) mean temperature, and iii) precipitation seasonality. All models predicted that birds would not be found in areas that had a minimum temperature of below 0ºC. They also predicted that birds were most likely to be found in areas with a mean temperature of between 16ºC and 22ºC. These temperatures coincide with a subtropical climate which is where white-backed vultures are found across Africa. Another indication of this was precipitation seasonality. The eastern half of South Africa has high seasonality with warm, wet summers and cold, dry winters which coincides with the high precipitation seasonality which the models predicted. It also coincides with the typical climate of South African savannas (Mucina and Rutherford 2010).

The SABAP2 data indicate that portions of suitable habitat were missed by the models, suggesting that the model is too conservative. These areas are largely in the Eastern Cape and KwaZulu-Natal provinces which may have been underpredicted by the models. The average habitat suitability values for all of the white-backed vulture models were below the suitable habitat cut-off. The models without climate variables were slightly more successful in correctly identifying areas where white-backed vultures were present than the models with climate variables. This is likely because the models without climate variables predicted a larger area and identified more regions than those with climate variables. This may indicate that the climate variables importance have been over-exaggerated in the models due to the fact that the birds are from one portion of their total range suggesting elevation and biome may be more suitable predictors.

2.5.2: Cape vulture model

All the Cape vulture models had high AUC values, and showed similar areas where the birds were likely to be found. Suitable areas in all models include west of Kruger National Park, central Limpopo province, parts of North West province, and the Magaliesberg mountain range in Gauteng and North West provinces. These areas have consistent feeding stations, many game and livestock farms, and mountain ranges with suitable nesting habitat. The climate models missed parts of the Cape vulture range such as the highlands of KwaZulu-Natal province and the majority of the Eastern Cape province. Both of these areas have large breeding populations of Cape vultures (Mundy et al. 1992). The model also missed the population at De Hoop Nature Reserve in the Western Cape province. This is likely because the tracked vultures used in the models were all trapped in far off Limpopo province and did not frequent these areas. The provincial models covered the majority of where Cape vultures (particularly the tracked sub-population) are known to occur.

Six different variables contributed over 10% to at least one of the Cape vulture models. Only one was consistent through all four models, suggesting there were major differences in terms of scale for the provincial and South African models. At the provincial scale, the important variables were minimum temperature, temperature seasonality, and distance to protected area. At the country scale, the important variables were precipitation seasonality and biome. Precipitation seasonality is a strong driver of vegetation type in southern Africa and this combined with biome, is very important on the larger scale for

vulture habitat use. Temperature and protected areas are likely to be more important on a smaller scale.

The variable that was important in all the models was distance to feeding station. It contributed heavily to the modelled distribution, particularly in those without climatic variables, suggesting that Cape vultures rely heavily on vulture feeding stations while white-backed vultures do not. The model indicates that it is unlikely that a Cape vulture would be more than 150 kilometres from a feeding station. This strong contribution from feeding stations may be because all of the birds that were tracked were trapped at feeding stations. This may mean that the tracked population is a sub-population of vultures that utilise feeding stations more regularly than vulture population generally. This would inflate the importance of feeding stations for the species as a whole, and interpretation needs to be undertaken cautiously. To assess whether there is a country-wide reliance on feeding stations would require more tracking data from other parts of the country, and from birds trapped away from feeding stations (or nestlings).

The SABAP2 data indicated that the Cape vulture models were more accurate than the white-backed vultures in predicting vulture presence, particularly those without climate variables. The maximum values for pentads with Cape vultures present, based on the national and provincial models without climate variables, were above 0.5. Again, the climate models were less accurate than the no-climate models suggesting climate variables may not be as important in determining habitat suitability, especially on a large scale, as the models are indicate and may be underpredicting suitability in some areas.

2.5.3: Differences between species

The Cape vulture models predicted more suitable area than the white-backed vulture models in all cases. They also had lower AUC values in all cases. This may be because the Cape vulture has a less specific habitat type than the white-backed vultures and therefore were less constrained by variables like biome and temperature. For instance, white-backed vultures are generally restricted to savanna (particularly for breeding) while Cape vultures are found in savanna and grassland (Mundy et al. 1992). Adult Cape vultures are also found at a greater variety of elevations (and habitats) than adult white-backed vultures (Mundy et al. 1992). The other major difference between the two species is their use of feeding stations. Feeding stations contributed little to White-backed vulture models but in Cape vultures', the

contribution was very high, suggesting the latter were heavily reliant on feeding stations in comparison to white-backed vultures. This may be a function of proximity to feeding stations with many feeding stations being located close to the breeding and roosting cliffs of Cape vultures allowing for better access.

Based on the SABAP2 data, the Cape vulture models more accurately reflect the actual range of the species than the white-backed vulture models. As discussed above, the white-backed vulture models underpredict suitable habitat, probably because the vast majority of the white-backed vulture points were in a small area, implying a small area of suitability, while the Cape vulture points were more widely spread across the country. This could be remedied with more tracking paths from different white-backed vulture sub-populations, elsewhere in South Africa. Although the birds do move large distances, the breeding adults seem more likely to remain around their breeding areas.

2.5.4: Differences between models

The models without climatic variables consistently predicted larger areas with smaller AUC values and better fit the SABAP2 data. Many of the non-climatic variables likely served as proxies for climate variables in the no-climate models (e.g. elevation correlates well to temperature; biome with temperature and rainfall). Hence, the core suitable habitat was very similar from both climatic and non-climatic variable models. Overall, the models were similar in their predictions of suitable habitat and consistently emphasised the lack of importance of human population variables and the importance of habitat variables like biome, elevation, feeding stations, and protected areas.

2.5.5: Conservation implications

These models show predicted, currently suitable habitat for two threatened vulture species. Conservationists should aim to manage areas of high suitability for vultures. This includes providing safe food at feeding stations, particularly for Cape vultures that seem reliant on these, educating the public to reduce poisoning and capture for the traditional medicine trade, and carefully placing power infrastructure to avoid electrocution and collision. The birds do not appear to avoid areas of human development and therefore human population and land use is not, in itself, a problem as long as proper steps are taken to reduce mortality from

power lines and poisoning. By increasing the number of feeding stations in the country, it may not be necessary to conserve large areas of habitat (with the exception of breeding areas) as the birds are more likely to remain close to consistent (and safe) food resources.

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Chapter 3: Seasonal movements of Cape (*Gyps coprotheres*) and white-backed (*Gyps africanus*) vultures in southern Africa

3.1: Abstract

Vultures have been shown to exhibit seasonal movements elsewhere in Africa in response to carcass availability. I tracked eight Cape (*Gyps coprotheres*) and five white-backed (*G. africanus*) vultures in southern Africa for 19 months (2013-2014). Birds were trapped at two sites in Limpopo province in South Africa and fitted with GSM-GPS trackers, DUCK-4A or BUBO-4A (Ecotone Telemetry, Sopot, Poland). Variations in home range, displacement, feeding station use, and diversity of habitat use were compared over four seasons: winter (June-August), spring (September-November), summer (December-February), and autumn (March-May). There were few significant differences between seasons for either species. During the winter, white-backed vultures decreased their displacement and home range, and increased their use of feeding stations which may be linked to the breeding season when birds were restricted to their nest sites. White-backed vultures showed more changes in seasonal movement than Cape vultures perhaps due to differences in habitat use. The lack of significant differences between seasons suggests that food availability may not be a limiting factor for the current South African population of white-backed and Cape vultures. Understanding seasonal movements of vultures may assist conservationists and managers to support vultures during the periods when food availability is low.

3.2: Introduction

Vultures, both Old World and New World, are the only obligate vertebrate scavengers on earth (Ruxton and Houston 2004, Dermody et al. 2011). Their large wingspan and keen eyesight allows them to take advantage of carcass resources in a unique way travelling large distances to locate carrion, a resource that varies in availability, both spatially and temporally (Mundy et al. 1992, Ruxton and Houston 2004, Dermody et al. 2011, Duriez et al. 2014). Food availability is thought to be the primary limiting factor in scavenger populations (as

predation events are uncommon) (Ruxton and Houston 2004, Wilson and Wolkovich 2010). Vultures must adopt specific strategies to take advantage of limited food resources, including focusing on habitats where visibility is better, using social cues to locate carcasses, and perhaps, adapting foraging patterns seasonally (Ruxton and Houston 2004, Dermody et al. 2011, Kendall et al. 2013, Cortes-Avizanda et al. 2014, Duriez et al. 2014).

White-backed (*Gyps africanus*) and Cape (*G. coprotheres*) vultures are the most common vulture species in southern Africa (Mundy et al. 1992, IUCN 2015). Both species are listed in Threatened categories by the International Union of Conservation of Nature (IUCN) Red List with severe population declines due to poisoning, electrocution by power lines, declines in food availability, and habitat loss (Ledger and Annegarn 1981, Mundy et al. 1992, Dean 2004, Boshoff et al. 2011, McKean et al. 2013, IUCN 2015). The Cape vulture, an endemic species to southern Africa, is currently listed as Endangered (IUCN 2015). The white-backed vulture, distributed across Africa, has recently been listed as Critically Endangered (IUCN 2015). Both birds are highly gregarious, gathering in large numbers at carcasses, at breeding sites, and occasionally water points (Mundy et al. 1992). Sub-adult birds of both species travel widely throughout southern Africa while adults tend to have smaller home ranges around their nest (during the winter breeding season) or roost sites (Bamford et al. 2007, Phipps et al. 2013a, Phipps et al. 2013b).

A recent study examined the seasonal movements of Rüppell's (*G. rueppellii*), white-backed, and lappet-faced (*Torgos tracheliotos*) vultures in the Masai Mara National Reserve in Kenya (Kendall et al. 2013). It was long believed that vultures followed seasonal movements of the migratory western white-bearded wildebeest (*Connochaetes taurinus*) (Houston 1974, Kendall et al. 2013). It is, however, a much more complex relationship with vultures only following wildebeest during the dry season when rates of mortality are naturally high from starvation, dehydration, and disease (Gallivan et al. 1995, Fynn and O'Connor 2000). During the wet season, Rüppell's and lappet-faced vultures targeted dry areas where herbivore mortality was higher rather than following the wildebeest herds (Kendall et al. 2013). Kendall et al. (2013) suggest this is adaptive foraging by both species related to food availability. Boshoff et al. (2009) suggest there is migratory behaviour in the Cape vultures of the Eastern Cape province, South Africa, the vultures vacating winter, breeding cliffs during the summer, non-breeding season. They hypothesise that birds move east during the breeding season into the south-eastern Eastern Cape and far western KwaZulu-Natal provinces, though this has not been assessed using tracking devices or tagged birds (Boshoff et al. 2009).

In northern and eastern portions (the summer rain fall areas) of southern Africa, there are two main seasons: the wet, warm summer season (November to April) and the cooler, dry winter season (May to October) (Fauchereau et al. 2003, Zhang et al. 2005). The majority of free-range livestock and wild herbivore mortality occurs in the dry season due to the limited water and food resources (Gallivan et al. 1995, Fynn and O'Connor 2000, Cronje et al. 2002, Owen-Smith 2008). During the wet season, when grazing and water are normally plentiful, many young ungulates are born and the vegetation is thick which allows for heavy predation (Cronje et al. 2002, Owen-Smith 2008). Vultures, however, are less likely to access predated carcasses as predators chase the birds off or even kill them. Southern Africa supports a large number of scavenger species including black-backed jackal (*Canis mesomelas*), spotted (*Crocuta crocuta*) and brown (*Hyaena brunnea*) hyenas, and opportunistic lion (*Panthera leo*), leopard (*P. pardus*), and cheetah (*Acinonyx jubatus*) (Smithers 2000). Common avian scavengers include six vulture species, bateleur (*Terathopius ecaudatus*), several *Aquila* and other eagle species, and pied crows (*Corvus albus*) (Hockey et al. 2005). These species create a diverse scavenger community that takes advantage of the large amount of carrion available in the southern African system and likely results in high levels of competition for carcasses.

I examined seasonal movements of white-backed and Cape vultures in southern Africa. Changes in movements and habitat use may be caused by fluctuations in food availability, which may be result from seasonal variations of temperature and rainfall. If rainfall is low, food availability is likely to be high, due to high ungulate mortality. In the case of the summer rainfall regions of southern Africa, this is likely to be in the winter season. If food availability is greater in one season (i.e. winter), vultures should reduce their home ranges and displacement because carrion is easier to find. During the wet season, ungulates are more dispersed and therefore vultures may need to travel greater distances to find carrion. Although if the birds are no longer tied to nesting sites and therefore may be able to stay in areas where food is available and travel less. Vultures may reduce their use of feeding stations when natural food availability is higher because they are more likely to encounter more carrion naturally. Lastly, if natural carrion is widely available, white-backed and Cape vultures may use fewer vegetation types because their home ranges are smaller. I predicted that if food availability is greater in one season (i.e. winter), a) vultures' home range and displacement will shrink, b) they will reduce their use of feeding stations, and c) their use of vegetation types will be less diverse. These hypotheses were tested using white-backed and Cape vulture tracking points through southern Africa.

Documenting the seasonal movements of these two species will provide a better understanding of their resource use in southern Africa and facilitate management of their populations, by enabling better provisioning at feeding stations during times of food scarcity, and improving protection of areas important to their survival throughout the year. Vultures forage over vast areas, putting them at risk of poisoning from carcasses (Verdoorn et al. 2004). Poisoning of carcasses has been the greatest cause of vulture decline in Africa (Ogada et al. 2015). Poisoning includes targeted incidents, e.g. poachers aiming to avoid detection and traditional healers capturing birds for the traditional medicine market, and inadvertent incidents e.g. farmers poisoning carcasses to reduce predator populations. Providing safe carcasses at feeding stations reduced poisoning in India (Gilbert et al. 2007). This is especially important during times of low food availability. With these two species (and other African vulture species), declining rapidly throughout their ranges, it is important to implement effective conservation measures. This can be more effectively done by understanding their behaviour at a landscape level.

3.3: Methods

3.3.1: Tracking data

Thirteen individuals, five white-backed vultures (three female and two male), and eight Cape vultures (two female, five male, one unknown) were trapped at Moholoholo Rehabilitation Centre (S24.5134º, E30.9048º) or Mockford Farms (S24.0628º, E29.2992º) feeding stations in Limpopo province by the Endangered Wildlife Trust (EWT) under a ToPs (Threatened or Protected Species) permit for the Limpopo Vulture Project. Feeding stations are locations where poison-free carcasses are placed out for vultures and other avian scavengers to feed on (Donazar et al. 2010). Besides one sub-adult white-backed vulture, all birds were adults. Their breeding status was unknown. Birds were trapped in walk-in traps set up at each location. Each individual was fitted with GSM-GPS tracking devices, either DUCK-4A or BUBO-4A (Ecotone Telemetry, Sopot, Poland; www.ecotone-telemetry.com). In addition, birds were patagial tagged (a numbered plastic tag attached to both wings) and ringed, and blood was collected to sex the birds (Hewitt and Austin-Smith 1966, Wallace et al. 1980, Kendall and Virani 2012). Data points were collected hourly (5:00-17:00) each day from

April 2013 to October 2014. Vultures with insufficient points (<500) to create accurate home ranges and displacement values, were excluded from analyses.

3.3.2 Weather data analysis

Months were divided into four seasons: winter (June-August), spring (September-November), summer (December-February), and autumn (March-May) based on typical rainfall patterns in the summer rainfall regions of southern Africa where the vultures were caught (Kendall et al. 2013). South African Weather Service (SAWS) data from 2000 to 2014 for Polokwane, Limpopo province and Nelspruit, Mpumalanga province (the two weather stations closest to the capture points of the vultures) The data included average daily maximum and minimum temperatures and total rainfall for each month. In addition to testing differences between seasons, the climate during the vulture tracking months was examined relative to the average values of those months to assess whether the climate of the tracked year was typical.

