Identifying drivers of Cape vulture (*Gyps coprotheres*) space use in southern Africa

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Chapter 2 is published in the peer-reviewed journal *PLoS ONE* with William Louis Phipps as first and corresponding author. Co-authors were Kerri Wolter, Michael Michael, Lynne MacTavish and Richard Yarnell. W L Phipps collected and analyzed the data and wrote the article, and R W Yarnell was his director of postgraduate studies. K Wolter and L M MacTavish assisted with data collection. W L Phipps was the corresponding author for the published article and all authors listed above provided comments on article drafts prior to publication.

Abstract

The decline of worldwide vulture populations due to multiple anthropogenic threats is recognised as one of the most important issues in avian conservation due to the loss of the important ecosystem services that they provide. The Cape vulture (*Gyps coprotheres*) is endemic to southern Africa and is listed as Vulnerable by the International Union for Conservation of Nature due to declines across its range largely attributed to poisoning and fatal interactions with the expanding power line network.

In this thesis I provide a first insight into the factors that drive the space use patterns of Cape vultures in an effort to inform future conservation strategies. I deployed Global Positioning System (GPS) tracking units attached to vultures caught from the wild in the main breeding range of the species in northern South Africa, and in north-central Namibia where the species has recently been declared extinct as a breeding species but a small population remains. Tracking units were also deployed on three Cape vultures released in Namibia as part of a pilot reintroduction program. The GPS tracking data were used to delineate the size and extent of the vulture home ranges and to identify key factors influencing their movement patterns. Their relative use of unprotected and protected areas was assessed, as well as the influence of vegetation characteristics. Finally, I present the first approximation of the spatial niche of Cape vultures using ecological niche modelling methods and provide a first assessment of the potential impacts of climate change on their future occurrence.

Immature individuals and two of the reintroduced vultures traversed extensive ranges (maximum home range >975,000 km^2) and regularly crossed international borders, while wild-caught adult vultures tended to show a higher degree of site fidelity while foraging across more restricted ranges (maximum home range <150,000 km^2) closer to known breeding colonies. The vultures tracked from South Africa regularly used transmission line towers as roost and perch sites which has allowed them to extend their foraging range beyond their historical distribution into areas previously devoid of suitable perches. Although some adults often roosted at breeding colonies inside officially protected areas, all of the vultures foraged primarily on unprotected or privately managed land. The vultures generally tended to forage in more open habitats. The ecological niche models indicated that bioclimatic variables such as precipitation seasonality were the key factors that influenced the space use of the tracked vultures. The models predicted that climate change could potentially result in significant pole-wards shifts of up to 333 km in Cape vulture occurrence patterns, putting the core breeding colonies in the north of their range under threat.

This study has provided a first insight into the ranging patterns of Cape vultures using GPS tracking methods and has identified that their extensive ranges, frequent use of unprotected land and close association with power lines puts them at serious risk from multiple threats during their regular foraging activity. The findings of this study confirm for the first time that the threat of climate change to Cape vultures should be seriously considered when planning future conservation measures. This research has demonstrated the ability of GPS tracking methods to identify new threats and key areas for the implementation of conservation measures.

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Pencil drawing by Rory McCann, 2012

"I saw others spiralling on motionless wings high in the sky. Swarms of them, with ever more arriving as if from nowhere – first as barely visible specks in the sky – until they overpowered my senses."

Professor Bernd Heinrich, Life Everlasting – The Animal Way of Death.

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CHAPTER 1: INTRODUCTION

1.1. General introduction

Global biodiversity loss is increasing at unprecedented rates primarily driven by anthropogenic activities that cause widespread habitat loss and degradation, as well as direct persecution and over-exploitation of threatened species (Butchart *et al.* 2010; Dirzo *et al.* 2014). Of all described species, 41% of amphibians, 26% of mammals and 13% of bird species are threatened with extinction (Monastersky 2014), with an estimated 25% average decline in the abundance of terrestrial vertebrate species since 1500 AD (Dirzo *et al.* 2014). Current estimates indicate that the sixth mass extinction (defined as a loss of 75% of species) in the planet's history might occur as soon as the year 2200, despite increasing conservation efforts (Butchart *et al.* 2010; Monastersky 2014). Such catastrophic species losses are likely to reduce the stability of ecological communities, with associated cascading effects that could lead to the loss of vital ecosystem services on which we depend (Dirzo *et al.* 2014; Seddon *et al.* 2014).

Scavenging vertebrates are a particularly threatened guild, with avian scavengers being the most at risk of extinction of all avian functional groups (Sekercioglu *et al.* 2004; Hoffmann *et al.* 2010). Scavenging birds such as vultures are highly specialised to rapidly consume the carcasses of large animals and provide vital ecosystem services by recycling nutrients, leading other scavengers to carrion, and ultimately limiting the development and spread of diseases to human communities (DeVault *et al.* 2003a; Sekercioglu *et al.* 2004; Sekercioglu 2006a; Ogada *et al.* 2012a). It is widely recognised that the dynamics of scavenger communities would be drastically altered following vulture population declines and that diseases such as anthrax would be likely to develop and spread much more rapidly (Sekercioglu *et al.* 2004; Markandya *et al.* 2008; Ogada *et al.* 2012b). It has recently been estimated in Spain that replacing the carcass removal service naturally provided by vultures with carcass removal by vehicles would lead to significantly increased greenhouse gas emissions and higher government expenditure (Morales-Reyes *et al.* 2015).

The potential ecological and human health consequences of vulture declines have recently been observed in South Asia where some populations of vulture species in the *Gyps* genus declined by up to 99.9% in a 15 year period after being accidentally poisoned by the non-steroidal anti-inflammatory drug (NSAID) diclofenac which was widely used to treat livestock at the time (Prakash *et al.* 2007; Pain *et al.* 2008). The vulture population decline gave rise to substantial increases in feral dog numbers as they faced reduced competition at carcass dumps, leading to significant increases in cases of rabies both within the dog population and in humans as the frequency of dog bites also increased (Markandya *et al.* 2008). The "Asian vulture crisis" generated considerable concern and urgent calls for further research into vulture ecology and conservation to prevent similar catastrophes in the future (Koenig 2006; Pain *et al.* 2008; Ogada *et al.* 2012b).

Vulture populations in Africa are also declining across the continent due to multiple anthropogenic threats including poisoning, fatal interactions with power lines, harvesting for the illegal wildlife trade and habitat loss and degradation (Virani *et al.* 2011; Ogada *et al.* 2012b; Ogada 2014). Although protected areas are thought to be vital for the persistence of vultures in many regions of Africa (Thiollay 2006b; Virani *et al.* 2011; Kendall and Virani 2012), their role throughout the continent remains unclear, particularly in southern Africa where vultures frequently forage outside national parks and wildlife reserves and thus encounter the full range of threats (Bamford *et al.* 2007; Phipps *et al.* 2013a). The conservation of wide-ranging species is particularly difficult without reliable information about their spatial ecology and movement patterns (Runge *et al.* 2014). Increasing our knowledge about vulture ranging behaviour and identifying potential threats in key areas have been acknowledged as priorities for the effective conservation of all vulture species in Africa (Virani *et al.* 2011; Ogada *et al.* 2012a).

The rapidly developing field of remote wildlife tracking using Global Positioning System (GPS) technology offers the opportunity to study the spatial ecology of wide ranging species for conservation purposes (Kie *et al.* 2010; Tomkiewicz *et al.* 2010; Wall *et al.* 2014). The aim of this study is to provide a first insight into the movement patterns of the threatened Cape vulture *Gyps coprotheres* (listed as Vulnerable by the IUCN (BirdLife International 2013)) using GPS tracking units fitted to wild-caught vultures in northern South Africa and north-central Namibia. The influence of protected areas, power lines, land use practices and other environmental factors on Cape vulture ranging behaviour are assessed and a first assessment of the potential impact of climate change on Cape vulture occurrence is provided. Ultimately it is hoped that the findings of this study will inform Cape vulture conservation measures and stimulate further research.

1.2. *Gyps* vultures in Africa: ecology, threats and conservation

1.2.1. *Gyps* vultures: an introduction

The eight species of vulture in the *Gyps* genus occur only in the Old World and are characteristically large in body size and wingspan, with almost featherless elongated necks and heads, and brown or cream coloured plumage which becomes lighter with age (Mundy *et al.* 1992; Duriez *et al.* 2011) (Fig. 1.1.). All species show very limited sexual dimorphism in appearance and foraging behaviour (Bose *et al.* 2007; Bose *et al.* 2012). *Gyps* vultures are generally gregarious and are regarded as obligate scavengers because they feed exclusively on the carcasses of dead animals, primarily large ungulates (Houston 1974b, a; Dermody *et al.* 2011). The spatial and temporal unpredictability of the availability and distribution of this ephemeral food source has given rise to several morphological and behavioural adaptations that allow *Gyps* vultures to efficiently locate and consume carcasses, often before their terrestrial competitors (Houston 1979; Ruxton and Houston 2004; Dermody *et al.* 2011; Moleon *et al.* 2014a). For example, their large body size and long and broad wings (e.g. Cape vultures can weigh more than 10.6 kg and have a wingspan of 2.5 m (Mundy *et al.* 1992)) result in a high wing loading (e.g. 112 $N \cdot m^{-2}$ for Cape vultures (Pennycuick 1972)) that is well adapted for an energy efficient soaring flight that allows them to travel relatively long distances in short periods by making use of thermals and orographic lift (Pennycuick 1972; Duriez *et al.* 2014). *Gyps* vultures are therefore able to traverse large foraging ranges and it is not unusual for them to travel more than 150 km in a day from their nest or roost sites (Houston 1976), with flight speeds of over 100 kmh^{-1} and daily distances of over 250 km recently recorded in immature African white-backed vultures *Gyps africanus* (Phipps *et al.* 2013a).

Figure 1.1. Adult Cape vulture (A) in flight and (B) showing the characteristically long, almost featherless head and neck.

In contrast to New World vultures and most mammalian scavengers that use their sense of smell to locate carrion (Houston 1979, 1986), *Gyps* vultures do not use olfaction and are reliant on their high visual acuity to detect carcasses from distances of at least 4 km (Pennycuick 1972; Houston 1974a). The search efficiency of *Gyps* vultures is increased further by their use of social foraging networks whereby they monitor the movements of other soaring vultures and immediately move towards any bird rapidly descending to a carcass (Pennycuick 1972; Houston 1974a). This process of social facilitation and information transfer between vultures gives rise to a chain reaction of many individuals arriving at a carcass from distances of more than 35 km away and partially explains their gregarious feeding, breeding and roosting behaviour (Houston 1974a; Ruxton and Houston 2004; Jackson *et al.* 2008b; Dermody *et al.* 2011). In this way hundreds of vultures can gather at a single carcass (Fig. 1.2.) creating a highly competitive feeding event, during which they use their long powerful necks, sharp bills and serrated-edged tongues to fill their large crops with >1 kg of soft tissue within 2 minutes (Houston 1974b; Houston and Cooper 1975; Mundy *et al.* 1992). The unpredictability of the carrion supply is reflected in this rapid speed of consumption as the vultures need to gain as much energy as possible at each feeding event, and also provides a further evolutionary explanation for their large body size which allows them to build up stored energy reserves to sustain them through periods of low food availability or poor weather when they are unable to fly (Houston 1976, 1979; Ruxton and Houston 2004; Duriez *et al.* 2014). This is particularly important for breeding adults that are restricted to foraging within a certain distance of their nest sites and often experience food shortages at critical periods of chick-rearing (Houston 1976). In contrast, immature vultures are able to travel more freely in a nomadic manner between areas of fluctuating carrion availability (Houston 1976; Phipps *et al.* 2013a).

Gyps vultures are therefore highly specialised to efficiently locate and rapidly consume ungulate carcasses, and are consequently the main consumers of ungulate carrion in the African savannah ecosystem (Houston 1974b, 1979). For example, it was estimated that *ca.* 26 million tonnes of non-predated ungulate carrion were available to scavengers each year in the Serengeti ecosystem in Tanzania, of which more than half was consumed by vultures, with the remainder eaten by mammalian carnivores such as spotted hyaena (*Crocuta crocuta*) and lions (*Panthera leo*), or invertebrates and bacteria (Houston 1979). In many parts of southern Africa where large carnivores have been extirpated and are now largely restricted to fenced reserves (Packer *et al.* 2013), it is likely that vultures consume a larger proportion of available carrion in the wider landscape than in the past (Benson *et al.* 2004).

The ecological relationship between mammalian carnivores and vultures is therefore complex and varies in space and time (Moleon *et* *al.* 2014b; Pereira *et al.* 2014). Although vultures do derive some food from large predator kills in areas where they persist (Kruuk 1967; Kendall 2013), the majority of ungulate deaths are caused by malnutrition, disease or injury (Houston 1974b; Moleon *et al.* 2014b). Most large predators are facultative scavengers to some degree and consequently directly compete with vultures for carrion (Moleon *et al.* 2014b), often actively defending a carcass and preventing vultures from feeding (Hunter *et al.* 2007; Kendall *et al.* 2012). It has recently been recognised that the intricate network of facilitative and competitive interactions between vultures and mammalian carnivores is poorly understood and further research into scavenger dynamics has been encouraged, particularly given the potential implications of the loss of vultures and other scavengers for ecosystem function and stability (Wilson and Wolkovich 2011; Ogada *et al.* 2012b; Moleon *et al.* 2014b; Pereira *et al.* 2014).

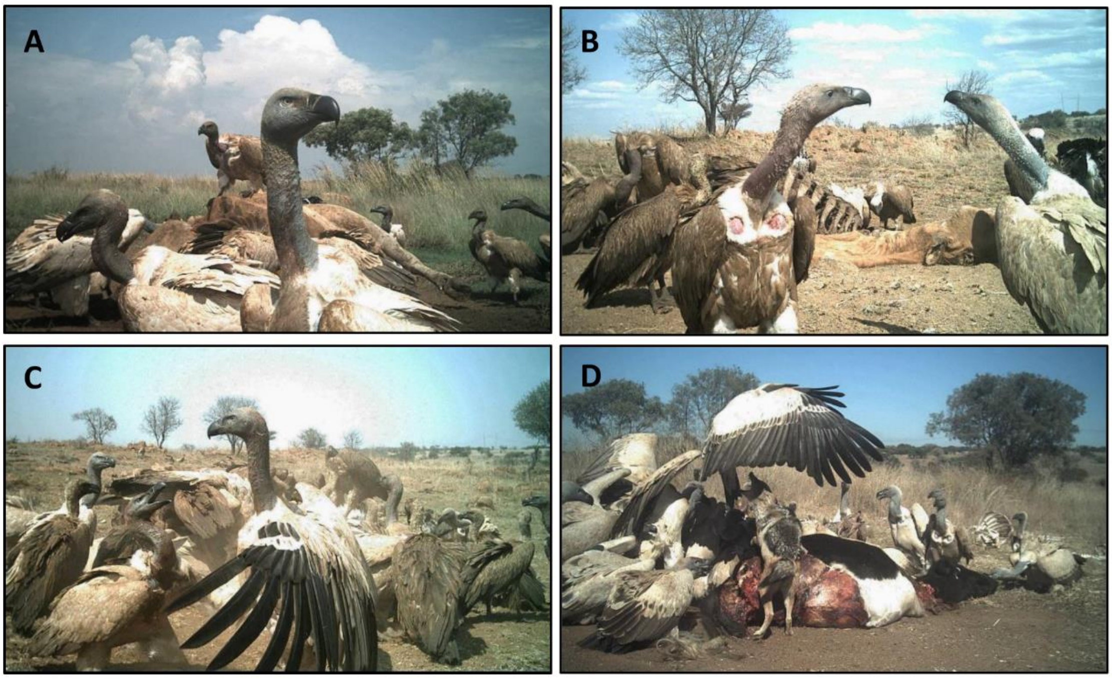

Figure 1.2. Camera trap photographs from a vulture feeding site at Mankwe Wildlife Reserve, South Africa, showing: (A) an adult Cape vulture with full crop partially visible; (B) a characteristically dark brown immature Cape vulture on the left compared to a paler adult on the right (a juvenile African white-backed vulture is immediately behind the immature Cape vulture); (C) an adult Cape vulture adopting a dominant posture towards a younger individual; (D) a black-backed jackal competing for food with a group of Cape vultures.

1.2.2. The Cape vulture in southern Africa

The Cape vulture is a gregarious, cliff-nesting species endemic to southern Africa where the main breeding range occurs in mountainous areas of the north-east and south-east of South Africa and south-east Botswana (Fig. 1.3; (Mundy *et al.* 1992; Whittington-Jones *et al.* 2011; BirdLife International 2015)). The population has been estimated at 8,000 – 10,000 individuals, with less than 4,000 breeding pairs, 80% of which nest at 18 core colonies, the largest being located in the North West and Limpopo Provinces of northern South Africa (Boshoff and Anderson 2007; Whittington-Jones *et al.* 2011; BirdLife International 2015). Due to continuing declines across its range the Cape vulture is now listed as Vulnerable on the IUCN Red List and is considered extinct as a breeding species in Swaziland, Zimbabwe and Namibia, although the species does still forage in those countries (BirdLife International 2015).

In the north of its current range the Cape vulture coexists with the morphologically and ecologically similar African white-backed vulture (*Gyps africanus*), although the latter is smaller and considered more of a lowland savannah species where it nests in trees in loose colonies (Mundy *et al.* 1992; Bamford *et al.* 2009b, a). Despite this degree of habitat partitioning between the two species they do compete for the same food supply in certain areas, particularly in north-east South Africa and south-east Botswana where both species breed (Houston

1975; Mundy *et al.* 1992; Hertel 1994). A similar scenario occurs in East Africa where the cliff-nesting Rüppell's vulture (*Gyps rueppellii*) competes at carcasses with the African white-backed vulture (Kendall *et al.* 2012). Other vulture species that frequently feed at carcasses in the range of the Cape vulture are the lappet-faced vulture (*Torgos tracheliotos*), the white-headed vulture (*Trigonoceps occipitalis*), and the bearded vulture (*Gypaetus barbatus meridionalis*), although they all occur at lower densities and are less gregarious than *Gyps* species (Kendall *et al.* 2012; Kendall 2013, 2014; Krueger *et al.* 2015). The hooded vulture (*Necrosyrtes monachus*) also occurs in the north and east of the Cape vulture distribution.

Most early research into the feeding ecology of African vultures was carried out in the largely protected Serengeti-Mara ecosystem in East Africa which has been suggested as the most suitable model for conditions in southern Africa prior to modern social and economic development (Houston 1974b, a, 1975, 1979; Benson *et al.* 2004). In that environment vultures consumed the wild ungulate species that naturally occurred in the area, with a significant proportion of their energy requirements being obtained from carcasses of migratory species such as wildebeest (*Connochaetes taurinus*) and zebra (*Equus quagga*), as well as more sedentary species such as impala (*Aepyceros melampus*) and Thomson's gazelle (*Eudorcas thomsonii*) (Houston 1974b, 1979).

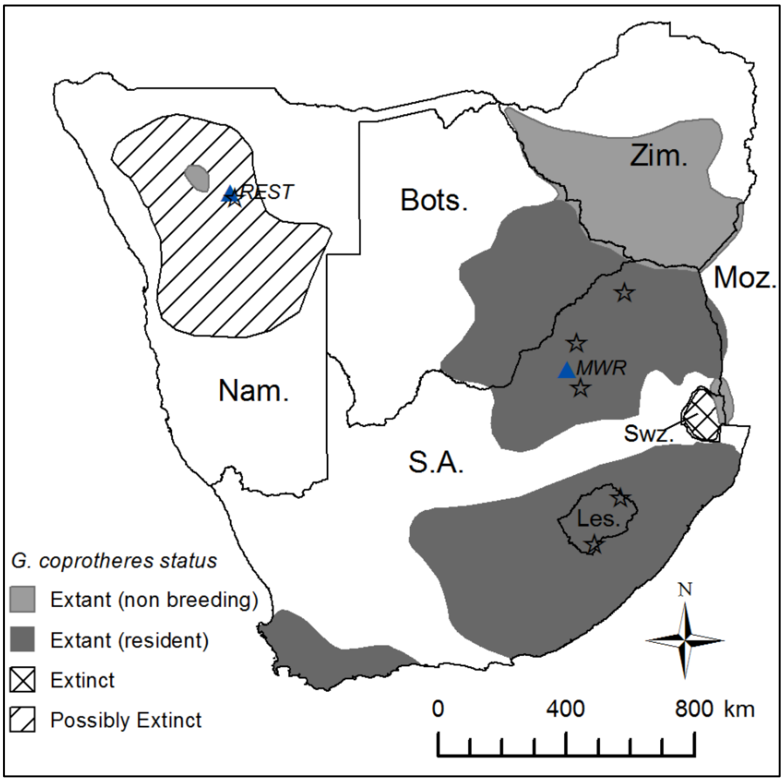

Figure 1.3. Species range map for the Cape vulture *Gyps coprotheres*. Species status is shown as shaded polygons according to the map legend (BirdLife International and Natureserve 2011). Country names are abbreviated to three letters or initials. Stars indicate some of the major Cape vulture breeding colonies. Blue triangles indicate the capture site at Mankwe Wildlife Reserve (MWR) and the Rare and Endangered Species Trust (REST).

In the last few centuries southern Africa has undergone rapid economic development and concurrent changes to land use and farming practices have resulted in significant changes to ungulate abundance and distribution (Biggs *et al.* 2008). Between the 18th and 20th centuries vultures were forced to feed more frequently on domestic livestock as wild ungulates were removed from much of southern Africa to make way for modern farming practices (Boshoff and Vernon 1980; Mundy *et al.* 1992). The onset of commercial livestock farming and the associated improvement in animal husbandry led to a decrease in carrion availability for vultures and has been identified as an important factor contributing to widespread vulture population declines in the region (Boshoff and Vernon 1980; Mundy *et al.* 1992; Boshoff and Anderson 2007). More recently wild ungulate species have been reintroduced in high numbers to large areas of their former ranges for the game farming, hunting and ecotourism industries, particularly in South Africa and Namibia (Van der Waal and Dekker 2000; Van der Merwe and Saayman 2005; Lindsey *et al.* 2013b). In addition, supplementary feeding sites, termed “vulture restaurants”, have recently been established in southern Africa to provide an additional source of carrion for vulture conservation and monitoring purposes (Piper *et al.* 1999; Yarnell *et al.* 2015). Although such feeding sites are regularly visited by large numbers of vultures, their wider impacts on the ecology of vultures and other scavengers are poorly understood (Phipps *et al.* 2013a; Yarnell *et al.* 2015). Therefore, in modern times vultures in southern Africa have adapted their foraging behaviour to exploit a number of food sources consisting of both wild ungulate species and domestic livestock carcasses (Mundy *et al.* 1992; Benson *et al.* 2004; Murn and Anderson 2008).

The local abundance and mortality rates of ungulates, and therefore carrion availability, are primarily driven by seasonal rainfall patterns (Owen-Smith *et al.* 2005; Ogutu *et al.* 2008; Owen-Smith 2008) and have been shown to influence the breeding activity of *Gyps* vultures in addition to their foraging behaviour (Virani *et al.* 2012; Kendall *et al.* 2014). The typical nesting season for Cape vultures is from April to October and coincides with the dry winter months when ungulate mortality, and therefore food availability, is highest due to nutritional stress when nutrient availability in vegetation is limited (Houston 1976; Mundy *et al.* 1992; Owen-Smith *et al.* 2005). A single egg is incubated by each pair for approximately 57 days after which the nestling is fed regurgitated soft tissue and bone fragments for approximately 140 days when it fledges in October or November having gained approximately 8 kg in weight (Mundy *et al.* 1992; Benson *et al.* 2004). On average between 45% and 78% of breeding pairs that lay an egg successfully fledge a chick (Mundy *et al.* 1992; Whittington-Jones *et al.* 2011). Over the next three months the fledgling vultures continue to forage with their parents and the other vultures from the breeding colony during the post-fledging dependence period (Mundy *et al.* 1992). Therefore, breeding adults spend up to 10 months nesting or raising their chicks each year and are normally restricted to foraging in relative proximity to the colony (Houston 1976; Mundy *et al.* 1992). In contrast, once juvenile Cape vultures can forage independently they are able to disperse away from their natal areas and move in a nomadic manner between areas of fluctuating food availability, which is typical of other *Gyps* vultures and other raptor species (Newton 1979; Mundy *et al.* 1992; Phipps *et al.* 2013a). The first year after fledging is the most risky for Cape vultures, with survival rates estimated at 29-56%, increasing to 58-76% for vultures aged four years or more (Piper *et al.* 1999). Cape vultures generally only breed after six years when adult survival rates are estimated at more than 90% (Piper *et al.* 1999; Monadjem *et al.* 2014). Despite the relatively high survival rates estimated for adult Cape vultures, continuing economic development and associated urbanisation and land use change, particularly in their core breeding areas, makes them increasingly susceptible to multiple threats across their range (Biggs *et al.* 2008; Naidoo *et al.* 2011; Monadjem *et al.* 2014).

1.2.3. Threats to Cape vultures

Vulture populations are particularly vulnerable to elevated mortality rates and potential extinction due to their large body size, slow life history, low population density, relatively restricted ranges and their occupation of an ecological niche at a high trophic level (Purvis *et al.* 2000; Ogada *et al.* 2012a). Multiple anthropogenic factors have caused

61% of vulture species found worldwide to be threatened with extinction (Ogada *et al.* 2012a). For example, lead poisoning from hunting activity continues to threaten the California condor (*Gymnogyps californianus*) in the USA despite its partial recovery from near-extinction (Finkelstein *et al.* 2012), and now other New World vulture species are also showing signs of chronic lead exposure (Behmke *et al.* 2015). The rapid decline of up to 99.9% of three species of vultures in the *Gyps* genus in the Asian subcontinent after they were accidentally poisoned by the veterinary drug diclofenac further illustrated the vulnerability of vultures to anthropogenic threats, as well as the potential ecological and socio-economic consequences (Prakash *et al.* 2007; Pain *et al.* 2008; Ogada *et al.* 2012b).

African vulture species are also under serious threat of extinction, with declines of up to 98% recorded for some species in West Africa (Thiollay 2007b) and declines of 50-60% in East and southern Africa in the last 30 years (Virani *et al.* 2011; Ogada *et al.* 2012a). The Cape vulture has declined by more than 20% over three generations, with declines of up to 70% estimated in parts of eastern South Africa (BirdLife International 2015). Most strikingly the population of Cape vultures in Namibia, where it is now extinct as a breeding species, declined from *ca.* 2000 birds in the 1950s to only 13 breeding birds in the 1980s and approximately 25 individuals in 2006 (Brown 1985; BirdLife International 2015). Experimental small scale (<20 individuals) reintroductions of captive or rehabilitated vultures to

Namibia from South Africa in 2005 are thought to have failed due to high mortality or dispersal rates (Diekmann and Strachan 2006; BirdLife International 2015).

In an effort to stabilise the Cape vulture population the Cape Vulture Task Force (CVTF), consisting of vulture researchers and conservation practitioners, was established in 2006 to gather information to inform future conservation actions (Boshoff and Anderson 2007). During the first CVTF meeting consensus was reached that the most serious threats to the persistence of Cape vultures were poisoning, fatal interactions with power lines, unsustainable harvesting for the traditional beliefs trade and habitat degradation and food shortages (Boshoff and Anderson 2007). Subsequently it was established that Cape vultures were also potentially under threat from the toxic effects of certain veterinary drugs (Naidoo *et al.* 2009). Although climate change had been previously implicated in Cape vulture declines (Simmons and Jenkins 2007), it was not identified as an important threat by the CVTF (Boshoff and Anderson 2007). It is clear that the threats facing Cape vultures are multifaceted and dynamic, and calls for further research and conservation measures aimed at African vultures (Koenig 2006; Virani *et al.* 2011; Ogada *et al.* 2012a) resulted in the establishment of the Vulture Specialist Group (VSG) of the IUCN Species Survival Commission in 2011. The following paragraphs discuss some of the threats to Cape vultures considered to be most important by the CVTF and VSG, as well as the potential impact of climate change.

1.2.3.1 Poisoning

The use of poisons to kill wildlife has a long history worldwide (Ogada 2014). Recently poisoning has been recognised as an increasingly serious threat to wildlife populations, particularly in Africa where agricultural pesticides (e.g. carbamates and organophosphates) are illegally used to kill damage-causing animals and for harvesting animals for food and the illegal trade in wildlife products (Mander *et al.* 2007; Kissui 2008; Groom *et al.* 2013; Ogada 2014). Carnivores are frequently targeted using poisoned baits or carcasses either to prevent or to retaliate against livestock depredations (Kissui 2008; St John *et al.* 2012), and such illegal activity is now regarded as one of the most serious threats to carnivore populations worldwide (Marquez *et al.* 2013; Ripple *et al.* 2014). Lethal predator control has been widespread in southern Africa since the arrival of European settlers in the seventeenth century, which resulted in the eradication of wild dogs (*Lycaon pictus*), lions, spotted hyaena and cheetahs (*Acinonyx jubatus*) from most of their historical range (Riggio *et al.* 2013; Ogada 2014). More recently meso-carnivores such as caracals (*Caracal caracal*) and black-backed jackals (*Canis mesomelas*) continue to be intensively persecuted, most frequently by small stock farmers (Blaum *et al.* 2009; St John *et al.* 2012).

The use of poisoned carcasses for predator control is indiscriminate and vultures are particularly vulnerable to inadvertent mass poisoning incidents due to their highly efficient social foraging behaviour (Mundy *et al.* 1992; Ogada *et al.* 2012a). Vultures are also poisoned intentionally due to fears that they could kill newly born lambs (Mundy *et al.* 1992; Bridgeford 2001; Margalida *et al.* 2014) or for the harvesting of their body parts for the traditional beliefs trade (Groom *et al.* 2013; Williams *et al.* 2014). Consequently, many mass poisoning incidents of vultures have been recorded in southern Africa, with *Gyps* species being the most numerous victims due to their high relative abundance and tendency to feed in large groups (Mundy *et al.* 1992; Ogada *et al.* 2012a). For example, Mundy *et al.* (1992) estimated that at least 1,250 vultures were killed at 33 poisoning events in southern Africa over a 12 year period. In recent years a poaching epidemic has swept across southern Africa and poison is being increasingly used to kill elephants for ivory or to kill vultures to prevent them from indicating the locations of poached carcasses (Roxburgh and McDougall 2012; Ogada 2014). In one incident in July 2013 it was conservatively estimated that 400-600 vultures, mainly African white-backed vultures, were fatally poisoned after feeding on a poisoned elephant carcass in the vicinity of Bwabwata National Park in the Caprivi region of Namibia (IUCN 2013, 2014). The harvesting of vulture body parts for the traditional beliefs trade is also increasingly prevalent across Africa (Pfeiffer *et al.* 2014; Williams *et al.* 2014), and in July 2012 more than 200 vultures were killed at a poisoned elephant carcass in Gonarezhou National Park in southern Zimbabwe, with evidence of the removal of body parts (e.g. upper bills) from many individuals (Groom *et al.* 2013). In the four years prior to 2014 more than 1000 vultures were poisoned and beheaded in four different countries for the illegal wildlife trade (Ogada 2014).

Poisoning has thus been identified as one of the main factors leading to the observed population declines of Cape vultures (Boshoff and Anderson 2007), and is likely to have played a major role in the demise of the breeding population in Namibia and elsewhere in southern Africa (Boshoff and Vernon 1980; Brown 1985; Mander *et al.* 2007). Given that more than 1,500 vultures were poisoned in southern Africa between 2012 and 2014 (Ogada 2014), previous calls for further research into vulture feeding ecology and movement patterns to inform effective conservation strategies are increasingly valid (Koenig 2006; Pain *et al.* 2008; Virani *et al.* 2011; Ogada *et al.* 2012b).