3.3.3: Tracking data analysis

Tracking points were categorised by month for each vulture. Monthly displacement, minimum convex polygon (MCP) and 50%, and 95% kernels were calculated for each month using Geospatial Modelling Environment (Spatial Ecology LLC, 2014, vers. 0.7.4.0). These measures assess changes in foraging patterns across seasons (Worton 1989). Because there was extremely high variability in the data, MCP and both kernels were log transformed in order to better visualise the trends across seasons.

Vulture feeding stations were plotted in ArcGIS 10.2 (ESRI Inc., 2015, vers. 10.2.0.3348) from the EWT Vulture Restaurant database. A buffer of 500 metres was created around each feeding station. The buffer provided a small margin of error for the tracking and GPS points of the feeding stations. The proportion of vulture tracking points in the buffer was calculated for each month to assess whether vultures were more likely to rely on feeding stations in some seasons.

Both biome use and vegetation diversity were calculated for each month. The South African National Biodiversity Institute (SANBI) vegetation layer was used (Mucina and Rutherford 2010). The vegetation and biome type were extracted for each point within South Africa, Lesotho, and Swaziland, the countries covered by the layer. All tracking points

outside of these countries were excluded from this analysis. The total number of points in each biome for each species and each season was counted to investigate if biome use was different across seasons and between species. If the birds were tracked at a point it was considered to be using that biome or vegetation type. Even if the birds were flying at the point, it is likely that they were foraging, and, therefore, using that particular vegetation type. The vegetation type was extracted for each point and monthly vegetation diversity was calculated for each tracking month of each bird. Vegetation diversity was calculated using the Shannon Diversity Index on Land Uses (Laiola 2005). The following formula was used: $H' = -\sum p_i \times logp_i$ where p is the proportion of land type i. All months were assigned to seasons for analysis. All statistics were calculated using R (The R Foundation for Statistical Computing Platform, 2015, vers. 3.2.2). All values are presented as means ± standard deviation.

3.4: Results

3.4.1: Seasonal climate

A total of 180 months of climate data from Polokwane was analysed. One hundred and sixty four months of temperature data and 161 months of rainfall data were analysed from Nelspruit.

In Polokwane, maximum temperature during the tracking months was one standard deviation above the mean in two months (June and September 2013) and one standard deviation below the mean in two months (December 2013 and January 2014) (Figure 3.1). Minimum temperature was one standard deviation below the mean in five months (April, May, June, October, and November 2013). Minimum temperature was two standard deviations below the mean in one month (October 2013). Monthly rainfall was one standard deviation above the mean in two months (April 2013 and March 2014).

In Nelspruit, maximum temperature during the tracking months was one standard deviation above the mean in two months (January 2013 and June 2014) and one standard deviation below the mean in two months (December 2013 and October 2014). Minimum temperature was one standard deviation above the mean in one month (July 2013). Monthly rainfall was one standard deviation above the mean in four months (April, May, and August 2013 and March 2014) and one standard deviation below the mean in one month (January

2014). Monthly rainfall was two standard deviations above the mean for two months (May 2013 and March 2014).

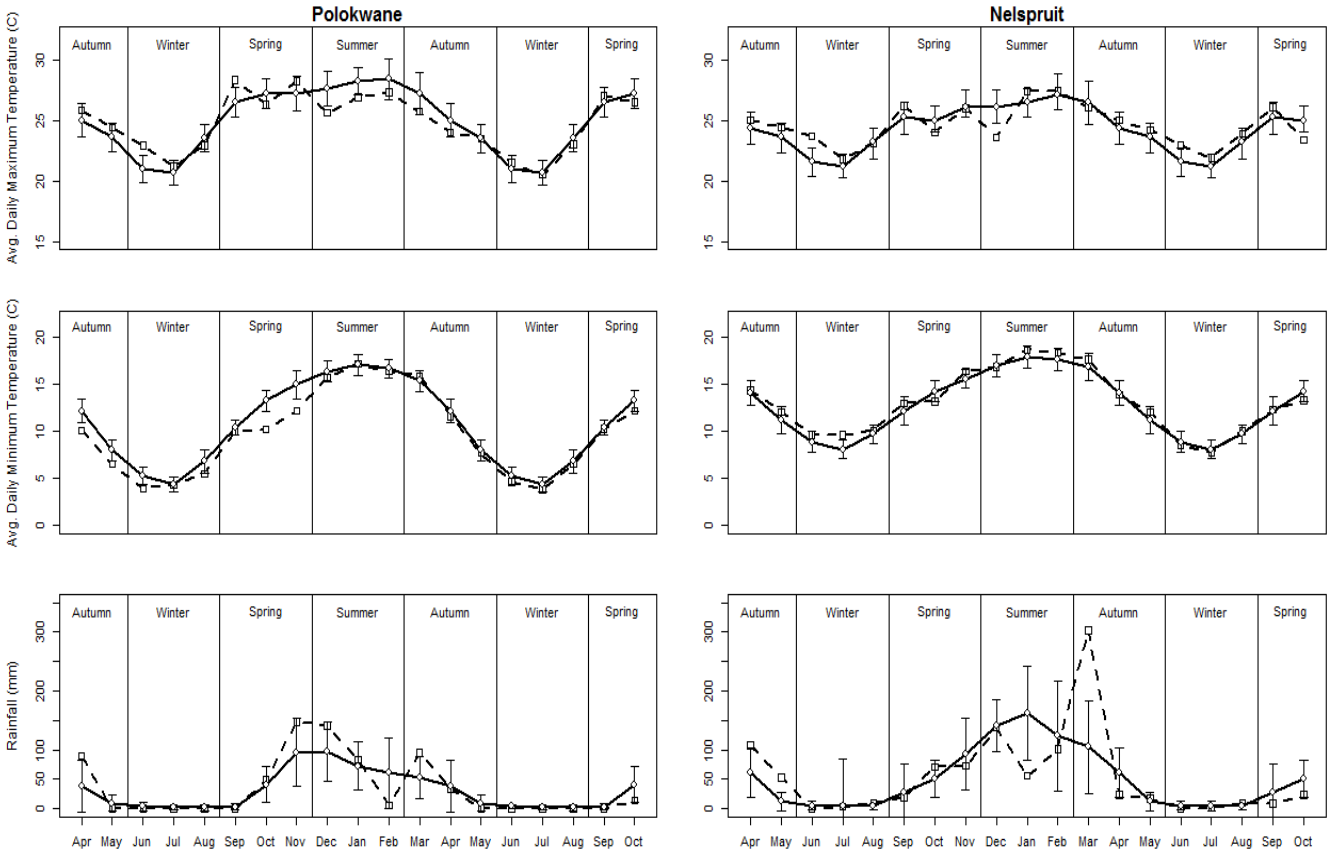


Figure 3.1: The mean monthly average maximum and minimum temperature and monthly rainfall values (solid lines with open circles) and the monthly average maximum and minimum temperature and monthly rainfall values for vulture tracking months (dashed line with open squares) from April 2013 to October 2014 for Nelspruit and Polokwane. Error bars represent one standard deviation above and below the mean.

In Polokwane, monthly average maximum temperatures were significantly different in all seasons ($F=128.5(3, 176)$, $p<0.001$). Summer had the highest monthly average maximum temperatures while winter had the lowest (Figure 3.2). Monthly average minimum temperatures were significantly different for all seasons except spring and autumn ($H=137.79$, d.f.=3, $p=0.05$). Monthly average minimum temperatures were highest in the summer and lowest in the winter. Monthly rainfall values were significantly different in all seasons except spring and autumn ($H=78.21$, d.f.=3, $p=0.05$). The rainfall was highest in summer, and the lowest in winter.

In Nelspruit, monthly average maximum temperatures were significantly different in all seasons except spring and autumn ($F=71.52(3, 160)$, $p<0.01$). Highest average maximum temperatures were recorded in summer, and lowest in winter. Monthly average minimum temperatures were significantly different in all seasons except spring and autumn ($F=157.9(3,160)$, $p<0.01$). Summer had the highest average minimum temperatures, and winter had the lowest. Monthly rainfall values were significantly different in all seasons except spring and autumn ($H=87.36$, d.f.$=3$, $p<0.01$). Rainfall values were highest in summer, and lowest in winter.

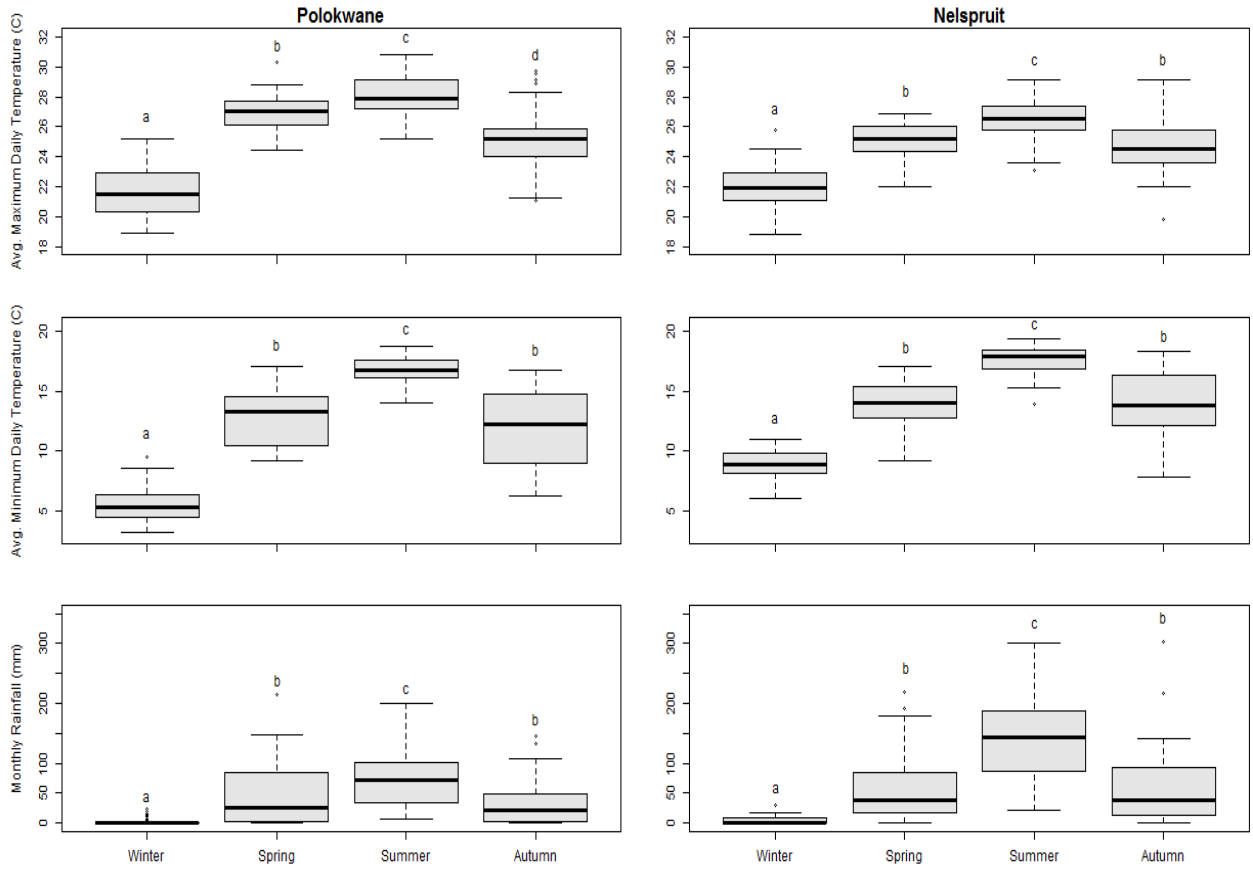


Figure 3.2: The mean monthly average maximum and minimum temperature and monthly rainfall values for each season in Polokwane and Nelspruit. The letters represent significant differences within not between the models. The boxes represent the 25% and 75% quantiles. The line across the box represents the mean. The open circles are outliers.

3.4.2: Tracking data

The white-backed vultures were tracked for an average of 12.4 ± 3.7 months. A total of 62 tracking months were used in analysis for white-backed vultures (Table 3.1).

The Cape vultures were tracked for an average of 9.9 ± 5.9 months. A total of 89 tracking months were used in analysis for Cape vultures (Table 3.1).

Table 3.1: The number of vulture tracking months and tracking points per season for white-backed and Cape vultures.

Season	**White-backed vulture**		**Cape vulture**	
	Number of tracking months	*Number of tracking points*	*Number of tracking months*	*Number of tracking points*
Winter	15	4882	20	5855
Spring	14	4268	22	6746
Summer	15	4715	23	6657
Autumn	18	4762	24	6147
Total	**62**	**18,627**	**89**	**25,405**

Birds were tracked in six countries (South Africa, Botswana, Zimbabwe, Mozambique, Lesotho, and Swaziland (Figure 3.3). The total MCP of all the white-backed vultures was 1,002,603 km^2 and the total MCP of all the Cape vultures was 1,168,602 km^2.

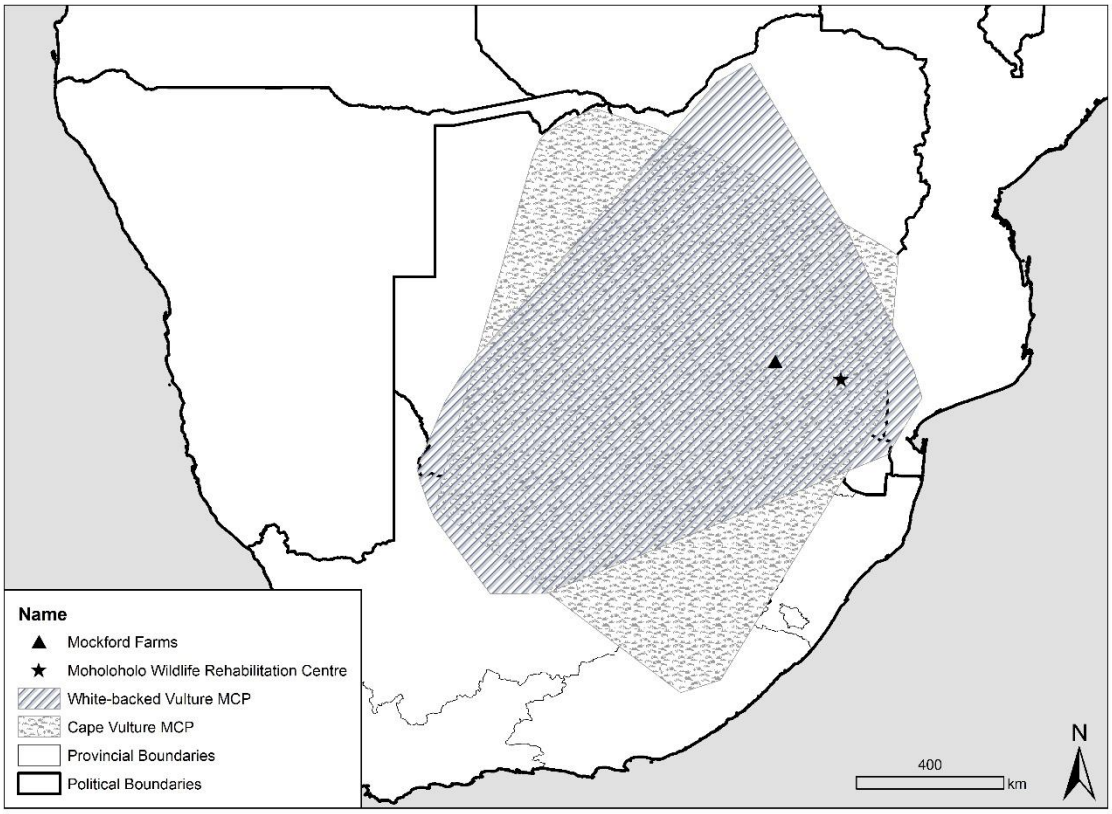


Figure 3.3: The MCP of all white-backed and Cape vultures with the capture points of the birds marked.