1.2.3.2 Power lines: collisions and electrocutions

The utilities infrastructure is expanding across southern Africa as the region continues to undergo rapid economic development, with hundreds of kilometres of new power lines being constructed each year, particularly in South Africa (Biggs *et al.* 2008; Jenkins *et al.* 2010). The construction of power lines introduces ecological costs and benefits which are often indicated by changes to avian community dynamics and spatial distributions (Lehman *et al.* 2007; Mainwaring 2015). The potential for newly constructed power lines to increase mortality rates in local bird populations through fatal electrocutions or collisions with overhead cables is widely recognised (Janss 2000; Lehman *et al.* 2007), and has been identified as a major factor leading to the decline of crane (*Anthropoides* species) and bustard (*Neotis* species) populations in parts of South Africa (Shaw *et al.* 2010a; Shaw *et al.* 2010b; Jenkins *et al.* 2011). However, some species, including some vultures (Anderson and Hohne 2008), benefit from the construction of power lines which can provide nest sites or perches for roosting or foraging (Fig. 1.4.), particularly in areas which are otherwise devoid of natural perches, although negative impacts on competitors or prey species often result (Lammers and Collopy 2007; Mainwaring 2015). For example, in North America ravens (*Corvus corax*) concentrate their foraging activity in the vicinity of transmission line pylons on which they preferentially nest, which potentially limits the population of greater sage-grouse (*Centrocercus urophasianus*) through elevated nest predation rates (Howe *et al.* 2014). It has also been suggested that power lines can act as ecological traps by attracting birds to suboptimal locations that ultimately reduce their breeding success or increase mortality rates (Gilroy and Sutherland 2007; Mainwaring 2015). This has been demonstrated for white storks (*Ciconia ciconia*) which nest on pylons in large numbers but collisions and electrocutions with power lines account for the mortality of more than 25% of juveniles and 8% of adults in some areas of Europe (Garrido and Fernandez-Cruz 2003; Kaluga *et al.* 2011).

Large, gregarious bird species that primarily employ soaring flight are particularly vulnerable to fatal interactions with power lines (Janss 2000). It has also recently been shown that the visual fields of some species, including vultures, often cause them to be blind in the direction of travel when foraging, leaving them especially prone to collisions (Martin 2011; Martin *et al.* 2012). Consequently the Cape vulture and African white-backed vulture are two of the species most frequently recorded as killed or injured by collisions or electrocutions with power lines in South Africa since studies began in the 1970s (Markus 1972; Ledger and Annegarn 1981; Jenkins *et al.* 2010). For example, more than 300 *Gyps* vultures were killed by power lines in the eastern region of the North West Province between 1970 and 1977 (Ledger and Annegarn 1981) and it is conservatively estimated that power lines kill 4% of the local population of Cape vultures in the Eastern Cape Province each year, with the possibility of rapid local extinctions in high risk areas (Boshoff *et al.* 2011). Fatal interactions are expected to be most common in open habitats lacking natural perches, and in areas with locally abundant carrion where vultures gather in larger numbers and crowding and competition for perches can lead to numerous electrocutions or collisions (Ledger and Annegarn 1981; Lehman *et al.* 2007; Jenkins *et al.* 2010; Guil *et al.* 2011). While mitigation measures are regularly installed in such areas, their effectiveness is often limited and studies used to inform their implementation are often retrospective rather than prospective, especially in terms of identifying high risk areas (Lehman *et al.* 2007; Jenkins *et al.* 2010).

Although fatal interactions with the expanding power line network are considered a major threat to Cape vultures (Boshoff and Anderson 2007; Naidoo *et al.* 2011), it is possible that they may also provide some benefits. For example, while Cape vultures do not nest on transmission line pylons in the same way as African white-backed vultures, they do frequently use them as perches (Anderson and Hohne 2008), and Mundy *et al.* (1992) suggested that the construction of power lines in largely treeless and cliff-less areas might have allowed the Cape vulture to extend its foraging range into areas previously devoid of suitable perches.

Consequently, the influences of power lines on Cape vulture spatial ecology are not fully understood and further research has been encouraged, particularly in order to inform the implementation of effective mitigation strategies (Lehman *et al.* 2007; Jenkins *et al.* 2010; Boshoff *et al.* 2011; Guil *et al.* 2011; Mainwaring 2015). This is especially pertinent given that recent studies indicate that the construction of power lines has contributed to the abandonment of territories of other vulture species in the region (Krueger *et al.* 2015), and that proposed wind farm developments will threaten Cape vultures further (Rushworth and Krueger 2014).

Figure 1.4. Twenty two Cape vultures perching on a newly constructed transmission line tower at Mankwe Wildlife Reserve, North West Province, South Africa. The overhead cables that pose a serious collision risk to the vultures were not yet fitted to the structure at the time the photograph was taken. (Photograph credit: Lynne MacTavish)

1.2.3.3 Loss of foraging habitat due to bush encroachment

Habitat degradation and land use change are key drivers of biodiversity loss, both globally and regionally in southern Africa (Biggs *et al.* 2008; Butchart *et al.* 2010). Changing land use practices have not only led to reduced availability of ungulate carcasses for vultures due to over-hunting and improved animal husbandry, but also to bush encroachment as a result of overgrazing, which has been identified as a threat to vultures in southern Africa through a reduction in suitable foraging habitat (Boshoff and Anderson 2007; Schultz 2007; Bamford *et al.* 2009a).

Bush encroachment typically occurs when overgrazing depletes the grass layer and allows fast-growing woody shrubs, such as sickle bush (*Dichrostachys cinerea*), to rapidly become the dominant vegetation type, leading to the conversion of open grassland to a closed canopy of woody shrubs and trees (Sankaran *et al.* 2005). Bush encroachment has a range of ecological impacts including lowering carrying capacity for grazing herbivores, reducing avian diversity and altering carnivore community dynamics and predation rates (Muntifering *et al.* 2006; Blaum *et al.* 2007; Sirami *et al.* 2009). It has been demonstrated that Cape vultures do not feed at carcasses in tree cover of more than 2600 trees·ha^{-1} and that they require a take-off angle (i.e. the angle from the carcass to the top of surrounding trees) of no more than 4^{o} (Schultz 2007; Bamford *et al.* 2009a). In contrast, the smaller African white-backed vulture is able to land at carcasses in higher tree densities (Bamford *et al.* 2009a). Consequently, this supports suggestions that bush encroachment has played a role in the decline of Cape vultures in Namibia while African white-backed vulture populations remain relatively stable, despite high levels of bush encroachment (Bamford *et al.* 2007; Bamford *et al.* 2009a). In addition, given that vultures locate carcasses by sight alone, it is likely that bush encroachment will hinder their ability to detect carcasses from above (Bamford *et al.* 2007; Bamford *et al.* 2009a). However, the effects of vegetation structure on Cape vulture foraging patterns are not fully understood, and further research into the potential impacts of bush encroachment are required (Bamford *et al.* 2007; Boshoff and Anderson 2007).

1.2.3.4 Climate change

Climate change has been identified as a key driver of alterations to the distribution, phenology and abundance of many species worldwide (Parmesan and Yohe 2003; Thomas *et al.* 2004; Hockey *et al.* 2011). Although some species are predicted to expand their ranges under future climatic conditions, many are likely to experience significant range loss and consequently be at higher risk of extinction, particularly if coverage of their ranges by protected areas is reduced (Hole *et al.* 2009; Pereira *et al.* 2010; Hole *et al.* 2011). Southern Africa is expected to experience particularly extreme climate change and records show that significant warming and changes to rainfall patterns have occurred in recent decades (Warburton *et al.* 2005; Williams *et al.* 2007; Kruger and Sekele 2013). Consequently, future changes to community composition across a range of taxa have been predicted, with pole-ward shifts in suitable climatic conditions expected for many species (Midgley *et al.* 2003; Simmons *et al.* 2004; Thuiller *et al.* 2006a; Thuiller *et al.* 2006b; Walther and van Niekerk 2015). For example, the distributions of at least 56 bird species in South Africa have already changed in recent decades, often with range expansions and contractions of several hundred kilometres, predominantly in southwards and westwards directions (Hockey *et al.* 2011).

Large, mobile species such as vultures are expected to be more resilient to the effects of climate change than smaller, more restricted species as they are pre-adapted to respond more readily to environmental change to exploit novel opportunities (Hockey *et al.* 2011; Walther and van Niekerk 2015). However, bearded vulture and Cape vulture nesting sites are more likely to have been recently abandoned at lower elevations and at more northerly colonies where the effects of warming and changing precipitation patterns have been most pronounced (Simmons and Jenkins 2007; Williams *et al.* 2007). Simmons and Jenkins (2007) thus suggested that climate change potentially played a role in the extinction of the northernmost Cape vulture colonies in Namibia and Zimbabwe possibly because vultures nesting on cliffs that experienced higher temperatures and longer sunlight exposures (northerly aspects) showed significantly higher heat-stress than those nesting on cliffs with lower temperatures and reduced exposure to sunlight (southerly aspects) (Chaudhry 2007). Considering that weather conditions influence the flight performance (Duriez *et al.* 2014) and cliff site selection of similar species (Lambertucci and Ruggiero 2013), and potentially the distribution of a whole guild of avian scavengers in South America (Shepard and Lambertucci 2013), it is reasonable to assume that climate change will influence Cape vultures to some degree. In addition, the breeding success of African vulture species has been linked to changing rainfall patterns, with higher success following years of lower rainfall when ungulate mortality, and therefore food availability, was likely to be highest (Bridgeford and Bridgeford 2003; Virani *et al.* 2012; Kendall *et al.* 2014).

Although a recent study identified the presence of power lines and poisoning, rather than climate change, as the main factors leading to territory abandonment by bearded vultures (Krueger *et al.* 2015), the impacts of climate change on Cape vulture occurrence remain unknown and the threat is potentially under-appreciated and warrants further research (Simmons and Jenkins 2007). Furthermore, climate change is likely to influence bush encroachment and ungulate mortality rates through changing rainfall patterns (Sankaran *et al.* 2005; Thuiller *et al.* 2006a), and such interactions should be considered when assessing potential threats to vultures (Simmons and Jenkins 2007).

1.2.4. The role of protected areas for vulture conservation

Protected areas are important for mitigating the continuing loss of biodiversity caused by habitat degradation, fragmentation, hunting and other anthropogenic pressures (Hoffmann *et al.* 2010; Montesino Pouzols *et al.* 2014). Although the primary objective of protected areas is usually to conserve threatened species, important habitats and overall biodiversity, they also contribute to the livelihood of local communities and national economies through tourism revenues (Watson *et al.* 2014). From a conservation perspective it is generally recognised that species with a higher proportion of their range covered by protected areas are more likely to persist in the face of greater threats in the wider landscape (Butchart *et al.* 2010; Cantu-Salazar *et al.* 2013). Currently, 12.5% of the Earth's terrestrial surface is covered by protected areas (Watson *et al.* 2014) which falls short of the Convention of Biological Diversity's (CBD) target of 17% by 2020 (http://www.cbd.int/sp/targets). Therefore, it is widely recognised that the protected area network should be expanded to provide more effective conservation measures for threatened species (Hoffmann *et al.* 2010; Cantu-Salazar *et al.* 2013; Montesino Pouzols *et al.* 2014; Watson *et al.* 2014). This is particularly true across Africa where over-hunting and other anthropogenic threats are causing widespread declines of whole wildlife communities both inside and outside protected areas (Lindsey *et al.* 2009; Craigie *et al.* 2010; Winterbach *et al.* 2013; Tranquilli *et al.* 2014).

While 12% of terrestrial sub-Saharan Africa is covered by protected areas, the degree of coverage varies substantially between countries (Loucks *et al.* 2008; Trimble and van Aarde 2014). This is particularly true in southern Africa where 45% of Botswana is listed under some form of environmental management status and consists of a network of relatively large wildlife reserves, while only 6.5% of South Africa is covered by many small, often isolated reserves (Newmark 2008; Trimble and van Aarde 2014; CBD 2015a, b). Traditionally southern African protected areas are perceived as highly managed, often fenced reserves, with prescribed fire and water management regimes and some degree of artificial control of wildlife populations, which contrasts with a more "hands off" approach in the larger, mostly unenclosed protected areas in East Africa (Newmark 2008; Beale *et al.* 2013; Winterbach *et al.* 2013). While fenced protected areas can be effective at separating biodiversity from threats such as human-wildlife conflict, invasive species and disease, they also create significant financial and ecological costs such as blocking migration and dispersal routes, and may result in some wildlife populations exceeding natural carrying capacity or becoming inbred (Hayward and Kerley 2009). The use of fences for large carnivore conservation has been thoroughly debated in recent years, with suggestions that fences are fundamental for effectively managing carnivore populations in an increasingly human-modified landscape despite potentially leading to declines in ungulate populations through over-predation when carnivores exceed their carrying capacities, among other negative impacts (Hayward *et al.* 2007; Newmark 2008; Hayward *et al.* 2009; Hayward and Kerley 2009; Creel *et al.* 2013; Packer *et al.* 2013; Riggio *et al.* 2013; Massey *et al.* 2014; Pfeifer *et al.* 2014; Woodroffe *et al.* 2014).

The role of protected areas for vulture conservation remains unclear. It has been suggested that high levels of competition and declines of ungulate populations caused by unusually high densities of apex predators in protected areas in northern South Africa (Tambling and Du Toit 2005; Hayward *et al.* 2007) might have contributed to their limited use by African white-backed vultures tracked in northern South Africa (Phipps *et al.* 2013a). Although firm evidence was lacking, this would be consistent with previous observations that vultures were rarely seen feeding in the Ngorongoro Crater in Tanzania due to intense competition from mammalian carnivores (Houston 1974b). In contrast, in parts of East and West Africa vulture populations persist inside protected areas but are now rarely seen in unprotected areas where mortality rates are considerably higher due to poisoning and food shortages (Thiollay 2006b; Thiollay 2007a; Virani *et al.* 2011; Kendall and Virani 2012; Ogada *et al.* 2012a). In southern Africa protected areas are certainly important for breeding vultures where they are afforded protection from anthropogenic disturbance, and many of the remaining Cape vulture breeding colonies are located within National Parks (NPs) such as Marakele, Blouberg, Magaliesberg and the Maloti-Drakensberg (Benson *et al.* 2004; Monadjem and Garcelon 2005;

Bamford *et al.* 2009b; Whittington-Jones *et al.* 2011; Krueger *et al.* 2014b; Krueger *et al.* 2015).

However, vultures do frequently breed and forage on unprotected farmland, sometimes preferentially, and so are likely to be exposed to a wide range of threats in the wider landscape (Herremans and Herremans-Tonnoeyr 2000; Murn *et al.* 2002; Benson *et al.* 2004; Murn and Anderson 2008; Kendall and Virani 2012; Phipps *et al.* 2013a). Given that 88% of southern Africa is not covered by protected areas, it is clear that the future conservation of vultures, and biodiversity in general, will rely heavily on land that is unprotected (Beale *et al.* 2013; Trimble and van Aarde 2014). This is particularly pertinent in the face of climate change as the ranges of many species are expected to lose coverage by protected areas (Hole *et al.* 2009; Hole *et al.* 2011). However, the expanding network of private and communal conservancies across southern Africa might create new opportunities for the conservation of vultures and other carnivores by increasing food availability and protecting important habitats, although persistent threats such as widespread illegal poisoning must be addressed first (Lindsey *et al.* 2009; Lindsey *et al.* 2013a; Lindsey *et al.* 2013b).

The relative importance of protected and unprotected areas for Cape vulture activity has not yet been assessed and has been identified as a research priority to inform effective conservation strategies in key areas (Boshoff and Anderson 2007; Murn and Anderson 2008; Beale *et al.* 2013; Phipps *et al.* 2013a). The use of tracking technology to efficiently and accurately assess patterns of land use and other aspects of avian ecology is now widespread and is discussed in the next section (Laver and Kelly 2008; Wilson *et al.* 2015).

1.3. Tracking methods for conservation research

Regional, national and international threat assessments (e.g. the IUCN Red List) require basic information about species distributions, movement patterns, mortality rates, behaviour and habitat use, and it is increasingly necessary to identify key areas for targeted conservation measures in the face of global habitat degradation (Cooke 2008; Hoffmann *et al.* 2010). Remote tracking methods to study the spatial ecology, behaviour, and habitat requirements of free-living animals has rapidly developed since the 1970s and such data are now widely used to inform species conservation and management strategies (Cooke 2008; Wilson *et al.* 2015).

The use of tracking technology for ecological studies has been extensively reviewed and there is a general trend towards much smaller devices being able to collect more accurate data at much finer spatial and temporal scales, for longer tracking periods and for lower financial costs (Cooke *et al.* 2004; Cooke 2008; Rutz and Hays 2009; Cagnacci *et al.* 2010; Tomkiewicz *et al.* 2010; Guilford *et al.* 2011; Sokolov 2011; Wilson *et al.* 2015). The incorporation of GPS (global positioning system) technology and remote data retrieval systems such as GSM-SMS (global system for mobile communications-short message service) and Argos DCLS (data collection and location system) into tracking units was "revolutionary" for obtaining highly accurate (<10 m) animal location data, particularly for species capable of large scale movements (Cooke 2008; Tomkiewicz *et al.* 2010), and was relatively recent at the onset of this study.

The recent miniaturisation of GPS tracking units and the incorporation of accelerometers and other sensors has allowed detailed studies of the physiology, locomotion and energetics of free-living animals in their natural environment (Wilson *et al.* 2008; Guilford *et al.* 2011; Sokolov 2011). However, the majority of studies aiming to provide data to inform conservation measures generally assess the spatial requirements of a species in terms of the size and extent of home ranges, patterns of habitat use and selection, site fidelity and the potential impacts of environmental change and existing mortality factors (Cooke 2008; Kie *et al.* 2010; Wilson *et al.* 2015). The following paragraphs discuss some of the common methods used to assess home ranges, resource selection and ecological niche modelling using GPS tracking data.

1.3.1. Home range analysis

The size and extent of animal home ranges are essentially spatial expressions of the link between animal movements and the distribution of the resources necessary for their survival and reproduction, and are therefore dependent on factors such as food availability, the distribution of suitable foraging and breeding habitat, and the level of intra- and interspecific competition (Boerger *et al.* 2008; Kie *et al.* 2010; Perez-Garcia *et al.* 2013). Consequently, the delineation of home ranges in combination with further analysis relating to resource use provides important information about the behavioural and spatial ecology of a species, and is valuable for conservation planning (Cooke 2008; Hebblewhite and Haydon 2010).

Numerous methods are used for estimating home ranges from tracking data and the method of choice is largely dependent on the aims of the study and the temporal and spatial resolution of the data (Laver and Kelly 2008; Hebblewhite and Haydon 2010; Kie *et al.* 2010; Powell and Mitchell 2012). For conservation studies relatively simplistic but easily interpreted analytical methods are often used to delineate home ranges (Hebblewhite and Haydon 2010), with the two most frequent being the creation of minimum convex polygons (MCPs) and utilization distribution contours by kernel density estimation (KDE) (Laver and Kelly 2008; Kie *et al.* 2010).

The MCP method has been widely used since the onset of tracking studies and provides a basic representation of the outer limits of the home range of an animal by connecting adjacent peripheral GPS locations with all internal angles being less than 180^{o} to create a polygon representing the assumed overall or maximum home range (Mohr 1947; Harris *et al.* 1990). However, MCPs unrealistically assume uniform space use within the polygon boundary and have been criticised due to their sensitivity to the sample size of location data and the incorporation of outlying locations often results in the inclusion of large areas that were never visited by the tracked animal (Borger *et al.* 2006; Downs and Horner 2008). Although MCPs continue to be used for comparative purposes with earlier studies (Harris *et al.* 1990), the use of more robust methods that identify variations in the intensity of space use within a home range have been advocated (Laver and Kelly 2008; Kie *et al.* 2010).

The KDE method is the method of choice for many studies due to its ability to identify multiple centres of activity and exclude unused areas, resulting in a more accurate and useful depiction of space use (Hemson *et al.* 2005; Laver and Kelly 2008; Kie *et al.* 2010). KDE calculates the intensity of use across the home range by placing a probability density, or kernel, over each GPS location, superimposing a grid of a selected scale (determined by a "smoothing factor"), and averaging the densities of all the kernels that overlap at each grid intersection to produce an estimated kernel density, or probability of occurrence of the tracked animal at that point (Worton 1989; Seaman and Powell 1996). Areas with a high number of GPS locations, and therefore overlapping kernels, will produce higher estimated probabilities of occurrence than those with few (Worton 1989; Seaman and Powell

1996). Subsequently contours, or isopleths, are created that correspond to the estimated probabilities of occurrence, and provide an approximation of the amount of time that the tracked animal spent within that contour (Hemson *et al.* 2005; Wauters *et al.* 2007). The majority of studies represent the overall home range boundary with a contour that contains probabilities of occurrence of 95% or more, while 50% contours typically identify core areas of intensive use (Laver and Kelly 2008; Kie *et al.* 2010).

Following the delineation of home range boundaries it is possible to estimate resource use and selection patterns by combining additional environmental datasets to identify the factors that determine the relative intensities of space use across the wider landscape (Kie *et al.* 2010). In addition, overlap between home ranges of different individuals or species can provide information about inter- and intraspecific competition, and can also identify key breeding or foraging areas of conservation importance (Fieberg and Kochanny 2005; Cooke 2008; Catry *et al.* 2013). Furthermore, the overlap between the home ranges of an individual calculated in multiple time periods (e.g. in consecutive years or breeding seasons) provides valuable information about site fidelity and resource availability and predictability (Fieberg and Kochanny 2005; Weimerskirch 2007; Monsarrat *et al.* 2013). The delineation of core areas of space use also allows the identification and possible mitigation of key threats within a species’ range, such as the risk of collisions with man-made structures (Desholm and Kahlert 2005; Rushworth and Krueger 2014).

1.3.2. Resource selection analysis

A thorough understanding of how animals use and select resources, such as different habitats, within their home ranges is important when planning conservation measures for threatened species (Cooke 2008; Burgess *et al.* 2009). It is generally assumed that the disproportionate use of a resource compared to its availability (i.e. selection) is likely to arise because that resource improves the fitness, survival or reproduction of the animal (Thomas and Taylor 2006). Therefore, resource selection studies generally aim to determine which resources are selected preferentially by the study species by comparing use and availability of discrete resource categories (Manly *et al.* 2002; Warton and Aarts 2013).

When analysing resource selection, resource *use* and *availability* must be clearly defined (Beyer *et al.* 2010). For studies that use GPS tracking data to analyse habitat or land use selection by animals, use of a habitat is most often represented by the relative proportions of GPS locations recorded within each habitat category (Thomas and Taylor 2006; Warton and Aarts 2013). The use of each habitat category by the animal is then compared to its availability within the home range boundary (i.e. third order selection (Johnson 1980)) (Manly *et al.* 2002; Thomas and Taylor 2006). In addition, the proportion of a home range covered by given habitats (i.e. use) can be compared to their proportional availability in the overall study area (i.e. second order selection (Johnson 1980)) for analysis at a broader scale (Thomas and Taylor 2006).

Patterns of selection can be tested for significance in terms of deviating from random use of resources by comparing the use and availability of given resource categories using a variety of methods depending on the aims and design of the study and the available data (Manly *et al.* 2002; Warton and Aarts 2013). Suitable methods range from relatively simplistic pairwise statistical tests (e.g. Wilcoxon signed-rank test) and electivity indices (e.g. Ivlev's electivity index (Ivlev 1961)) to more complex logistic regression modelling based on calculations of resource selection functions (RSFs) and resource selection probability functions (RPPFs) (Manly *et al.* 2002; Thomas and Taylor 2006; Warton and Aarts 2013). Compositional analysis is an application of multivariate analysis of variance (MANOVA) that uses individual animals as replicates (Aebischer *et al.* 1993; Manly *et al.* 2002) and is one of the most commonly used methods for telemetry studies owing to its robustness against: pseudo-replication; the unit-sum constraint, whereby the avoidance of one resource inherently leads to some selection for alternatives; and the differential use of resources by different animals (Aebischer *et al.* 1993; Manly *et al.* 2002; Thomas and Taylor 2006).

When combined with environmental data, therefore, resource selection analyses provide valuable information about what drives ranging patterns of tracked animals and can inform conservation decisions based on establishing the basic requirements of a species and how they might be threatened by environmental change (Jones 2001; Warton and Aarts 2013). The next section introduces a closely related method for investigating the factors that determine the distribution or niche of a species in more depth using GPS tracking data (Warton and Aarts 2013).

1.3.3. Ecological niche modelling using GPS data

Ecological niche modelling (ENM; also known as species distribution modelling, SDM) is a relatively recent and rapidly developing method that has become an important tool for conservation planning and natural resource management (Franklin 2013; Guisan *et al.* 2013; McDonald *et al.* 2013). ENMs typically correlate the presence of a species at multiple locations with relevant environmental covariates to provide a spatial representation of the potential or realised niche occupied by that species (Araujo and Guisan 2006; Franklin 2010; Guillera-Arroita *et al.* 2015). While resource selection studies often estimate the probability that a given resource will be used, ENMs generally predict the likelihood that a species occurs at a given location (i.e. the probability of species presence) and allow the estimation of a species' ecological requirements (Araujo and Guisan 2006; Franklin

2010; McDonald *et al.* 2013). Consequently, ENMs are able to identify the key environmental conditions or critical habitats required for the existence of a species, and are used to predict the impacts of environmental change (e.g. climate change; biological invasions) and inform decisions related to reserve design, species translocation, and the general management of threatened species and habitats (Addison *et al.* 2013; Guisan *et al.* 2013; Guillera-Arroita *et al.* 2015).

Maxent, a presence-only machine learning method (Phillips *et al.* 2006), is one of the most frequently used methods for ENM studies when using GPS tracking data for presence locations because it was developed specifically for presence-only data and repeatedly outperforms other methods in terms of predictive accuracy, even with limited sample sizes (Elith *et al.* 2006; Phillips and Dudik 2008; Elith *et al.* 2011). Maxent uses the principal from statistical mechanics that a probability distribution with maximum entropy (i.e. closest to uniform), subject to known constraints, is the best estimation of an unknown distribution because it agrees with everything that is known but avoids assuming anything that is unknown (Phillips *et al.* 2006; Franklin 2010). For ENMs the distribution being estimated is the multivariate distribution of suitable environmental conditions associated with species presence locations (Franklin 2010; Elith *et al.* 2011). The unconstrained distribution is that of all environmental variables in the study area (e.g. a geographical area delineated by country borders), and the constraint is that the expected value is approximated by the set of presence locations, represented by GPS locations for telemetry studies (Phillips *et al.* 2006; Phillips and Dudik 2008; Franklin 2010). Maxent has been successfully applied to GPS tracking data to assess the characteristics, extent and level of protection of suitable environmental conditions for threatened species, as well as the potential impacts of environmental change, and is widely considered to be a useful tool for conservation planning (Gschweng *et al.* 2012; Liminana *et al.* 2012; Franklin 2013; Kassara *et al.* 2013; Swanepoel *et al.* 2013; Liminana *et al.* 2014; Guillera-Arroita *et al.* 2015).

1.4. Cape vulture space use: existing knowledge

Findings from a wide range of studies relating to Cape vulture morphology, distribution, breeding biology, feeding behaviour, survival rates and threats were thoroughly collated and summarised in the comprehensive text *"The vultures of Africa"* by Mundy and colleagues (1992). Since then most studies specifically on Cape vultures have focussed on the impacts of threats and conservation measures on survival rates (Piper *et al.* 1999; Anderson *et al.* 2005; Simmons and Jenkins 2007; Boshoff *et al.* 2011; Monadjem *et al.* 2014; Pfeiffer *et al.* 2014; Rushworth and Krueger 2014), the status of breeding colonies (Vernon 1999; Borello and Borello 2002; Whittington-Jones *et al.* 2011; Boshoff 2012), and toxicology studies (Van Wyk *et al.* 1993;

Van Wyk *et al.* 2001a; Van Wyk *et al.* 2001b; Naidoo *et al.* 2010a; Naidoo *et al.* 2010b).

Following the recent collapse of Asian vulture populations and widespread declines of African vulture species, it is widely acknowledged that further research into vulture ecology and movement patterns is required to inform effective conservation strategies (Boshoff and Anderson 2007; Pain *et al.* 2008; Boshoff and Minnie 2011; Virani *et al.* 2011; Ogada *et al.* 2012a). However, despite an overall increase in studies on vulture species worldwide (Koenig 2006) and the recent publication of findings from several tracking studies on other African vulture species since the onset of this study (Kendall and Virani 2012; Nathan *et al.* 2012; Phipps *et al.* 2013a; Spiegel *et al.* 2013; Kendall *et al.* 2014; Krueger *et al.* 2014a), the spatial ecology of the Cape vulture remains poorly understood and key areas for conservation have not been fully identified (Boshoff and Anderson 2007; Boshoff and Minnie 2011).

The first study on the ranging patterns of wild-caught Cape vultures using GPS tracking techniques was carried out between 2004 and 2005 in the Waterberg region of north-central Namibia where a small (<20 breeding adults) population was soon to become extinct as a breeding species (Bamford *et al.* 2007). The findings published in 2007 were from the initial tracking periods (less than one year) and the mean home range (MCPs) of five adults was estimated at 21,320 km^2 where they foraged primarily on private farmland adjacent to the Waterberg Plateau Park and fed on wild ungulates and domestic livestock, and avoided communal farmland (Bamford *et al.* 2007; Schultz 2007). Investigation of the ground sites from the tracking data and the placement of experimental carcasses revealed that Cape vultures were unlikely to land and feed at carcasses in tree densities of 2,600 trees ·ha^{-1} (Schultz 2007), which corresponded with a subsequent study in Swaziland (Bamford *et al.* 2009a). The two immature vultures traversed vast foraging ranges (mean MCP = 482,276 km^2) and regularly crossed international borders (Bamford *et al.* 2007) in a similar way to immature African white-backed vultures tracked from South Africa (Phipps *et al.* 2013a). In addition, recoveries and re-sightings of marked and ringed individuals indicate that immature Cape vultures range much further than breeding adults (Mundy *et al.* 1992), as expected from natal dispersal patterns in other vulture and raptor species (Newton 1979; Dwyer *et al.* 2013). Mundy *et al.* (1992) suggested that immature vultures might disperse to "nursery areas" away from breeding colonies to avoid competition from more dominant adults for scarce carrion sources, as seen in other species (Negro *et al.* 1997; Dwyer *et al.* 2013).

A recent study that tracked two adult Cape vultures in the Drakensberg region of South Africa estimated that their normal foraging distance averaged 15 km and extended up to 40 km from the breeding colony (Rushworth and Krueger 2014). That estimate corresponds to previous suggestions that breeding Cape vultures are most likely to forage within 35-40 km of a colony, although those findings were based on direct observations, re-sightings of marked individuals, questionnaire surveys and an early telemetry study on a single vulture (Boshoff *et al.* 1984; Robertson and Boshoff 1986; Brown and Piper 1988; Boshoff and Minnie 2011), and so should not be considered as accurate as estimates from modern GPS tracking studies (Bamford *et al.* 2007). A study based on opportunistic observations, questionnaires and colony surveys suggested that the Cape vulture population in the Eastern Cape province of South Africa is partially migratory, possibly due to seasonal ungulate mortality patterns driven by rainfall and calving or lambing seasonality (Boshoff *et al.* 2009).

Previous studies relating to the foraging ecology of Cape vultures suggest that they feed on livestock and mixed game farms as well as wildlife reserves and officially protected areas (Robertson and Boshoff 1986; Mundy *et al.* 1992; Benson *et al.* 2004), which corresponds with studies on African white-backed vultures in the region (Murn and Anderson 2008; Phipps *et al.* 2013a). However, their relative use of different land uses has not been accurately quantified across their range and the role of protected areas for their foraging activity remains unclear (Bamford *et al.* 2007). If immature Cape vultures range as widely as expected then they are likely to encounter the full range of threats in the region from poisoning to collisions with power lines (Phipps *et al.* 2013a). Although the potential impacts of power line mortalities has been assessed (Boshoff *et al.* 2011), and a recent study indicated that Cape vultures will be at risk of colliding with proposed wind turbines (Rushworth and Krueger 2014), the influence of power lines on their movement patterns has not been investigated. In addition, no study has investigated which environmental factors such as bioclimatic conditions or habitat characteristics (but see Bamford *et al.* (2009a)) drive Cape vulture distribution patterns.

In summary, although aspects of Cape vulture ecology have been relatively well studied, their movement patterns and spatial ecology remain poorly understood and merit further investigation to inform effective conservation strategies (Boshoff and Anderson 2007; Boshoff and Minnie 2011).

1.5. Thesis rationale and structure

It has recently been recognised that the importance of the ecosystem services that scavengers provide has been underestimated and urgently requires further investigation (Wilson and Wolkovich 2011; Moleon *et al.* 2014a). Vultures are among the most threatened species on the planet, with global declines largely driven by anthropogenic activities (Ogada *et al.* 2012a). In order to plan and implement effective conservation strategies in key areas it is essential to have a thorough understanding of the spatial ecology of threatened species and determine their vulnerability to threats across their range (Cooke 2008; Balme *et al.* 2014).

The aim of this study is to increase our understanding of the spatial ecology of Cape vultures in southern Africa by using GPS tracking methods to identify the key factors that influence their movement patterns in the core of their current range in northern South Africa, and in north-central Namibia where a small population remains but no longer breeds. The primary objective of this study is to inform effective vulture conservation strategies and to stimulate further research.

The thesis is divided into the following three chapters which are written as original research articles, described below. The final chapter presents a synopsis and discussion of the overall findings in the context of vulture conservation with recommendations for future research.

Chapter 2: Do power lines and protected areas present a Catch-22 situation for Cape vultures (*Gyps coprotheres*)?

Chapter 2 presents the findings from the first GPS tracking study of Cape vultures caught from the wild in northern South Africa. The home ranges traversed by nine vultures (five adults and four immatures) were delineated and the influence of transmission power lines on their movement patterns was assessed, as well as their use of officially protected areas.

This chapter is published in *PLoS ONE* (Appendix 3)*:*

Phipps, W. L., Wolter, K., Michael, M. D., MacTavish, L. M. & Yarnell R. W (2013). Do Power Lines and Protected Areas Present a Catch-22 Situation for Cape Vultures (*Gyps coprotheres*)? PLoS ONE 8(10): e76794. doi:10.1371/journal.pone.0076794

Chapter 3: Ranging and land use patterns of a remnant population of Cape vultures *Gyps coprotheres* in Namibia.

Chapter 3 presents results from the analysis of the full tracking periods of Cape vultures caught from the wild in north-central Namibia, extending the analysis of Bamford *et al.* (2007) who reported findings from the first year of the study. The ranging patterns of the wild-caught vultures were also compared with those of three vultures that were released as part of a pilot reintroduction program. The relative use of freehold conservancies, communal conservancies, officially protected areas and unprotected farmlands was assessed, as well as the influence of vegetation structure on space use patterns. Site fidelity was assessed for vultures that were tracked for multiple years.

This chapter is prepared for submission to *Bird Conservation International.*

Chapter 4: Due South: A first assessment of the potential impacts of climate change on Cape vulture occurrence.

In Chapter 4 the GPS locations from the wild-caught tracked vultures from Chapters 2 and 3 were used to create an ecological niche model using Maxent modelling procedures. The key environmental factors driving the occurrence of the tracked vultures were identified, and a first assessment of the potential impacts of climate change on Cape vulture occurrence was conducted. The coverage of areas predicted to be suitable for Cape vultures by protected areas under current and future climatic conditions was also assessed.

This chapter is prepared for submission to *Biological Conservation.*

Chapter 5: Discussion

Synopsis and discussion of the findings in the context of conservation implications.

CHAPTER 2: Do power lines and protected areas present a Catch-22 situation for Cape vultures (*Gyps coprotheres*)?

Citation: Phipps, W. L., Wolter, K., Michael, M. D., MacTavish, L. M. & Yarnell R. W (2013). Do Power Lines and Protected Areas Present a Catch-22 Situation for Cape Vultures (*Gyps coprotheres*)? PLoS ONE 8(10): e76794. doi:10.1371/journal.pone.0076794

Statement of author contributions: W L Phipps collected and analyzed the data and wrote the article, with R W Yarnell as doctoral supervisor. K Wolter and L M MacTavish assisted with data collection. W L Phipps was the corresponding author for the published article and all authors listed above provided comments on article drafts prior to publication.

2.1. Abstract

Cape vulture *Gyps coprotheres* populations have declined across their range due to multiple anthropogenic threats. Their susceptibility to fatal collisions with the expanding power line network and the prevalence of carcasses contaminated with illegal poisons and other threats outside protected areas are thought to be the primary drivers of declines in southern Africa. We used GPS-GSM units to track the movements and delineate the home ranges of five adult (mean ±SD minimum convex polygon area = 121,655±90,845 km^2) and four

immature (mean ±SD minimum convex polygon area = 492,300±259,427 km^2) Cape vultures to investigate the influence of power lines and their use of protected areas. The vultures travelled more than 1,000 km from the capture site and collectively entered five different countries in southern Africa. Their movement patterns and core foraging ranges were closely associated with the spatial distribution of transmission power lines and we present evidence that the construction of power lines has allowed the species to extend its range to areas previously devoid of suitable perches. The distribution of locations of known Cape vulture mortalities caused by interactions with power lines corresponded to the core ranges of the tracked vultures. Although some of the vultures regularly roosted at breeding colonies located inside protected areas the majority of foraging activity took place on unprotected farmland. Their ability to travel vast distances very quickly and the high proportion of time they spend in the vicinity of power lines and outside protected areas make Cape vultures especially vulnerable to negative interactions with the expanding power line network and the full range of threats across the region. Co-ordinated cross-border conservation strategies beyond the protected area network will therefore be necessary to ensure the future survival of threatened vultures in Africa.

2.2. Introduction

Vultures in the *Gyps* genus are obligate scavengers of vertebrate carcasses and provide vital ecosystem services by recycling carrion, thereby limiting the development and spread of disease and maintaining energy transfer through food webs (Houston 1974b; DeVault *et al.* 2003a). Their longevity, delayed maturity and low reproductive rates mean that even minimal reductions in adult survival rates or the proportion of immatures reaching breeding age could result in population declines (Mundy *et al.* 1992; Martinez-Abrain *et al.* 2012). As a consequence all eight species of *Gyps* vultures found globally are declining (Ogada *et al.* 2012a) because of multiple threats such as reduced food availability (Donazar *et al.* 2009; Margalida and Angels Colomer 2012), illegal poisoning (Margalida 2012), and collisions with wind turbines (Carrete *et al.* 2012; Martinez-Abrain *et al.* 2012) and power lines (Guil *et al.* 2011). The recent collapse of *Gyps* vulture populations in Asia caused by accidental contamination of their food supply (Pain *et al.* 2008) has resulted in major changes to scavenger community dynamics and a wide range of human health and socio-economic impacts in the region (Markandya *et al.* 2008). The urgency to prevent similar ecological catastrophes from occurring elsewhere is widely acknowledged (Pain *et al.* 2008; Ogada *et al.* 2012a).

African vulture populations have also declined considerably, with land use change and illegal poisoning identified as widespread mortality factors (Herremans and Herremans-Tonnoeyr 2000; Thiollay 2006a; Virani *et al.* 2011). For example, a 52% decline in *Gyps* vulture numbers in the Masai Mara region of Kenya over a 30 year period was largely attributed to secondary poisoning after they fed on carcasses illegally laced with poisons to kill livestock predators (Virani *et al.* 2011). Electrocutions and collisions with the expanding power line network are also frequent causes of vulture mortality and injury in Africa (Boshoff *et al.* 2011; Naidoo *et al.* 2011). *Gyps* vultures are especially prone to fatal interactions with power lines in southern Africa due to their frequent use of power line towers for perching and roosting (Mundy *et al.* 1992; Jenkins *et al.* 2010). For example, in the Eastern Cape Province of South Africa it is conservatively estimated that fatal interactions with power lines kill *ca.* 4% of the local population of Cape vultures *G. coprotheres* per year, with the possibility of rapid local extinctions in some high risk areas (Boshoff *et al.* 2011). Despite this vultures might have derived some benefits from the presence of power lines. For example, African white-backed vultures *G. africanus* nest on pylons (Anderson and Hohne 2008) and it has even been suggested that some areas previously devoid of suitable perches might become newly accessible as vultures utilise power line towers as roost sites and vantage points (Mundy *et al.* 1992). Under the current rate of expansion of the power line network it is important to investigate the relationship between power lines and vultures in southern Africa, particularly in a spatial context to allow mitigation measures to be implemented in key areas (Boshoff *et al.* 2011; Guil *et al.* 2011).

Vultures and other raptors in Africa are thought to be increasingly restricted to protected areas where they are less exposed to multiple threats that persist in the wider landscape (Herremans and Herremans-Tonnoeyr 2000; Thiollay 2006a; Virani *et al.* 2011). For example, in several African countries increasing prevalence of anthropogenic mortality factors such as illegal poisoning have led to higher vulture mortality rates and population declines outside compared to inside protected areas (Thiollay 2006a; Virani *et al.* 2011; Kendall and Virani 2012). While protected areas often provide safe breeding and roosting sites for vultures (Benson *et al.* 1990; Monadjem and Garcelon 2005; Bamford *et al.* 2009b; Virani *et al.* 2011), they frequently forage far beyond protected area boundaries, leaving them exposed to numerous threats (Kendall and Virani 2012; Phipps *et al.* 2013a). The role and effectiveness of protected areas for vulture ecology and conservation remains unclear, therefore, and merits further investigation.

In this study we use Global Positioning System (GPS) telemetry techniques to provide a first insight into the size and extent of Cape vulture home ranges in relation to the network of power lines and protected areas in southern Africa. The Cape vulture is endemic to southern Africa and is listed as Vulnerable on the IUCN Red List due to declines across its range (BirdLife International 2013). It is a gregarious cliff-nesting species with a global population estimated at 8,000–10,000 individuals (*ca.* 4,000 breeding pairs) (BirdLife International 2013). The largest remaining breeding colonies are located in the north-eastern provinces of South Africa (Benson *et al.* 1990; Mundy *et al.* 1992; Whittington-Jones *et al.* 2011; BirdLife International 2013), where increasing urbanisation and land use change has caused habitat loss, food shortages and an increasing incidence of negative vulture-power line interactions (Naidoo *et al.* 2011). We hypothesize that frequent use of transmission line pylons as perching and roosting sites by Cape vultures will influence the extent of their home ranges and the location of their core foraging areas. We also assess the ability of GPS tracking data to identify potentially high risk areas of vulture-power line interactions in order to inform future mitigation strategies. We predict that Cape vultures regularly roost and forage outside protected areas, but expect adults to traverse smaller home ranges in closer proximity to protected breeding colonies compared to the less restricted movements of immature individuals (Bamford *et al.* 2007).

2.3. Methods

2.3.1. Vulture Captures and GPS Tracking

A walk-in cage trap (6 x 3 x 3 m; Appendix 1) baited with ungulate carcasses was used to catch vultures at a supplementary feeding site for vultures at Mankwe Wildlife Reserve (MWR; 25°13’S, 27 °18’E) in the North West Province of South Africa (Fig. 2.1) (Phipps *et al.* 2013a). Ten Cape vultures were caught between November 2009 and June 2010 during seven separate captures. Owing to the difficulty in ageing *Gyps* vultures individuals could only be identified as adults (>5 years), immatures (2-5 years) or juveniles (first year) based on characteristic plumage traits and eye colouration (Duriez *et al.* 2011). For statistical analyses juveniles (n=1) were pooled with immatures. The genders of vultures were not confirmed by molecular analysis as blood or feather samples were not taken from each individual and *Gyps* vultures exhibit no obvious sexual dimorphism in plumage or body characteristics (Bose *et al.* 2007). Furthermore, Bosé *et al.* (2007) found no difference in male or female life history or movement patterns in a closely related species and so this was not investigated during this study. Teflon® ribbon backpack-style harnesses were used to secure Hawk105 GPS-GSM (Global System for Mobile communications) tracking units (Africa Wildlife Tracking Ltd., Pretoria, South Africa; www.awt.co.za; Appendix 2) onto the back of each vulture (Diekmann *et al.* 2004; Phipps *et al.* 2013a). Each unit recorded GPS locations (~10 m accuracy, verified by a positional dilution of precision (PDOP) measure of accuracy (D'Eon and Delparte 2005)), altitude above sea level, speed, direction of travel, date, time and temperature three times per day at 07:00, 11:00 and 15:00 Central Africa Time (CAT). One additional data point was recorded per day at 13:00 CAT for three adult vultures (AG314, AG349 and AG355) to account for foraging trips from cliff roosts between the

11:00 and 15:00 readings. The units were expected to record and transmit data for approximately one year. Patagial tags with unique numeric codes were attached to both wings of each vulture to allow identification of individuals following release.

2.3.2. Ethics Statement

The procedures were approved by the ethical review committee of the School of Animal, Rural and Environmental Science, Nottingham Trent University. Permits for the capture and handling of vultures and the fitting of tracking units were granted by the Department of Agriculture, Conservation, Environment and Rural Development, North West Provincial Government, Republic of South Africa (Permit: 000085 NW-09). All procedures were carried out by South African Bird Ringing Unit permit holders (KW and WLP). All necessary measures were taken to minimise any potential discomfort to the birds. Each tracking unit weighed 170g which is *ca.* 1.8% of the mean mass of an adult Cape vulture (Mundy *et al.* 1992), and less than the 3% recommended for flying birds. A weak point was included on each harness to allow it to eventually fall off, releasing the tracking unit from the bird.

2.3.3. Data Analysis

GPS locations were projected to the Universal Transverse Mercator (UTM) coordinate system for all spatial analyses. Stationary and moving GPS locations were defined as all those recorded with a speed $<$ or $\geq$ 10 $\mathrm{km \cdot h^{-1}}$, respectively. Distances travelled between consecutive GPS locations were calculated for each vulture. Two methods were used to delineate the home ranges of each vulture.

Firstly, Minimum Convex Polygons (MCPs) were created using the Home Range Tools extension (Rodgers *et al.* 2007) for ArcGIS® using all recorded GPS locations to allow comparisons to be made with other *Gyps* vulture tracking studies (Harris *et al.* 1990; Bamford *et al.* 2007). Incremental area analysis was performed for each vulture by creating MCPs using sequentially added consecutive GPS locations until all locations were used to create an MCP for the total tracking period. Home range area curves were then plotted to identify whether the home range areas reached asymptotes by the end of the tracking period (Harris *et al.* 1990). Secondly, fixed kernel density estimation (KDE) was carried out using the Geospatial Modelling Environment (GME) program (Beyer 2012) to delineate 99% and 50% contours to represent the overall and core foraging ranges, respectively (Worton 1989). The plug-in method of bandwidth selection was used following preliminary analyses that indicated that the least-squares cross-validation (LSCV) method failed to select a bandwidth due to numerous identical GPS locations and use of the reference bandwidth resulted in over-smoothed home range boundaries (Gitzen *et al.* 2006). A 1 km^2 cell size was used for KDE calculations. The 99% KDE contours were used instead of the 95% contours to represent the overall home ranges as the latter generally produced undersmoothed and more fragmented outer contours. The size of the 99% KDE contours and MCPs of the adult and immature vultures were compared using Mann-Whitney tests. The spatial extent of the home ranges were compared to the IUCN Cape vulture species distribution map (BirdLife International and Natureserve 2011) and the proportion of GPS locations recorded within the IUCN distribution were compared between adults and immatures using Mann-Whitney tests to determine whether either age class travelled beyond the known species distribution more or less frequently than the other.

The use of transmission power lines and associated stuctures for perching and roosting by vultures was estimated by calculating the proportion of stationary (i.e. < 10 km▪h^{-1}) GPS locations recorded within 50 m of transmission power lines within each vulture's home range. Analyses were performed in ArcMap v9.3 (ESRI 2008) and spatial data for transmission power lines were sourced from Eskom (South Africa), the Africa Infrastructure Knowledge Program (Botswana and Zimbabwe; http://www.infrastructureafrica.org) and the Environmental Information Service (Namibia; http://www.the-eis.com). We assumed that if a vulture was recorded as being stationary within 50 m of a transmission line or pylon it was likely to be using it as a roost or perch site. To test whether vulture perching or roosting activity was more closely associated with transmission line corridors than other features in the wider landscape the density of stationary GPS locations within a 50 m buffer each side of the transmission line network was compared with the density of stationary

GPS locations in the overall home range (i.e. 99% KDE contour) for each vulture. The density of stationary GPS locations within the 50 m transmission line buffer inside each vulture's core area (i.e. 50% KDE contour) was also compared to the density inside the total core area to identify whether stationary locations were concentrated in the vicinity of power lines inside core areas. Wilcoxon signed-rank tests were used to identify significant differences in GPS location densities at the different scales with each vulture considered as a sampling unit. The proportion of stationary GPS locations recorded within 50 m of transmission lines was compared between adult and immature vultures using a Mann-Whitney test. To assess the potential for GPS tracking data to identify possible high risk areas of vulture-power line interactions the proportion of locations of Cape vulture-power line incidents with known GPS co-ordinates (437 mortalities at 126 locations) recorded in the Central Incident Register (CIR) of the Endangered Wildlife Trust (EWT) and Eskom (the main electricity distributor in the country) between May 1996 and July 2012 (Jenkins *et al.* 2010; Boshoff *et al.* 2011; Eskom-EWT 2012) that overlapped with the vultures' core foraging ranges was calculated.

To assess vulture use of protected areas a polygon shapefile was created comprising all IUCN category I-VI protected areas and 'national other areas' (i.e. protected areas uncategorized by IUCN) polygons from the 2010 and 2003 World Database on Protected Areas (WDPA) (IUCN and UNEP 2003, 2014). Each vulture's use (U_i) of protected areas was then estimated as the proportion of stationary (< 10 km▪h^{-1}) GPS locations recorded inside the protected area polygons. The availability of protected areas (A_i) to each vulture was defined as the proportion of the 99% KDE contour covered by the protected areas polygons. Wilcoxon signed-rank tests were used to identify differences between U_i and A_i with each vulture considered as a sampling unit. Ivlev's electivity index (E_i) was then calculated as a measure of whether protected areas were visited more frequently than expected based on their availability at the overall home range scale: $E_i = (U_i - A_i) / (U_i + A_i)$ (Ivlev 1961). A value of zero indicated that use of protected areas was proportional to their availability, while positive (maximum = +1) and negative (minimum = -1) values indicated greater and lesser use of protected areas than expected, respectively. Use of protected areas was also assessed in the same way at the core range scale by defining U_i as the proportion of the 50% KDE contour covered by the protected areas. Adult and immature vulture use (U_i) of protected areas were compared using a Mann-Whitney test. The values reported in the Results section correspond to mean ± standard deviation unless stated otherwise.

2.4. Results

Ten Cape vultures, five adults, four immatures and one juvenile (hereafter considered as an immature) were captured and tracked using GPS-GSM tracking units for 300±178 days from November 2009 to August 2011 (Table 2.1). The average number of GPS locations recorded per individual was 1,052±578 with 78.35±9.47% recorded as stationary (< 10 km·h^{-1}) (Table 2.1). The mean and maximum speed of all moving (≥ 10 km·h^{-1}) locations (n = 2319) was 54.54±16.93 km·h^{-1} and 115 km·h^{-1}, respectively. Mean accuracy of all GPS locations on the PDOP scale was high at 2.17±1.97 (n = 9468). Tracking units stopped transmitting data prematurely (i.e. < 1 year) for five vultures for unknown reasons. The tracking unit on an immature vulture (AG351) stopped transmitting after only 12 days and the data were excluded from the analyses. Another immature vulture (AG352) travelled north through eastern Zimbabwe before heading west to an area 40 km east of Maun, Botswana, where its tracking unit ceased transmitting data. An adult vulture (AG382) was tracked for a month to an area west of the Kruger National Park *ca.* 400 km from the capture site, where its remains were found and the tracking unit recovered. The cause of death was unconfirmed. Tracking units on two adults functioned properly for more than 8 months before data transmission ceased.

2.4.1. Size and Extent of Home Ranges

The nine vultures occupied large home ranges (mean 99% KDE = 223,132±227,256 km^2; mean 50% KDE contour = 25,851±28,473 km^2; Table 2.1) and long distance cross-border movements were not unusual with a total of five countries (Namibia, Botswana, Zimbabwe, Lesotho and South Africa) entered by different vultures (Fig. 2.1A). The mean maximum distance recorded between two consecutive GPS locations for all vultures was 178±46 km (maximum = 254 km; Table 2.1.). Some individuals were recorded more than 1000 km straight-line distance from the capture site. Incremental area analysis indicated that the home range areas of most of the vultures had become stable by the end of their tracking periods (Fig. S2.1). The most intensively used areas, as indicated by the 50% KDE contours (Fig 2.1B), were located in the north-western Limpopo Province and north-eastern North West Provinces of South Africa, extending north into southern Botswana either side of the Limpopo River, and south to the Magaliesberg Mountains and Mafikeng district in North West Province, South Africa (Fig. 2.2). The 99% KDE contours (median = 353,717 km^2) and the MCPs (median = 413,722 km^2) of the four immature vultures were significantly larger than the 99% KDE contours (median = 69,254 km^2; $Z = -2.45$, $p = 0.014$) and MCPs (median = 92,092 km^2; $Z = -2.45$, $p = 0.014$) of the five adult vultures (Table 2.1, Fig. S2.2).

The combined 99% KDE contours for all individuals covered 1,052,467 km^2, of which 36% was located outside the extent of the IUCN distribution for the species, largely due to the movements of several individuals into the Northern Cape Province of South Africa and southern Namibia (Fig. 2.1A). A significantly higher proportion of GPS locations were recorded inside the extent of the IUCN Cape vulture distribution for adults (median = 98.41%) compared to immatures (median = 67.53%; $Z = -2.21$, $p = 0.027$; Fig. 2.1A), indicating that immatures travelled beyond the known distribution for the species more frequently than adults.

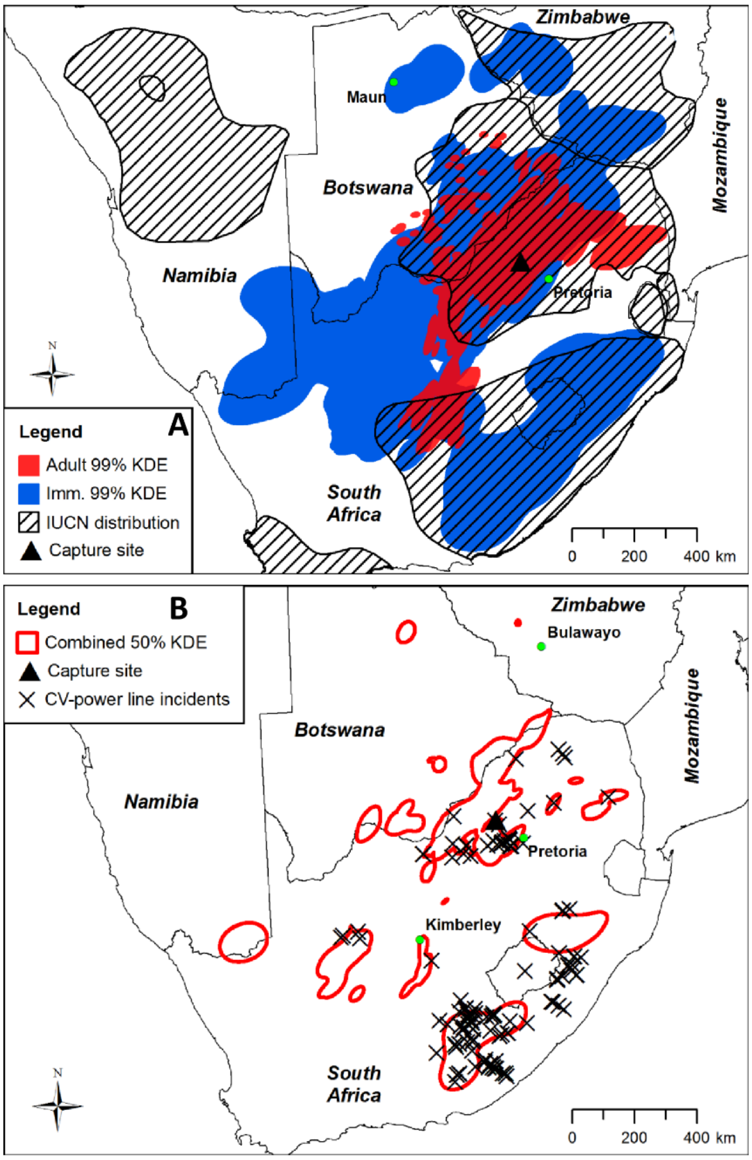

Figure 2.1. Home ranges of nine Cape vultures with species distribution map and Cape vulture-power line incidents. (A) Shaded red and dark blue polygons represent the combined 99% kernel density estimated (KDE) contours of all adult and immature vultures, respectively. The diagonal line shaded polygons represent the extent of the Cape vulture species distribution according to BirdLife International (BirdLife International and Natureserve 2011). The capture site is indicated by a black triangle. (B) The hollow red polygons represent the combined 50% KDE contours of all nine vultures. Black crosses show locations of Cape vulture-power line incidents recorded in the Central Incident Register of the EWT-Eskom strategic partnership (Eskom-EWT 2012).

Table 2.1. Home range and distance estimates for nine Cape vultures tracked by GPS-GSM units.*(full description overleaf)

				Home range estimates (km²)			Distance estimates (km)		
Vulture ID	**Age**	**Tracking period (days)**	**Number of GPS locations**	**MCP**	**99% KDE**	**50% KDE**	**Mean (± SD) distance between consecutive locations**	**Maximum distance between consecutive locations**	**Total distance travelled / tracking days**
AG314	Adult	479	1,636 (1,065)	165,337	69,254	3,056	21.34±26.49	212	73
AG329	Adult	267	793 (746)	92,092	78,847	11,113	5.17±15.58	156	15
AG349	Adult	234	752 (513)	56,152	52,385	5,998	20.07±28.63	185	64
AG355	Adult	490	1,860 (1,341)	258,294	149,687	10,071	16.70±25.35	174	63
AG382	Adult	31	84 (72)	36,401	53,589	6,691	9.35±18.22	84	25
Mean		300	1,025	121,655	80,752	7,385	14.53	162	48
SD		191	722	90,845	40,095	3,250	7.00	48	26
AG313	Imm.	315	922 (725)	273,946	161,311	10,722	13.32±25.96	254	39
AG352	Imm.	207	612 (538)	392,856	312,715	44,429	9.53±20.78	159	28
AG353	Juv.	558	1,654 (1,251)	434,588	392,719	59,927	15.25±23.71	184	45
AG383	Imm.	409	1,155 (898)	867,811	737,684	80,654	13.24±21.26	192	37
Mean		372	1,086	492,300	401,107	48,933	12.83	197	37
SD		149	439	259,427	244,042	29,481	2.39	40	7

*Minimum convex polygons (MCP) including all recorded GPS locations and 99% contours from kernel density estimation (KDE) represent overall foraging ranges. 50% KDE contours represent core foraging ranges. Mean (± SD) and maximum distances between consecutive GPS locations, and the total distance travelled divided by the number of tracking days are shown. The age (adult (>5 years), immature (2-5 years) or juvenile (first year)) of each vulture, the tracking period and number of GPS locations (number of stationary ($<10\ \mathrm{km \cdot h^{-1}}$) locations are given in parentheses) recorded are also shown.

2.4.2. Utilisation of Power Lines

The vultures were frequently recorded in the vicinity of transmission power lines. The 50 m transmission line buffer area covered only 0.52±0.14% of the 99% KDE contour areas of all nine vultures but contained 20.60±12.74% of the stationary GPS locations recorded by each tracking unit (Table S2.1). There was no significant difference in the proportion of stationary locations recorded within 50 m of transmission lines for adults (median = 19.17%) compared to immatures (median = 14.87%; $Z = -0.490$, $p = 0.730$). The density of stationary GPS locations within the 50 m transmission line buffer in the 99% KDE contours (median = 0.267 locations·km^{-2}) was significantly higher than the density in the overall 99% KDE contours (median = 0.005 locations·km^{-2}; $Z = -2.67$, $p = 0.008$; Table S2.1). The 50 m transmission line buffer covered significantly more of the 50% KDE contours (median = 0.80%) than the 99% KDE contours (median = 0.59%; $Z = -2.37$, $p = 0.018$), and the density of stationary GPS locations within the 50 m transmission line buffer in the 50% KDE contours (median = 0.827 locations·km^{-2}) was significantly higher than in the overall 50% KDE contours (median = 0.046 locations·km^{-2}; $Z = -2.67$, $p = 0.008$). This indicates that the vultures were more frequently in close proximity to transmission lines when stationary compared to the wider landscape, particularly in their core foraging areas. The stationary locations within the 50 m buffer were generally clustered along certain sections of transmission line that were repeatedly visited by several different individuals (Fig. 2.2 and 2.3). Out of 126 known locations of Cape vulture-power line incidents recorded in the Eskom-EWT CIR, 120 (95%) were inside the combined 99% KDE contours of all vultures, of which 67 (56%) were recorded inside the combined 50% KDE contours (Fig. 2.1B).

2.4.3. Utilisation of Protected Areas

All vultures spent the majority of their tracking periods outside protected areas but several regularly roosted on cliffs inside national parks or nature reserves. The difference in coverage of protected areas (Table 2.2) was not significantly different between the 99% (median = 4.53%) and 50% KDE contours (median = 9.72%; $Z = -1.36$, $p = 0.173$). Although the proportion of stationary GPS locations recorded inside protected areas (median = 27.31%) was higher than the proportion they covered of 99% KDE contours (median = 4.53%), the difference was not significant ($Z = -1.84$, $p = 0.066$). Ivlev's electivity index values indicated, however, that six vultures used protected areas more than expected based on their availability in their overall home ranges (Table 2.2).

Of the 1,496 stationary GPS locations recorded inside protected areas (21% of all stationary locations), 94% were in South African reserves, of which 68% were recorded in Marakele National Park (NP) in the Limpopo Province (24^{o}24'S, 27^{o}35'E), and 11% were recorded in the Magaliesberg Nature Reserve (NR) (25^{o}44'S, 27^{o}45'E), both of which encompass large Cape vulture breeding colonies (Fig. 2.2) (Benson *et al.* 1990; Whittington-Jones *et al.* 2011). Marakele NP was visited by a total of seven vultures but the majority (96%) of stationary locations recorded inside the park were from three adult vultures (AG314, AG349, AG355) that frequently roosted on the breeding cliffs. 93% of stationary locations recorded inside Marakele NP were situated on the Kransberg nesting cliffs. Breeding attempts by those vultures could not be confirmed during colony observations, however, and so the influence of breeding status could not be investigated. Similarly, all stationary locations recorded in the Magaliesberg NR were situated on known breeding or roosting cliffs, the majority (87%) of which were from one immature vulture (AG313). Beyond the breeding colonies 15 other protected areas were visited in South Africa (Fig. 2.2), although only six contained more than 10 stationary GPS locations. Outside South Africa one immature vulture (AG383) briefly entered two protected areas in south-west Zimbabwe, another (AG353) visited the Central Kalahari GR in Botswana, while a third (AG352) entered several protected areas in eastern Zimbabwe and central Botswana. Despite the more frequent use of roost sites within protected areas by the adult vultures there was no significant difference in the proportion of stationary locations recorded within protected areas for adults (median = 36.45%) compared to immatures (median = 11.71%; $Z = -1.470$, $p = 0.190$).

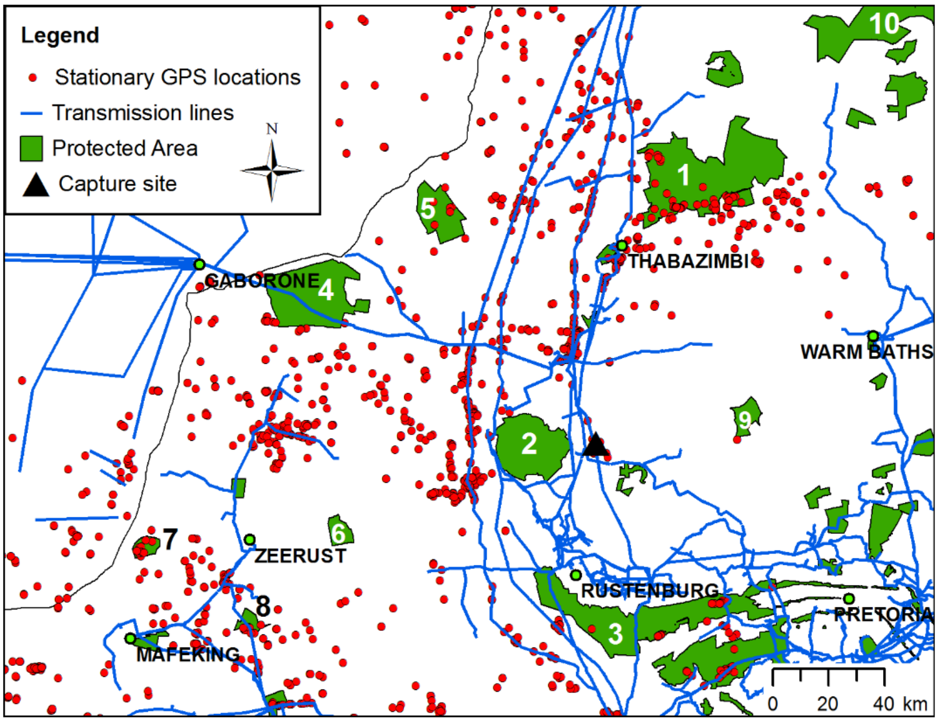

Figure 2.2. Stationary GPS locations in relation to protected areas and transmission power lines in the northern provinces of South Africa. Stationary GPS locations (red circles) from nine Cape vultures tracked by GPS-GSM tracking units are shown with transmission power lines (blue lines) and protected areas (green ploygons (IUCN and UNEP 2003, 2014)). 1 = Marakele NP and Welgevonden NR; 2 = Pilanesberg NP; 3 = Magaliesberg NR; 4 = Madikwe GR; 5 = Atherstone NR; 6 = Marico-Bosveld NR; 7 = Botsalano GR; 8 = Oog van Malmanie GR; 9 = Borakalalo GR; 10 = Lapalala, Moepel *et al.* reserves. The capture site is indicated by a black triangle.