3.4.3: Displacement

White-backed vulture data showed seasonal differences in total monthly displacement ($H=10.73$, d.f.=3, $p=0.01$). They travelled greater distances in the spring than in the autumn (Figure 3.4). Cape vulture data did not show seasonal differences in total monthly displacement (Figure 3.4). There were no significant differences between the two species.

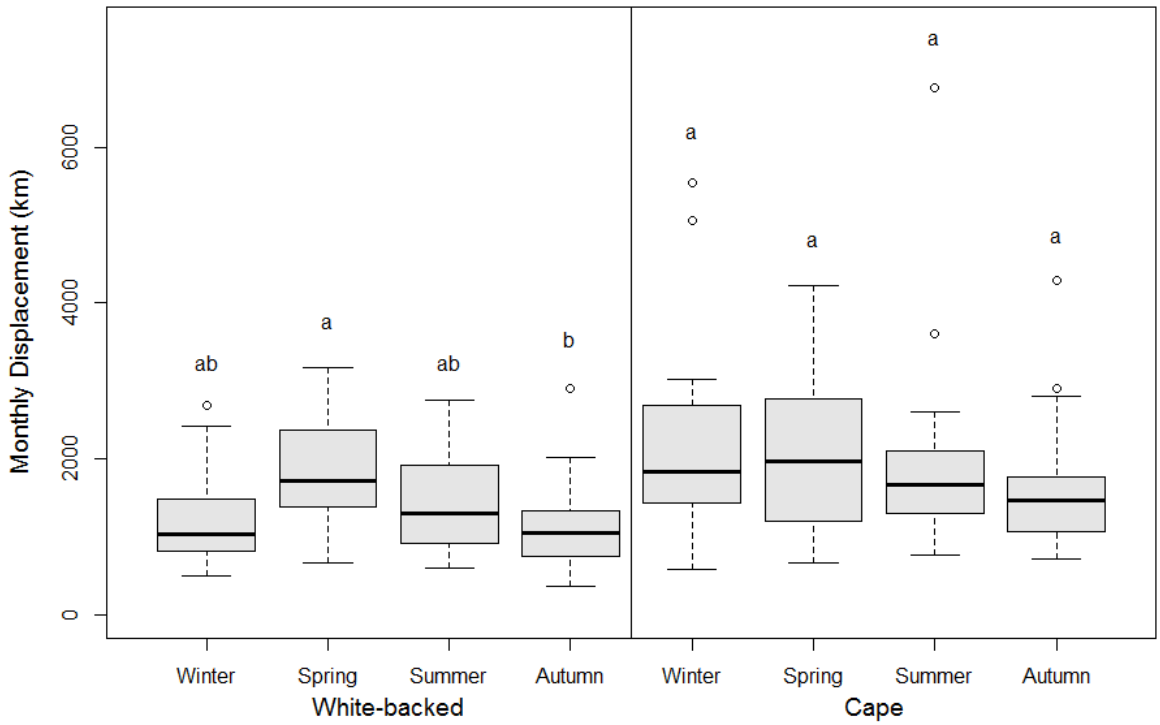


Figure 3.4: The average monthly displacement across seasons of tracked white-backed vultures and Cape vultures. The letters represent significant differences within not between the models. The boxes represent the 25% and 75% quantiles. The line across the box represents the mean. The open circles are outliers.

3.4.4: Home Range

Both white-backed and Cape vultures showed no significant seasonal differences in home range kernel areas. However, there is a consistent peak in home range during the spring for Cape vultures and during the summer and autumn seasons for white-backed vultures (Figure 3.5). There were no significant differences between species.

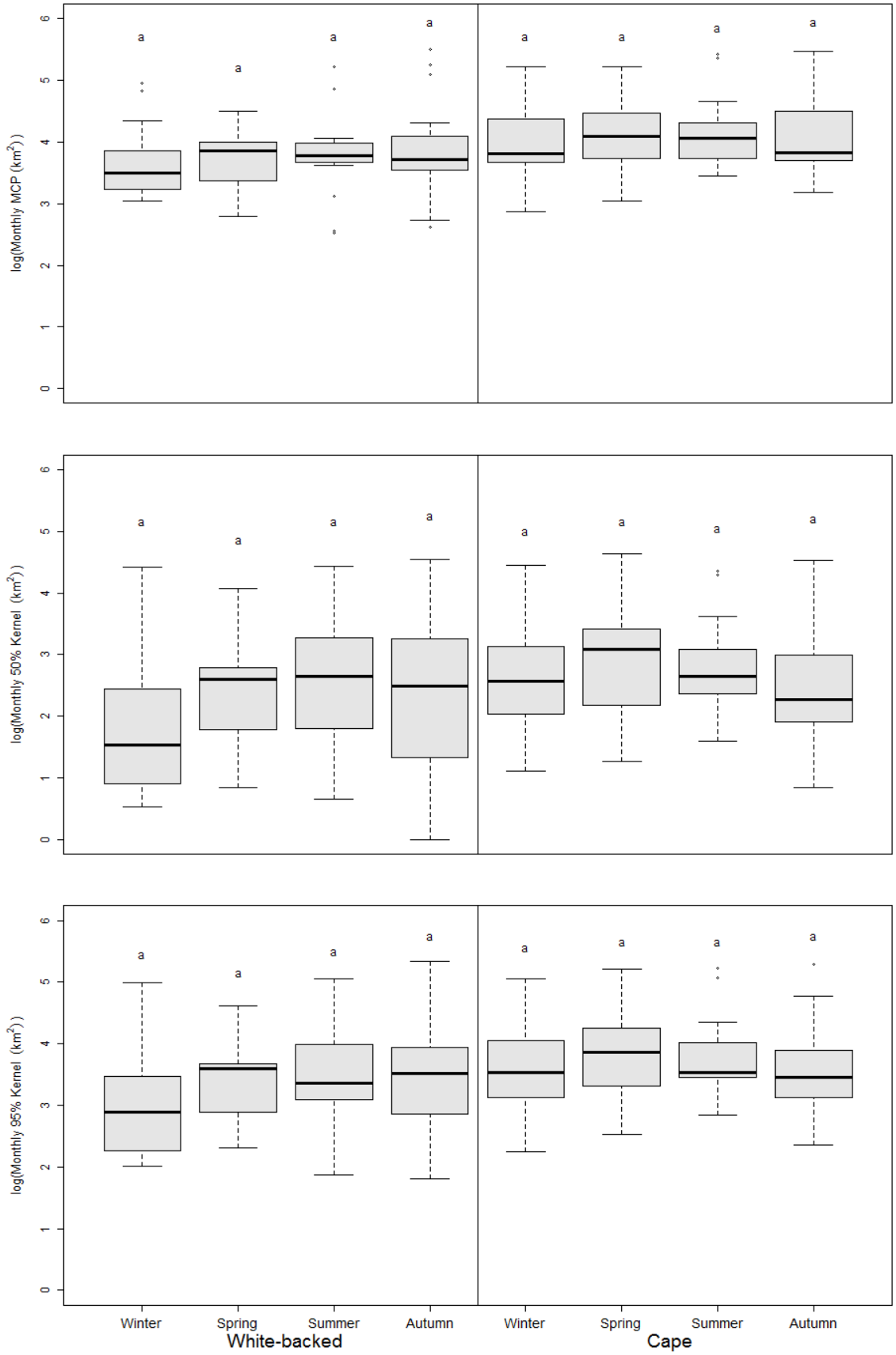


Figure 3.5: The average monthly logMCP, log50% kernel, and log95% kernel across seasons of tracked white-backed vultures and Cape vultures. The letters represent significant differences within not between the models. The boxes represent the 25% and 75% quantiles. The line across the box represents the mean. The open circles are outliers.

3.4.5: Feeding station use

There were no significant differences in the proportion of time spent by white-backed vultures at feeding stations across seasons. The same was true for Cape vultures. White-backed vultures showed a peak in use during the winter (Figure 3.6). There were no significant differences between species.

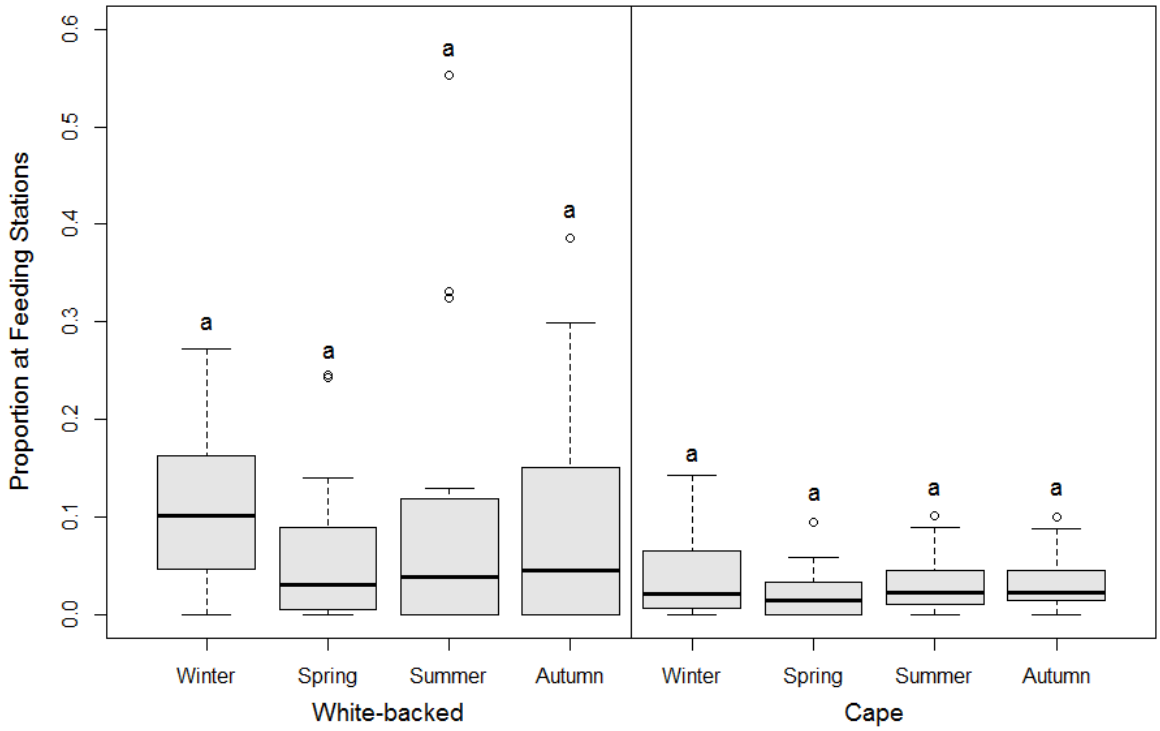


Figure 3.6: The average monthly proportion of points at feeding stations across seasons of tracked white-backed vultures and Cape vultures. The letters represent significant differences within not between the models. The boxes represent the 25% and 75% quantiles. The line across the box represents the mean. The open circles are outliers.

3.4.6: Vegetation diversity

Totals of 59 months for white-backed vultures and 80 months for Cape vultures were used for the vegetation and biome use analysis. White-backed and Cape vultures used five biomes: i) savanna, ii) grassland, iii) Nama-karoo, iv) forests, and v) azonal vegetation (Figure 3.7). Because of low counts in several biomes, white-backed vulture data were combined into two categories: i) savanna and ii) other. The Cape vulture data were combined into three categories: i) savanna, ii) grassland and iii) other. Biome use differed significantly between

the species over the tracking period (χ^2=3680.7, d.f.=2, p<0.001). Cape vultures used more grassland and other vegetation types than white-backed vultures. White-backed and Cape vultures both showed significant differences in biome use between seasons (χ^2=963.29, d.f.=6, p<0.001 and χ^2=151.96, d.f=3, p<0.001). White-backed vultures used only savanna in the spring and more of other biomes in the summer. Cape vultures used more grassland and other biomes in the summer and less grassland and other vegetation types in the winter.

Both white-backed and Cape vultures showed no significant differences in vegetation use diversity between seasons (Figure 3.8). White-backed vultures showed a small peak during the summer. There was a significant difference in vegetation use between species during spring.

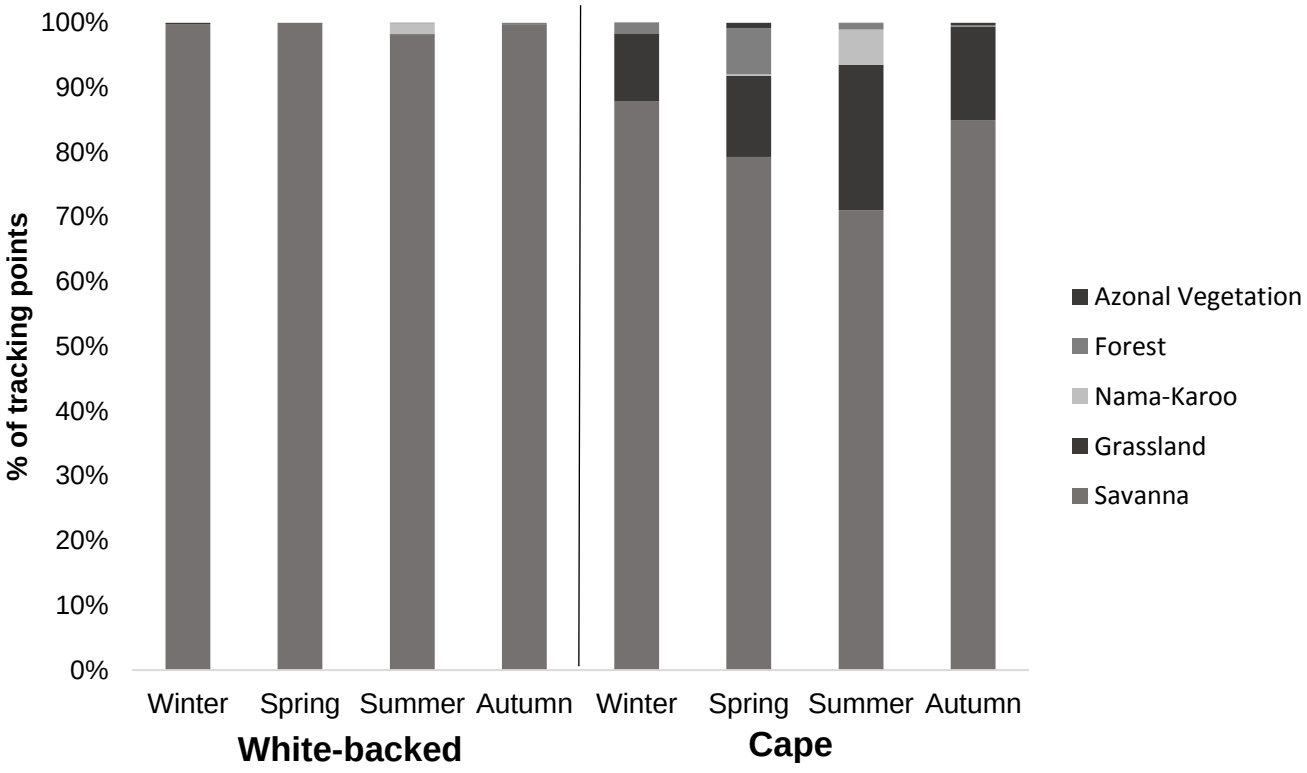


Figure 3.7: The percentage of tracking points in each biome for each season for white-backed and Cape vultures.

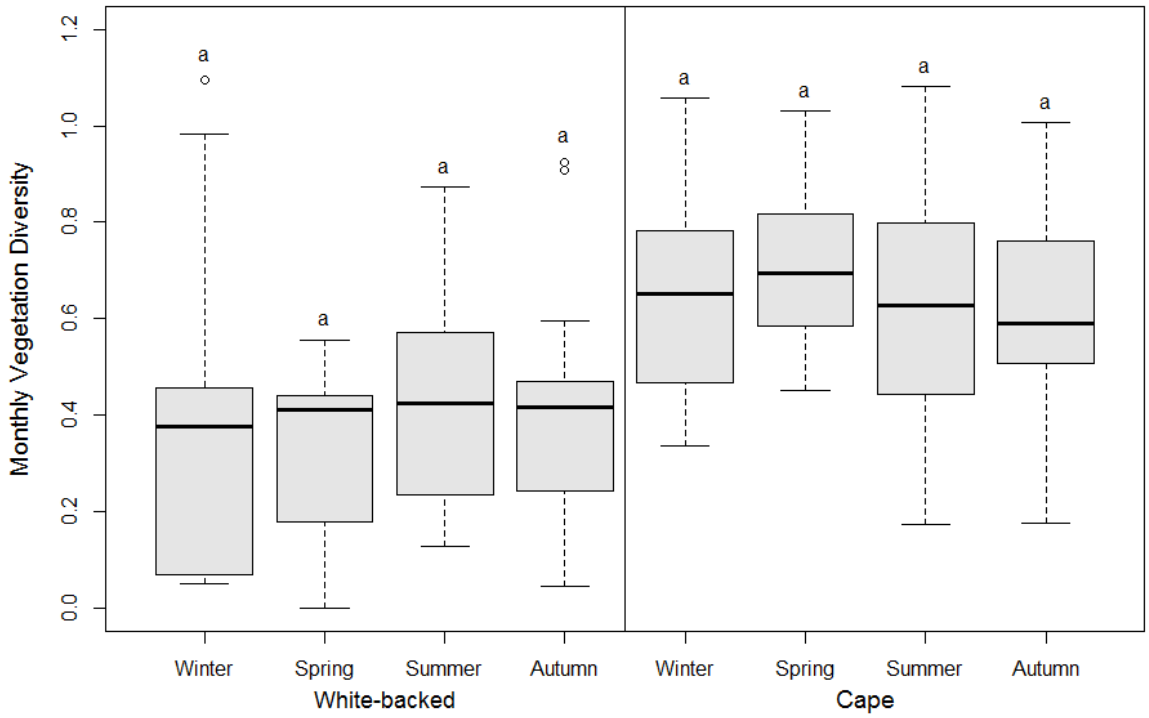


Figure 3.8: The average monthly vegetation diversity across seasons of tracked white-backed and Cape vultures.

3.5: Discussion

There was little change in seasonal foraging movements in the southern African white-backed and Cape vultures observed in this study. White-backed vultures showed more variation throughout the year, with lower displacement and home range values, and the highest use of feeding stations in winter. Cape vultures showed similar displacement, home range, and use of feeding stations throughout the year. There was high variation within each season for both species.

The lack of strong seasonal changes in movement is in contrast to what previous studies in South Africa, Namibia, Kenya, and Europe have found (Robertson and Boshoff 1986, Bamford et al. 2007, Kendall et al. 2013, Monsarrat et al. 2013). Seasonal movements of Cape vultures in the Western Cape province, South Africa, and in Namibia were linked to breeding behaviour and food availability (Robertson and Boshoff 1986, Bamford et al. 2007). Kendall et al. (2013) found changes in Kenyan vulture foraging behaviour and where they foraged but did not examine displacement, or home range.

3.5.1: Seasonal climate differences

The data from the Polokwane and Nelspruit weather stations supported the divisions of the data into four seasons. Seasons were significantly different from each other (with the exception of spring and fall) in temperature and rainfall. Winter was the driest and coldest season as expected. This supports the idea that vultures may be less able to fly in winter due to cold weather leading to less thermal lift and the view that mortality of mammals due to starvation and dehydration is likely to be greater (Gallivan et al. 1995, Fynn and O'Connor 2000). The nineteen months that vultures were tracked were fairly typical of the last decade. The one major exception was the extreme rainfall in March 2014. This may have resulted in the autumn results reflecting more of a summer signal due to the high rainfall. It may also have resulted in a winter season with reduced mammal mortality due to high surface water and ground water availability. These factors may have changed the vultures' foraging patterns for this season. This supports the need for more seasons of tracking data to better understand the changes and variability between and across years.

3.5.2: Drivers of seasonal movement in vultures

There appear to be three primary drivers of seasonal changes in vulture movements: i) weather, ii) breeding behaviour, and iii) food availability (Robertson and Boshoff 1986, Bamford et al. 2007, Monsarrat et al. 2013). Because vultures are large, heavy birds, weather patterns have a great effect on their ability to forage (Mundy et al. 1992, Ruxton and Houston 2004, Shepard and Lambertucci 2013, Duriez et al. 2014). In conditions that do not facilitate updrafts, such as cold or windless days, vultures may have to remain at their roosting sites (Mundy et al. 1992, Shepard and Lambertucci 2013, Duriez et al. 2014). Winters in southern Africa are cold and dry, and the days are short (Fauchereau et al. 2003). Vultures tend to leave their nests later as a result of poor flying conditions (Robertson and Boshoff 1986, Mundy et al. 1992). This results in shorter foraging days for the birds which may mean that they move shorter distances to find food. The slight decline in white-backed vulture home range and displacement supports this idea. One possible explanation for the lack of change in the movement of the Cape vultures could be that their roosting and breeding cliffs are in mountainous areas which are windier and would produce ridge lift that Cape vultures could

exploit to get aloft (Mundy et al. 1992). It also may be possible that the area they forage in is sufficient regardless of the time of year.

Both white-backed and Cape vultures begin breeding in late summer and early autumn (Mundy et al. 1992). During the incubation phase, one parent is constantly on the nest while the other forages (Mundy et al. 1992). This continues through the nestling phase (Mundy et al. 1992). However, at this point the demands of feeding the young increase (Mundy et al. 1992). Both species also feed their fledgling after they leave the nests (Mundy et al. 1992). This results in a very intensive period of foraging from the time the chick hatches until the post fledging dependence period is over which coincides with winter into early spring (Mundy et al. 1992, Bamford et al. 2007). At the Potberg colony in the Western Cape province, Cape vultures spent the most time foraging in January and February, when food was scarcest (Robertson and Boshoff 1986). The shortest foraging time was recorded in March, April, and May, which is lambing season in the Western Cape province and therefore, there is high food availability due to high lamb mortality (Robertson and Boshoff 1986). For a single radio-tracked vulture from Potberg the mean furthest foraging site was twice as far from the colony in summer as it was in the winter (Boshoff et al. 1984).

A pattern similar to the Potberg Cape vultures occurred in the white-backed vultures of this study, with slightly lower home range and displacement in the winter and a sharp increase in feeding station uses. This suggests that breeding vultures are using a reliable food resource available close to their nests. It also implies that there are more feeding stations per km^2 in the vultures' home range. This pattern is very similar to that found in griffon vultures (*G. fulvus*) in the Grand Causse region of France where adult birds decreased their home range and displacement during the winter but the density of feeding stations in their ranges increased (Monserrat et al. 2013). Monserrat et al. (2013) suggested that they were cutting out areas from their summer home range during the winter but only areas without feeding stations, leading to an increase in feeding station density in their home ranges. This was hypothesised to be because of a combination of weather, food availability, and breeding behaviour. But in my study, Cape vultures showed very little change in the scale of their movements during the breeding season.

Food availability is a major factor determining seasonal movements of vultures(Robertson and Boshoff 1986, Monsarrat et al. 2013). Southern Africa has a large population of wild and domestic ungulates (Smithers 2000). Adult ungulate mortality from starvations varies throughout the year, peaking in winter (the dry season), and early spring (Gallivan et al. 1995, Fynn and O'Connor 2000). High mortality of young ungulates,

particularly impala (*Aepyceros melampus*), in spring produces another peak in carrion availability (Gallivan et al. 1995, Smithers 2000). Summer and autumn are the wet, green periods with lower herbivore mortality (Gallivan et al. 1995, Fynn and O'Connor 2000, Fauchereau et al. 2003). Winter and spring should be periods with the largest amount of food biomass available to vultures.

Despite the likely changes in food availability, the birds did not drastically change their foraging habits throughout the year. White-backed vultures moved shorter distances in a smaller area but relied more heavily on feeding stations. Cape vultures showed very little change. This may be because even if there is a change in the amount of food throughout the year, there is still more than enough for the current population. There may be little competition between vultures due to the drastic population decline (across most areas) over the past several decades and a possible increase in food provisioning through feeding stations although this is currently unclear. Food availability may not be a limiting factor for white-backed and Cape vultures, and therefore, seasonal movements may not be dictated by food availability. Another possible hypothesis is that vulture breeding is linked to the season with the highest food availability to meet their energy demands. During the summer season, birds are no longer breeding, and therefore, their energy requirements (and those of the chicks they were feeding) are lower. So that despite the decrease in food availability, a concurrent decline in energy demands means the birds fly similar distances to fulfil their needs.

3.5.3: Differences between species

White-backed and Cape vultures showed very little difference in. This is probably because both species have similar breeding and feeding habits (Mundy et al. 1992). Cape vultures use a greater variety of habitats, explaining the higher diversity in the use of vegetation types. This may also explain the lack of seasonal changes. Cape vultures move between habitats, negating seasonal effects by exploiting a greater variety of food resources. White-backed vultures tend to remain only in savanna and therefore may be more susceptible to seasonal changes in this particular biome (Mundy et al. 1992).

3.5.4: Conservation implications

Understanding the seasonal movements of vultures and the drivers behind provides information for evidence-based conservation initiatives for both species. In my study, white-backed and Cape vultures showed little seasonal change in movement, either in the distances they travelled to find food or in the habitat types in which they foraged. The two species differed in the types of habitat that they used, with Cape vulture using savanna, and grassland while white-backed vultures almost exclusively used savanna habitats. White-backed vultures used feeding stations more frequently than Cape vultures, particularly during the winter breeding season. This does not support my hypotheses. In periods when vultures are using feeding stations most, it is particularly important to provide safe carcasses at these sites. Because Cape vultures use feeding stations less, they may be at greater risk of poisoning year-round. The lack of strong seasonal changes in foraging patterns of these two vultures seemingly supports the hypothesis that there is more food available to vultures than the population needs. This may be because of the sharp declines in vulture populations over the past three decades, allowing for a greater volume of food per vulture. Despite the availability of natural food, provisioning feeding stations may be an important step to avoid poisoning deaths of these two species.

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Chapter 4: Using landscape factors to model vulture power line electrocutions and collisions in South Africa

4.1: Abstract

Recent assessments of vulture mortality in Africa have shown that electrical infrastructure (such as power lines and wind turbines) is the third greatest source of unnatural mortality. With the populations of white-backed and Cape vultures decreasing by ~90% over the past three decades, it is important to reduce mortality where possible. To reduce vulture mortality from power lines, high risk constructions must be identified and retrofitted. This study aimed to identify high risk power lines in South Africa using landscape scale factors. Models were created using collision and electrocution data for white-backed and Cape vultures from the Endangered Wildlife/Eskom Wildlife and Energy Programme from 1996-2013 and the presence-only modelling program, MaxEnt. High risk collision areas were identified in the Kruger National Park, northern Limpopo province, and north-eastern KwaZulu-Natal province for white-backed vultures and western Eastern Cape province, and the area around the Potberg colony in Western Cape province for Cape vultures. High risk electrocution areas were found in northern North West province, Kruger National Park, north-western Limpopo province, and the border between the Free State and Northern Cape provinces for white-backed vultures and western Limpopo province, the western side of the Eastern Cape province, and the border between the Free State and Northern Cape provinces. Voltage contributed to risk in every model for both collision and electrocution. Land use contributed to the white-backed vulture collision model, and slope and population density contributed to the white-backed electrocution model. Population density and feeding station contributed to both Cape vulture models, and elevation contributed to the Cape vulture electrocution model. These variables are probably related to both the likelihood of vulture presence in the area, and their behaviour (e.g. low foraging in low population areas putting them at risk for collision). High risk constructions should be retrofitted in an appropriate way, and should be prioritised by site. There should also be increased monitoring of power line mortality through surveys of land owners or personnel walking under rural lines to add to the available data to create risk models.

4.2: Introduction

Old world vultures are large, soaring scavengers found in Asia, Africa, and Europe (Ruxton and Houston 2004, Dermody et al. 2011). They provide many ecosystem services including attracting tourism, cleaning up carcasses, recycling nutrients, and reducing the risk of disease transmission in mammals and human beings, and are a cultural symbol for many people (Becker et al. 2005, Markandya et al. 2008, Ogada et al. 2011, Dupont et al. 2012, Ganz et al. 2012, Ogada et al. 2012). In India, a drastic decline in vulture populations has cost the Indian economy an estimated 34 billion US dollars in increased human health care costs over 14 years due to higher rates of rabies and other mammalian diseases (Markandya et al. 2008). These escalating disease rates have accompanied a burgeoning feral dog (*Canis lupus familiaris*) population that has benefited from an increase in available food once fed on by vultures (Markandya et al. 2008).

Vulture populations are declining across the Old World (Prakash et al. 2003, Green et al. 2004, Oaks et al. 2004, Thiollay 2006, 2007, Ogada and Keesing 2010, Virani et al. 2011, Ogada et al. 2015). India experienced a 92% decline in vulture populations from 1990 to 2000 and populations in Africa are falling equally quickly (Ogada et al. 2015). Eleven of the 16 Old World vulture species are listed in Threatened categories by the International Union of Conservation of Nature (IUCN) including seven out of ten African species (IUCN 2015, Ogada et al. 2015). Both white-backed vultures (*Gyps africanus*) and Cape (*G. coprotheres*) have experienced massive declines and are listed as Critically Endangered and Endangered respectively (IUCN 2015). Ogada et al. (2015) estimate Cape and white-backed vulture populations have fallen 92% and 90% respectively over three decades.

Threats to vultures in Africa are varied and widespread, including habitat loss, decrease in food availability, poisoning, use in traditional medicine, and electrocution by and collision with power lines (Benson 1984, Piper et al. 1999, van Wyk et al. 2001, Verdoorn et al. 2004, Beilis and Esterhuizen 2005, Camina and Montelio 2006, Simmons et al. 2007, Boshoff et al. 2011, McKean et al. 2013, Ogada et al. 2015). Poisoning is believed to be the top threat to vultures in Africa due to its diverse drivers (Ogada et al. 2015). Poisoning includes accidental poisoning by commercial farmers (targeting mammalian carnivores such as black-backed jackals (*Canis mesomelas*), targeted poisoning by poachers (attempting to avoid detection by authorities), and environmental poisoning from veterinary medicine and lead (Benson 1984 Verdoorn et al. 2004, Ogada et al. 2015). Power lines are the third major

threat to vultures in Africa behind poisoning and use in the traditional medicine trade (Ogada et al. 2015).

Power lines pose a threat to a variety of bird species around the world including flamingos, bustards, storks, and many species of raptors (Benson 1982, Bevanger 1998, Janns 2000, Rubolini et al. 2005, Jenkins et al. 2010, Shaw et al. 2010, Boshoff et al. 2011). Currently, most research on the effects of power lines has been focused in the United States and Europe (Benson 1982, Lehman et al. 2007, Jenkins et al. 2010). Power lines are known to kill birds through both collisions with power lines and electrocution by power lines (Jenkins et al. 2010). Large and/or heavy birds with wide wings and birds with rapid flight are much more likely to conflict with power lines (Janns 2000). In southern Africa, this includes all species of vultures (except hooded vultures (*Necrosyrtes monachus*), blue crane (*Anthropoides paradiseus*), Ludwig's (*Neotis ludwigii*) and Denham's bustards (*N. denhami*), lesser (*Phoeniconaias minor*) and greater flamingos (*P. minor*), and many large raptor species (Jenkins et al. 2010, Shaw et al. 2010). Raptors, including vultures, are susceptible to both collisions from flying into power lines due to their large wings, and electrocutions from perching on power lines (Jenkins et al. 2010, Boshoff et al. 2011). When the birds extend their wings to take off, they can create a circuit with any energised part of the pylon and are then electrocuted (Markus 1972, Ledger and Annegarn 1981). Whether they get electrocuted depends on weather, voltage and other factors (Lehman et al. 2007). Both collision and electrocution can result in severe injury or death to the birds (Markus 1972, Ledger and Annegarn 1981).