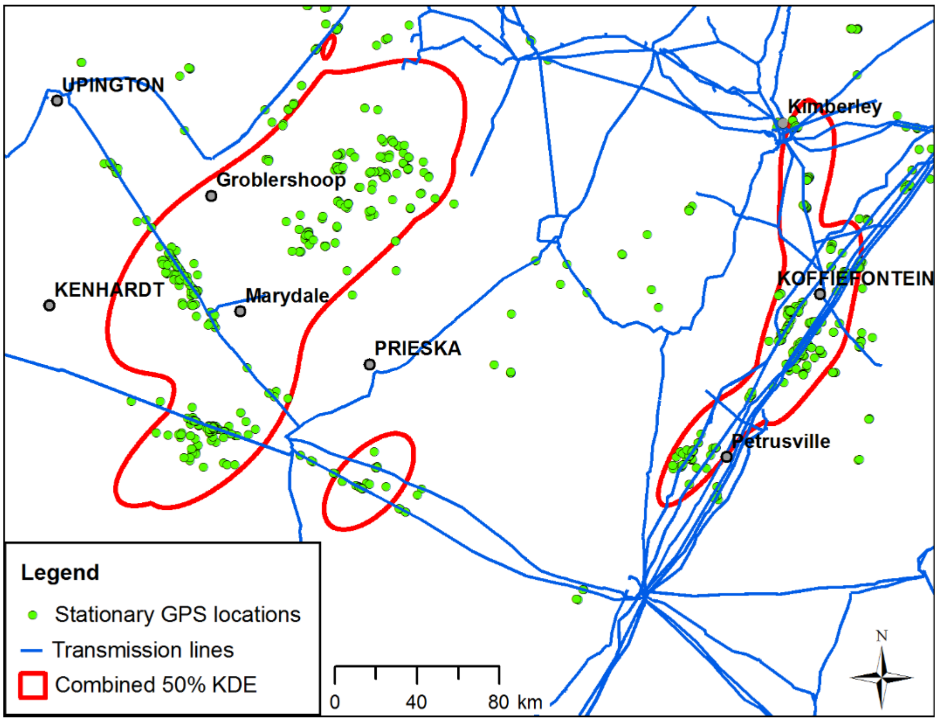

Figure 2.3. Stationary GPS locations and core areas in relation to transmission power lines in the Northern Cape Province, South Africa. Stationary GPS locations (green circles) and merged 50% kernel density estimated (KDE) contours (hollow red polygons) from nine Cape vultures are shown in relation to transmission power lines (blue lines).

Table 2.2. Availability and use of protected areas by nine Cape vultures at the overall and core home range scales.*

Vulture ID	PA coverage in 99% KDE (%)	PA coverage in 50% KDE (%)	Ivlev's electivity index at core range scale	Proportion of stationary locations inside PAs (%)	Ivlev's electivity index at home range scale
AG314	3.47	18.43	0.68	38.78	0.84
AG329	3.84	3.20	-0.09	3.49	-0.05
AG349	5.55	13.71	0.42	36.45	0.74
AG355	4.53	9.72	0.36	32.14	0.75
AG382	16.89	32.47	0.32	40.28	0.41
AG313	3.37	11.74	0.55	27.31	0.78
AG352	19.55	8.32	-0.40	16.54	-0.08
AG353	3.97	5.43	0.16	6.87	0.27
AG383	6.02	3.21	-0.30	4.12	-0.19
Mean	7.47	11.80	0.19	22.89	0.38
SD	6.20	9.21	0.38	15.29	0.41

*The proportion of each vulture's 99% kernel density estimated (KDE) contour occupied by protected areas (PAs) defined their availability (A_i) to each vulture. At the overall home range scale use (U_i) of protected areas was defined as the proportion of stationary (i.e. < 10 km▪h^{-1}) GPS locations within the 99% KDE contour that were recorded inside protected areas. The proportion of each vulture's 50% KDE contours occupied by protected areas defined their use at the core foraging range scale. Ivlev's electivity index values range from -1 to +1, with zero indicating use in proportion to availability, while positive and negative values indicate use more or less than expected, respectively.

2.5. Discussion

This study uses GPS tracking methods to provide the first description of the relationship between the power line network and ranging behaviour of Cape vultures in southern Africa, together with their use of protected areas. The vultures, particularly immature individuals, traversed large home ranges that closely followed the spatial distribution of transmission power lines. The core foraging areas overlapped with known locations of negative vulture-power line interactions. All vultures spent the majority of their tracking periods outside protected areas, although some regularly used roost sites at breeding colonies within national parks or nature reserves.

The home ranges recorded during this study are among the largest for any vulture species. Although the five adult vultures traversed larger home ranges (mean MCP = 121,655±90,845 km^2) than five adult Cape vultures tracked in Namibia (mean MCP = 21,320 km^2 (Bamford *et al.* 2007)), such comparisons should be considered with caution because breeding attempts by the vultures from this study could not be confirmed during colony surveys. If they were non-breeding birds their foraging movements would not have been restricted by the need to return to a nest site, allowing them to range further than breeding individuals from the Namibian study (Houston 1974b; Bamford *et al.* 2007). The four immature vultures occupied similarly extensive home ranges (mean MCP = 492,300±259,427 km^2) to two immature Cape vultures from the Namibian study (mean MCP = 482,276 km^2) (Bamford *et al.* 2007)), but larger than those of six immature African white-backed vultures tracked from South Africa (mean MCP = 269,103±197,187 km^2 (Phipps *et al.* 2013a)). Compared to *Gyps* species outside Africa the home ranges recorded here exceeded those of Eurasian griffon vultures (*G. fulvus*) tracked in France (combined MCP = *ca.* 1,000 km^2 (n=28) (Monsarrat *et al.* 2013)) and Spain (median MCP = 7,419 km^2 (n=8) (Garcia-Ripolles *et al.* 2011)), and Asian white-backed vultures (*G. bengalensis*) in Pakistan (mean MCP = 24,155 km^2 (n=6) (Gilbert *et al.* 2007)). A recent study in Israel reported that while the majority of 43 tagged *G. fulvus* did not travel more than 200 km from the centre of their home range, a few individuals undertook infrequent "long-range forays" of more than 1,700 km from their home range centres (Nathan *et al.* 2012). Such comparisons must be considered with caution, however, as factors that determine home range characteristics such as food availability, habitat quality, topography and levels of competition are likely to vary geographically and between species (Monsarrat *et al.* 2013), and could not be fully investigated here due to limited data availability. Nevertheless, the similar long-distance cross-border movements and large distances travelled on a daily basis during this study confirm that *Gyps* vultures and Cape vultures in particular, are among the widest ranging bird species probably due to their reliance on a sparsely and unpredictably distributed food source (Houston 1974b; Meretsky and Snyder 1992).

The high densities of stationary GPS locations recorded in close proximity to transmission lines provide strong evidence that the movement patterns of Cape vultures are closely linked to the spatial extent of the transmission power line network in southern Africa and suggest that they prefer to perch, roost and forage in the vicinity of transmission line towers rather than moving randomly throughout their home ranges as might be expected from a typical central-place forager (Monsarrat *et al.* 2013). For instance, although the spatial extent of the core ranges (Fig. 2.1B) corresponded with areas known to be important foraging grounds for *Gyps* vultures in southern Africa (Benson *et al.* 1990; Mundy *et al.* 1997; Whittington-Jones *et al.* 2011; Phipps *et al.* 2013a), the core area used by three immature vultures in the Marydale region of the Northern Cape Province (Fig. 2.3) extended more than 100 km west of the IUCN distribution range for the species (BirdLife International 2013). The close association of the vultures' movements with the transmission lines in that area provides strong evidence that the construction of power line "towers have proved ideal as roosting sites.....in places devoid of cliffs", allowing the species to expand its range into new foraging areas (Mundy *et al.* 1992). It is possible that the construction of power lines in that area has provided a "nursery area" where immature Cape vultures forage away from the competition imposed by dominant adult vultures at carcasses nearer breeding colonies (Mundy *et al.* 1992; Duriez *et al.* 2012). A similar finding was recorded in immature Spanish imperial eagles *Aquila adalberti* which frequently perched on pylons where alternative perching sites were limited in dispersal areas away from adult competition (Gonzalez *et al.* 2007). This could also partially explain why the immature vultures traversed more extensive home ranges than the adults, as seen elsewhere (Meretsky and Snyder 1992; Bamford *et al.* 2007; Duriez *et al.* 2012). Although the breeding status of the adult vultures was unknown it is likely that they would have remained in closer proximity to nesting colonies in order to encounter potential breeding opportunities, compared to the immature vultures which could range further between food sources (Houston 1974b; Duriez *et al.* 2012). However, further research is required to determine the primary factors driving the long-distance movements of immature vultures.

Although power line towers provide vultures with additional roost sites and vantage points, the large proportion of time that they spend in the vicinity of overhead cables associated with the structures, in combination with their large size, susceptibility to collisions with man-made structures and their gregarious nature puts them at significant risk of injury or death (Janss 2000; Martin *et al.* 2012). These factors explain the high and increasing number of collision-related injuries and fatalities of vultures recorded in South Africa (Boshoff *et al.* 2011; Naidoo *et al.* 2011). In some regions it is conservatively estimated that power lines kill at least 4% of the local population of Cape vultures annually (Boshoff *et al.* 2011). The number of vultures killed by collisions is thought to be significantly under-recorded as they rarely cause electricity supply faults and are therefore not investigated, and the vast majority of vulture carcasses are likely to be removed by terrestrial scavengers before they are detected (Jenkins *et al.* 2010; Boshoff *et al.* 2011). If the estimate of only 2.6% of power line mortalities of blue cranes *Anthropoides paradiseus* and Denham's bustards *Neotis denhami* being recorded in part of South Africa (Shaw *et al.* 2010a) is repeated for Cape vultures, then such a prevalent unnatural mortality factor is likely to cause severe population declines (Boshoff *et al.* 2011) as witnessed in other species (Shaw *et al.* 2010b). For example, negative interactions with power lines are a major cause of mortality in Spanish imperial eagles, particularly in sub-adults which frequently perch on electricity pylons in areas lacking suitable alternatives (Gonzalez *et al.* 2007).

Although organizations such as Eskom have invested significant resources in an attempt to reduce vulture mortalities, more widespread mitigation measures are required to prevent vulture population declines caused by the expanding power line network (Boshoff *et al.* 2011; Naidoo *et al.* 2011). For example, marking wires with bird flight diverters to increase their visibility and reduce the risk of collision has been carried out in many areas with some success (Jenkins *et al.* 2010; Barrientos *et al.* 2012). It is a costly measure (e.g. 1,100-2,600 US$

km^{-1} (Kruger 2001)), however, and it is therefore essential to target high risk areas. The ease of identifying repeatedly visited sections of power line and the relatively high degree of overlap between the vulture core ranges and the known fatalities recorded in the CIR recorded during this study demonstrate the ability of GPS tracking data to inform the implementation of such mitigation measures. For example, additional surveys for vulture carcasses could be carried out at frequently visited sections of power line to determine whether mitigation measures (e.g. bird flight diverters) are required or to assess their effectiveness after installation.

Although protected areas away from breeding colonies were rarely visited by any of the vultures during this study (Fig. 2.2), breeding cliffs inside two protected areas were regularly used as roost sites by three adults and one immature, confirming that protected areas are important for reducing anthropogenic disturbance at nest and roost sites (Herremans and Herremans-Tonnoeyr 2000; Borello and Borello 2002; Monadjem and Garcelon 2005; Bamford *et al.* 2009b; Virani *et al.* 2011). The most intensively used areas by the vultures were located in a south-westerly direction from the Kransberg colony (Marakele NP) on private and communal farmland, and rarely included protected wildlife reserves. Although data relating to food availability were not available, this supports suggestions that Cape vultures from the Kransberg colony regularly feed on domestic livestock carcasses (Benson *et al.* 2004) and are therefore at risk of exposure to harmful veterinary drugs (Naidoo *et al.* 2009; Naidoo *et al.* 2010b). The vultures also frequently travelled to the northern Limpopo Province and elsewhere in South Africa where game farming is common (St John *et al.* 2012) and so it is likely that they also consumed wild ungulate species as seen previously (Murn and Anderson 2008). Consequently, during their regular foraging activity the vultures would have been afforded very little protection from widespread threats such as consuming ungulate carcasses contaminated with veterinary drugs, illegal poisons used for predator control or lead bullet fragments from hunting activity on unprotected farmland (Garcia-Fernandez *et al.* 2005; Virani *et al.* 2011; St John *et al.* 2012). A similar pattern of limited use of protected areas was observed for immature African white-backed vultures tracked in the same area (Phipps *et al.* 2013a). Thus these findings further emphasise the need to establish vulture monitoring and conservation measures outside protected areas.

The small sample size of tracked vultures (n = 10) limited by financial constraints mean that the results from this study provide a first, rather than a comprehensive insight into the movement patterns of Cape vultures and their relationship with the power line network and protected areas in southern Africa. Although the findings allow preliminary comparisons between adult and immature movement patterns, future research should aim to elucidate the influence of additional individual characteristics such as breeding status and gender on Cape vulture ranging behaviour. Moreover, the effect of food availability on vulture movement patterns was not assessed during this study because of a lack of accurate data relating to ungulate densities and mortality rates. As an important factor in determining home range characteristics (Harris *et al.* 1990) and the risk posed by power lines at a local scale (Bevanger 1998), this issue should be investigated further. Nonetheless, the regular sampling intervals and highly accurate GPS location data have demonstrated the ability of GPS tracking data to delineate the home ranges of vultures and assess their exposure to potential threats in the region.

2.6. Conclusions

The findings from this study demonstrate that Cape vultures have extended their range by using transmission power line structures for roosting and perching in areas otherwise devoid of suitable perches, but must frequently face the risk of colliding with overhead wires. If the extensive movement patterns and limited use of protected areas recorded during this study are representative across the species' geographical range then it is likely that the population is regularly exposed to multiple threats such as negative interactions with power lines and poisoning from contaminated carcasses on private farmland. We suggest that co-ordinated cross-border conservation measures beyond the boundaries of the protected area network will be necessary to ensure the future survival of threatened vultures in Africa. Specifically, additional monitoring and mitigation of negative interactions with power lines will be required, as well as a concerted effort to remove contaminants from the food supply. The use of GPS tracking data to inform conservation management of other threatened species is also advocated.

2.7. Supplementary information

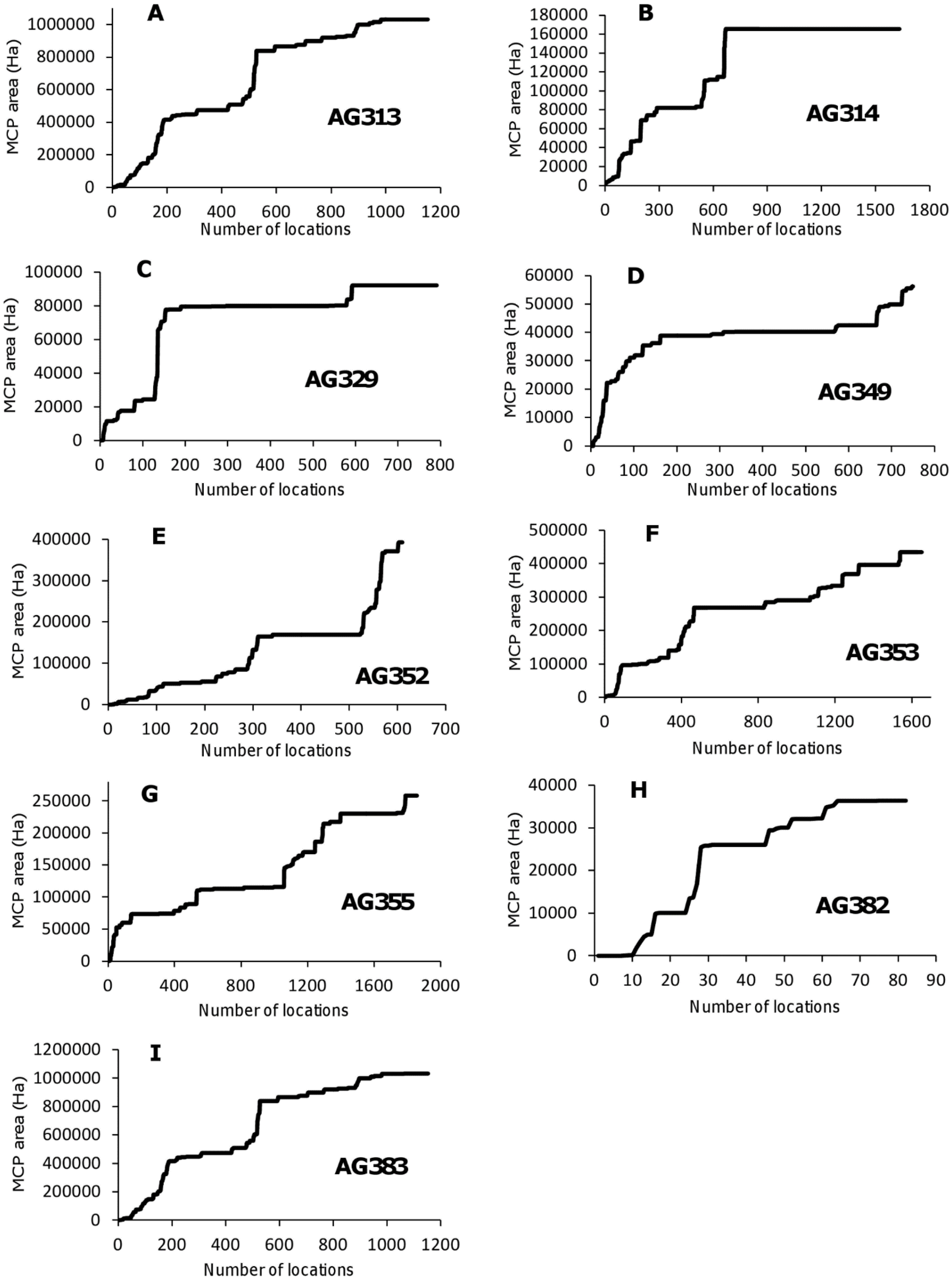

Figure S2.1. Home range area curves from incremental area analysis of GPS locations from nine Cape vultures. The number of GPS locations used to generate minimum convex polygons (MCPs) by adding consecutive locations until all locations were used is plotted against the area of each MCP. (A) – (I) represent different vultures (refer to Table 2.1).

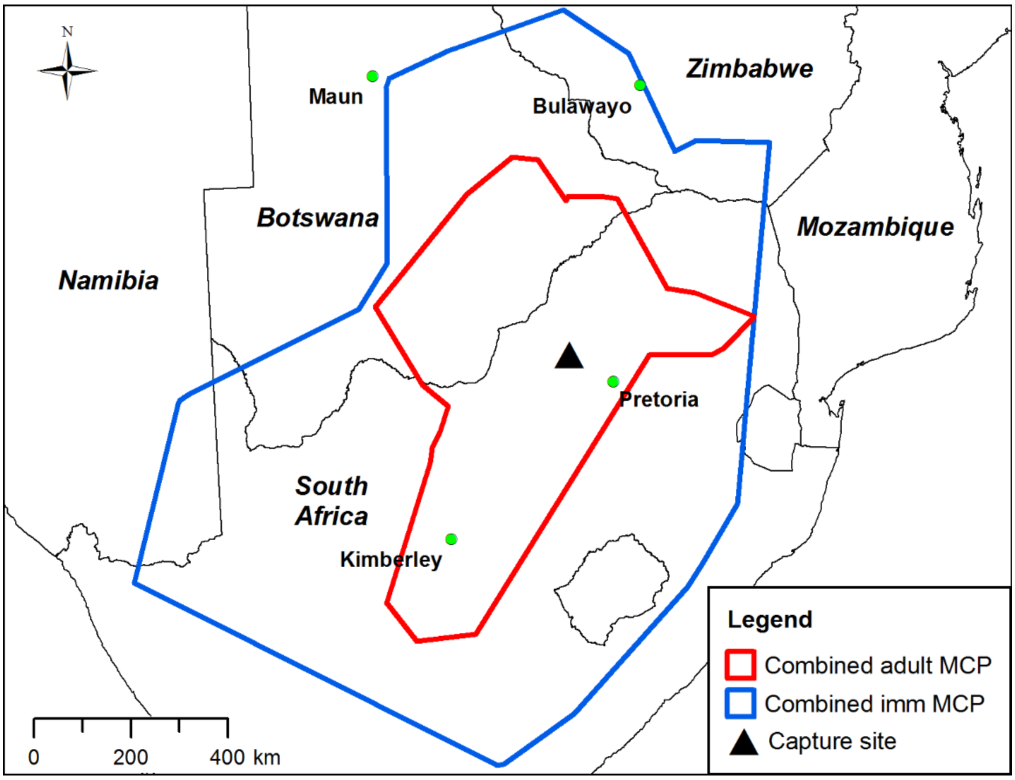

Figure S2.2. Minimum convex polygons of five adult and four immature Cape vultures tracked by GPS-GSM tracking units. Hollow red and blue polygons represent merged minimum convex polygons (MCPs) using all locations from five adult and four immature Cape vultures tracked using GPS-GSM tracking units, respectively. The capture site is indicated by a black triangle.

Table S2.1. Association of GPS tracking locations and home ranges of nine Cape vultures with the transmission power line network. The proportion of the 99% and 50% kernel density estimated (KDE) contours covered by the 50 m transmission line (Tx) buffer, and the proportion of stationary GPS locations recorded within the Tx buffer are shown, as well as the corresponding stationary GPS location densities within the 99% and 50% contours and the Tx buffer.

					Stationary location density (locations·km^{-2})			
Vulture ID	**Proportion of 99% KDE occupied by Tx buffer (%)**	**Proportion of stationary locations in 99% KDE in Tx buffer (%)**	**Proportion of 50% KDE occupied by Tx buffer (%)**	**Proportion of stationary locations in 50% KDE in Tx buffer (%)**	**99% KDE**	**99% KDE Tx buffer**	**50% KDE**	**50% KDE Tx buffer**
AG314	0.39	18.31	0.98	18.70	0.015	0.730	0.222	4.233
AG329	0.68	19.17	1.25	20.65	0.009	0.267	0.050	0.827
AG349	0.59	30.99	0.80	30.60	0.010	0.513	0.067	2.563
AG355	0.63	32.07	1.18	32.08	0.009	0.458	0.098	2.647
AG382	0.66	2.78	0.51	1.56	0.001	0.006	0.010	0.029
AG313	0.63	43.59	0.95	46.73	0.004	0.312	0.046	2.245
AG352	0.35	8.74	0.61	10.71	0.002	0.043	0.009	0.156
AG353	0.39	14.71	0.45	17.77	0.003	0.121	0.013	0.530
AG383	0.37	15.03	0.52	19.04	0.001	0.050	0.008	0.294
Mean±	0.52	20.60	0.81	21.98	0.006	0.278	0.058	1.503
SD	0.14	12.74	0.30	13.09	0.005	0.250	0.069	1.470

2.8. Acknowledgements

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Author Contributions

Conceived and designed the experiments: WLP KW RWY MM LM. Performed the experiments: WLP KW LM. Analyzed the data: WLP. Wrote the paper: WLP RWY. Acted as the first author’s study supervisor: RWY.

CHAPTER 3: Ranging and land use patterns of a remnant population of Cape vultures *Gyps coprotheres* in Namibia

Prepared for submission to *Bird Conservation International.*

3.1. Abstract

Vulture populations are declining worldwide due to multiple anthropogenic threats. Illegal poisoning is now considered to be the most serious threat to African vultures although other mortality factors such as electrocutions and collisions with power lines, food shortages and loss of foraging habitat are also widespread. The severity of the problem is illustrated by the decline of the Cape vulture (*Gyps coprotheres*) in Namibia where it no longer breeds and is now considered Critically Endangered nationally and Vulnerable globally. From 2004 to 2008 satellite tracking units were fitted to five adult and one immature Cape vulture caught from the wild in their former breeding range in north-central Namibia, as well as three adults released as part of a pilot reintroduction program. The wild-caught adults and one of the reintroduced adults concentrated their activity in the former core breeding area of the species in north-central Namibia, while two of the reintroduced adults dispersed more than 500 km to south-east Namibia. The immature vulture initially travelled extensively across southern Africa before occupying a consistent dry season range in south-east Botswana and a wet season range in south-east Namibia over consecutive years. The adult vultures also made occasional long-distance forays into neighbouring countries. All of the vultures spent the majority of their tracking periods beyond the boundaries of officially protected areas, foraging predominantly on freehold conservancies and unprotected farmland. Officially protected areas and communal conservancies were used rarely. Vegetation cover did not appear to influence the local movement patterns of the vultures, and vulture restaurants were rarely visited. This study indicates that unprotected farmlands and freehold conservancies are important foraging areas for vultures in north-central Namibia, and that the mitigation of widespread problems associated with human-wildlife conflict such as illegal poisoning should be a conservation priority in the region.

3.2. Introduction

As the main consumers of ungulate carcasses in the savannah ecosystem (Houston 1974c) vultures in the *Gyps* genus provide vital ecosystem services related to maintaining nutrient cycles and limiting the development and spread of disease (DeVault *et al.* 2003b; Sekercioglu 2006b). The importance of *Gyps* vultures to environmental health has been widely recognised since the collapse of their populations in Asia due to accidental poisoning by the veterinary drug diclofenac (Oaks *et al.* 2004; Markandya *et al.* 2008; Ogada *et al.* 2012a). Widespread and rapid declines of vulture populations have also been reported across sub-Saharan Africa (Herremans and Herremans-Tonnoeyr 2000; Thiollay 2006a; Virani *et al.* 2011), largely attributed to illegal poisoning either through direct persecution or when vultures consume poisoned carcasses intended to kill livestock predators (Virani *et al.* 2011; Ogada *et al.* 2012a).

The Cape vulture (*Gyps coprotheres*) is endemic to southern Africa and is currently listed as Vulnerable by the IUCN due to continuing declines across its range (BirdLife International 2013). The two remaining core breeding areas (*ca.* 4,000 breeding pairs total) are located in the mountains of the northern provinces of South Africa and southern Botswana, and the Drakensberg Mountains in Lesotho and south-eastern South Africa (Borello and Borello 2002; Whittington-Jones *et al.* 2011; BirdLife International 2013). The Cape vulture is now considered Critically Endangered and extinct as a breeding species in Namibia (Robertson *et al.* 1998; BirdLife International 2013) where it formerly nested on the cliffs of the Waterberg Plateau Park (WPP) in the north-central region (Brown 1985). The population decline in Namibia from approximately 500 breeding birds in 1940 to just 13 adults in 1985 was one of the first and most severe declines of a *Gyps* species to be reported in Africa, and has been mainly attributed to the widespread use of poisons aimed at killing livestock predators (Brown 1985; Mundy *et al.* 1992; Bamford *et al.* 2007; Schumann *et al.* 2008). It has also been suggested that bush encroachment due to overgrazing, which is widespread in north-central Namibia and results in a closed canopy of woody vegetation (e.g. *Senegalia mellifera*; (Joubert *et al.* 2008)), has reduced foraging habitat availability by making it difficult for Cape vultures to visually locate and land at carcasses (Brown 1985; Bamford *et al.* 2007; Bamford *et al.* 2009a). However, the exact mechanism behind the decline is not fully understood and is likely to be multifaceted (Simmons and Jenkins 2007). Local conservation measures include the establishment of supplementary feeding sites, or "vulture restaurants", where uncontaminated carrion is provided at regular intervals (Brown and Jones 1989; Piper *et al.* 1999), although their effectiveness as a conservation tool is not fully understood (Deygout *et al.* 2009).

Recent GPS (Global Positioning System) tracking studies have shown that *Gyps* vultures are able to travel extensively across southern Africa and forage most frequently beyond the boundaries of officially protected areas (Phipps *et al.* 2013a; Phipps *et al.* 2013b). However, vulture use of privately owned and communally managed conservancies has not been assessed in the region. Conservancies are legally defined protected areas made up of co-operatively managed neighbouring properties with the aim of collaboratively using natural resources sustainably (CANAM 2010). Conservancies are widespread in north-central Namibia where they are divided into privately owned commercial (or freehold) conservancies managed for intensive and extensive livestock and game farming; and communal conservancies that are owned by the government but managed by traditional authorities and pastoral livestock farmers (Schumann *et al.* 2012; Rust and Marker 2014). Although conservancies provide a refuge for free-roaming wildlife, particularly carnivores, human-wildlife conflict still remains prevalent and illegal predator control methods, including poisoning, are widespread across southern Africa (Schumann *et al.* 2008; Schumann *et al.* 2012; St John *et al.* 2012; Lindsey *et al.* 2013a; Rust and Marker 2014).

Knowledge of space use patterns by far-ranging animals, such as vultures, is fundamental to understanding their behavioural ecology and for informing conservation strategies (Marker *et al.* 2008). In this study I report the ranging patterns of a sample of the remnant population of Cape vultures in Namibia that were tracked for several consecutive years using satellite transmitters. While the findings from the initial (<1 year) tracking periods were reported previously (Bamford *et al.* 2007), this study analyses data from the full tracking period of the six wild-caught individuals over several years, as well as three additional adults that were released as part of a pilot reintroduction program (Diekmann and Strachan 2006; BirdLife International 2013). I estimate the size and extent of vulture home ranges, assess site fidelity based on the overlap of seasonal ranges for vultures tracked for several years, and assess vulture use of different protected area categories, including freehold and communal conservancies. To test whether bush encroachment influenced vulture foraging activity I determine if they used open or closed vegetation cover in proportion to their respective availabilities. Finally, I assessed how frequently the vultures used vulture restaurants. This study therefore provides a first insight into the long-term ranging and land use patterns of wild Cape vultures tracked continuously for several consecutive years, as well as the first report of the movement patterns of reintroduced vultures in Namibia. It is hoped that the findings will inform strategies to assist any future re-establishment of breeding Cape vultures in north-central Namibia.

3.3. Methods

3.3.1. Satellite tracking data

The data analysed for this study are comprised of GPS tracking locations from five adult males (hereafter referred to as CV1 – CV5) and one immature female (CV6) Cape vulture captured between January 2004 and February 2005 using a walk-in cage trap at the Rare and Endangered Species Trust (REST) property to the west of the Waterberg Plateau Park (WPP) in north-central Namibia (20°15′54″S, 17°03′53″E) (Bamford *et al.* 2007). The sample of wild-caught vultures potentially represented half of the estimated population of adult Cape vultures remaining in Namibia at the onset of the study (Bamford *et al.* 2007; BirdLife International 2013). Bamford *et al.* (2007) reported findings from the initial tracking periods of these vultures using data collected from January 2004 until September 2005. For this study GPS tracking data from three adult Cape vultures that were released at the

REST capture site as part of a pilot reintroduction program were also analysed. Two of the reintroduced vultures were females bred in captivity in South Africa, transferred to REST and released as adults (CV7, released in October 2005; CV9, released in May 2008), while one was a formerly captive adult male (CV8, released in August 2006) (Diekmann and Strachan 2006). Tracking data collection ceased in May 2010.

The vultures were each fitted with a solar-powered Argos/GPS PTT-100 tracking unit made by Microwave Telemetry Inc. (Columbia, Maryland), attached using a Teflon ribbon backpack harness (Diekmann *et al.* 2004; Bamford *et al.* 2007). Each unit weighed 70 g (<1 % of Cape vulture body mass) and recorded GPS locations accurate to ± 10 m as well as simultaneous speed, direction and altitude readings. The units fitted to the wild-caught vultures (CV1 – CV6) were programmed to record one GPS location every hour from 04h00 to 19h00 GMT, while the units fitted to the reintroduced vultures recorded GPS locations every 2 hours from 07h00 to 15h00 GMT. Data from all units were therefore filtered to only include GPS locations recorded every two hours from 07h00 to 15h00 GMT to reduce spatial autocorrelation and to correspond with the active foraging times of the vultures (Bamford *et al.* 2007). The tracking units were solar-powered and were expected to record data for several years. The capture of vultures and fitting of tracking units was carried out by SAFRING permit holders under permits from the Namibian Ministry of Environment and Tourism (Bamford *et al.* 2007).