Very few methods have proved effective in the mitigation of collisions (Jenkins et al. 2010). Markers on power lines, both with and without lights, are the primary means of preventing collisions (Jenkins et al. 2010). Another option is removing the ground wire, the top wire on a power line, which is responsible for a large portion of collisions (Jenkins et al. 2010). Electrocution mitigation has proved slightly more successful (Jenkins et al. 2010). Options include adding alternate perches or removing dangerous perches, or insulating dangerous energised elements (Jenkins et al. 2010).

As of 1996, South Africa had 255,745 kilometres of power lines managed exclusively by the South African parastatal Eskom (Electrical Supply Commission) (van Rooyen and Ledger 1997). Owing to growing demand, the network of power lines is expanding rapidly (Perkins et al. 2005). Vulture electrocutions in South Africa were first recorded by Markus (1972) in modern day Limpopo province on 88kV kite structures. Since then, hundreds more incidents have been recorded, especially for the most numerous species, white-backed and

Cape vultures (Ledger and Annegarn 1981, Boshoff et al. 2009). White-backed vultures occasionally nest on, and both species commonly perch on pylons, making electrocutions more likely (Anderson and Hohne 2007). Jann (2000) suggests vulture collision are common because they focus below them rather than in the direction they are flying.

The most thorough examination of the impact of power lines on vultures was Boshoff et al. (Boshoff et al. 2011). This study used a combination of a power line mortality dataset and interviews of people living in the area to estimate vulture mortalities on power lines per year. Although 14 vultures were recorded dead in the WEP database, using the surveys, this increased 5.7 fold to an estimated 80 birds/year. This is around 4% of the Eastern Cape province population (Boshoff et al. 2011). This level of mortality is enough to cause an annual decrease in the Eastern Cape province Cape vulture populations (Boshoff et al. 2011). Although power lines do cause mortality, they also have allowed the expansion of white-backed vulture populations to new areas in South Africa, providing predator-free nesting sites particularly in the arid Northern Cape province, where suitable large trees are few (Anderson and Hohne 2007).

Very little is known of the landscape scale factors contributing to South African vulture mortality on power lines. There has been a concerted effort to document power line deaths of all bird species by the Endangered Wildlife Trust's (EWT) Wildlife and Energy Programme (WEP). All known power line mortality data of white-backed and Cape vultures in South Africa have been collected since 1996. The present study aims to model the likelihood of white-backed and Cape vulture mortality on power lines based on landscape scale variables (e.g. biome, land use, elevation, etc.), and to apply these findings to the current power line grid. These models also examined the differences in factors related to collision and electrocution risk to help engineers and conservationists identify places to avoid for future power line expansions and where to retrofit to make constructions safer for vultures.

4.3: Methods

4.3.1: Electrocution and collision dataset

Vulture power line electrocution and collision data have been opportunistically collected by the WEP since 1996. The data used in the present study were collected between 1996 and

2013. The dataset included the species killed, the cause of death (collision or electrocution), the number of birds killed, the date discovered, and the GPS location of birds for the entirety of South Africa. There was no power construction or line height data included.

4.3.2: Power line dataset

The power line dataset detailed all Eskom power lines in South Africa. The layer included the name of the line, whether it was active, and the voltage. There was no construction or line height data included.

4.3.3: Environmental datasets

To create the models, the following variables were used.

4.3.3.1: Topography

Two topographic variables were used: elevation and slope. There is higher wind at areas of greater slope and elevation which may make vultures vulnerable to collision with power lines. A 90m DEM model from BioClim was used for elevation and slope was derived from elevation using ArcGIS 10.2 (ESRI Inc., 2015, vers. 10.2.0.3348) (Hijmans et al. 2005).

4.3.3.2: Distance to resources

Three resource variables were used, i) distance to fresh water, ii) distance to feeding station, and iii) distance to protected area (SANBI 2009, 2010, 2011). These variables may contribute to how likely a vulture is to be in a specific location. Birds taking off from water points or feeding stations may also be more likely to collide with power lines or may use power lines to roost on, increasing their risk of electrocution. To calculate distance to water, the South African National Biodiversity Institute (SANBI) and the South African vegetation map water class were combined. This water feature dataset was then used to create a Euclidean distance raster. Distance to feeding station was measured using a Euclidean distance function applied to the EWT dataset of all known feeding stations in southern

Africa. Lastly, formal (national and provincial parks) and informal (private reserves) protected areas from the SANBI protected area layers were combined and the resulting dataset was used to create a Euclidean distance raster.

4.3.3.3: Cattle density

All vulture species feed on domestic livestock carcasses (Mundy et al. 1992). In areas where vultures are most likely to find food (e.g. areas of high livestock mortality), birds may fly lower increasing their risk of collision with power lines. Birds may also perch on power lines near carcasses, increasing their risk of electrocution. In South Africa, the largest livestock biomass is cattle (i.e. 13.9 million animals in 2012) (DAFF 2013). The cattle density dataset is from the Food and Agriculture Organization's (FAO) Animal Production and Health department (FAO 2005). The cattle density layer is a model using various environmental variables and livestock counts.

4.3.3.4: Population density

If vultures avoid densely populated areas, locations with high human population may have a lower likelihood of electrocution and collision. Data on South African human population were obtained from the Council for Scientific and Industrial Research (CSIR) Geospatial Analysis Platform (Naude et al. 2007). The human densities for each mesozone were calculated from area and population counts.

4.3.3.5: Land use

Different land use types may also indicate varying levels of human disturbance to vultures. Land use data were obtained from the SANBI Land Cover map from 2009 (SANBI 2009). They include seven categories: i) natural, ii) cultivated, iii) urban, iv) degraded, v) water, vi) plantation, and vii) mines. Land use types were defined using data from provincial governments as well as data sources from the Department of Water Affairs and Forestry, the Agricultural Research Council, and Eskom.

4.3.3.6: Biome

In open, treeless areas, vultures/raptors are more likely to perch on power lines, increasing their electrocution risk. Biome data were obtained from the SANBI vegetation map and included eleven categories: i) savanna, ii) grassland, iii) Albany thicket, iv) azonal vegetation, v) desert, vi) forest, vii) fynbos, viii) Indian Ocean coastal belt, ix) Nama-karoo, x) succulent karoo, and xi) water (Mucina and Rutherford 2010).

4.3.4: Preparing data

Two datasets, using GPS points were created, one each for collisions and electrocutions. Using the GPS data, each power line (both distribution and transmission) segment was assessed to determine if vulture mortality incident had occurred there, and a dataset of lines where deaths occurred was created. A random set of 10,000 both distribution and transmission lines where mortalities had not occurred was created for both collisions and electrocutions. Four additional presence and absence datasets were created, one each for the two species; collision and electrocution records. In total six presence and six absence datasets were created, as well as a dataset of all South African power lines. Environmental data (from all thirteen datasets), as well as voltage, were extracted for each segment of power line. The categorical variables were assigned based on the biome or land use that covered the majority of the segment. The continuous variables were based on the average value for the segment.

4.3.5: Power line risk modelling

MaxEnt (2015, vers. 3.3.3k), a software aimed at creating models with presence-only data, was used to create all six models (Phillips and Dudik 2008), (Elith et al. 2011). It is particularly useful for small datasets of presence-only data, and is robust to overfitting (modelling of random noise rather than the underlying pattern) even with correlated environmental variables. MaxEnt maximises entropy between two probability densities, the landscape data and the presence-only data. It then uses a maximum likelihood approach to plot likelihood values for each landscape variable in the model. For categorical variables (e.g. biome or land use), each category is given a likelihood value. For this study, the standard setting of MaxEnt were used. The models used a *samples with data* method which involved

using the power lines in a datasheet with the environmental variables already assigned (Elith et al. 2011). All models were applied to all power lines in South Africa. All statistics were calculated in R (The R Foundation for Statistical Computing Platform, 2015, vers. 3.2.2). Values of above 0.5 were considered high risk and values of above 0.75 were considered very high risk (Liminana et al. 2012, Liminana et al. 2014). Averages are presented with ± standard deviation.

4.4: Results

Between 1996 and 2013, 837 vultures were reported killed in 331 power line mortality incidents, in the study area. Sixty-nine (20.8%) were collision events, killing 91 birds, and 262 (79.2%) were electrocution incidents, killing 746 birds (Table 4.1). One hundred and two of the incidents (30.8%) involved white-backed vultures, killing 245 birds, and 229 episodes (69.2%) killed 592 Cape vultures.

Table 4.1: The total number of incidents of power line death of vultures divided by both cause of death and species of vulture. The number in parentheses is the percent of the total number of incidents.

	Electrocution	**Collision**	**Total**
White-backed vulture	88 (26.6%)	14 (4.2%)	102 (30.8%)
Cape vulture	174 (52.6%)	55 (16.6%)	229 (69.2%)
Total	262 (79.2%)	69 (20.8%)	331 (100%)

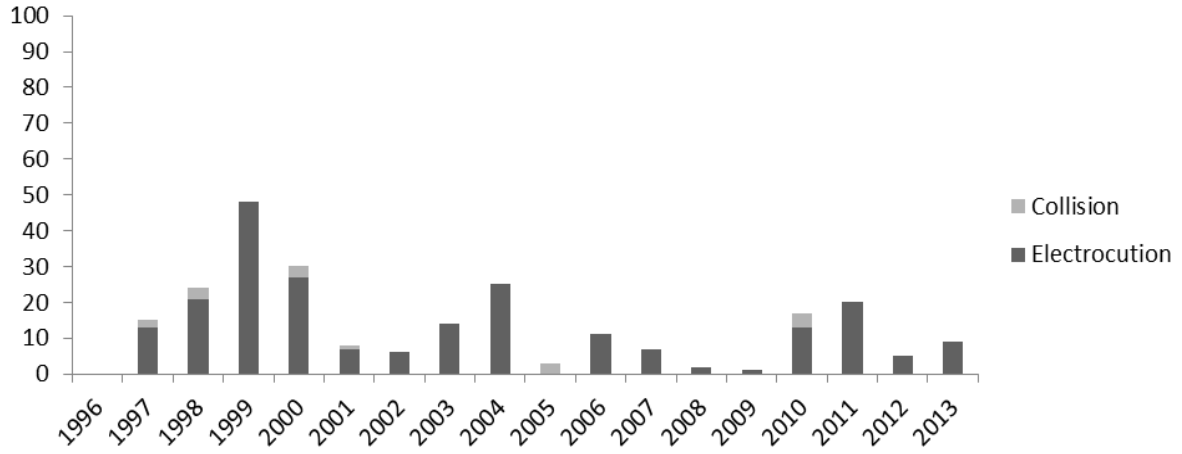
There were significant differences between the number of birds killed per incident across species and cause of death ($H=27.44$, d.f.=3, $p<0.01$). Significantly more Cape vultures were killed per electrocution killed than collisions (electrocutions – mean = 2.98 ± 4.91; collisions – mean = 1.36 ± 0.97) There was no significant difference the number of birds kill per electrocution and collision events for white-backed vultures (electrocutions – mean = 2.71 ± 2.69; collision – mean = 1.14 ± 0.53).

There were GPS coordinates for 178 (53.8%) incidents (white-backed vulture – electrocutions = 25 (28%) and collisions = 9 (64%); Cape vulture – electrocutions = 44 (80%) and collisions = 100 (57%)).

4.4.1: Annual mortality

The white-backed vultures' annual mean mortality rates were 12.72 ± 12.09 for electrocutions and 0.89 ± 1.41 for collisions. For Cape vultures, the annual mean values were 28.72 ± 19.01 for electrocutions and 4.17 ± 3.55 for collisions. There was a decrease in overall white-backed vulture powerline mortality and an increase in overall Cape vulture mortality over the study period (Figure 4.1).

A.



B.

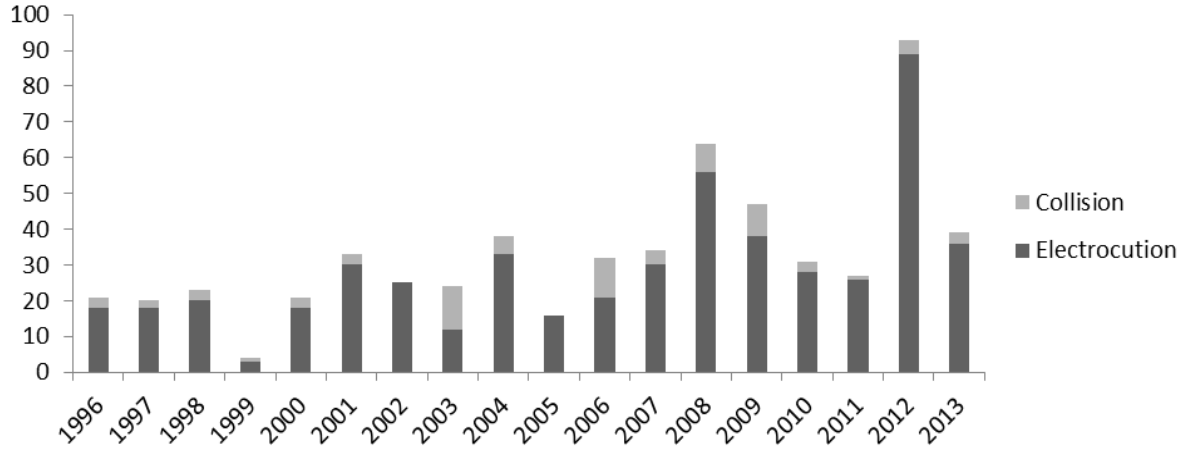


Figure 4.1: The annual mortality of A) white-backed vultures and B) Cape vultures due to collision with and electrocution by power lines from 1996 to 2013.

4.4.2: Spatial patterns of power line mortality

Vulture power line mortalities have been recorded in all nine South African provinces (Figure 4.2). White-backed vulture mortalities were the highest in the North West and Northern Cape provinces (Figure 4.3). Most Cape vulture mortalities were in the Eastern Cape and North West provinces (Figure 4.3).

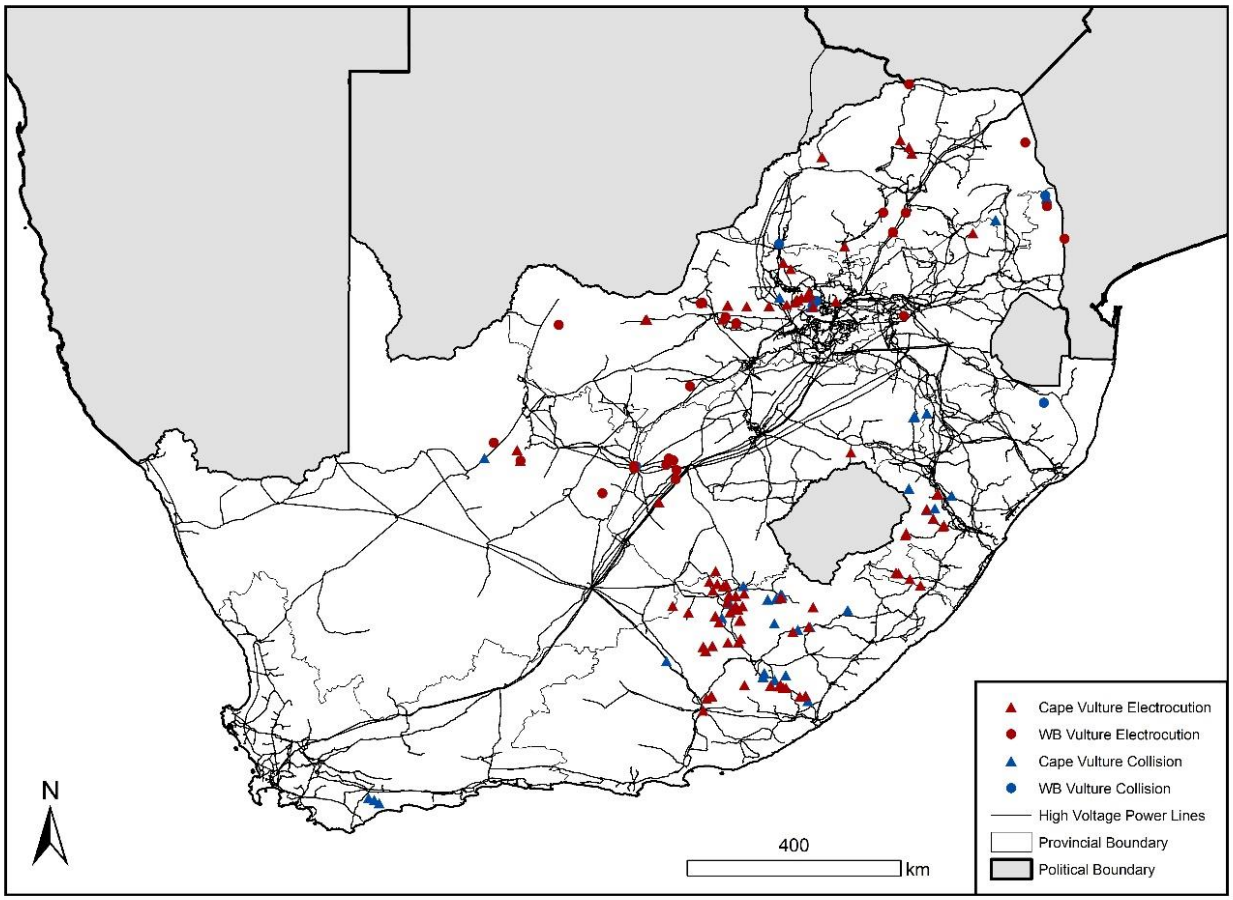


Figure 4.2: A map illustrating all major power lines in South Africa with all power line mortality points (collision and electrocution) marked.

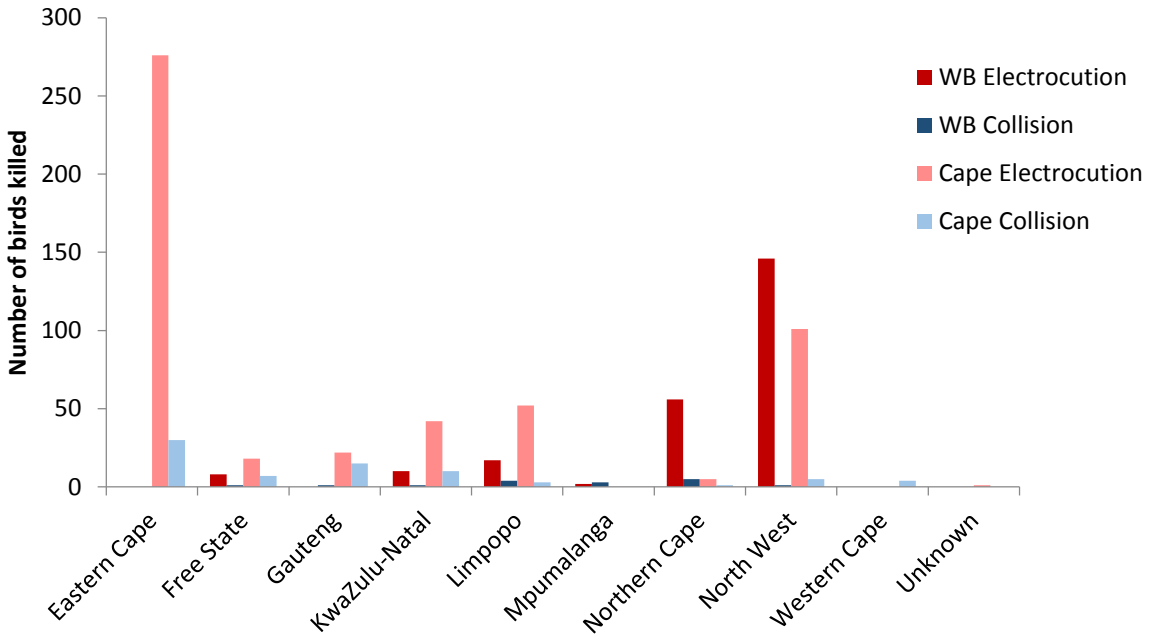


Figure 4.3: The total mortality of white-backed (WB) and Cape vultures from both collision with and electrocution by power lines in each province from 1996 to 2013.

4.4.3: Collision models

The model for collision for both species had a strong AUC value of 0.97 (range: 0.00 – 0.99). A total of 24,336 kilometres of power line had a value of over 0.75 (very high risk) and a total of 42,450 kilometres of power line had a value of over 0.50 (high risk). High risk areas were in western Eastern Cape province, the area around the Potberg Cape vulture colony (Western Cape province), Kruger National Park, and many of the large power lines across the country (Figure 4.4). Distance to feeding station, land use, population density, and voltage each contributed over 10% to the model (Table 4.2).

The model for collision for white-backed vultures had a strong AUC value of 0.98 (range: 0.00 – 0.99). A total of 18,954 kilometres of power line had a value of over 0.75 (very high risk) and a total of 33,856 kilometres of power line had a value of over 0.50 (high risk). High risk areas included northern Limpopo province, Kruger National Park and northern KwaZulu-Natal province (Zululand) (Figure 4.5). The high voltage, long distance lines (transmission lines) are also included. Land use and voltage each contributed over 10% to the model (Table 4.2).

The model for collision for Cape vultures had a strong AUC value of 0.96 (range: 0.00 – 0.99). A total of 19,221 kilometres of power line had a value of over 0.75 (very high

risk) and a total of 32,060 kilometres of power line had a value of over 0.50 (high risk). High risk areas were around the Potberg colony (Western Cape province), and western Eastern Cape province (Figure 4.6). The high voltage, long distance lines (transmission lines) are also included. Distance to feeding station, population density, and voltage each contributed over 10% to the model (Table 4.2).

Table 4.2: Percent contribution of individual variables to three collision MaxEnt models. Values in bold contributed over 10% to the model. The signs next to the percent indicate how the lines were shaped. "-" indicates negative. "+" indicates positive. "-/+" indicates an initial decrease followed by an increase. "+/-" indicates an initial increase followed by a decrease. "n" indicates no clear pattern.

Variable	Both		White-backed vulture		Cape vulture	
Voltage	**45.8**		**45.2**		**45.2**	
Elevation	0.6	+/-	0.3	-	0.1	+/-
Slope	3.1	-	3.1	-	3.9	+
Distance to Water	0.3	-	<0.1	+	1.4	-/+
Distance to Feeding station	**14.3**	-	7.3	-	**19.3**	-
Distance to Protected Area	1.8	+	1.4	-	0.8	+
Cattle Density	0.8	+	0.0	n	1.5	+
Population Density	**16.6**	-	4.5	-	**13.2**	-
Land use	**14.6**		**31.1**		8.8	
Biome	2.1		7.2		5.9	

4.4.4: Electrocution Models

The model for electrocution for both white-backed and Cape vultures had a strong AUC value of 0.95 (range: 0.00 – 1.00). A total of 24,281 kilometres of power line had a value of over 0.75 (very high risk) and a total of 48,732 kilometres of power line had a value of over 0.50 (high risk). High risk areas were border area of the Free State and Northern Cape provinces, northern Limpopo province, and western Eastern Cape province (Figure 4.7). Distance to feeding station, land use, population density, and voltage each contributed over 10% to the model (Table 3.3).

The model for electrocution for white-backed vultures had a strong AUC value of 0.99 (range: 0.00 – 1.00). A total of 6,370 kilometres of power line had a value of over 0.75 (very high risk) and a total of 15,766 kilometres of power line had a value of over 0.50 (high risk). High risk areas were the border of the Free State and Northern Cape provinces,

northern North West province, and Kruger National Park (Figure 4.8). Population density, slope, and voltage each contributed over 10% to the model (Table 4.3).

The model for collision for Cape vultures had a strong AUC value of 0.96 (range: 0.00 – 1.00). A total of 19,481 kilometres of power line had a value of over 0.75 (very high risk) and a total of 40,206 kilometres of power line had a value of over 0.50 (high risk). High risk areas were the border between Free State and Northern Cape provinces, the west of the Eastern Cape province, the Drakensberg region of KwaZulu-Natal province, and north-central Limpopo province. (Figure 4.9). Elevation, distance to feeding station, population density, and voltage each contributed over 10% to the model (Table 4.3).

Table 4.3: Percent contribution of individual variables to three electrocution MaxEnt models. Values in bold contributed over 10% to the model. The signs next to the percent indicate how the lines were shaped. "-" indicates negative. "+" indicates positive. "-/+" indicates an initial decrease followed by an increase. "+/-" indicates an initial increase followed by a decrease. "n" indicates no clear pattern.

Variable	Both		White-backed vulture		Cape vulture	
Voltage	**23.4**		**27.8**		**19.2**	
Elevation	8.1	+	0.0	n	**12.3**	+
Slope	0.6	+/-	**24.6**	-	1.9	+
Distance to Water	0.3	+/-	3.3	+/-	5.1	+
Distance to Feeding Station	**11.9**	-	3.3	-	**14.1**	-
Distance to Protected Area	1.7	-	5.8	-	0.8	-
Cattle Density	1.0	-	0.4	-	1.0	-
Population Density	**35.3**	-	**25.9**	-	**31.1**	-
Land Use	**11.1**		7.3		9.5	
Biome	2.6		1.5		5.0	

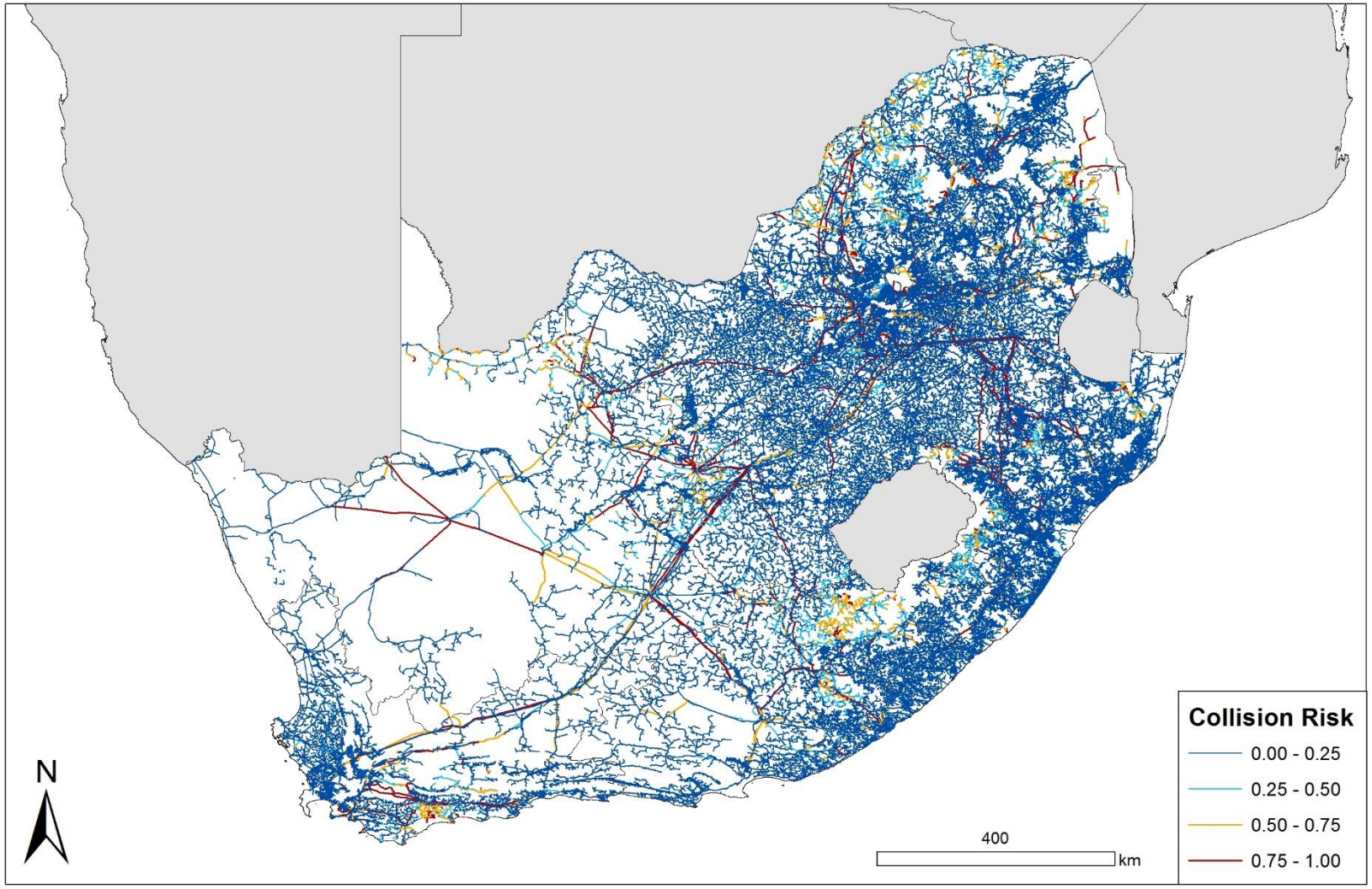


Figure 4.4: Model of power line collision risk in South Africa for both species (white-backed and Cape vultures). Warm colours (red and orange) represent high risk lines while cool colours (blues) represent lower risk lines.

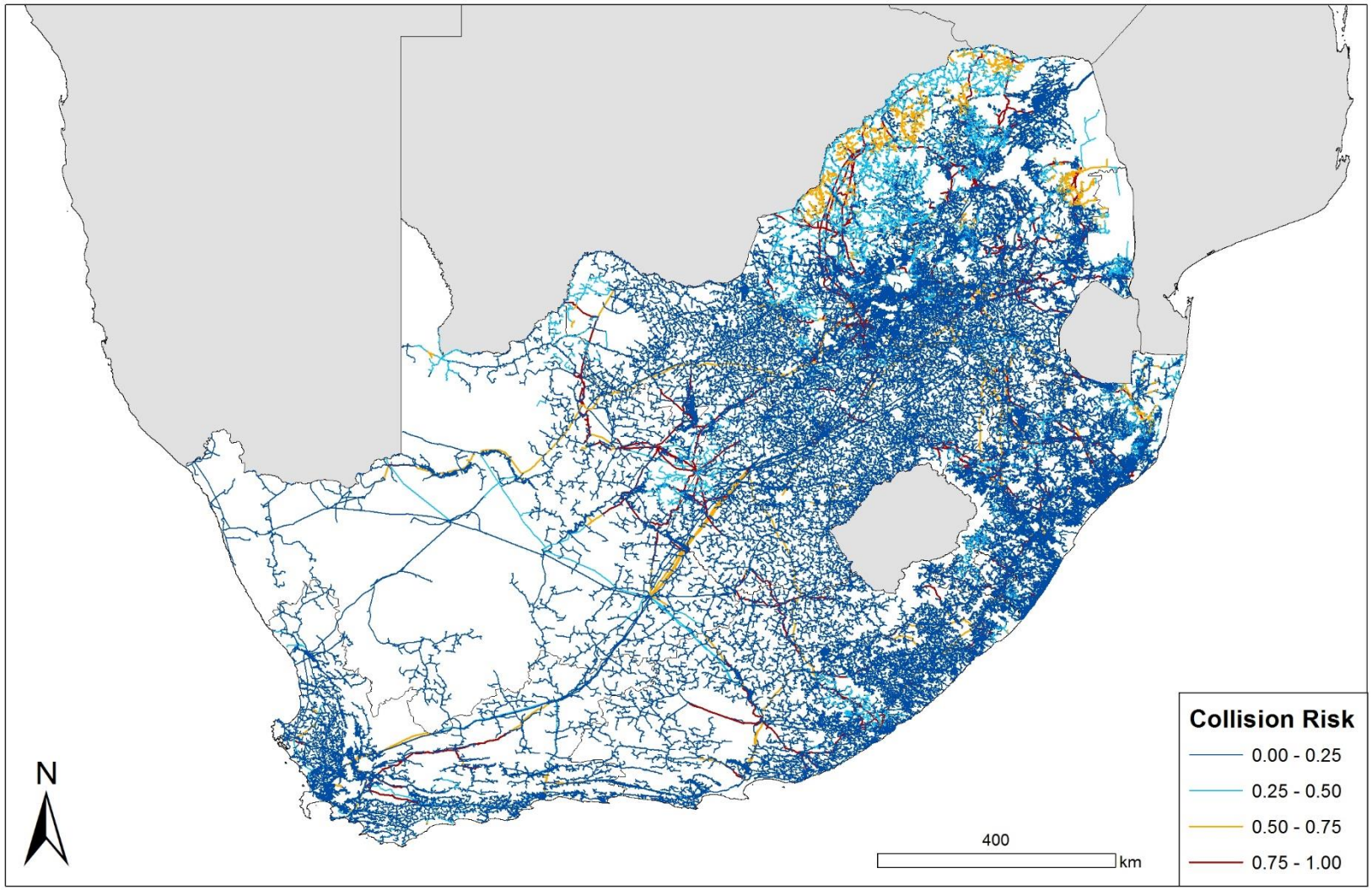


Figure 4.5: Model of power line collision risk in South Africa for white-backed vultures. Warm colours (red and orange) represent high risk lines while cool colours (blues) represent lower risk lines.