3.3.2. Space use estimation

GPS locations were converted to the Universal Tranverse Mercator (UTM) coordinate system for all spatial analyses. The overall home and core ranges were estimated for each vulture using the 95% and 50% contours, respectively, calculated by fixed kernel density estimation (KDE) using the Home Range Tools (HRT) extension (Rodgers *et al.* 2007) for ArcGIS 9.3 (ESRI 2008). Following preliminary analyses the reference bandwidth was selected as the most appropriate smoothing parameter (Gitzen *et al.* 2006; Kie *et al.* 2010). A 1 km^2 cell size was used for KDE calculations. The Minimum Convex Polygon (MCP) encompassing all of the time-filtered GPS locations was also calculated for each vulture using HRT to allow comparisons to be made with previous studies (Kie *et al.* 2010). Incremental area analysis using MCPs constructed by sequentially adding GPS locations was performed to establish whether vulture home ranges had stabilised by the end of the tracking period (Harris *et al.* 1990).

For vultures that were tracked for more than one year (CV3, CV4, CV5, CV6) KDE contours were also delineated for individual wet (November – April) and dry seasons (May – October) which corresponded to seasonal rainfall patterns in the region (Chase *et al.* 2012). The dry and wet seasons also correspond approximately to the nesting and non-nesting periods for the Cape vulture in the region, respectively (Mundy *et al.* 1992). To quantify site fidelity between overall wet and dry seasonal ranges and between consecutive seasons, the amount of overlap between the corresponding KDE contours was calculated as follows: $HR_{1,2} = \left(\frac{\left((AO_{1,2}/A_1) + (AO_{1,2}/A_2)\right)}{2}\right) \times 100$ where $AO_{1,2}$ is the the area of overlap between the two KDE contours, and A_1 and A_2 are the KDE contour areas for season 1 and 2 (Kernohan *et al.* 2001). This was performed for both 95% and 50% KDE contours.

The average distance of each GPS location from the arithmetic mean centre of all GPS locations was calculated as a measure of the spread of the overall and seasonal home ranges (hereafter termed “range spread”, RS), and also acted as a linear indicator of home range size (Bosch *et al.* 2010; López-López *et al.* 2013).

The daily distance travelled by each vulture was estimated by summing the distances between consecutive GPS locations recorded every 2 hours from 07h00 to 15h00 on a single day using Hawth’s Analysis Tools (Beyer 2009).

3.3.3. Land use selection

Two aspects of land use selection patterns were investigated separately based on use-availability analysis (Thomas and Taylor 2006). Firstly, the vultures’ use of different categories of Protected Areas (PAs) was assessed. The PA data were derived from the 2014 World Database on

Protected Areas (WDPA; (IUCN and UNEP 2014)) and imported into ArcMap 9.3. Following verification of the location and designation of the PA boundaries, three categories of PA were created from the PAs that occurred within the 95% KDE contours of the vultures based on different ownership and management criteria (refer to Introduction): Freehold PAs, consisting mainly of privately owned conservancies or game reserves; Communal PAs, consisting of government owned land managed by traditional authorities; Official PAs, consisting mainly of government owned and managed category I - VI Protected Areas such as National Parks (IUCN and UNEP 2014). The remaining area of each 95% KDE contour not covered by any PAs was defined as non-protected area (Non-PA).

Secondly, the vultures' use of different land-cover categories related to vegetation cover were assessed. Land-cover data were derived from the Global Land Cover 2000 (GLC 2000) dataset which consists of a map of vegetation cover of Africa in the year 2000 at 1 km^2 spatial resolution based on the spectral response and temporal profile of the vegetation cover (Mayaux *et al.* 2004). The land-cover classes within the 95% KDE contours of each vulture were further classified into three categories of vegetation cover based on the estimated percentage tree cover: Open (<15% tree cover), Closed (>15% tree cover) and Other (e.g. cities, croplands).

Land use selection was subsequently analysed using use-availability based methods at the home range scale, with the availability of each PA or land-cover category being defined as the proportion of the 95% KDE contour that it covered for each vulture (Thomas and Taylor 2006). Use of a PA or land-cover category was defined as the proportion of stationary (<10 kmh^{-1}) GPS locations within the 95% KDE contour recorded within each category (Thomas and Taylor 2006). To determine land use selection during foraging activity, GPS locations recorded within 2 km of regularly used roost and nest sites were eliminated from the analysis, based on preliminary ground surveys (Schultz 2007). Roost and nest sites were identified from a combination of field visits and by identifying very localised sites that were frequently returned to by a vulture over the course of its tracking period by analysis of flight paths in ArcMap. The vulture restaurant at REST was included as a roost site for CV7 but no other vulture. Use of a PA or land-cover category including roost and nest GPS locations was also assessed as described below.

Compositional analysis using ComposAnalysis version 6.3 (Smith Ecology Ltd, Monmouthshire, Wales, UK) was used to evaluate whether the vultures used the different PA and land-cover categories disproportionally to their availability consistently across the group, based on the above definitions of use (U_i) and availability (A_i) (Aebischer *et al.* 1993). ComposAnalaysis calculated the significance of

Wilk's Λ with 1000 iterations, and if a PA or land-cover category availability was zero, a value of 0.01 substituted it (Aebischer *et al.* 1993; Manly *et al.* 2002). While selection of all PA categories was assessed using compositional analysis, only the Open and Closed land-cover categories were considered for the land-cover selection analysis due to the low availability and use of the "Other" land-cover category.

To assess whether Closed or Open vegetation cover were used disproportionally to their availability at the individual vulture level, Ivlev's electivity indices (Ivlev 1961) were calculated as $E_i = (U_i - A_i) / (U_i + A_i)$, where A_i and U_i represent the availability and use of each category, respectively, as defined above. Ivlev's electivity indices ranged from -1 (complete avoidance) to +1 (maximum positive selection), with zero indicating proportional use (Ivlev 1961).

For each vulture the proportion of stationary (<10 kmh^{-1}) GPS locations recorded within 1 km of two vulture restaurants was calculated to estimate their use of supplementary carrion. One site was located at the capture site at REST (20°15′54″S, 17°03′53″E) while the other was within the Waterberg Plateau Park (20°19′16″S, 17°18′16″E). Reliable data on carrion provisioning rates were not available for either site.

Statistical analyses were performed in SPSS Statistics version 21.0 (SPSS Inc, 2012) or Microsoft Excel (2007). Average values are presented as means ± SD unless otherwise stated. Level of significance was set at $p = 0.05$.

3.4. Results

A total of nine Cape vultures comprising five adult males (CV1 – CV5) and one immature female (CV6) captured from the wild and three previously captive, reintroduced adults (CV7 – CV9) were fitted with tracking units between January 2004 and May 2008 (Table 3.1). The tracking unit attached to CV2 fell off after only two months and so meaningful home range estimates could not be calculated and are not reported in the main text. One wild caught vulture (CV1) was tracked for 208 days before its unit stopped transmitting data, while the other four were tracked for several consecutive years (mean ± SD = 1,592 ± 205 tracking days; Table 3.1). The three reintroduced vultures were tracked for 306 ± 133 days (Table 3.1). For all nine vultures the mean number of GPS locations recorded every two hours between 07h00 and 15h00 was 3,385 ± 2,989, of which 65.44 ± 8.57% were recorded as stationary (< 10 kmh^{-1}; Table 3.1). The average speed of all moving GPS locations from all vultures (n = 22,706) was 57.43 ± 19.36 kmh^{-1}, at a maximum flight speed of 127 kmh^{-1}. The mean distance travelled per day by all vultures was 67.43 ± 17.76 km.

3.4.1. Home ranges

The wild-caught adult vultures occupied home ranges (median 95% KDE contour area = 9,271 km^2; Table 3.1) largely concentrated in the areas surrounding the Waterberg Plateau Park (WPP; Figure 3.1). The core ranges as indicated by the 50% KDE contours were located around several roost and nest sites that were regularly used over the extended tracking periods, mainly to the west of WPP (Figure 3.1). The 50% KDE contours of all of the adult vultures overlapped with the Waterberg Freehold Conservancy, indicating that they spent a significant proportion of their tracking periods in that area (Figure 3.1; Figure S3.2). The bimodal 50% KDE contour of CV4 also overlapped one of its nest sites 100 km north-east of WPP in the Omirunga Freehold Conservancy (Figure S3.2), while the bimodal 50% KDE contour for CV3 overlapped with the Ozonahi Communal Conservancy *ca.* 40 km south-east of WPP (Figure S3.2).

The three reintroduced adult vultures traversed larger overall home ranges as indicated by the 95% KDE contours (median = 36,590 km^2) compared to the four wild-caught adults (median = 9,271 km^2; Table 3.1; Figure 3.1). All three of the reintroduced vultures travelled much further away from the release site in a shorter tracking period than most of the wild-caught adults, with CV9 travelling *ca.* 400 km north into southern Angola and both CV7 and CV8 travelling more than 650 km to south-east Namibia (Figure 3.1). The larger Range Spread (RS) values for the reintroduced vultures (median RS = 53 km) compared to the wild-caught adults (median RS = 28 km) further emphasise the more restricted movements of the wild-caught adults (Table 3.1). However, the wild-caught adults did make occasional relatively long-distance forays beyond their established home range boundaries even towards the end of the tracking periods, as shown by the home range area curves generated by incremental area analysis (Figure S3.1). CV5 was the longest ranging wild-caught adult, travelling as far as Etosha National Park (>200 km north-west of WPP), >350 km north into southern Angola, and over 680 km east to the Okavango Delta in northern Botswana. Nevertheless such forays were rare and the wild-caught adults always returned to their core ranges in the WPP vicinity, unlike the reintroduced vultures that spent extended periods elsewhere. Reintroduced CV7 and CV8 were both located 840 km and 563 km south of the release site, respectively, when their tracking units stopped transmitting data in southern Namibia.

The immature vulture (CV6) traversed a very large range (95% KDE contour area = 975,731 km^2) extending across six different countries (Figure 3.2), reflected by the high RS value of 483.65 km. After being fitted with the tracking unit in February 2005 CV6 travelled in a generally nomadic manner across an extensive area throughout northern Namibia (spending extended periods in the Omusati region and Etosha NP), to the Hardap region of south-east Namibia and the Okavango and Chobe regions of northern Botswana with occasional forays into southern Angola and Zambia (Figure 3.2). In August 2006 CV6 travelled from the Hardap region of south-east Namibia to the Chobe region of northern Botswana before travelling to south-east Botswana in September 2006. From September 2006 until the end of the tracking period in May 2010 CV6 showed a clear pattern of spending the dry season (April – October) each year in the Serowe-

Palapye region of south-east Botswana (>1000 km south-east of release site), regularly roosting at a single site *ca.* 30 km north-east of Serowe (22°18′40″S, 26°58′22″E), before travelling more than 800 km to the Mariental-Gochas-Stampriet region of south-east Namibia (>450 km south of release site) in November or December (Figure 3.2). CV6 then remained in south-east Namibia each year until March when it would return to the same area of south-east Botswana, but usually via a more northerly route (Figure 3.2). Thus, from September 2006 until the end of the tracking period in May 2010, CV6 occupied distinct dry and wet season ranges in south-east Botswana and south-east Namibia, respectively, and never returned to northern Namibia (Figure 3.2).

The three wild-caught adult vultures that were tracked for several years (CV3, CV4, CV5) showed a high degree of spatial overlap between their overall wet and dry season 95% (mean overlap = 81.71 ± 12.77%) and 50% KDE contours (mean overlap = 77.87 ± 3.90 %), while the immature vulture's overall seasonal ranges overlapped to a lesser degree (overall wet–dry season 95% and 50% KDE contour overlap = 64.16% and 72.74%, respectively). The level of spatial overlap of the 95% (mean overlap = 76.25 ± 10.72%) and 50% KDE contours (mean overlap = 64.90 ± 3.26%) between consecutive seasons was also higher for the adults compared to the immature vulture (95% and 50% KDE contour overlap between consecutive seasons = 56.57 ± 12.66% and 51.21 ± 19.51%, respectively). The individual wet (median 95% KDE contour area = 9,200 km^2; n = 11) and dry (median 95% KDE contour area = 10,247 km^2; n = 13) season ranges traversed by the three wild-caught adults were not significantly different in size (Wilcoxon signed-rank test: $Z = -0.533$, $p = 0.637$).

Table 3.1. Individual characteristics, tracking details and ranging metrics for nine Cape vultures tracked using satellite tracking units fitted in north-central Namibia. *(Full description overleaf)

Vulture	Status, age, sex	Tracking period	Tracking days	2 hour locations from 07h00 - 15h00	95% KDE area (km²)	50% KDE area (km²)	MCP area (km²)	Range Spread (km)	Mean ±SE distance per day (km)
CV1	Wild, Ad., Male	Jan-Oct 2004	203	725 (504)	8420	308	16820	16.60 ±21.28	52.08 ±3.94
CV2	Wild, Ad., Male	Mar-May 2004	57	218 (163)	31230	2615	31329	48.64 ±35.64	75.66 ±11.82
CV3	Wild, Ad., Male	Nov 2004 - Nov 2009	1615	5158 (2596)	6168	742	27163	23.00 ±15.74	57.36 ±1.02
CV4	Wild, Ad., Male	Nov 2004 - May 2008	1231	5449 (3786)	10122	1127	30085	52.44 ±16.30	87.34 ±2.26
CV5	Wild, Ad., Male	Jan 2005 - Dec 2009	1656	6310 (4150)	18409	1625	271873	33.60 ±37.59	70.19 ±1.48
CV6	Wild, Im., Fem.	Feb 2005 - May 2010	1866	8451 (4724)	975731	86846	1626515	483.65 ±187.82	87.00 ±1.44
CV7	Reintro., Ad., Fem.	Oct 2005 - Feb 2007	359	1629 (1202)	36590	2960	188684	53.28 ±62.77	43.70 ±2.74
CV8	Reintro., Ad., Male	Aug 2006 - Feb 2007	155	688 (505)	223083	50664	134913	232.22 ±71.00	47.17 ±3.76
CV9	Reintro., Ad., Fem.	May 2008 - Jul 2009	404	1840 (1031)	31220	3267	162219	43.78 ±47.36	86.37 ±3.03

*Table 3.1. The status (wild or reintroduced), age (adult (Ad.) or immature (Im.)) and sex are provided, as well as the tracking start and end dates and duration in days on which data were recorded. The number of GPS locations recorded every 2 hours from 07h00 – 15h00 GMT are given with the number of stationary (<10 kmh^{-1}) GPS locations provided in parentheses. Overall home range estimates are represented by 95% kernel density estimated (KDE) contours and minimum convex polygons (MCP) and core ranges are represented by 50% KDE contours. Range spread is calculated as the mean distance of each GPS location from the arithmetic centre of all GPS locations. The mean distance travelled per day is also provided. CV2 was not tracked for a sufficient period for meaningful home range estimates to be calculated and they are therefore not reported in the main text.

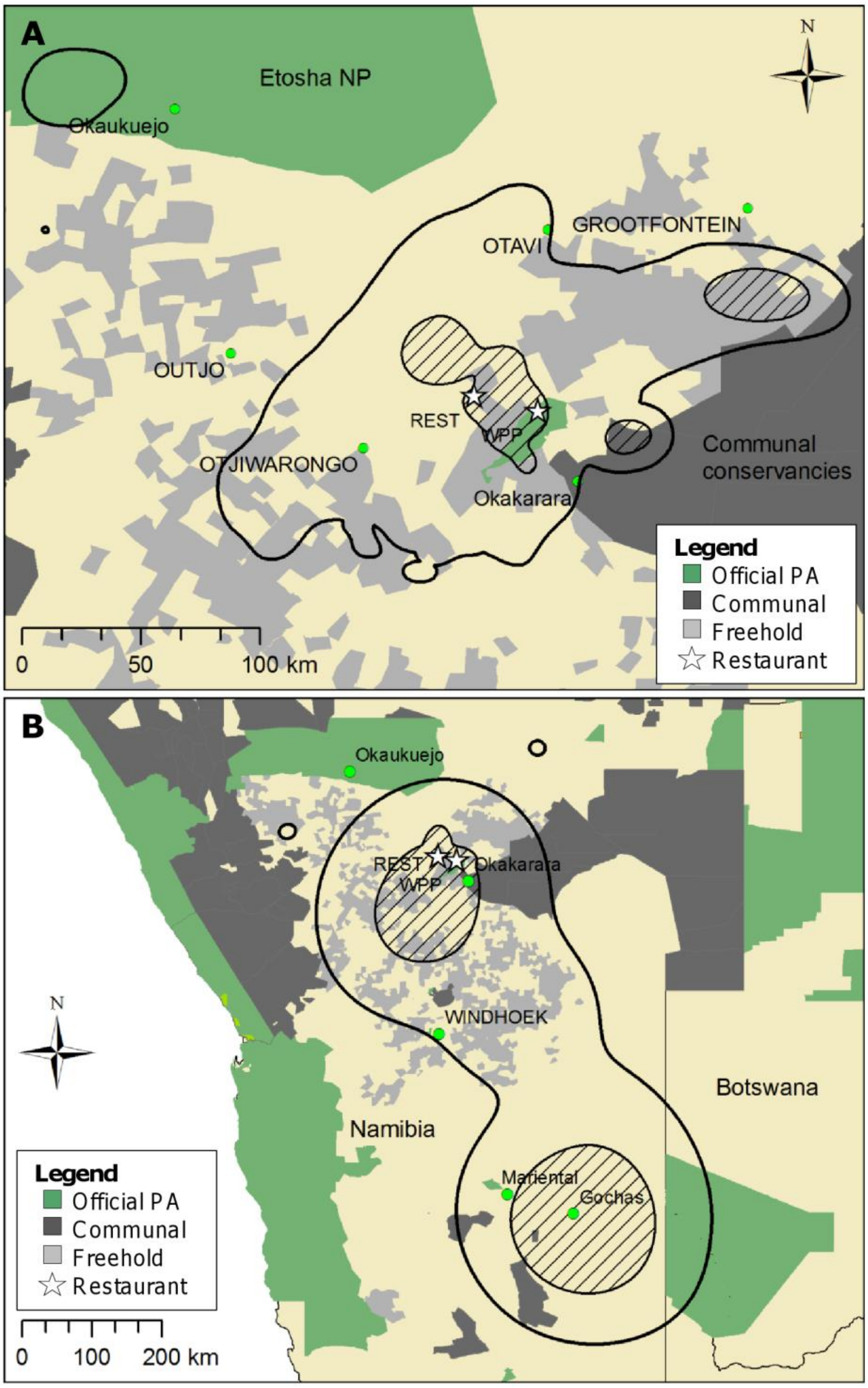

Figure 3.1. Merged 95% kernel density estimated (KDE) contours (black outlined polygons) and merged 50% KDE contours (black hatched polygons) for (A) four wild adult Cape vultures and (B) three reintroduced adult Cape vultures in relation to official protected areas (PA), communal and freehold conservancies, unprotected areas (beige) and vulture restaurants (stars) (REST = Rare and Endangered Species Trust capture site; WPP = Waterberg Plateau Park; green circles indicate towns).

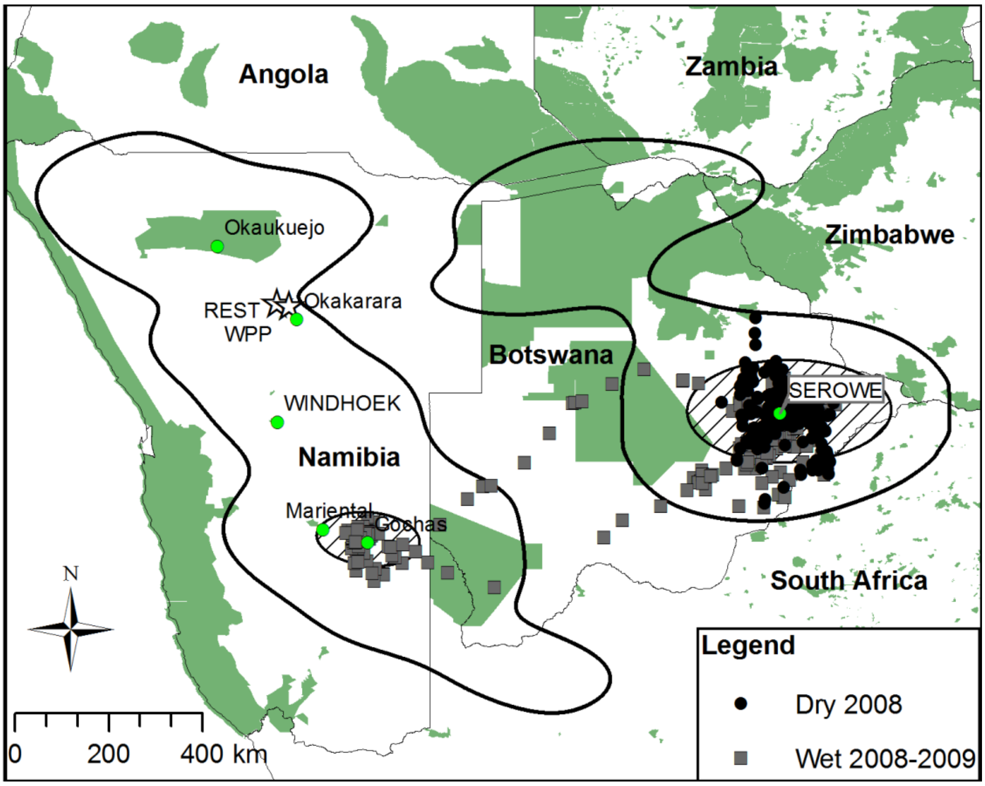

Figure 3.2. Overall home range (95% kernel density estimated (KDE) contours (black outlined polygon)) and core range (50% KDE contours (black hatched polygons)) estimated from the total tracking period (1,866 days) of an immature Cape vulture (CV6) tracked from north-central Namibia. Black circles and grey squares represent the GPS locations recorded during the dry season 2008 (May – October) and the wet season 2008 – 2009 (November – April), respectively. Green shaded polygons show official protected areas. White stars show the vulture restaurants in north-central Namibia (REST = Rare and Endangered Species Trust capture site; WPP = Waterberg Plateau Park; green circles indicate towns).

3.4.2. Land use selection

Across the eight vultures a mean of 45.48 ± 21.43% of stationary non-roost GPS locations were recorded within PAs, with the remainder being recorded in Non-PAs (Figure 3.3). For all vultures apart from the immature vulture (CV6) the majority of stationary non-roost GPS locations that were recorded within PAs were recorded within Freehold PAs (mean = 40.51 ± 17.26% stationary non-roost GPS locations; Figure 3.3). The four wild-caught adults spent less time within PAs of any kind (median = 39.44% stationary GPS locations) than the reintroduced adults (median = 71.29% stationary GPS locations). When data from the seven adult vultures were analysed, compositional analysis indicated that the PA categories were used significantly out of proportion to their availability based on non-roost GPS locations ($\Lambda = 0.295$, $X^2_3 = 8.555$, $P = 0.036$), but no significant selection was found when data from the immature vulture (CV6) were included ($\Lambda = 0.456$, $X^2_3 = 6.277$, $P = 0.099$). However, when GPS locations at roost and nest sites were also analysed with the foraging locations across all eight vultures the PA categories were used significantly out of proportion to their availability ($\Lambda = 0.244$, $X^2_3 = 11.286$, $P = 0.010$). The PA categories were ranked in order of most selected across the group as Freehold PA > Non-PA > Official PA > Communal PA, with Freehold PA being selected significantly more than all other categories when GPS locations at roost and nest sites were included in the analyses.

The Waterberg Conservancy directly to the west of the Waterberg Plateau Park official PA was the most regularly utilised Freehold PA and formed part of all of the adult vultures' core foraging ranges. Other Freehold Conservancies utilised relatively regularly included Kalkfeld and Owipuka to the south of Otjiwarongo, and Ngarangombe to the north-east of WPP (Figure S3.2). CV4 also occupied a nest and roost site on Omirunga Freehold Conservancy *ca.* 40 km south of Grootfontein and *ca.* 100 km north-east of WPP (19°53'12"S, 18°08'33"E), and frequently foraged there (Figure S3.2). Although CV5 used Freehold PAs regularly it also visited the south-east region of Etosha NP, over 200 km north-west of WPP, in two consecutive dry seasons. CV5 was the only vulture tracked during this study to frequently use a transmission line to the north-east of Otjiwarongo for roosting, accounting for many of its stationary GPS locations recorded in Non-PAs. CV6 used Official PAs (15.18% of non-roost stationary GPS locations) more frequently than the adult vultures, with Etosha NP in Namibia and the Okavango Delta and Chobe NP in northern Botswana accounting for the majority. From September 2006 until May 2010 CV6 spent the majority of its tracking period in Non-PAs in south-east Botswana and south-east Namibia (Figure 3.2). The three reintroduced vultures utilised Freehold PAs in the Waterberg region, as well as some further south, such as Ombotuzu. CV3 was the only vulture to utilise Communal PAs relatively frequently (21.58% of non-roost stationary GPS locations), mainly accounted for by its frequent use of three areas in the Ozonahi Communal Conservancy *ca.* 30 km south-east of WPP (Figure S3.2). All other vultures rarely, if ever, visited Communal PAs (Figure 3.3). Although CV3 and CV5 regularly roosted on the cliffs of the former breeding colony at WPP, they were the only vultures to do so and no breeding attempts could be confirmed. All other identified regular roost and nest sites were located in trees. No breeding attempts were verified after the study conducted by Bamford *et al.* (2007).

Closed vegetation (mean availability = 24.19 ± 9.17%) covered less of the eight individual home ranges than Open vegetation (mean availability = 73.99 ± 8.78%). When stationary GPS locations at roost sites were removed the eight vultures used both Closed (mean use = 21.95 ± 9.77%) and Open vegetation cover (mean use = 76.72 ± 8.80%) in similar proportions to their availability, confirmed by compositional analysis ($\Lambda = 0.677$, $X^2_1 = 3.124$, $P = 0.077$). There was also no significant selection for either category when data from the immature vulture were excluded ($\Lambda = 0.766$, $X^2_1 = 1.863$, $P = 0.172$). Although when GPS locations at roost sites were included in the analysis use of Closed vegetation cover was higher than its availability (mean use = 37.57 ± 30.35), and use of Open vegetation cover was lower than its availability (mean use = 61.34 ± 29.33%), the difference was not significant across all eight vultures ($\Lambda = 0.875$, $X^2_1 = 1.065$, $P = 0.302$) or for adults only ($\Lambda = 0.787$, $X^2_1 = 1.674$, $P = 0.196$). At the individual level Ivlev's electivity indices did not reflect any strong patterns of selection or avoidance of either Open or Closed vegetation cover by foraging vultures, although three of the wild adults frequently roosted or nested in areas of Closed vegetation (Figure S3.3).

Apart from one reintroduced vulture (CV7) that remained in the vicinity of the vulture restaurant at REST for more than 2 months following its release and regularly returned there during its tracking period (54% of stationary GPS locations recorded <1 km from the vulture restaurant at REST), the remaining eight vultures were recorded relatively rarely in the vicinity of either vulture restaurant (6.51 ± 3.44 % of stationary non-roost GPS locations recorded <1 km from vulture restaurants).

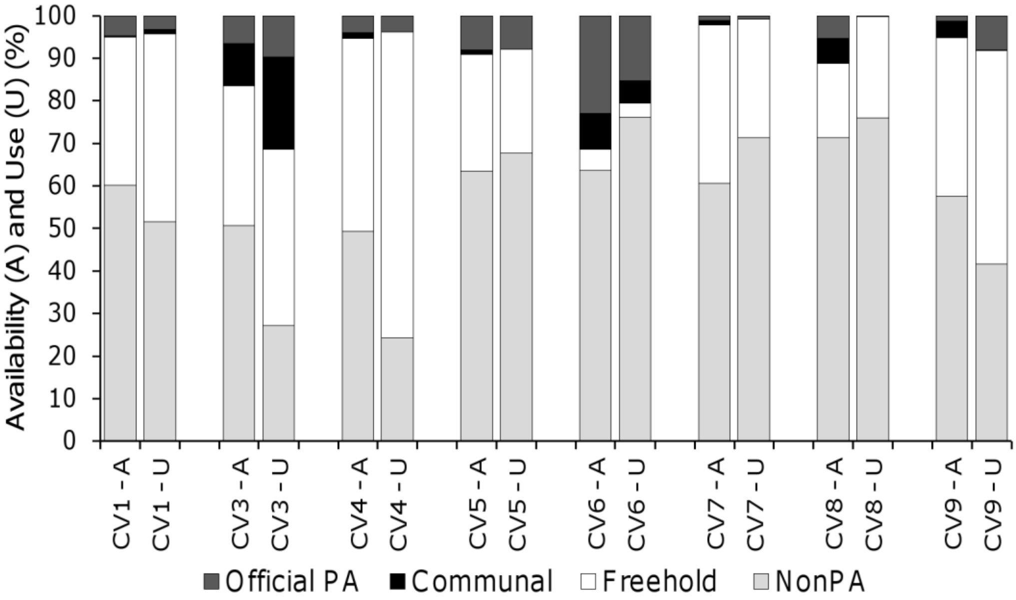

Figure 3.3. Availability (A) and use (U) of different protected area (PA) categories by eight Cape vultures tracked by satellite telemetry. The PA categories included communal and freehold conservancies, official category I-VI protected areas (Official PA) and unprotected areas (NonPA). Availability was defined as the proportion of each vulture's overall home range (95% KDE contour) covered by each PA category, and use was defined as the proportion of stationary non-roost GPS locations recorded within each PA category.

3.5. Discussion

This study reports results from the analysis of satellite telemetry data from the complete tracking periods of five adult and one immature Cape vulture from the isolated and critically endangered population in Namibia, as well as three adults that were released as part of a pilot reintroduction program. The findings confirm that *Gyps* vultures, particularly immatures, traverse extensive ranges in southern Africa, often cross international borders, and frequently forage outside the boundaries of officially protected areas (Phipps *et al.* 2013a; Phipps *et al.* 2013b).

The overall ranging patterns bore similarities to the findings from the initial tracking periods (Bamford *et al.* 2007), with the home ranges of the wild-caught adult vultures and one of the reintroduced adults being largely concentrated in relative proximity to the former breeding colony in the Waterberg area of north-central Namibia. Those vultures made only occasional long-range forays outside their relatively small home ranges, displayed a high degree of site fidelity between seasons and rarely utilised vulture restaurants, indicating that the area contained sufficient resources to support them over the extended tracking periods. Given that north-central Namibia has particularly high densities of both domestic and wild ungulates and is known to support a large proportion of Namibia's remaining free-roaming carnivores (Marker *et al.* 2003; Schumann *et al.* 2008; Stein *et al.* 2010), the availability of carrion was potentially relatively high compared to surrounding areas, limiting the need for the vultures to regularly forage further afield.

In accordance with the initial observations of Bamford *et al.* (2007), only two of the vultures regularly roosted on the cliffs of the former colony at Waterberg Plateau Park (WPP), while several regularly roosted and even attempted to nest in trees. Given the usual preference of adult Cape vultures to roost and nest on cliffs this confirms that the colony had been abandoned as a breeding and roosting site by the vultures as previously suggested (Mundy *et al.* 1992; Borello and Borello 2002; Bamford *et al.* 2007; Simmons and Jenkins 2007). In an ideal situation with a stable population, vultures forage most efficiently in groups in a network across the wider landscape to benefit from the effects of social facilitation (Jackson *et al.* 2008a; Deygout *et al.* 2010). However, because the population of Cape vultures in Namibia numbers less than 20 (BirdLife International 2013) it is possible that the remaining individuals might benefit by roosting and foraging in the vicinity of tree-roosting and nesting African white-backed vultures (*Gyps africanus*) that persist in relatively large numbers in the region and forage in a similar manner (Spiegel *et al.* 2013), which would partially explain their regular use of tree roosts. In contrast to a recent study that showed that Cape vultures frequently roost on power lines in South Africa (Phipps *et al.* 2013b), only one vulture tracked during this study did so which might be due to the lower availability of power lines in the area, or perhaps the absence of a learned behaviour through social facilitation.