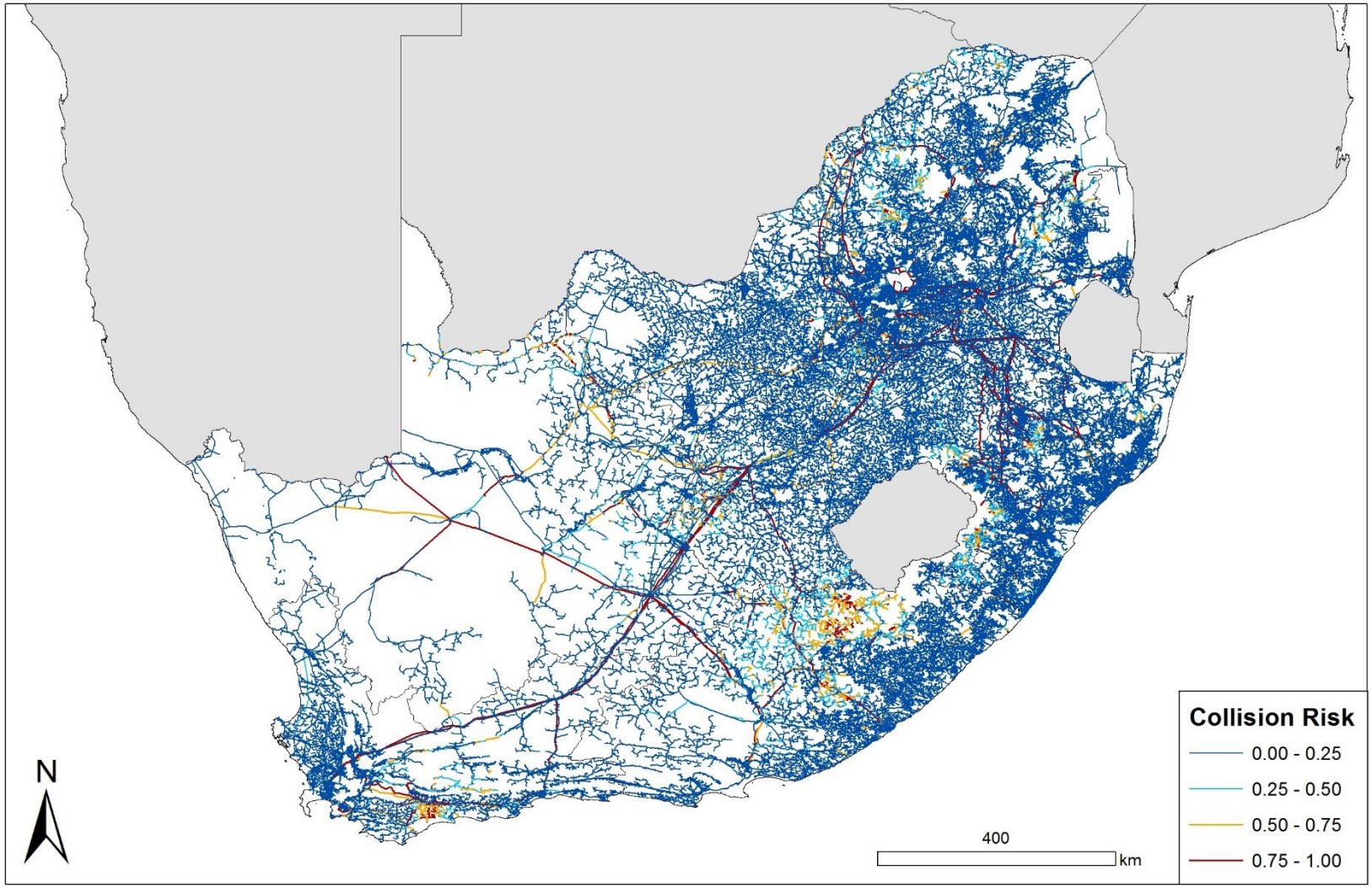


Figure 4.6: Model of power line collision risk in South Africa for Cape vultures. Warm colours (red and orange) represent high risk lines while cool colours (blues) represent lower risk lines.

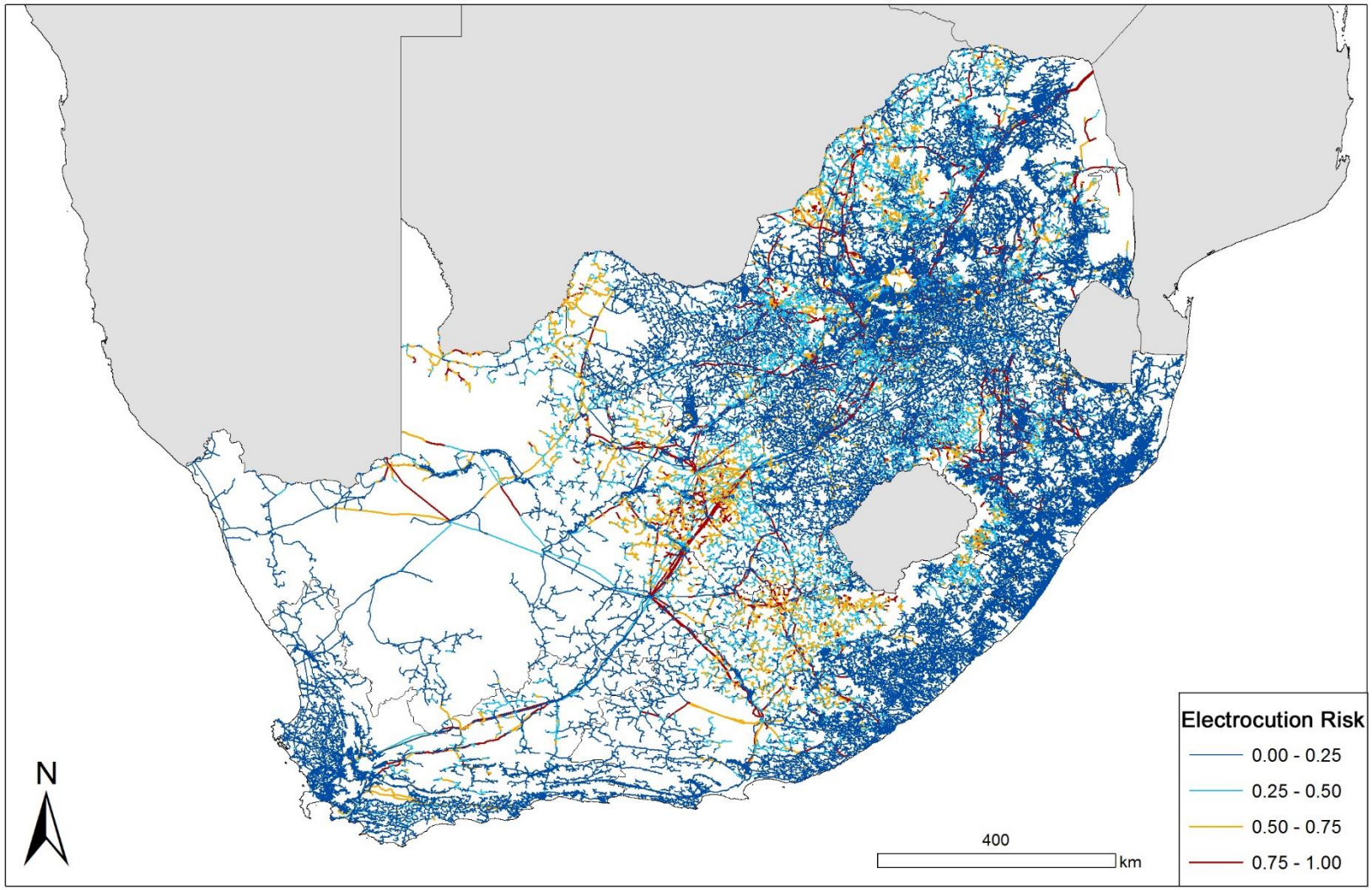


Figure 4.7: Model of power line electrocution risk in South Africa for both species (white-backed and Cape vultures). Warm colours (red and orange) represent high risk lines while cool colours (blues) represent lower risk lines.

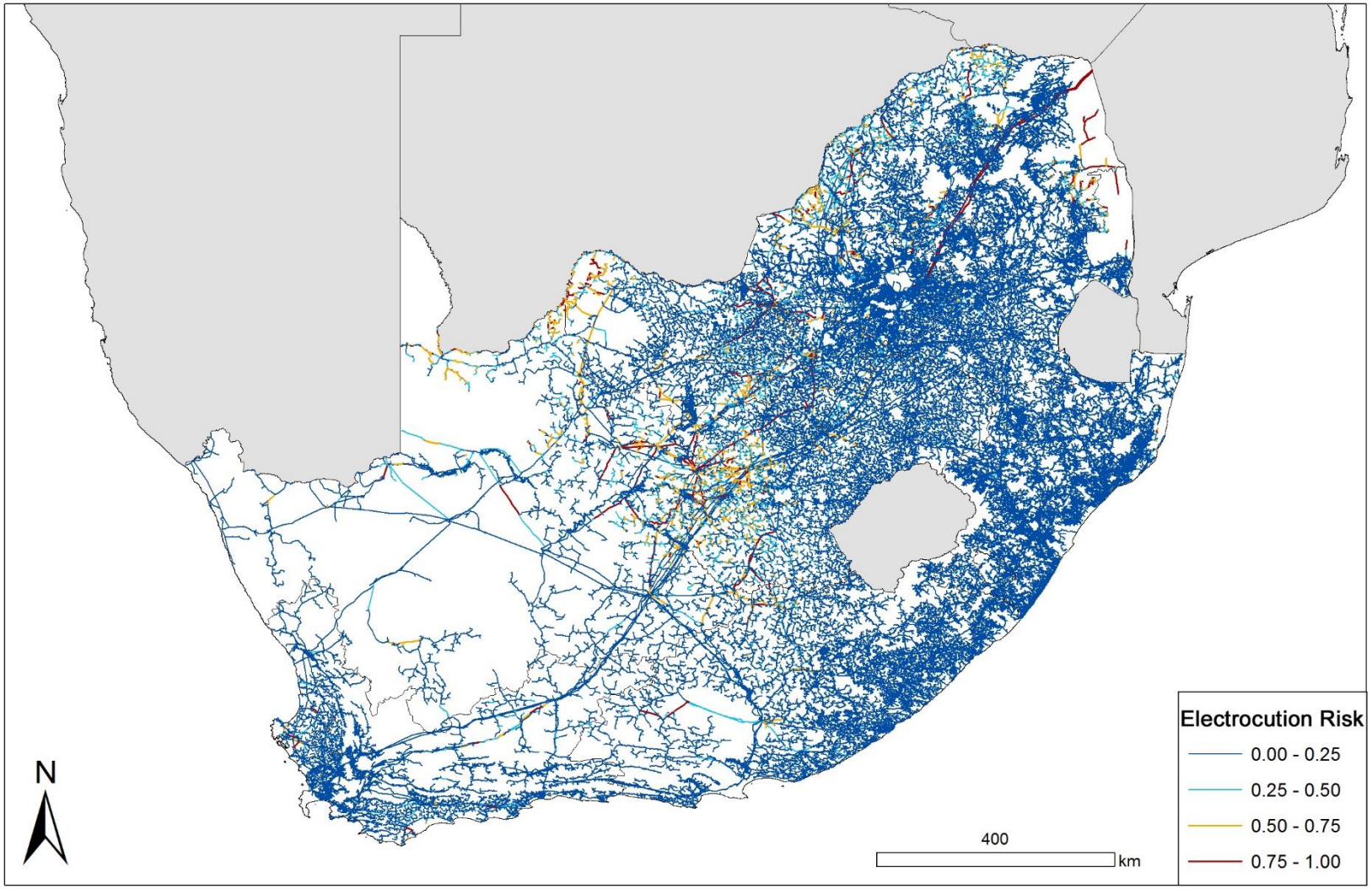


Figure 4.8: Model of power line electrocution risk in South Africa for white-backed vultures. Warm colours (red and orange) represent high risk lines while cool colours (blues) represent lower risk lines.

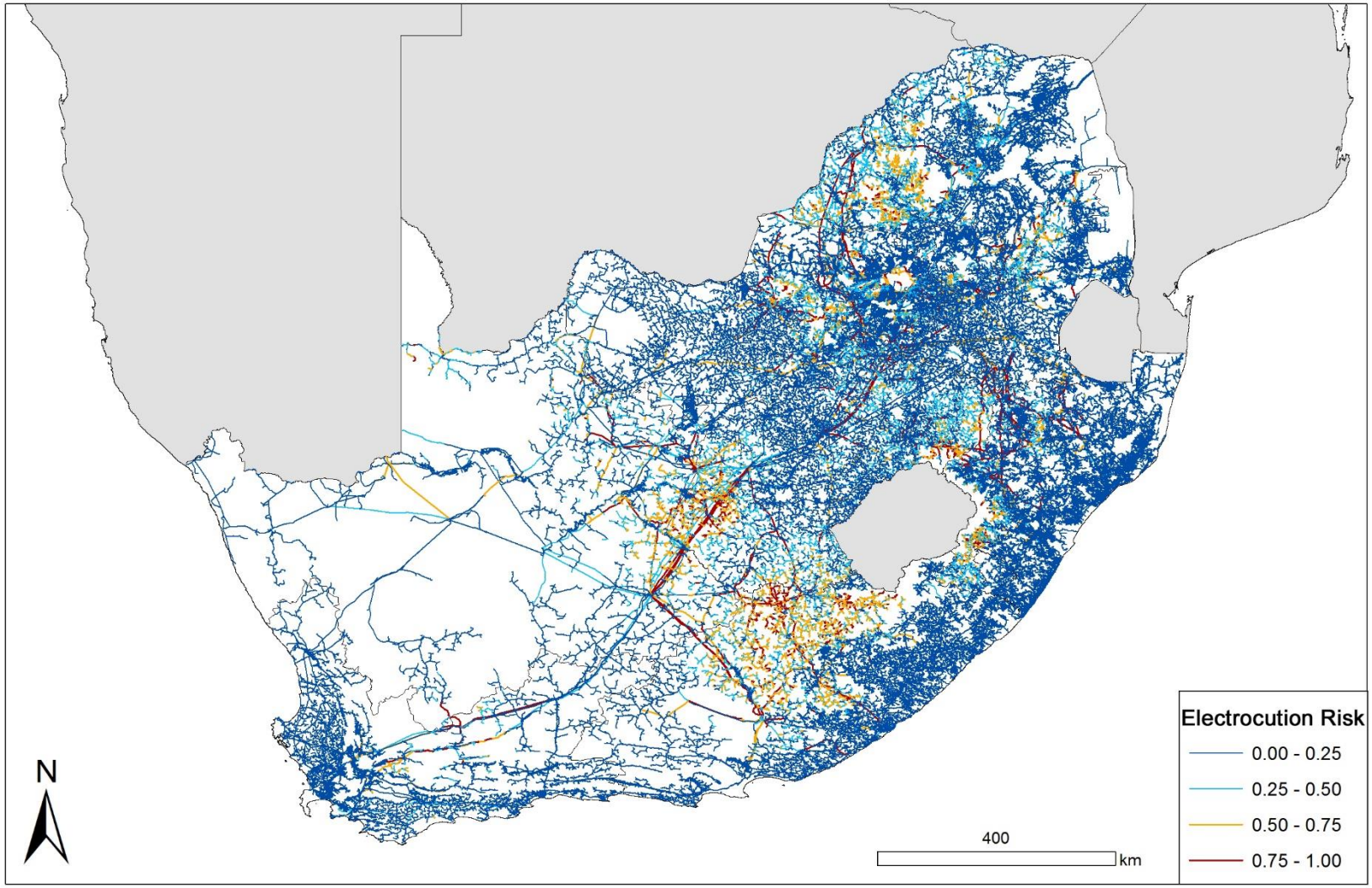


Figure 4.9: Model of power line electrocution risk in South Africa for Cape vultures. Warm colours (red and orange) represent high risk lines while cool colours (blues) represent lower risk lines.

4.5: Discussion

4.5.1: Variables contributing to collision risk

These models identify high risk collision and electrocution areas using large scale landscape variables. The variables that contributed to the model, with the exception of voltage, are largely those that affect the likelihood of vultures being in the area. However, these variables may also be contributing disproportionately to the model due not only to the probability of vultures being an area but also to a real increase collision or electrocution risk.

For the collision models, voltage was the highest contributing variable. High voltage (transmission) lines had the highest risk for collision for both species. This is most likely due to the configurations that are commonly used for the high voltage lines. These lines are more likely to have a ground wire and are generally greater in height. These greater heights may be more similar to the height that vultures are flying at, putting them at greater risk of collision. When vultures are foraging, they are less likely to focus directly in front of them as they are looking at the ground which further increases the risk of the large lines at the foraging height of vultures (Martin et al. 2012).

For white-backed vultures, the other contributing factor to collision risk was land use type with birds being most at risk in natural areas. This may relate not only to where the birds are more likely to be found but also to a change in behaviour when they are in natural areas. The white-backed vultures may be more likely to be foraging in these areas where there are natural carrion sources, and this in turn may put them at higher risk as they are flying lower (e.g. closer in height to power lines). In addition, they are at risk when taking off from a carcass, particularly when frightened (Mundy et al. 1992). Therefore, if they are more likely to be feeding in these areas, they may be more likely to collide with power lines.

Two other major contributing factors to Cape vulture collision risk are 1) distance to feeding station and 2) human population density. Human population density may have a similar function to land use as natural areas are likely to coincide with low human population density areas. The Cape vultures' behaviour may change in a similar way to the white-backed vultures in natural areas (e.g. lower flight height while searching for carrion). Distance to feeding station may also contribute due to the behaviour of Cape vultures in the areas around the site. In many cases the birds are at high risk of collision when taking off from the ground,

especially in cases where they are scared off of a carcass (Mundy et al. 1992). With large numbers of vultures feeding at a designated feeding station, the risk of collision may be higher simply due to increased vulture density.

4.5.2: Variables contributing to electrocution risk

As in the collision risk models, voltage contributed heavily to the electrocution models, with middle voltage lines being the highest risk for both species. This is not consistent with what is known about electrocution risk in vultures. Low voltage (distribution) power lines (22kV and 33kV) are generally believed to be of highest risk due to the arrangement of conductors (Markus 1972, Ledger and Annegarn 1981, Benson 1982, Lehman et al. 2007, Boshoff et al. 2011). The 22kV and 33kV lines were not placed in the low risk category by the model but were not put in particularly high risk categories either. The large lines are more likely to electrocute birds in the case of streamers, when bird excrement connects the conductors and the bird, resulting (rarely) in electrocution (Lehman et al. 2007). An exaggeration of risk on middle voltage lines may be a function of inaccurate geospatial information for some points. This means that all data must be analysed with caution.

Two other variables were major contributing factors to white-backed vulture electrocution risk, slope and human population density. This species tends to be found in flat areas and this is reflected by the model in Chapter 2 (Mundy et al. 1992). Vultures are more likely to be found in flat, open areas (Mundy et al. 1992). They may also be more likely to be perched on power lines in flat areas as this would allow them a good view of the surrounding area and a safe place from predators. In the flat, open areas surrounding Kimberly in the Northern Cape province, white-backed vultures are thought to be expanding their range by using power lines to perch and nest on (Anderson and Hohne 2007). The use of power lines for perching puts the birds at risk of electrocution.

Three other variables were major contributing factors to the Cape vulture model, 1) human population density, 2) distance to feeding station, and 3) elevation. These factors probably strongly influence both the presence and the behaviour of Cape vultures. The effect of elevation is more likely to be a function of presence than a function of behaviour. Cape vultures are often found in mountainous (and sometimes high elevation) areas, particularly in the Eastern Cape and KwaZulu-Natal provinces where they forage in montane grassland areas (Mundy et al. 1992). In terms of electrocution risk, human population density is also

more likely to be function of likelihood of presence rather than a change in behaviour. Distance to feeding station may increase power line mortality risk in vultures due to their behaviour after feeding. Birds often perch on trees or power line structures after eating (Mundy et al. 1992). In the case of feeding stations, there are often many birds which increases the risk of each individual getting electrocuted due to interactions between birds (Lehman et al. 2007, Boshoff et al. 2011).

4.5.3: Conservation implications

Many of the high risk areas for electrocution and collision are in regions with large vulture populations, particularly around important breeding sites. This highlights that many of the important contributing factors likely relate to the density of vultures in a given locale. These locations must be prioritised for retrofitting of lines to reduce risk as much as possible. In many areas, such as Kruger National Park, Eskom has already begun retrofitting lines in spots where birds have been electrocuted or have collided with power lines. It is important to continue this process but it also is important to take a proactive approach to better identify high risk lines before vultures are killed and to build only raptor safe constructions in the future.

Power lines have been retrofitted in a variety of ways. For collision, flappers, spirals and other objects that make the power lines more visible to birds have been attached to lines in high risk areas (Jenkins et al. 2010). Although they are not 100% effective, they do reduce collision risk (Lehman et al. 2007, Jenkins et al. 2010). The ground wire has also been removed as this puts birds particularly at risk (Jenkins et al. 2010). For electrocution risk, insulation of conductors at the insulators has been used as a cost-effective method of reducing electrocution risk (Lehman et al. 2007). If this proves ineffective, the structure can also be changed to a lower risk type structure, although this is much more expensive (Lehman et al. 2007).

It is also important to take these models into account when expanding electrical infrastructure. Areas where vultures occur in high densities and where the risk factors identified are present need to either be avoided or mitigation needs to be put in place from the beginning. This is particularly true in areas where vultures are breeding or near feeding stations. The locations of vulture feeding stations must also be carefully examined to reduce risk for the large number of vultures feeding.

4.5.4: Improving the models

There are many ways of improving these models and our current knowledge of power line mortality in vultures. The easiest way to improve the models would be to increase the number of points included in the models as well as to better include areas where human population is lower. Currently the data for the models were opportunistically collected which leads to bias towards certain areas where either research is being done on power line mortality or there is a large population centre nearby, e.g. around Kimberly in the Northern Cape province. As Boshoff et al. (2011) found, there is a vast underreporting of these incidents. There are several ways that this knowledge could be improved, the first would be to send out surveys to people in order to assess whether they have seen incidents that went unreported. The second option would be to have personnel walking under power lines periodically and regularly to assess the number of carcasses found below the power lines, particularly in areas that are rarely visited. A combination of these methods would likely vastly improve the dataset, particularly for white-backed vultures where there are relatively few incidents recorded. It would also help to assess the overall numbers of birds being killed each year by power lines.

Increasing the accuracy of the geospatial data for each incident would also be useful to identify the responsible lines. These models highlight three things 1) the variables contributing to vulture power line risk, 2) the need for retrofitting in specific areas, and 3) the need to improve data collection. By further investigating each of these factors and implementing solutions based on the data, power line mortality can be reduced for all vulture species which will greatly help with the conservation of these birds.

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Chapter 5: Conclusion

I examined how the habitat choices and movements of South African white-backed (*Gyps africanus*) and Cape (*G. coprotheres*) vultures put them at risk of mortality from interactions with power lines. These species are threatened by a variety of mortality sources including poisoning, habitat loss, declines in food availability, wind turbines, and power lines (Verdoorn et al. 2004, Boshoff et al. 2011, Ogada et al. 2015). Their declines have been extreme over the past three decades. Their loss could be catastrophic and expensive for human and wildlife health (Markandya et al. 2008, Ogada et al. 2011). It is imperative that we understand more about the drivers of the birds' habitat choices and movement, and where they are most at risk. This was a three part study aimed at better understanding these species and their interactions with the environment and power lines. The first chapter examined the habitat choices of both white-backed and Cape vultures on multiple spatial scales. The second chapter studied whether these species exhibit seasonal movements possibly linked to food availability in their environment. The third chapter investigated where vultures are most at risk of power line mortality by electrocution and collision.

Results from the first chapter indicate there were many climatic and non-climatic drivers influencing the habitat choices of both white-backed and Cape vultures. Biome and distance to a feeding station were the key drivers while temperature and precipitation variables were less important. The majority of the predicted suitable habitat for white-backed vultures was in South Africa's largest protected area, the Kruger National Park, with additional areas located in northern Limpopo province. This was true at all scales examined. The Kruger National Park has the largest population of white-backed vultures in South Africa while the areas along the western Limpopo River have highly suitable nesting habitat (Tarboton & Allan 1984). This range means that they spend a large amount of time in protected areas, although this may be a function of this particular sub-population. Cape vultures were predicted to be far more widespread with suitable habitat in Eastern Cape, KwaZulu-Natal, Gauteng, North West, and Limpopo provinces. This suggests that this species is more at risk because they spend less time in large protected areas.

Distance to a feeding station was very important to the Cape vulture habitat models suggesting these sites are extremely important to this species. This allows conservationists to utilize feeding stations to better conserve the species. Feeding stations may reduce the

species' exposure to poisoned carcasses and additional food may improve their breeding success and attract individuals that might increase population recruitment (Robertson and Boshoff 1986, Gilbert et al. 2007, Oro et al. 2008). They may also help manipulate where vultures are likely to be found by reducing the area which birds need to locate food. It is also interesting to note variables that were less important. None of the *human variables* (cattle density, land use, and population density) were major contributors suggesting that birds are not strongly avoiding human developments which may put them at risk of poisoning or power line mortality.

These models must be examined with caution as they underpredict the range of both species. This is probably because the data were from only a portion of both species' overall range. To improve the models, more tracking data needs to be collected and incorporated into the models. More individuals of both species, from different regions, tracked for longer periods of time would strengthen the models. This is particularly true for white-backed vultures in Zululand (Kwa-Zulu-Natal province) and the Northern Cape province. For Cape vultures, the Drakensberg Mountains in KwaZulu-Natal province and the Eastern Cape province, where my tracked birds rarely ventured, needs more investigation. Increased cooperation and data sharing from multiple conservation organisations, research institutions, and government nature conservation authorities in South Africa would greatly improve this effort to obtain more data.

The second chapter examined whether white-backed and Cape vultures were moving seasonally to better exploit food resources. There were very few significant differences in the seasonal movement of white-backed or Cape vultures over the study period. This may suggest that there is more than enough food available for the birds throughout the year. Consistent food availability may relate to several factors including an increase in the amount of livestock on farms and communal grazing areas in South Africa, an increase in the number of game farms, or perhaps an increase in the number of reliable vulture feeding stations (DAFF 2013). In addition, the populations of all vulture species, as well as other scavengers have declined in many areas, perhaps leading to less competition at carcasses (Ogada et al. 2015). Whether there is sufficient food to feed the vulture population or not, vulture feeding stations are still important, providing a safe, poison-free food source and perhaps supplementing younger, less competitive birds.

The final chapter modelled power line risk to white-backed and Cape vultures across South Africa. Across the models the greatest predictor of power line risk across models was voltage, which relates to the height and design of a power line structure. Certain structures

are much more dangerous than others, and voltage may relate to the type of structure (Benson 1982, Bevanger 1998, Lehman et al. 2007, Boshoff et al. 2011). At least one variable related to human influence, land use or human population density, was found to be a major contributor in every model. Vultures tend to be electrocuted in natural or low human population areas. I believe that this is not just a function of where vultures are more likely to be found, as my habitat models suggest little association with natural areas. It may be a function of behaviour in these areas where birds are likely to be doing the majority of their foraging, flying at lower altitudes and spending more time perched or on the ground.

Because my models are predicting electrocutions and collisions in low population areas, it is extremely important to increase monitoring in rural regions. Boshoff et al. (2011) indicated that only a small percentage of power line mortalities are being reported. To improve this number, an active campaign of education should be undertaken to better inform people in rural areas about the Wildlife and Energy Programme (WEP), and emphasis on surveying people in rural areas to detect a greater number of mortalities. Eskom personnel properly surveying a number of power lines a year may also help better understand where birds are at risk. These efforts can be focused in high risk predicted in my models. Increasing the electrocution and collision datasets will make the models more robust, particularly for white-backed vultures where the data are very limited.

Despite the different drivers in the habitat suitability and power line mortality models, it is clear that many of the areas that are most suitable to white-backed and Cape vultures are also areas of high power line mortality risk. This supports the idea that vulture density is one of the drivers of power line mortality risk, as we would expect. The different important variables from both models suggest that density is not the sole predictor of electrocution and collision risk in vultures. It is important to note the places where the models overlap to prioritise retrofitting of power lines in these areas. Many of these regions of overlap are in important breeding areas or near vulture feeding stations.

There are many lessons to be learned from this study about the conservation of and research on vultures. Firstly, it highlights the importance of vulture feeding stations. It is documented that feeding stations reduce the risk of poisoning, as well as provide reliable food sources for vultures (Gilbert et al. 2007, Oro et al. 2008). It also appears, based on my habitat suitability model, that feeding stations may be profoundly changing how vultures move through their environment at sub-continental scales. This may allow conservationists and managers to change where vultures spend their time through the use of feeding stations.

It is important to place feeding stations in areas where the birds are safe, particularly from power lines, to avoid mortality.

Secondly, it highlights that mitigation actions are required to address power line induced vulture mortality. These models may allow Eskom to take a more proactive approach to vulture power line mortality by identifying high risk lines which they can manage accordingly. With the populations of white-backed and Cape vultures declining rapidly, reducing mortality in any way possible is extremely important to both species' long term survival. It is also important to assess these models through ground-truthing of power line mortality to improve them and to better predict high risk areas.

The biggest lesson from a research point of view is that it is important to have large, comprehensive datasets to improve habitat suitability models, and other spatial analyses of vultures. These datasets can be created through cooperation and data sharing between the many vulture stakeholders such as conservation organisations, researchers, and government agencies. To better conserve both species, it is extremely important to holistically understand vulture foraging, nesting and roosting, and where they are at greatest mortality risk to poisoning and/or power lines.

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