Compared to the wild-caught adults two of the reintroduced adults ranged much further south into central and south-east Namibia over a relatively short period, and the third undertook a long-range foray into southern Angola. Although comparisons are difficult due to the small sample size and the disparity in tracking periods (1,592 ± 205 days and 306 ± 133 days for the wild and reintroduced adults, respectively), it is clear that two out of the three reintroduced adults dispersed further over a shorter period than the more "settled" wild-caught adults which were more restricted to the Waterberg region partly due to breeding attempts (Clobert *et al.* 2001). A recent study in southern Europe also showed that reintroduced bearded vultures (*Gypaetus barbatus*) dispersed further than wild individuals, emphasising the need to carefully consider individual variation in dispersal abilities when planning reintroduction strategies (Le Gouar *et al.* 2008b; Margalida *et al.* 2013). Although our findings are based on a very small sample of individuals reintroduced as part of a pilot project, their outward dispersal patterns demonstrate that further applied research is required if reintroduction is to be considered as a tool for Cape vulture conservation in Namibia (Converse *et al.* 2013; Margalida *et al.* 2013; Mihoub *et al.* 2014). Most importantly the exact mechanism that drove the decline of the breeding population and apparent abandonment of the former breeding colony must be identified and mitigated before population augmentation can be considered as a viable strategy.

The extensive movements of the immature vulture confirm that immature *Gyps* vultures range widely across southern Africa, leaving them susceptible to the full range of threats in the region (Phipps *et al.* 2013a; Phipps *et al.* 2013b). The long distance movements (>1000 km) from the capture site also illustrate the high dispersal capability of immatures which may allow them to exploit locally abundant sources of carrion and potentially settle in more favourable areas (Phipps *et al.* 2013a). An interesting aspect of the movement patterns of the immature vulture was its utilisation of distinct wet and dry season ranges, exhibiting movement characteristics potentially indicative of partial migration (Clobert *et al.* 2001; Boshoff *et al.* 2009). While migratory movements have been recorded in *Gyps* vultures elsewhere (Bildstein *et al.* 2009), they have only recently been proposed to occur in Cape vultures in the Eastern Cape province of South Africa where they are thought to be driven by seasonal peaks in carrion abundance on livestock farms due to calving and lambing mortalities in the early wet season (Boshoff *et al.* 2009). It is possible that the immature vulture was also moving between two seasonal ranges in response to fluctations in carrion supply (Boshoff *et al.* 2009). For example, seasonal peaks in carrion abundance due to calving mortalities potentially occur in the wet season range in the south-east of Namibia where the density of both livestock and game species (especially springbok, *Antidorcas marsupilais*) is very high (Lindsey *et al.* 2013b). Carrion abundance also fluctuates with the widespread seasonal hunting activity in south-east Namibia which is known to be linked to increased vulture activity elsewhere (Murn and Anderson 2008; Mateo-Tomas and Olea 2010). As *Gyps* vultures are highly gregarious, it is likely that the movements of the immature vulture also represent similar movements of other vultures in the region and ongoing studies indicate that south-east Namibia is freqently visited by other GPS-tracked vulture species (P. Hancock, personal communication). Considering this together with the southerly movements of the two reintroduced vultures, and the long-distance movement of a GPS tracked immature African white-backed vulture to the same area of south-east Namibia from South Africa (Phipps *et al.* 2013a), further investigation into the importance of this area to vultures is required, particularly as human-wildlife conflict is widespread in the region (Lindsey *et al.* 2013b).

As shown previously in southern Africa all of the vultures spent the majority of their tracking periods beyond the boundaries of official protected areas (Phipps *et al.* 2013a; Phipps *et al.* 2013b), and they visited freehold conservancies more often than expected based on their availability, followed by unprotected areas. This pattern was particularly pronounced for the wild-caught vultures that frequently roosted and foraged in the Waterberg Conservancy, and other freehold conservancies surrounding the Waterberg Plateau Park, as well as unprotected farmland. The densities of livestock and wild ungulates are high in the Waterberg region of north-central Namibia which is considered to be a vital area for the persistence of free-roaming large carnivores such as the cheetah (*Acinonyx jubatus*) owing to this abundant prey base and favourable environmental conditions (Marker *et al.* 2008; Schumann *et al.* 2008; Lindsey *et al.* 2013a). The farms directly to the west of WPP that now make up the Waterberg Conservancy were also identified as the most intensively used areas by 41 radio-collared cheetah (Marker *et al.* 2008). The main source of food for vultures (i.e. ungulates) also forms a major component of the diet of cheetah and other mammalian carnivores (Hayward and Kerley 2008; Marker *et al.* 2008), and so it is perhaps not surpising that there was a very high degree of overlap between the vulture and cheetah core ranges (Figure S3.2). Consequently, it is clear that, as in the case of cheetahs and other carnivores, privately owned farms in north-central Namibia, both within and outside conservancies, provided the tracked vultures with vitally important foraging areas and food sources (Marker *et al.* 2008; Schumann *et al.* 2008; Lindsey *et al.* 2013b). This has also been demonstrated in South Africa where mixed livestock and game farming and associated land use practices (e.g. hunting) are important for vulture activity (Murn and Anderson 2008). This region of Namibia should therefore be considered a key area for the future conservation of vultures and other carnivores in general (Marker *et al.* 2008; Schumann *et al.* 2008).

It is widely recognised, however, that human-wildlife conflict is prevalent on privately owned farms in Namibia and that a large proportion of farmers are prepared to use illegal poisons and other means to remove unwanted carnivores (Schumann *et al.* 2012; Lindsey *et al.* 2013a; Lindsey *et al.* 2013b; Rust and Marker 2014). Such illegal activity has been suggested as the main factor leading to the decline of Cape vultures in the country (Brown 1985) and other species elsewhere in Africa (Virani *et al.* 2011), either intentionally or inadvertently (Ogada *et al.* 2012a). As privately owned farms, especially within conservancies, were clearly important foraging grounds for the tracked vultures, resolving human-wildlife conflicts and eliminating illegal poisoning of predators is vital for vulture conservation in the region (Ogada *et al.* 2012a; Ogada 2014). Although communal conservancies have the potential to be important for carnivore conservation (Rust and Marker 2014), their limited use by all but one of the vultures was most likely because of the much lower densities of livestock and wild ungulates, and therefore carrion availability, compared to privately owned farmland (Rust and Marker 2014). Etosha NP was the only official protected area to be visited repeatedly by any of the adult vultures other than WPP, which itself was very rarely visited. The immature vulture also visited the south-east of Etosha NP which is known to be a favoured area for African white-backed vultures and lappet-faced vultures (*Torgos tracheilotus*) due to an unusually high abundance of ungulate carrion caused by disease outbreaks and high levels of predation (Spiegel *et al.* 2013). It is likely that the other vultures did not travel the relatively long distance to Etosha to forage as they were able to locate sufficient carcasses within their core ranges in the wider Waterberg region.

Previous studies have suggested that bush encroachment, whereby overgrazing causes grassland savannah to be dominated and enclosed by woody vegetation (Joubert *et al.* 2008), is likely to reduce the foraging efficiency of Cape vultures by hindering them from locating and landing at carcasses (Schultz 2007; Bamford *et al.* 2009a). Although our results do not show clear patterns of selection or avoidance of open or closed vegetation cover, other carnivore species in north-central Namibia, where bush encroachment is widespread (Joubert *et al.* 2008), have been affected by loss of suitable foraging habitat (Muntifering *et al.* 2006). It is possible that the vultures had to forage regularly over areas with relatively dense vegetation cover because that is where the browsing ungulate species upon which they fed most often (e.g. kudu, *Tragelaphus strepsiceros*) were most abundant (Schultz 2007; Marker *et al.* 2008). Thus it is plausible that the small sample of Cape vultures that were tracked during this study, and perhaps the few others that resided in the area, were able to persist in the heavily bush encroached landscape because they had adapted their foraging strategy to do so (Muntifering *et al.* 2006). Given the limited sample size, however, and considering evidence from previous studies and the wider effects of bush encroachment on ecosystem dynamics (Blaum *et al.* 2007; Schultz 2007; Bamford *et al.* 2009a), further research is required to determine the impact of vegetation structure on vulture foraging behaviour.

3.5.1. Conservation implications

Private conservancies and unprotected farmland in north-central Namibia played a central role in sustaining the tracked sample of the remnant Cape vulture population, and their management should therefore be considered a key component to successful vulture conservation in the future. This is widely acknowledged to be the case for other free-roaming carnivores in the region (Marker *et al.* 2008; Schumann *et al.* 2008; Lindsey *et al.* 2013a). As human-wildlife conflict persists and illegal poisoning is still prevalent (Schumann *et al.* 2008; Schumann *et al.* 2012; Lindsey *et al.* 2013a), the wide ranges and high degree of site fidelity displayed by the vultures leaves them susceptible to the illegal actions (intentional or inadvertent) of even a small number of individuals (Marker *et al.* 2008; Ogada *et al.* 2012a). Therefore the ongoing efforts to resolve human-wildlife conflict in the region (e.g. Schumann *et al.* (2006)) are not only essential for the persistence of mammalian predators (Lindsey *et al.* 2013a), but also for the future conservation of vultures (Ogada *et al.* 2012a). However, the population of Cape vultures is no longer considered to be a viable breeding population, and population augmentation has been suggested as a potential conservation action (BirdLife International 2013). While captive breeding and reintroduction of vultures can be successful (Le Gouar *et al.* 2008b), it is essential to first ensure that threats are mitigated before any such program begins (Converse *et al.* 2013). As it has not been possible to identify the exact mechanism behind the decline of the Cape vulture population and abandonment of the Waterberg breeding colony in north-central Namibia, further research is required if population augmentation or reintroduction strategies are to be successful. For example, it has been suggested that the warming climate has contributed to the abandonment of Cape vulture colonies in the north of their range (Simmons and Jenkins 2007) and increasing bush encroachment will also potentially impact on vulture foraging efficiency (Bamford *et al.* 2009a). Further investigation is therefore required to establish whether environmental conditions in Namibia remain suitable to support breeding Cape vultures. Ultimately, however, the ranging and land use patterns observed in this study confirm that the survival of vulture populations in Namibia and elsewhere in Africa will rely heavily on the curtailment of the increasing incidence of illegal poisoning across the continent (Ogada *et al.* 2012a; Ogada 2014).

3.6. Supplementary information

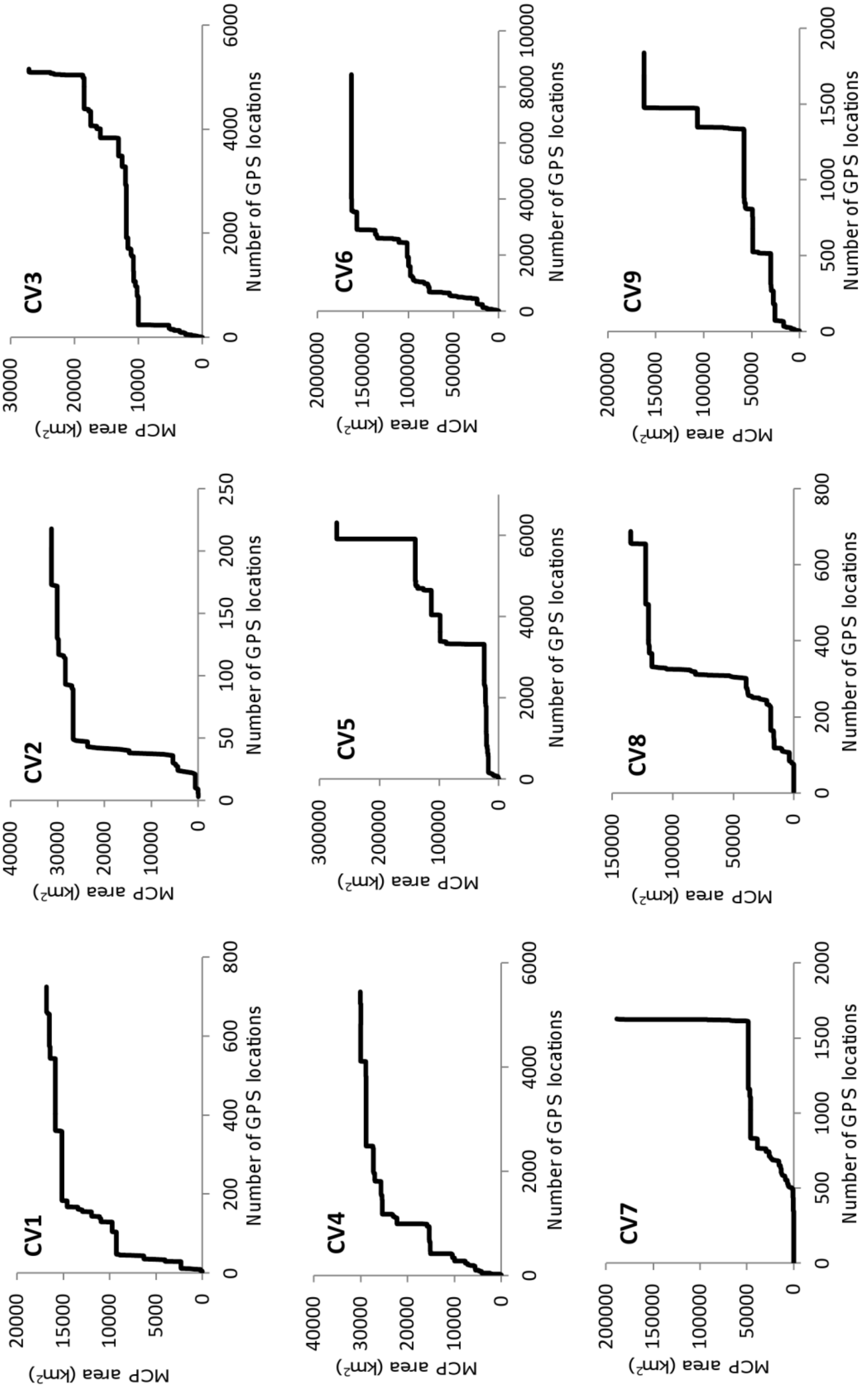

Figure S3.1. Home range area curves from incremental area analysis. Full legend overleaf.

Figure S3.1. Home range area curves from incremental area analysis for nine Cape vultures tracked using satellite tracking units from north-central Namibia. The number of GPS locations used to generate minimum convex polygons (MCP) by adding consecutive GPS locations until all recorded locations were used is plotted against the area of each MCP.

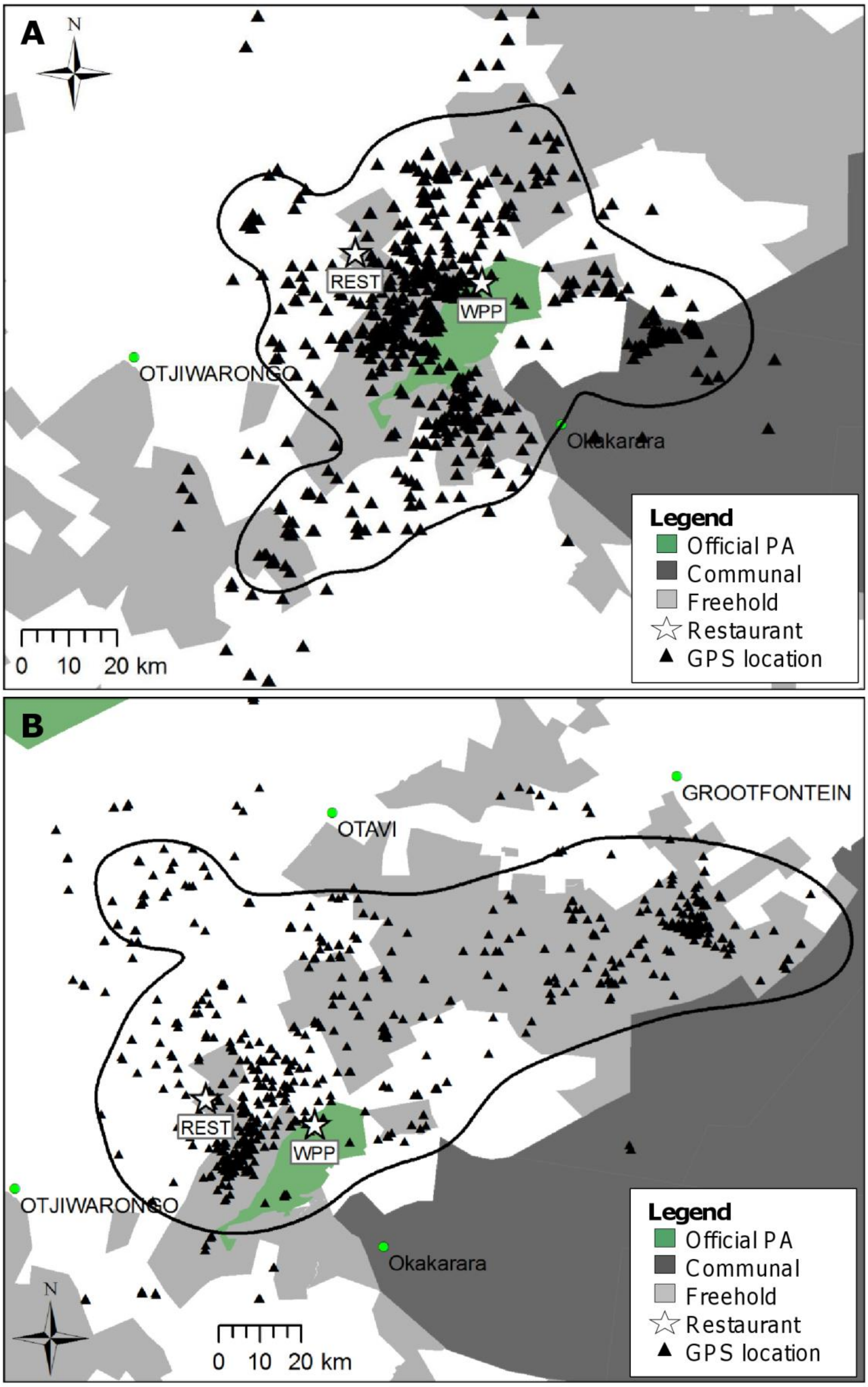

Figure S3.2. Overall home ranges contours and stationary GPS locations for two wild-caught Cape vultures tracked from north-central Namibia (A = CV3; B = CV4). Full legend overleaf.

Figure S3.2. Overall home ranges (95% kernel density estimated (KDE) contours (black outlined polygons)) and stationary GPS locations (black triangles) for two wild-caught Cape vultures tracked from north-central Namibia (A = CV3; B = CV4). Official protected areas (PA), communal and freehold conservancies, and vulture restaurants (REST = Rare and Endangered Species Trust capture site; WPP = Waterberg Plateau Park) are also shown.

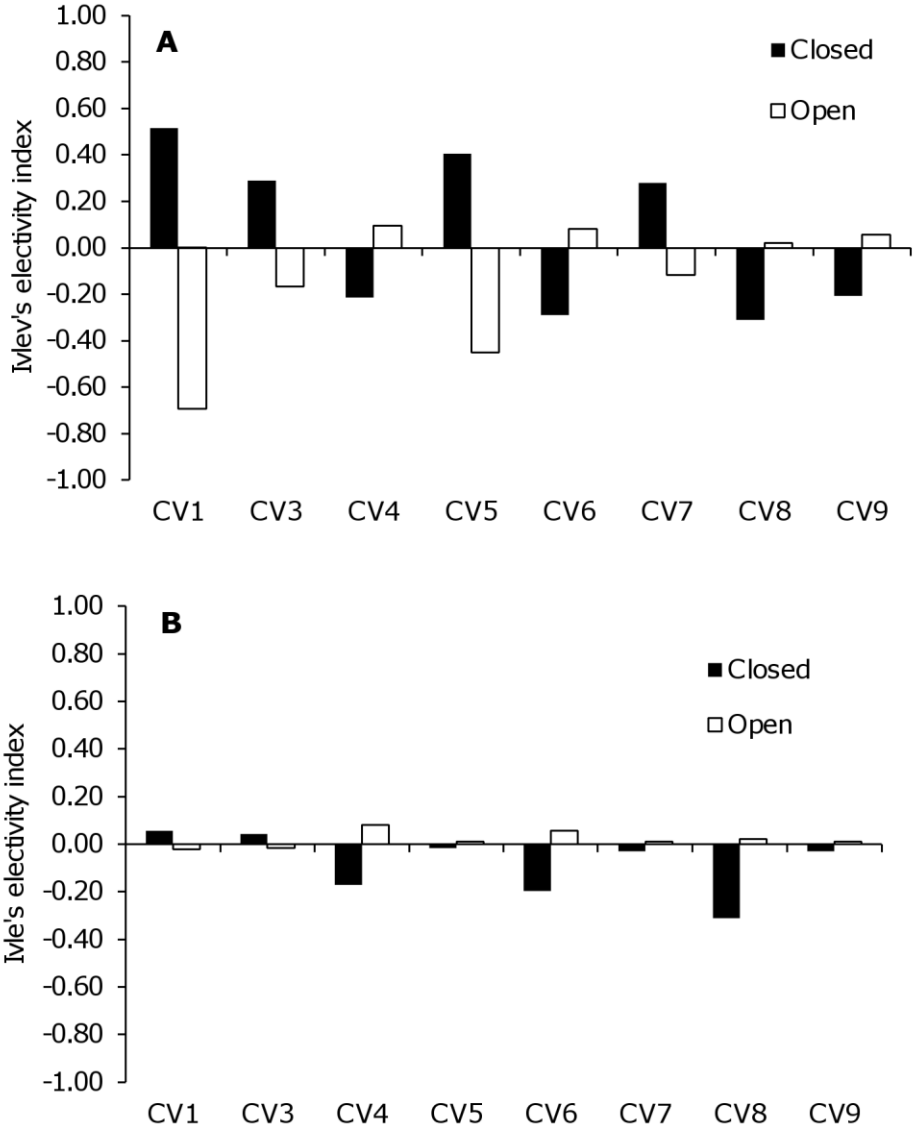

Figure S3.3. Ivlev’s electivity index values indicating selection or avoidance of Open (white bars) and Closed (black bars) vegetation cover by eight Cape vultures tracked by satellite telemetry from north-central Namibia. Ivlev’s electivity index values ranged from -1 to +1, indicating maximum avoidance and positive selection, respectively, and values of 0 indicating use in proportion to availability of each category. Availability was defined as the proportion of the 95% kernel density estimated (KDE) contour of each vulture covered by each category, and use was defined by the proportion of stationary GPS locations (A) including roost and nest locations and (B) excluding roost and nest locations recorded within each category.

3.7. Acknowledgements

I performed the data analysis and wrote the article with the permission of collaborative research partners Maria Diekmann (Rare and Endangered Species Trust, REST) and Dr John Mendelsohn (Research and Information Services of Namibia, RAISON) under the supervision of Dr Richard Yarnell, all of whom will be co-authors on resulting publications. I thank them for the opportunity to analyse these data and for their generous support both in the field and when writing up. Acknowledgements from Bamford *et al.* (2007) relating to funding: "All research and funding for the purchase of PTTs and Argos computer time was organized by the Rare and Endangered Species Trust (REST) and their donors: NedBank Namibia; Ned and Diana Twining; Steve Martin's Natural Encounters; Namibia Nature Foundation; Wilderness Safaris and Mr Jack Hanna. Construction of the walk-in trap was funded by NedBank Namibia. Mike Scott, Ann Scott, Tim Osborne and many others assisted with capturing the vultures and fitting the PTTs." Other funding partners of REST are also thanked for their generous support. I thank Nottingham Trent University for funding my studies through a Vice Chancellor's bursary and for providing funding for fieldwork in Namibia.

CHAPTER 4: Due South: A first assessment of the potential impacts of climate change on Cape vulture occurrence

Prepared for submission to *Biological Conservation.*

4.1. Abstract

Identifying and mapping environmental factors that determine the spatial distribution of a species are important aspects of conservation biology and allow effective management strategies to be implemented in appropriate areas. African vulture populations are declining across the continent due to multiple anthropogenic threats, particularly outside protected areas. The Cape vulture (*Gyps coprotheres*) has declined throughout its range and is now listed as being extinct as a breeding species in Namibia. In addition to known mortality factors (e.g. poisoning) it has been suggested that climate change might have contributed to the demise of Cape vultures in northern Namibia, and that other colonies towards the north of the current distribution might be under threat from regional warming and changing rainfall patterns. To provide a first assessment of the potential impacts of climate change on the occurrence of Cape vultures a presence-only ecological niche modelling method (Maxent) was used to predict the spatial occurrence patterns of wild-caught vultures fitted with GPS tracking units in northern Namibia and northern South Africa under current and future climatic conditions. The models showed high predictive power and precipitation seasonality and other bioclimatic variables were identified as the most important variables for predicting Cape vulture presence. Although an increase in the area predicted to be suitable for Cape vultures was predicted under future climate conditions, a pole-ward shift in the mean centre of the range of 151-333 km was predicted with significant range loss from the former breeding range in north-central Namibia and the core breeding range in northern South Africa. The coverage of predicted suitable areas by protected areas was small, confirming that vulture conservation measures must also be implemented on private land. This study provides the first indication that Cape vulture occurrence patterns will potentially be affected by the changing climate in southern Africa, and that northern colonies and foraging areas could be particularly under threat.

4.2. Introduction

Successful efforts to plan and implement conservation strategies in key areas are often reliant on the ability to describe the ecological niche and map the spatial distribution of a species to inform the management of endangered species, ecosystem restoration, reintroduction programs and population viability analysis (Elith *et al.* 2011; Razgour *et al.* 2011; Guillera-Arroita *et al.* 2015). Ecological niche modelling (ENM) or species distribution modelling (SDM) methods estimate the relationship between species presence records at sites and the environmental characteristics of those sites and are widely used in conservation biology and ecology (Elith *et al.* 2011). Increasingly Global Positioning System (GPS) tracking data provide the species presence records necessary for ENM analyses (Hebblewhite and Haydon 2010) for conservation themed studies on terrestrial (Swanepoel *et al.* 2013; Van Gils *et al.* 2014) and avian species (Jiguet *et al.* 2011; Gschweng *et al.* 2012; Liminana *et al.* 2014). Maxent (Phillips *et al.* 2006) is a common and favoured method for ENM analysis using tracking data because it does not require true absence data and has been shown repeatedly to outperform other presence-only modelling techniques (Elith *et al.* 2006; Hernandez *et al.* 2006). Examples of its successful application with avian tracking data include predicting the extent of suitable wintering habitats for pallid (*Circus macrourus*) and Montagu's (*Circus pygargus*) harriers in sub-Saharan Africa (Liminana *et al.* 2012; Liminana *et al.* 2014), and the response of Eleonora's falcons (*Falco eleonorae*) to environmental change (Gschweng *et al.* 2012).

African vulture populations are declining across the continent due to multiple anthropogenic threats such as poisoning (Ogada 2014), collisions and electrocutions on the expanding power line network (Boshoff *et al.* 2011) and food shortages due to depleted wild ungulate populations and improved livestock husbandry (Mundy *et al.* 1992; Ogada *et al.* 2012a; Krueger *et al.* 2015). The potential consequences of continuing declines are likely to be far reaching due to the essential ecosystem services that vultures provide (e.g. nutrient recycling; limiting the development and spread of disease (Sekercioglu 2006a; Moleon *et al.* 2014a; Morales-Reyes *et al.* 2015)). However, despite an increasing number of GPS tracking studies on African vulture species (Phipps *et al.* 2013a; Spiegel *et al.* 2013; Kendall *et al.* 2014; Krueger *et al.* 2014a) to our knowledge there has been no attempt to investigate what drives their spatial distribution using GPS tracking data and multivariate ENM methods.

The Cape vulture (*Gyps coprotheres*) is endemic to southern Africa and is listed as Vulnerable on the IUCN Red List due to declines across its range (BirdLife International 2013). It is a gregarious cliff-nesting species with a global population estimated at 8,000–10,000 individuals (*ca.* 4,000 breeding pairs) (BirdLife International 2013). The largest remaining breeding colonies are located in the north-eastern provinces of South Africa with smaller more dispersed colonies in the Maloti-Drakensberg mountains of Lesotho and south-east South Africa (Fig. 1.3) (Benson *et al.* 1990; Mundy *et al.* 1992; Whittington-Jones *et al.* 2011; BirdLife International 2013; Rushworth and Kruger 2014). An isolated breeding colony located on the cliffs of the Waterberg Plateau Park in north-central Namibia that numbered 500 Cape vultures in 1940 was reduced to as few as 13 individuals in 1985 (Brown 1985) and the species has recently been classified as extinct as a breeding species in the country (BirdLife International 2013). The declines have been mainly attributed to the widespread use of poisons for killing predators in the region and the loss of foraging habitat due to shrub encroachment (Brown 1985; Mundy *et al.* 1992; Bamford *et al.* 2007; Schumann *et al.* 2008; Bamford *et al.* 2009a). It has also been suggested that climate change may have played a role in the extinction of Cape vulture colonies in the north of their range since the 1950s due to the increasing temperatures and changing rainfall patterns recorded in the region during that time period (Simmons and Jenkins 2007; IPCC 2014). Southern Africa, and Namibia in particular, is predicted to experience particularly significant changes to climatic conditions (e.g. rising temperatures and altered rainfall patterns (Williams *et al.* 2007)) expected to drive pole-wards range shifts and loss of climatically suitable conditions for many species from different taxa (Simmons *et al.* 2004; Thuiller *et al.* 2006b; Garcia *et al.* 2012). Simmons and Jenkins (2007) therefore propose that climate change may work in concert with other factors to push Cape vultures away from their northernmost colonies in a southwards direction. However, although there is some evidence to suggest that breeding Cape vultures suffer increased levels of heat stress in higher temperatures and longer sunlight exposures (Chaudhry 2007), and rainfall patterns influence breeding success of other vulture species (Bridgeford and Bridgeford 2003; Virani *et al.* 2012), further work is required to investigate the potential impacts of climate change on Cape vulture occurrence (Simmons and Jenkins 2007; Krueger *et al.* 2015).

In this study I use Maxent modelling to provide a first description of spatial niche characteristics for Cape vultures and identify some of the environmental factors driving their occurrence. The presence locations were derived from GPS tracking data from wild caught vultures from northern South Africa (Phipps *et al.* 2013b) and from some of the last remaining Cape vultures in Namibia (Bamford *et al.* 2007). I investigate the potential influence of climate change on the extent of areas predicted to be currently suitable by projecting the models onto future bioclimatic conditions. I compare results from models using only data from South African tagged vultures with models from data from all vultures to assess whether conditions in north-central Namibia are predicted to be suitable for Cape vultures under current and future climate scenarios. I also evaluate the coverage provided by protected areas to areas modelled to be suitable for Cape vultures under current and future conditions as species turnover in protected areas is expected to be high in the region (Hole *et al.* 2009). The intention of this study is not to provide a definitive species distribution model for the Cape vulture, but to provide a first description of the spatial niche of a sample of vultures from the core breeding range of the species and to illustrate the potential impacts of climate change on their occurrence.

4.3. Methods

4.3.1. Modelling method and study area

The presence-only method Maxent (Phillips *et al.* 2006) was used to model the ecological niche of the Cape vulture as it does not require true absence data (Elith *et al.* 2011) and has been used previously with avian tracking data obtained from a small number of individuals (Gschweng *et al.* 2012; Liminana *et al.* 2012; Liminana *et al.* 2014). The geographical area used for ecological niche modelling was delineated by the national borders of South Africa, Lesotho, Swaziland, Zimbabwe, Botswana and Namibia, to correspond with the historical distribution of the Cape vulture (Mundy *et al.* 1992; BirdLife International 2013)(Fig. 1.3).

4.3.2. GPS tracking and presence data

Presence locations were derived from two studies that fitted GPS tracking units to wild-caught Cape vultures using walk-in cage traps (Bamford *et al.* 2007; Phipps *et al.* 2013b)(Chapters 2 and 3). The first capture site was located on a private livestock and game farm in the Waterberg region of north east Namibia (20°15’54”S, 17°03’53”E) while the second was on a private wildlife reserve in the North West Province of South Africa (25°13’S, 27 °18’E). Vultures captured in Namibia were fitted with solar-powered Argos/GPS PTT-100 tracking units made by Microwave Telemetry Inc. (Columbia, Maryland) programmed to record GPS locations every hour from 06:00 to 21:00

CAT (Bamford *et al.* 2007). The vultures captured in South Africa were fitted with battery-powered Hawk105 GPS-GSM tracking units programmed to record GPS locations up to four times per day at 07:00, 11:00, 13:00 and 15:00 CAT (Phipps *et al.* 2013b). Tracking units were fitted to vultures with Teflon® ribbon backpack-style harnesses and GPS locations were accurate to within 10 m. Data were derived from a total of five adult and four immature Cape vultures tagged in South Africa and five adults tagged in Namibia. The nine South African tagged vultures were tracked from 2009 to 2011 for a mean (±SD) tracking period of 332±167 days (1,052±578 GPS locations), and 952±771 days (11,031±8,884 GPS locations) for the five vultures tracked in Namibia from 2004 to 2009. This temporal difference was due to the ability of solar powered tracking units to generate more data points for longer periods than the battery-only units.

Two datasets of presence locations were selected for modelling purposes. Firstly, one dataset consisted of GPS locations only obtained from the nine South African tagged vultures, while the second consisted of GPS locations from all 14 vultures. This was done to compare results based on data from only South African tagged birds (i.e. captured in the "core" of the species' breeding range (Mundy *et al.* 1992; BirdLife International 2013)) to those that included presence locations from Namibia where the species formerly bred but is now considered extinct as a breeding species (Brown 1985; BirdLife International 2013). This provided an indication of the suitability of environmental conditions in northern Namibia compared to the rest of the study area and whether or not the region was predicted to be more or less affected by climate change compared to more southern areas during subsequent analyses.

Spatial preparation of GPS location and environmental variable data was performed in SDMtoolbox v1.1b (Brown 2014) in ArcMap (ESRI 2014) with all data projected to the Africa Albers Equal Area Conic coordinate system. For both presence datasets only stationary (<10 kmh^{-1}) GPS locations were selected to more accurately represent actual use of a given area. The Namibian tracking dataset was filtered further by only including GPS locations recorded every two hours from 09:00 to 17:00 CAT to reduce spatial autocorrelation and to correspond with the diurnal activity patterns of the vultures (Bamford *et al.* 2007)(Chapter 3). To further reduce spatial autocorrelation, which is known to influence species distribution model performance (Boria *et al.* 2014), the presence locations for each individual vulture were filtered by using the *spatially rarefy occurrence data* tool in SDMtoolbox v1.1b (Brown 2014) in ArcMap (ESRI 2014) to reduce clusters of presence locations to a single presence location within a Euclidian distance of 1 km. In order to reduce the influence of the disparity in tracking periods, and therefore the number of GPS locations per individual (Gschweng *et al.* 2012; Liminana *et al.* 2014), the mean number of stationary GPS locations rarefied by 1 km for the nine South African tagged vultures was calculated (mean±SD = 238±151 GPS locations individual^{-1}) and used to select a random subsample of 238 GPS locations for all individuals for which more than 238 stationary rarefied GPS locations were available using statistical software R v3.1.1 (R Core Team 2014). The maximum number of GPS locations per vulture was therefore limited to 238 and all stationary rarefied GPS locations were retained for vultures with less than 238 stationary rarefied GPS locations. Finally, the GPS locations for all individuals were merged into one shapefile and further spatially rarefied to a Euclidian distance of 1km. The two final presence location datasets consisted of 1,437 presence locations for the South African tagged individuals and 2,123 presence locations for the South African and Namibian tagged vultures combined (i.e. 686 presence locations for the five Namibian vultures).

Capture and tagging procedures were approved by the ethical review committee of the School of Animal, Rural and Environmental Science, Nottingham Trent University, and permits were granted by the Department of Agriculture, Conservation, Environment and Rural Development, North West Provincial Government, Republic of South Africa (Permit: 000085 NW-09) and the Namibian Ministry of Environment and Tourism. All procedures were carried out by South African Bird Ringing Unit permit holders (K. Wolter, M. Diekmann, W. L. Phipps).

4.3.3. Environmental variables

Only environmental variables with a pairwise Pearson's correlation coefficient of less than 0.7 (assessed using SDMtoolbox v1.1b (Brown 2014)) were included in the modelling process to reduce multi-collinearity effects (Phillips and Dudik 2008). Environmental variables were subsequently selected based on prior knowledge of their ecological relevance to Cape vultures and their contribution to preliminary models in an effort to achieve parsimony to reduce the risk of over-fitting (Anderson and Gonzalez 2011; Van Gils *et al.* 2014). Seven bioclimatic variables from the WorldClim database (http://www.worldclim.org/; (Hijmans *et al.* 2005)) were included in the models: annual mean temperature (*Bio_1*); mean diurnal temperature range (*Bio_2*); isothermality (*Bio_3*); minimum temperature of the coldest week (*Bio_6*); annual precipitation (*Bio_12*); precipitation seasonality (*Bio_15*); and precipitation of the coldest quarter (*Bio_19*). Such bioclimatic variables have previously performed well when modelling bird distributions (Barbet-Massin *et al.* 2009; Jiguet *et al.* 2011; Liminana *et al.* 2012; Liminana *et al.* 2014) and also influence vulture flight patterns (e.g. isothermality; (Pennycuick 1972; Ruxton and Houston 2002)) and the availability of carrion due to seasonal changes in ungulate mortality driven by fluctuations in vegetation productivity (Houston 1974b; Mduma *et al.* 1999; Owen-Smith *et al.* 2005; Ogutu *et al.* 2008).

Two topographic variables were included: altitude (*alt*) from the Digital Elevation Model (DEM) data from the BioClim database; and slope in percent (*slope_perc*) which was derived from the altitude DEM using the *slope* tool in ArcMap (ESRI 2014). Normalised Difference Vegetation Index (NDVI) is a reliable measure of greenness linked to forage availability (Boone *et al.* 2006) and was included as an indicator of vegetation structure (tree density or grass cover) and as a proxy for ungulate, and therefore carrion abundance (Ogutu *et al.* 2008), as used previously in vulture movement studies (Kendall *et al.* 2014). Monthly NDVI data were derived from the SPOT (Satellite Pour l'Observation de la Terre; http://www.cnes.fr/web/CNES-en/1415-spot.php) program by combining and averaging three layers per month for each year from 1998 – 2012 to give one NDVI dataset per month for the study area (R. Cooper-Bohannon, unpublished data). The August NDVI dataset (*ndvi_aug*) was included in the models after removing monthly NDVI layers with pairwise Pearson’s correlation coefficients of more than 0.7 and after identifying it as contributing the most to preliminary models that included only the twelve monthly NDVI layers. The Food and Agriculture Organisation (FAO) global cattle density dataset (*FAOcattle05*; http://www.fao.org; (Robinson *et al.* 2007)) was included as an indicator of potential livestock carrion supply. The FAO ruminant production systems dataset (*rum_prod_sys*) was used to include information about farming practices (e.g. mixed or livestock farming and water sources; (Robinson *et al.* 2011)). The Global Land Cover

2000 (*GLC2000*) dataset was included which consisted of vegetation cover data in the year 2000 based on spectral response and temporal profile (Mayaux *et al.* 2004). Finally, the World Wildlife Fund (WWF) terrestrial ecoregions of the world dataset classified by ecoregion ID code (*WWF_ecoregionID*; http://www.worldwildlife.org/biome-categories/terrestrial-ecoregions; (Olson *et al.* 2001)) was included to further assess the importance of vegetation characteristics. Therefore the models included a total of 14 environmental variables at a spatial resolution of 30 arc-seconds (approximately 1 km^2 at the equator).

For projections to future climatic conditions the current Bioclim variables were replaced with the corresponding Bioclim variables for the year 2050 from the WorldClim database from the HadGEM-AO model under emissions scenario RCP 8.5 which is a “worst case” scenario that predicts increasing greenhouse gas emissions and a likely global mean temperature increase of 1.4 – 2.6^{o}C between 2046 and 2065 (Riahi *et al.* 2007). The other environmental variables remained the same for projected models as for the current models, which I acknowledge is unlikely given projected climate, land use and socio-economic changes.

4.3.4. Ecological niche modelling procedure

Models were run using default settings in Maxent version 3.3.3 (Phillips *et al.* 2006) apart from the maximum number of iterations which was set at 5,000 to achieve algorithm convergence (Elith *et al.* 2011;

Kassara *et al.* 2013). Ten replicate models were run each using repeated random subsampling of 75% of the presence locations to train the model with the remaining 25% used to evaluate its predictive performance (i.e. test dataset). Results are presented as the mean and standard deviations of the ten replicate models. Two metrics were used to evaluate model performance (Elith and Graham 2009). Firstly, the area under the curve (AUC) of the receiver operating characteristics (ROC) was used to measure the model probability of correctly distinguishing presence from random locations, with values of 0.5 indicating models that predict no better than random and values greater than 0.75 for models with high model discrimination ability (Hanley and McNeil 1982; Phillips *et al.* 2006; Elith *et al.* 2011). The second metric, regularized training gain, describes how well the model prediction fits the presence data compared to a uniform distribution, with the exponential of the model gain indicating the sample likelihood compared to random background pixels (Phillips *et al.* 2006; Gormley *et al.* 2011).

Variable importance was assessed using two heuristic tests (percent contribution and permutation importance) and the jacknife procedure in Maxent. Percent contribution was calculated as the proportional contribution of each variable to the model training gain which is dependent on the path of the Maxent algorithm (Phillips *et al.* 2006). The permutation importance metric is independent of the algorithm path and represents the influence of the given variable on the training

AUC value, normalized to percentages (Phillips *et al.* 2006). For the jacknife tests variables were successively omitted and then used in isolation to measure their relative and absolute contribution to model gain, providing a measure of their explanatory power when considered alone (Elith *et al.* 2011; Gschweng *et al.* 2012).

4.3.5. Assessment of environmental suitability and impact of climate change

The logistic output from the Maxent model was used to display the spatial predictions of the probability of Cape vulture presence across the study area with values ranging from 0 to 1 (Fig. S4.1) (Phillips and Dudik 2008). To classify the model predictions into areas of binary suitability (1) and unsuitability (0) the mean (0.31) of the maximum training sensitivity plus specificity logistic threshold (*MaxTSS*) for the model with only South African tagged vulture presences (*MaxTSS* = 0.28) and the model with both presence datasets (*MaxTSS* = 0.33) was used. The *MaxTSS* threshold is independent of prevalence of presence locations and is recommended for use with presence only data as an objective method of binary suitability threshold selection (Jiguet *et al.* 2011; Liu *et al.* 2013). Binary maps of suitability were created using this method for both current and future (for the year 2050) climatic conditions for the two different presence datasets on which the models were based (i.e. *Model_SA* = presence locations from South African tagged vultures; *Model_NamSA* = presence locations from both South

African and Namibian tagged vultures). Subsequently the areas predicted to be unsuitable and suitable were compared for each model separately under the current and future environmental conditions. This was done in ArcMap to produce a raster dataset with areas predicted to be unsuitable in both current and future conditions; suitable under current but not future environmental conditions (range contraction); unsuitable under current conditions but suitable under future conditions (range expansion); and suitable under both current and future conditions (stable range). The distance between the mean centres of the extent of the suitable areas under current and future conditions was calculated in ArcMap to quantify the directional range shift from current to future conditions.

4.3.6. Evaluation of protected area coverage

To assess the level of protection afforded to areas predicted as suitable for Cape vultures based on the binary suitability maps, the number of suitable raster cells located within protected areas in the 2015 World Database on Protected Areas (IUCN and UNEP-WCMC 2015) were counted for current and future models in ArcMap (Liminana *et al.* 2012; Swanepoel *et al.* 2013; Liminana *et al.* 2014).

4.4. Results

4.4.1. Ecological niche model description and variable importance

The model constructed with the presence locations only from the South African tagged birds (Model_SA) and the model constructed with presence locations from South African and Namibian tagged birds (Model_NamSA) showed good predictive power based on mean AUC values of the 10 replicate runs (Model_SA AUC = 0.886±0.009; Model_NamSA AUC = 0.868±0.006), although the regularized training gain was lower for Model_NamSA (0.906±0.009) compared to Model_SA (1.084±0.009).

Model_SA classed 15.08% of the study area (*ca.* 460,801 km^2) as suitable for Cape vultures under current environmental conditions, while Model_NamSA classed 16.09% (*ca.* 491,655 km^2) of the area as suitable. The majority of the suitable area predicted by both models consisted of an almost continuous area in northern South Africa across most of the North West Province, the western half of the Limpopo Province and into south-east Botswana, corresponding with the extent of the known distribution for the species (Fig. 4.1b and c; Fig. 1.3). The suitable area also extended into the north-east of the Northern Cape Province and the western part of the Free State. A relatively narrow area of suitability was predicted along the south- and north-eastern edges of the Drakensberg escarpment bordering Lesotho in the north-eastern Eastern Cape and western edge of KwaZulu-Natal Provinces. This area was separated from the main region of suitability by an area of unsuitability estimated to extend in a south-west to north-easterly direction, almost 700 km long by 200 km wide across southern Gauteng, southern Free State and the south-west of Mpumulanga Province (Fig. 4.1b and c). In addition Model_NamSA predicted environmental suitability in an isolated area in north-central Namibia extending up to 300 km south and east of the Waterberg Mountains (Fig. 4.1c). Outlying areas of suitability were predicted in south-east Namibia, north-west Northern Cape and south-east Zimbabwe for Model_SA (Fig. 4.1b); and north-west Zimbabwe and an isolated area across the Namibia-Botswana Trans-Kalahari border for Model_NamSA (Fig. 4.1c).

According to the heuristic tests of variable importance bioclimatic variables were the most influential to model predictions in terms of percent contribution and permutation importance (Fig. 4.2a and b) with precipitation seasonality (*Bio_15*) contributing 29.88±2.14% (35.98±2.72% permutation importance) to Model_SA and five bioclimatic variables (*Bio_2, 12, 6, 3 and 1* in descending order) collectively contributing 73.70% to Model_NamSA (Fig. 4.2a and b). The four variables that contributed the most to Model_SA (*Bio_15, 6, 12 and 19* in descending order) collectively contributed 70.44% to the model. Altitude (*alt*) was also a relatively important variable with a permutation importance of 20.99% for Model_NamSA and 10.08% for

Model_SA. The jacknife tests for variable importance identified precipitation seasonality (*Bio_15*) as the most important variable for both models, followed by precipitation of the coldest quarter (*Bio_19*), minimum temperature of the coldest week (*Bio_6*) and WWF ecoregion ID for Model_SA (Fig. 4.2c). WWF ecoregion ID was also identified as an important variable for Model_NamSA, followed by altitude, minimum temperature of the coldest week (*Bio_6*) and NDVI in August (Fig. 4.2d). According to the jacknife tests exclusion of the variables from the models did not identify any obvious single variable that contained information that was lacking in the other variables, although the omission of *Bio_15* and *Bio_3* resulted in the greatest decrease in gain for Model_SA and Model_NamSA, respectively (Fig. 4.2c and d).

The average variable values for raster cells predicted to be suitable for Cape vultures were similar for Model_SA and Model_NamSA (Table 4.1) and the influence on the logistic probability of presence by the top eight variables identified as important to one or both models by the jacknife procedure are provided in Figure 4.3. When considered together the two models predicted that Cape vultures would be unlikely to occur below 517 m and above 3084 m above sea level (Model_NamSA mean *alt* = 1249 m above sea level) (Table 4.1; Fig. 4.3d). The minimum and maximum annual mean temperature (*Bio_1*) values were 5.8°C and 22.3°C, respectively (Table 4.1); the minimum and maximum annual precipitation was 81 mm and 1,605 mm, respectively (Model_NamSA mean *Bio_12* = 481 mm; Table 4.1; Fig.

4.3g); the minimum and maximum precipitation seasonality (*Bio_15*) values were 29% and 134%, respectively (Model_NamSA mean *Bio_15* = 76%; Table 4.1; Fig. 4.3a); the minimum and maximum precipitation of the coldest quarter (*Bio_19*) values were 0 mm and 326 mm, respectively (Model_NamSA mean = 17 mm; Table 4.1; Fig. 4.3b); the minimum and maximum minimum temperature of the coldest week (*Bio_6*) values were -5.9^{o}C and 9.9^{o}C, respectively (Table 4.1; Fig. 4.3c); and the highest probabilities of presence were predicted in Highveld grasslands (WWF ecoregion ID 31009), southern African bushveld (WWF ecoregion ID 30717) and Angolan mopane woodlands (WWF ecoregion ID 30702 (Model_NamSA only); Table 4.1; Fig. 4.3h) with a tendency for higher probability of presence in open grassland with sparse shrubs, closed grassland or croplands (*GLC2000*; Table 4.1) and in livestock only farming systems in arid land (*rum_prod_sys*; Table 4.1). The minimum and maximum NDVI (*NDVI_aug*) values were 10 and 245, respectively (Model_NamSA mean = 102; Table 4.1; Fig. 4.3e). The mean cattle density values were 10.53 cattle km^{-1} and 9.34 cattle km^{-1} for Model_SA and Model_NamSA, respectively (Table 4.1).

4.4.2. Projected extent of predicted environmental suitability

Of the 460,801 km^{2} predicted by Model_SA to be suitable for Cape vultures under current conditions, 28% was predicted to become unsuitable in 2050 with a pole-ward 151 km shift of the mean centre of the suitable area (Fig. 4.1b). However, under future conditions the overall suitable area was predicted to increase from 15% to 19% (594,964 km^2) of the study area, of which 44% (264,070 km^2) extended into areas predicted to be unsuitable in current conditions (Fig. 4.1b). For Model_NamSA a greater degree of current suitable range loss was predicted, with 55% of the 491,655 km^2 current suitable range predicted to become unsuitable in 2050, with a pole-ward 333 km shift of the mean centre of the suitable area (Fig. 4.1c). 56% (284,662 km^2) of the area predicted to be suitable in 2050 was predicted to be unsuitable in current conditions, resulting in a relatively small increase in the area predicted to be suitable across the study area to 504,911 km^2 (Fig. 4.1c). Both models predicted that the largest area of suitable range contraction would be in the western half of the Limpopo Province, South Africa, and south-east Botswana (Fig. 4.1c and d). Almost the whole area in north-central Namibia predicted to be suitable under current conditions by Model_NamSA was predicted to become unsuitable under climatic conditions in 2050 (Fig. 4.1c). The mean elevation (*alt*) for areas predicted to be suitable increased by 124 m and 171 m for Model_SA and Model_NamSA, respectively (Table 4.1).

4.4.3. Protected area coverage under current and projected suitability

Of the area predicted by Model_SA to be suitable for Cape vultures, 5.85% (26,961 km^2) and 3.79% (22,560 km^2) was included within protected areas under current and future conditions, respectively. The protected areas covering more than 1,000 km^2 of suitable area under current conditions were the Waterberg Biosphere Reserve (BR) in Limpopo Province, South Africa, the Drakensberg World Heritage Site (WHS), and the Central Kalahari Game Reserve (GR) in south-east Botswana, whereas under future conditions only the Kalahari-Gemsbok National Park (NP) and the Drakensberg WHS covered more than 1,000 km^2. For Model_NamSA, 7.91% (38,874 km^2) and 2.77% (13,963 km2) of the predicted suitable area was included within protected areas under current and future conditions, respectively. The protected areas covering more than 1,000 km^2 of suitable area under current conditions were several conservancies in north-central Namibia, the Waterberg BR in Limpopo Province, South Africa, and the Central Kalahari GR in south-east Botswana. Under future conditions only the Drakensberg WHS and the Waterberg BR in Limpopo Province, South Africa, covered more than 1,000 km^2 of suitable area.

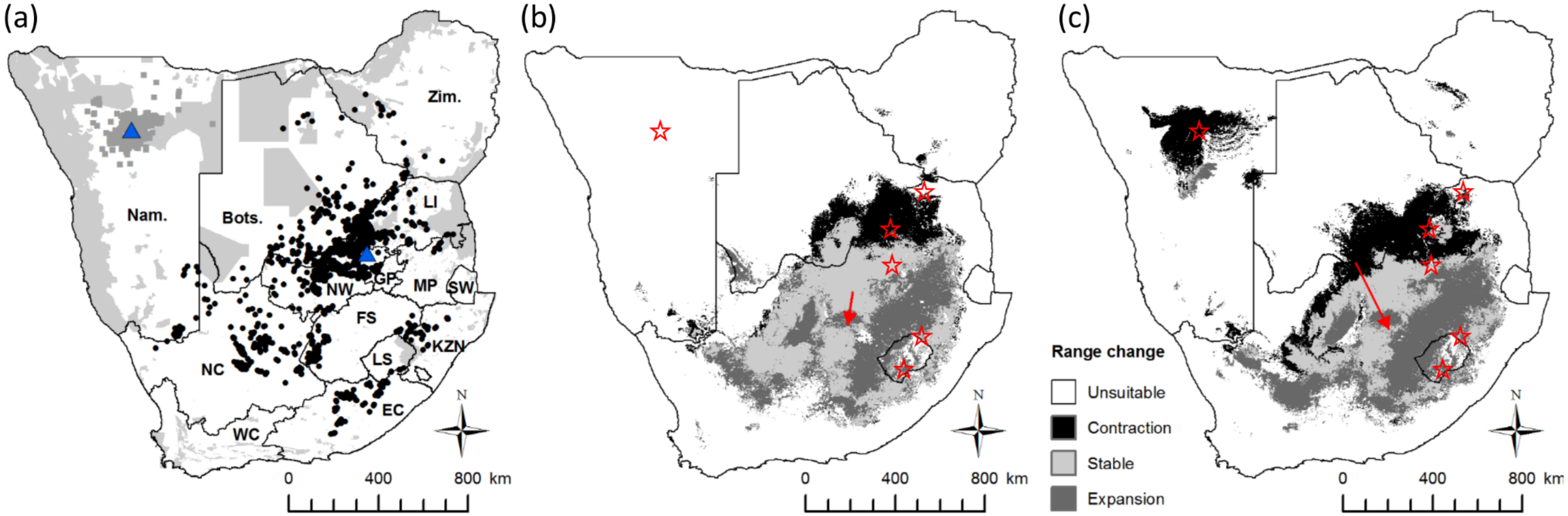

Figure 4.1. (a) Presence locations used for Maxent modelling from GPS tracking data from Cape vultures tagged in South Africa (black circles) and Namibia (dark grey squares). Capture sites are indicated by blue triangles and protected areas are shown by filled grey polygons. Letters indicated abbreviated country names and provinces of South Africa (NC = Northern Cape; WC = Western Cape; EC = Eastern Cape; KZN = KwaZulu-Natal; MP = Mpumulanga; NW = North West; LI = Limpopo; LS = Lesotho; SW = Swaziland; Nam. = Namibia; Bots. = Botswana; Zim. = Zimbabwe). Areas predicted by Maxent models to be unsuitable in both current and future (2050) climatic conditions (unsuitable), suitable in both (stable), suitable in current but not future conditions (range contraction) and suitable in future but not current conditions (range expansion) are shown by different shaded polygons for (b) Model_SA which was modelled with presence locations from South African tagged vultures only and (c) Model_NamSA which was modelled with all presence locations. The red arrows show to scale the movement of the mean centre of the suitable area under current conditions to the mean centre under future conditions. Red stars indicate some of the main Cape vulture colonies.

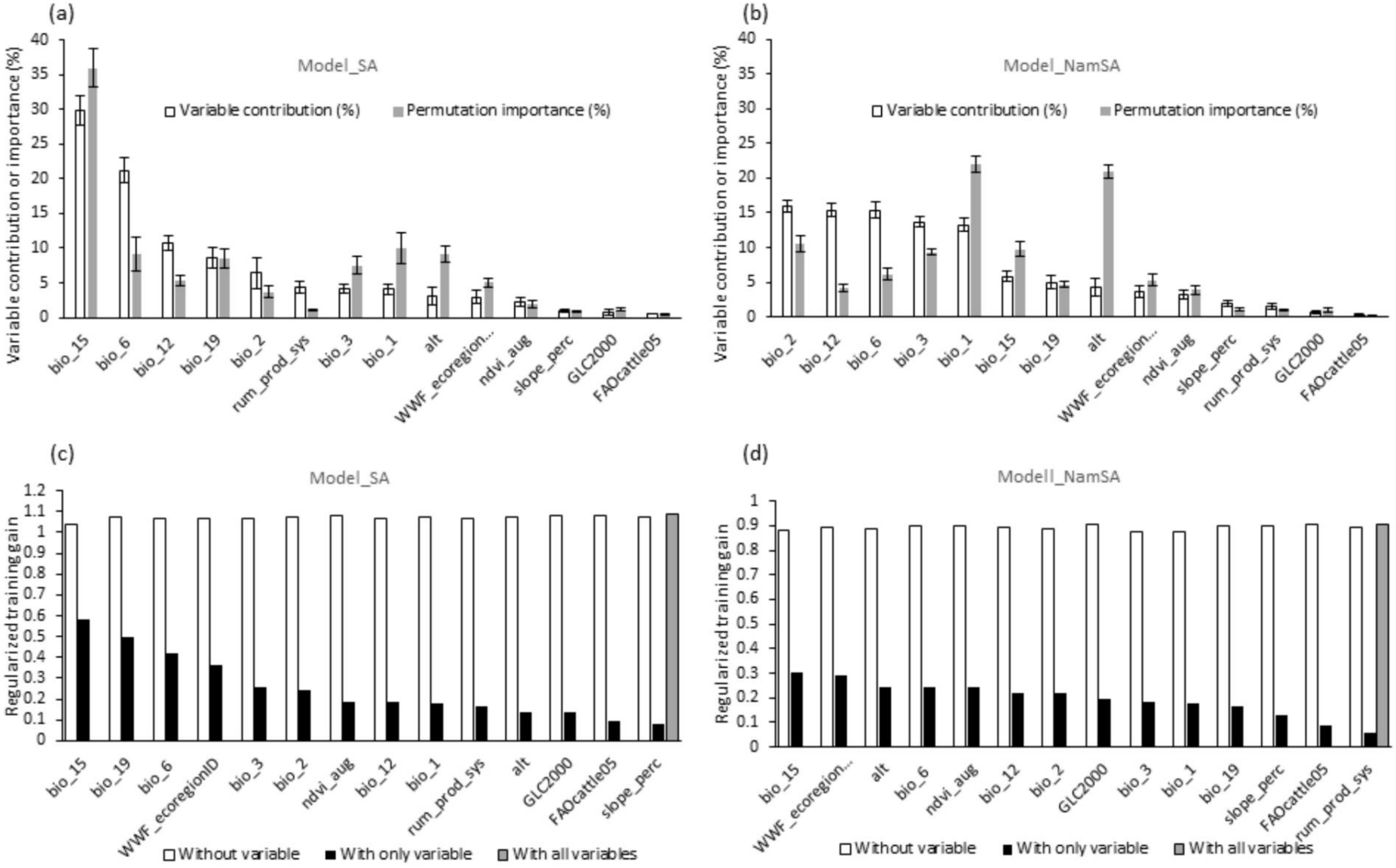

Figure 4.2. The mean (±SD) relative model contributions of variables based on (a – b) two heuristic tests (variable importance (white bars) and permutation importance (shaded bars) and (c – d) jacknife tests of variable importance based on 10 replicated models.*(Full legend shown overleaf)

* Figure 4.2. The mean (±SD) relative model contributions of variables based on (a – b) two heuristic tests (variable importance (white bars) and permutation importance (shaded bars) and (c – d) jacknife tests of variable importance based on 10 replicated Maxent models. Results in (c – d) express model gain in relation to the regularized training gain of each model with white bars showing gain for models with that variable omitted and black bars showing gain for models with only that variable. A low loss of training gain when one variable is omitted compared to the complete model indicates that the variable does not contain information that is not already provided in the other variables. A high training gain for models using only that variable indicates that the variable is useful for predicting Cape vulture presence. Model_SA used presence locations from only South African tagged vultures whereas Model_NamSA included presence locations from Namibian tagged vultures. [bio_1 = annual mean temperature; bio_2 = mean diurnal temperature range; bio_3 = isothermality; bio_6 = minimum temperature of the coldest week; bio_12 = annual precipitation; bio_15 = precipitation seasonality; bio_19 = precipitation of the coldest quarter; Alt = elevation above sea level; ndvi_aug = NDVI in August; slope_perc = slope percent rise; FAOcattle05 = FAO cattle density; rum_prod_sys = FAO ruminant production systems; GLC2000 = Global Land Cover from the year 2000; WWF_ecoregion_ID = WWF ecoregion.]

Table 4.1. Mean (±SE), minimum and maximum values for environmental variables* in raster cells modelled to be suitable under current and future (2050) climatic conditions using two presence location datasets from Cape vultures fitted with GPS tracking units in South Africa (n=9) and Namibia (n=5). Median and mode values are given for categorical variables. The mean (±SE), minimum and maximum values of the logistic probability of presence for each area of modelled suitability are also provided. The number of grid cells predicted to be suitable by each model are given in parentheses after the model name.

	Model_SA current (n=593,816)			Model_SA 2050 (n=766,707)			Model_NamSA current (n=633,576)			Model_NamSA 2050 (n=650,658)		
Variable*	Mean	Min.	Max.	Mean	Min.	Max.	Mean	Min.	Max.	Mean	Min.	Max.
bio_1 (°C)	17.88±0.0029	5.80	22.30	19.98±0.0026	7.50	24.40	18.41±0.0026	6.40	22.20	16.06±0.0022	5.60	21.50
bio_2 (°C)	15.69±0.0013	7.30	19.00	16.10±0.0014	9.90	19.20	15.90±0.0011	11.50	18.90	15.66±0.0013	10.40	18.10
bio_3	5.38±0.0004	4.40	6.40	5.44±0.0003	4.60	6.30	5.48±0.0005	4.40	7.30	5.32±0.0004	4.40	7.30
bio_6 (°C)	1.61±0.0025	-5.90	6.90	3.48±0.0019	-3.00	9.80	2.21±0.0027	-5.90	9.90	0.03±0.0020	-5.90	9.80
bio_12 (mm)	499.49±0.2286	81	1605	495.44±0.2316	77	1218	480.50±0.1938	103	1489	534.90±0.2408	105	1489
bio_15	72.74±0.0123	35	105	73.88±0.0121	34	98	78.51±0.0187	29	134	66.23±0.0130	20	136
bio_19 (mm)	21.58±0.0199	2	326	24.09±0.0172	3	333	17.47±0.0163	0	235	29.12±0.0157	0	233
Alt (m asl)	1222.61±0.3567	517	3084	1346.14±0.3225	596	3308	1248.70±0.3199	519	2946	1420.00±0.3349	389	3143
ndvi_aug	103.91±0.0189	10	245	100.67±0.0169	10	255	101.56±0.0157	10	185	101.06±0.0165	10	223
slope_perc (%)	2.23±0.0049	0	52.01	2.38±0.0042	0	52.01	1.75±0.0039	0	52.55	2.59±0.0047	0	52.55
FAOcattle05 (cattle·km^{-1})	10.53±0.0152	0	121.94	11.74±0.0165	0	468.60	9.34±0.0141	0	468.60	13.31±0.0234	0	468.60
Probability of presence	0.48±0.0001	0.31	0.89	0.55±0.0002	0.31	0.93	0.46±0.0001	0.31	0.88	0.59±0.0002	0.31	0.97
Categorical variables	Median (Mode)			Median (Mode)			Median (Mode)			Median (Mode)		
rum_prod_system	2 (2)			4 (2)			2 (2)			4 (2)		
GLC2000	14 (14)			14 (14)			14 (14)			14 (14)		
WWF_ecoregion_ID	31009 (31309)			31009 (31009)			31009 (31309)			31009 (31009)		

*bio_1 = annual mean temperature; bio_2 = mean diurnal temperature range; bio_3 = isothermality; bio_6 = minimum temperature of the coldest week; bio_12 = annual precipitation; bio_15 = precipitation seasonality; bio_19 = precipitation of the coldest quarter; Alt = elevation above sea level; ndvi_aug = NDVI in August; slope_perc = slope percent rise; FAOcattle05 = FAO cattle density; rum_prod_sys = FAO ruminant production systems (2 = Livestock-only systems in arid areas; 4 = Livestock-only systems in temperate areas or tropical highlands); GLC2000 = Global Land Cover from the year 2000 (14 = Open grassland with sparse shrubs); WWF_ecoregion_ID = WWF ecoregion (31009 = Highveld grasslands; 31309 = Kalahari xeric savannah).

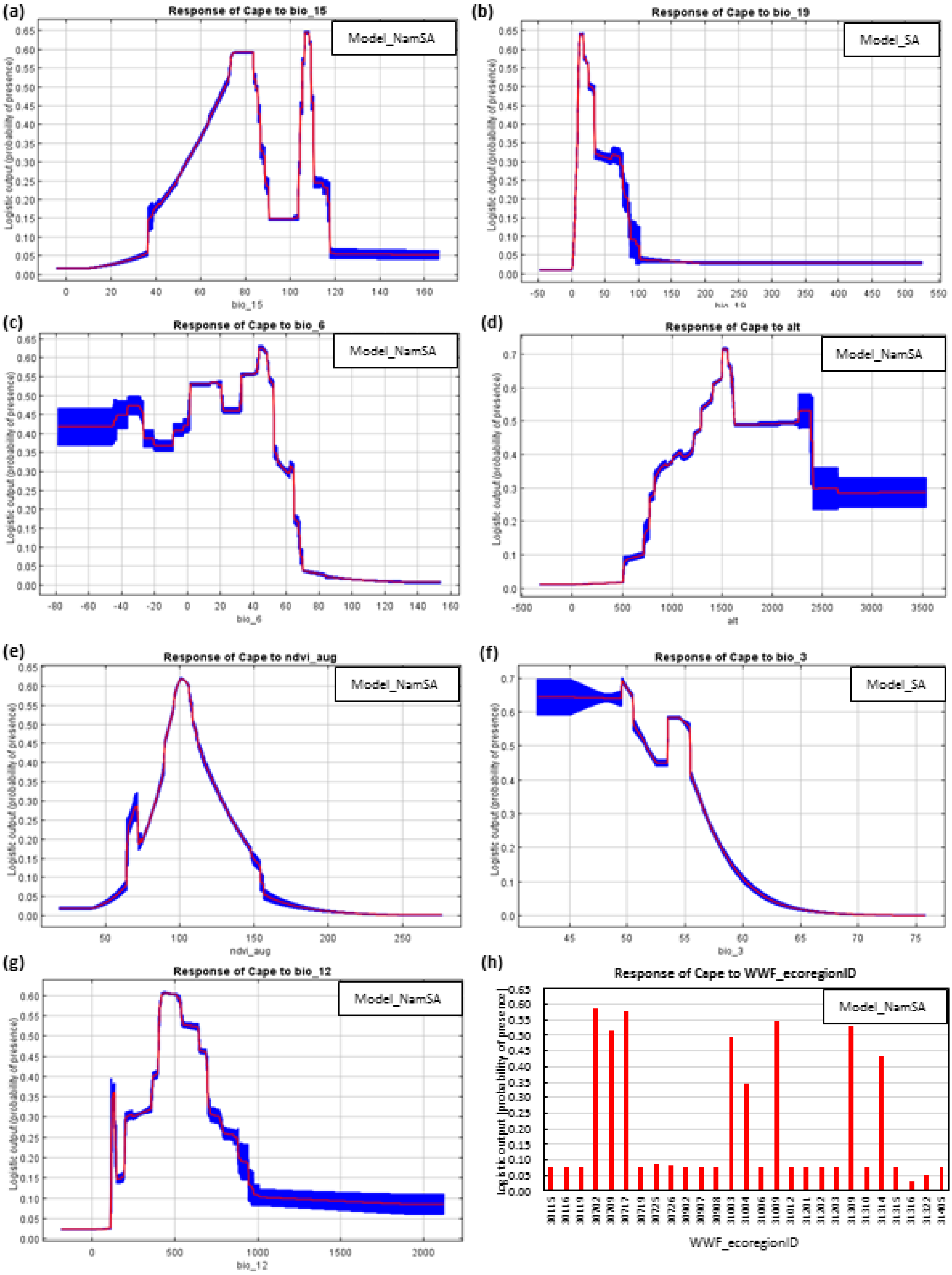

Figure 4.3. Response curves showing the predicted logistic probability of presence of the tagged Cape vultures in relation to the eight variables identified as the most important by jacknife tests.*(Full legend overleaf)

*Figure 4.3. Response curves showing the predicted logistic probability of presence of the tagged Cape vultures in relation to the eight variables identified as the most important by jacknife tests: (a) bio_15 (precipitation seasonality (%)); (b) bio_19 (precipitation of the coldest quarter(mm)); (c) bio_6 (minimum temperature of the coldest week (^{o}C*10)); (d) alt (elevation above sea level (m)); (e) ndvi_aug (NDVI in August); (f) bio_3 (Isothermality (^{o}C*10)); (g) bio_12 (Annual precipitation (mm)); (h) WWF_ecoregionID (WWF ecoregion ID). Red lines show the mean response curve and the blue shade areas show the standard deviation based on 10 replicated Maxent models.

4.5. Discussion

This study provides a first description of the environmental characteristics of the spatial niche occupied by the Cape vulture using a presence-only ecological niche modelling method based on GPS tracking locations from vultures caught from the wild in north-central Namibia and north-central South Africa. As with previous ecological niche modelling studies on raptor species the most important variables determining the limits of predicted suitability were bioclimatic variables, with precipitation seasonality consistently identified as one of the most influential variables (Gschweng *et al.* 2012; Liminana *et al.* 2012). The areas predicted to be suitable for Cape vultures by both models broadly corresponded with the known current and historical distribution of the species (Fig. 1.3), with a core range in the Highveld and bushveld of the northern provinces of South Africa and a secondary region of suitability in the more mountainous south-east of the country, mainly along the Maloti-Drakensberg escarpment (Mundy *et al.* 1992; BirdLife International 2013). The area of suitability also extended beyond the current western boundary of the recognised species distribution map (Fig. 1.3), which has been linked to the relatively recent construction of power lines in an area otherwise devoid of suitable roost sites (Mundy *et al.* 1992; Phipps *et al.* 2013b). A first estimate of the potential impact of climate change on the distribution of suitable areas for Cape vultures predicted a pole-ward shift in suitable conditions away from their core breeding and foraging range in northern South Africa, as expected based on projected patterns of bird species' responses to climate change in the region (Simmons *et al.* 2004; Hole *et al.* 2009). The model that included the presence locations from the vultures tagged in Namibia predicted that the majority of an isolated area of suitable conditions centred approximately on the former breeding colony in the Waterberg region would become unsuitable under future (2050) climatic conditions. In proportion to the regional coverage of protected areas in southern Africa (*ca.* 23% of land area, excluding Mozambique; *ca.* 9% of land area for South Africa, Lesotho and Swaziland (IUCN and UNEP-WCMC 2015)), the area predicted to be suitable for Cape vultures located within protected areas (5.85% of suitable area for the model based only on data from South African tagged vultures) was small and predicted to be reduced under future conditions.

4.5.1. Influence of environmental variables on predicted probability of presence

Overall, bioclimatic variables, and precipitation seasonality in particular, were the most influential in both models, which is consistent with previous studies that used GPS tracking data to model the ecological niche of raptors (Gschweng *et al.* 2012; Liminana *et al.* 2012). Vegetation production is dependent on climatic conditions and precipitation patterns determine forage abundance and quality, and subsequently nutrition-related mortality rates for ungulates (Boone *et* *al.* 2006; Ogutu *et al.* 2008; Chamaille-Jammes and Fritz 2009). Vulture movement patterns have recently been shown to be closely associated with seasonal ungulate mortality rates driven by seasonal changes in vegetation productivity indicated by changes in NDVI, with a clear preference by tracked vultures for areas of higher ungulate mortality during the dry season in the Masai Mara, Kenya (Kendall *et al.* 2014). NDVI in August (*NDVI_aug*) was identified as a variable of importance with a clear bell-shaped relationship between it and the predicted probability of presence for both models (Fig. 4.3e) which was similar to the response curves for mean annual precipitation (*Bio_12;* Fig. 4.3g) and precipitation seasonality (*Bio_15;* Fig. 4.3a). August is one of the coldest and driest months in southern Africa and mortality of both wild and domestic ungulates can be relatively high during that time as a consequence of nutritional stress (Owen-Smith *et al.* 2005; Mapiye *et al.* 2009). As August NDVI was identified as the most important variable in the preliminary model which included only the twelve monthly NDVI variables, it is likely that seasonal vegetation production influences the probability of Cape vulture occurrence. The interaction between climatic factors, vegetation production and probability of Cape vulture presence is further illustrated by the highest probability of presence being predicted in areas with very low levels of precipitation during the coldest quarter (*Bio_19*; Fig. 4.3b) and temperatures of 2^{o}C to 5^{o}C in the coldest week (*Bio_6*; Fig. 4.3c). This study therefore provides evidence that bioclimatic factors play a role in driving Cape vulture occurrence and movement patterns, most likely through climatic effects on vegetation production which directly influences the availability of food in the form of ungulate carrion, as reported for vultures in Kenya (Kendall *et al.* 2014). This provides a partial explanation (together with the availability of cliff nesting sites) for why the core breeding and foraging ranges of the species are located in the northern provinces of South Africa which are characterised by distinct wet summer (October – April) and dry winter (May – September) seasons (Benson *et al.* 1990; Mundy *et al.* 1992; Borello and Borello 2002), as Cape vultures and other *Gyps* species tend to coincide their breeding seasons with the highest availability of ungulate carrion in the dry season (Houston 1974b; Piper *et al.* 1999; Virani *et al.* 2010; Virani *et al.* 2012). This is consistent with previous studies that have found an inverse relationship between vulture breeding success and rainfall in the previous year due to reduced ungulate carrion availability (Bridgeford and Bridgeford 2003; Virani *et al.* 2012).

As large soaring fliers, vultures are reliant on suitable climatic conditions to provide sufficient air currents and thermals to allow them to cover the large distances required to locate their naturally ephemeral food source and it has been suggested that high rainfall and adverse weather conditions limit their ability to do so (Pennycuick 1972; Brown and Piper 1988; Mundy *et al.* 1992; Ruxton and Houston 2002; Monadjem and Bamford 2009; Lambertucci and Ruggiero 2013).

The influence of isothermality and other local climatic factors such as precipitation in determining the occurrence of large soaring birds has been shown for the Andean condor (*Vultur gryphus*), which should, according to a modelling study, prefer roost sites on climatically stable cliffs in areas of low rainfall (Lambertucci and Ruggiero 2013). The importance of isothermality in both models (*Bio_3*; Fig. 4.3f), together with higher probabilities of occurrence in areas with moderate seasonal rainfall, is consistent with this finding.

African vultures locate carcasses by sight alone (Houston 1974a) and it has been shown that high tree densities reduce their ability to locate and land at carcasses, decreasing their foraging efficiency (Schultz 2007; Bamford *et al.* 2009a). The results from this study provide further evidence that vegetation and habitat characteristics influence vulture movement and occurrence patterns. WWF ecoregion ID was identified as an important variable for both models, with higher probabilities of Cape vulture presence in habitats characterised by relatively limited tree density and more open habitats (e.g. Highveld grassland and southern African bushveld; Fig. 4.3h (Olson *et al.* 2001)). In addition, the most prevalent land cover type in the modelled suitable areas was open grassland with sparse shrubs which is also defined by relatively low tree densities (Table 4.1 (Mayaux *et al.* 2004)). These results correspond with previous descriptions of suitable Cape vulture habitat (Mundy *et al.* 1992) and support suggestions that they avoid heavily wooded areas and might be susceptible to the increasing rate and extent of bush encroachment in southern Africa (Schultz 2007; Bamford *et al.* 2009a).

Although variables related to land use and farming practices (FAO ruminant production systems; Global Land Cover 2000; FAO cattle density for 2005) were not identified as important variables for either model, relatively high probabilities of presence were predicted in livestock-only systems (as opposed to more arable dominated landscapes; Fig. S4.2b) and commercial agricultural areas (Fig. S4.2a), with an average cattle density of approximately 10 cattle km^{-2} in suitable areas (Fig. S4.2c). Furthermore, the probability of Cape vulture presence did not increase with increasing cattle density but decreased sharply after approximately 20 cattle km^{-2} (Fig. S4.2c), supporting suggestions that ungulate mortality rather than abundance is a main driver of vulture presence (Kendall *et al.* 2014), particularly as more intensive farming systems more frequently remove carcasses and reduce food availability for vultures (Murn and Anderson 2008; Margalida *et al.* 2014). These findings are consistent with suggestions that Cape vultures often utilise commercial farmland and are likely to exploit all sources of carrion as they become available across their range, including domestic livestock as well as wild ungulates (Benson *et al.* 2004; Murn and Anderson 2008; Phipps *et al.* 2013b).

4.5.2. Projected influence of climate change

The pole-ward shifts and increase in mean altitude of areas predicted to be suitable for Cape vultures in 2050 by both models correspond with previous studies that have predicted similar responses to changing climatic conditions in bird species in southern Africa (Simmons *et al.* 2004; Hole *et al.* 2009; Willis *et al.* 2009; BirdLife International and Durham University 2015). Although the model that used presence locations from Namibian tagged vultures predicted an area of suitability in the north-central region of the country (Fig. 4.1c and S4.1c), the model that only used presence locations from South African tagged vultures predicted a very low probability of presence in the same area (Fig. 4.1b and S4.1a). This confirms that bioclimatic conditions are very different in north-central Namibia compared to the majority of the predicted suitable area in South Africa and south-east Botswana (Williams *et al.* 2007). Under future conditions the area modelled to be suitable in north-central Namibia was predicted to contract severely away from its current extent in a southwards direction more than 170 km from the former Cape vulture breeding colony on the cliffs of the Waterberg Plateau (Fig. 4.1c). This is consistent with previous studies that predict that northern Namibia is likely to be particularly vulnerable to the effects of climate change as current climatic conditions shift pole-wards or even disappear, causing high rates of range loss for a high number of species from different taxa (Thuiller *et al.* 2006a; Thuiller *et al.* 2006b; Williams *et al.* 2007; Garcia *et al.* 2012). A similar level of range loss was predicted by both models in the current core breeding range of Cape vultures in northern South Africa and south-east Botswana (Fig. 4.1b and c; (Simmons and Jenkins 2007; BirdLife International 2013)) which have both previously been identified as areas expected to undergo high levels of bird and mammal species turnover and range loss driven by climate change (Thuiller *et al.* 2006a; Hole *et al.* 2009). These patterns provide evidence to support the suggestion that the most northerly Cape vulture breeding colonies could be at risk of becoming climatically unsuitable for the species in the future, and that climate change might have already played a role in the extinction of the only breeding colony in northern Namibia (Simmons and Jenkins 2007).

In contrast to the loss of suitable areas in the north of the modelled range, an increase in the overall extent of the suitable area was predicted by both models, largely as a result of a southwards range expansion into the Highveld grassland of the Free State and south-west Mpumalanga Provinces (Fig. 4.1b and c). This region is considered to be outside the historical distribution of the Cape vulture (Fig. 1.3) partly due to the relatively long distances from major breeding colonies but also due to the relatively low abundance of trees for roosting and perching after long-term overgrazing suppression and habitat degradation (Mundy *et al.* 1992; Low and Rebelo 1998; Olson *et al.* 2001). Therefore, although large bodied species, such as Cape vultures, that exhibit evidence of nomadic-like movements (Phipps *et* *al.* 2013a; Phipps *et al.* 2013b) are predicted to be more capable of dispersing to suitable areas under future climate change scenarios (Simmons *et al.* 2004; Dodge *et al.* 2014), dispersal capabilities were not considered in this study and so any predicted range expansions should be considered with caution, particularly as there are no active breeding colonies in the area and other factors such as land use change were not accounted for (Guisan and Thuiller 2005; BirdLife International 2013). Nevertheless, it was shown that the immature Cape vultures tracked in this study travelled beyond their historical distribution by perching on power line structures in areas previously devoid of natural perches (Phipps *et al.* 2013b), indicating that they might show a degree of plasticity in their movement patterns in response to future climate change as predicted for other vulture species (Simmons *et al.* 2004; Dodge *et al.* 2014).

4.5.3. The current and future role of protected areas

The limited coverage (<6% for Model_SA) of the modelled suitable Cape vulture range by protected areas under current climatic conditions reflects the distribution of relatively small, isolated protected areas in the majority of South Africa, particularly away from the east of the country, that cover just over 9% of the land surface (Fig. 4.1a (IUCN and UNEP-WCMC 2015)). This provides further evidence that vultures in southern Africa, and South Africa in particular, are likely to spend a significant amount of time foraging beyond the boundaries of protected areas, exposing them to multiple threats across the region (Murn and Anderson 2008; Phipps *et al.* 2013a; Phipps *et al.* 2013b).

Under future climate conditions the models predicted a decrease in the suitable area covered by protected areas to less than 4% for both models. The largest losses of protected area coverage were predicted in the core breeding range of the Cape vulture in the North West and Limpopo Provinces of South Africa (e.g. the Waterberg Biosphere Reserve), and in northern Namibia (Fig. 4.1b and c). In contrast, protected areas in the south of the range, such as the Maloti-Drakensberg mountain reserves, were predicted to retain or even gain areas predicted to be suitable under future climatic conditions. Two of the largest remaining Cape vulture colonies are located within protected areas adjacent to or part of the Waterberg Biosphere Reserve (Kransberg in Marakale National Park, and Blouberg in Polokwane Nature Reserve (Mundy *et al.* 1992; BirdLife International 2013)) and were predicted to become unsuitable in the future by both models (Fig. 4.1 b and c). Although breeding season monitoring does not suggest that the number of breeding pairs is declining at either colony (Cape Vulture Task Force, unpublished data), these findings do add further support to the suggestion that Cape vulture colonies are potentially at greater risk from the effects of climate change in the north of the range compared to the south, and that the Maloti-Drakensberg mountains could play an increasingly important role in providing nesting sites for vultures in the future (Simmons and Jenkins 2007).

4.5.4. Conservation implications and limitations

The modelling methods used in this study can only provide an approximation of the potential effects of climate change on the distribution of environmentally suitable conditions for Cape vultures and cannot provide definitive information about the underlying mechanisms driving those effects, or predict how vultures will respond to the changing climate in real circumstances (Thuiller *et al.* 2008; Elith and Leathwick 2009; Elith *et al.* 2011). Even so the findings from this study, based on accurate presence locations from tracking data, provide the first evidence to support suggestions that the northern bounds of the Cape vulture range are potentially highly vulnerable to the effects of future climate change (Simmons and Jenkins 2007). Considering higher temperatures and longer sunlight exposures have been shown to cause higher heat-stress on nesting Cape vultures (Chaudhry 2007) and rainfall patterns influence breeding success of other African vulture species (Bridgeford and Bridgeford 2003; Virani *et al.* 2012), it is reasonable to speculate that warming temperatures and changes to precipitation patterns over the last few decades (IPCC 2007) may have already affected the breeding distribution of Cape vultures by contributing to the extinction of the Waterberg Plateau breeding colony in north-central Namibia (Simmons and Jenkins 2007; Krueger *et al.* 2015). However, it is certainly not the case that climate change alone is responsible for the observed declines in Cape vultures in Namibia or elsewhere across their range, and the severe impacts of widespread poisoning (Ogada *et al.* 2012a; Ogada 2014), fatal interactions with power lines (Boshoff *et al.* 2011), habitat degradation (Bamford *et al.* 2009a), food shortages (Krueger *et al.* 2015), among other factors, are widely recognised. Our findings provide a first indication that climate change might pose an equally serious threat to vultures, however, particularly when considering the potential effects of climate driven changes to vegetation characteristics (Thuiller *et al.* 2006b; Chamaille-Jammes and Fritz 2009) and mammal distributions (Thuiller *et al.* 2006a) that could consequently reduce suitable foraging habitat and carrion availability.

It remains unknown exactly how Cape vultures will respond to future climate change in real terms and further related research is urgently required (Simmons and Jenkins 2007; Krueger *et al.* 2015), particularly as this study involves a relatively small sample of individuals. However, if southern areas such as the Maloti-Drakensberg mountains do become more important for Cape vultures in the future, then additional conservation measures to prevent or mitigate the impacts of proposed wind farms (Rushworth and Kruger 2014), power lines (Boshoff *et al.* 2011) and ongoing poisonings (Krueger *et al.* 2015) will be essential throughout their range. In addition, the small amount of suitable range predicted to occur within protected areas provides further evidence that it will be essential to direct vulture conservation measures to private land as well as to the existing protected area network, as acknowledged for other carnivore species (Lindsey *et al.* 2004; St John *et al.* 2012; Swanepoel *et al.* 2013).

4.6. Supplementary information

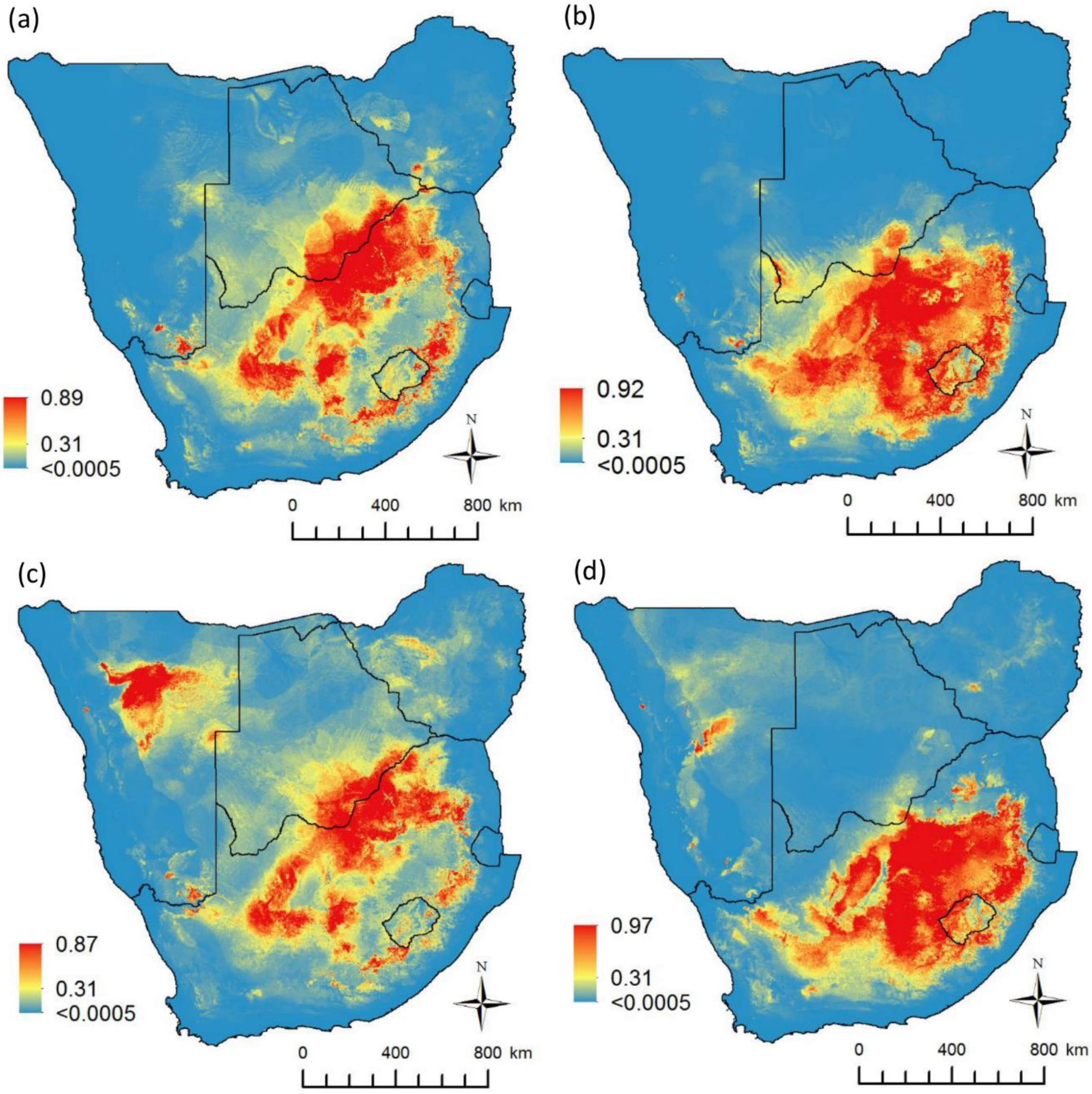

Figure S4.1. Maps showing logistic probability of presence of Cape vultures as predicted by Maxent models for (a) and (c) current and (b) and (d) future (2050) climatic conditions using GPS presence locations from (a-b) only South African tagged vultures and (c-d) South African and Namibian tagged vultures. Warmer colours represent higher predicted probability of presence and the suitability threshold as determined by the mean maximum training sensitivity plus specificity logistic threshold for the current models (0.31) is shown.

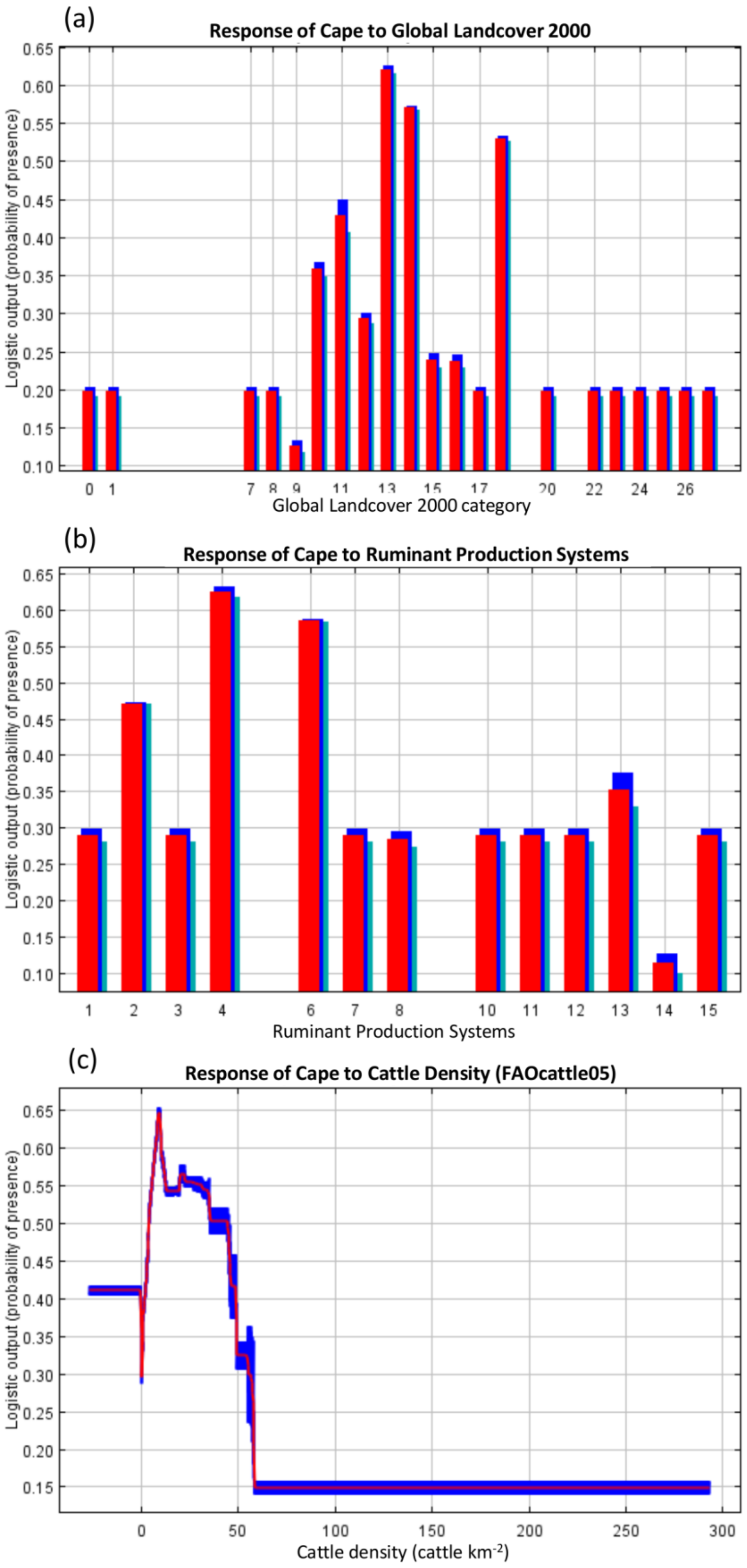

Figure S4.2. Response curves showing the predicted probability of presence of Cape vultures in relation to land use variables.*(Full legend overleaf)

Figure S4.2. Response curves showing the predicted probability of presence of Cape vultures in relation to (a) different land cover categories (GLC2000; 13 = closed grassland; 14 = open grassland with sparse shrubs; 18 = croplands (>50%) (Mayaux *et al.* 2004)); (b) different FAO defined ruminant production systems (rum_prod_sys; 2 = livestock-only systems in arid areas; 4 = livestock-only systems in Temperate areas or Tropical Highlands; 6 = mixed rainfed systems in arid areas (Robinson *et al.* 2011)); and (c) to FAO cattle density values for 2005 (FAOcattle05 = cattle·km^{-2} (Robinson *et al.* 2007)).

4.7. Acknowledgements

Acknowledgments for data collection, funding and other support relating to the GPS tracking data acquisition from Chapters 2 and 3 are also applied to this chapter. In particular I thank Maria Diekmann (Rare and Endangered Species Trust, REST), John Mendelsohn, Kerri Wolter (VulPro), Lynne and Dougal MacTavish (Mankwe Wildlife Reserve, MWR) for financial, logistical and general support directly or through their respective funding partners. I also thank Rachael Cooper-Bohannon for generously providing the NDVI datasets for modelling purposes. I also thank the University of Pretoria for additional support. I analysed the data and wrote the article under the supervision of Dr Richard Yarnell. I thank Nottingham Trent University for funding my studies through a Vice Chancellor's bursary and for providing funding for fieldwork in Namibia.

CHAPTER 5: DISCUSSION

5.1. Synopsis

Multiple anthropogenic factors have caused vulture populations to decline worldwide, with serious implications for ecosystem and human health, and ultimately socio-economic well-being in the future (Ogada *et al.* 2012a; Morales-Reyes *et al.* 2015). It is widely recognised that further research into the ecology of African vultures is required to inform the implementation of effective conservation measures in key areas and avoid catastrophic population declines similar to those seen in Asia (Boshoff and Anderson 2007; Ogada *et al.* 2012a).

In this thesis I have used GPS tracking methods to delineate the home ranges of Cape vultures in southern Africa and identified key factors that influenced their movement patterns. This study is the first, to my knowledge, to use GPS technology to track the movements of Cape vultures caught from the wild in the North West Province of South Africa, and the findings from Chapter 2 have already been used by the national power distributor to identify target areas for additional surveys and the installation of mitigation measures on certain transmission power lines (Phipps *et al.* 2010; Phipps *et al.* 2013b). This study also provides a first assessment of the use of protected areas by Cape vultures using accurate movement data, the first description of the environmental characteristics of their spatial niche, and a first estimate of the potential impacts of climate change on their future distribution. The initial findings of this research have contributed to an increasing interest in vulture research in southern Africa and will inform the planning of effective conservation measures in the future. The following section discusses the findings of this study in a conservation context.

5.2. Conservation implications

One of the first stages in assessing the conservation status of a species is to determine the size and extent of its range, both at the individual and the population level, and GPS tracking data are increasingly being used to inform such assessments (Cooke 2008; Mace *et al.* 2008). The analyses performed in Chapter 2 suggested that the IUCN species distribution might currently underestimate the overall range of the Cape vulture in South Africa, illustrated by the movements of several immature individuals westwards into the Northern Cape Province which was formerly thought to be outside the current range of the species in South Africa (Mundy *et al.* 1992; BirdLife International 2015). Given the close association of the movements of the immature vultures with power lines in the area, it is likely that the relatively recent construction of transmission lines has provided additional roosting and perching sites for vultures and allowed them to extend their overall range beyond their historical distribution in areas previously devoid of suitable perches, as suggested by Mundy and colleagues (1992).

Although the extent of the combined home ranges of the individuals tracked in Chapter 2 was larger (1,052,407 km^2) than the IUCN distribution (860,000 km^2 (BirdLife International 2015)), the area predicted to be suitable for the tracked vultures in Chapter 4 by ecological niche modelling methods was much smaller (460,801 - 491,655 km^2). Given the limited sample size of tracked vultures and the differences between these estimates, the IUCN range area estimate remains reasonable. However, further research is required to confirm the importance of the Northern Cape and Free State Provinces for foraging Cape vultures, particularly immature individuals, which will potentially result in the current IUCN distribution being extended westwards. Furthermore, the pole-ward shifts and contractions of suitable environmental conditions predicted in Chapter 4 illustrate the potential for climate change to alter the distribution range of the Cape vulture, particularly in the core breeding range in northern South Africa. However, the resilience and adaptability of Cape vultures to climate change remains poorly understood (Simmons and Jenkins 2007) and such modelling studies provide a best estimate as opposed to definitive predictions (Guillera-Arroita *et al.* 2015), and further study is required (Krueger *et al.* 2015).

Identifying important foraging and breeding areas for threatened species is essential for implementing effective conservation measures (Chevallier *et al.* 2011). The core ranges of the vultures tracked in Chapter 2 corresponded with areas known to be important for Cape vultures based on their historical distribution and previous studies. For example, the largest area of overlapping core ranges was located either side of the Limpopo River, which forms the border between south-east Botswana and the Limpopo and North West Provinces of South Africa, and extended south to the Magaliesberg Mountains, north-west of Pretoria (Fig. 2.1). This region forms the core breeding range of the species, with the largest colonies located at Blouberg (>1,000 breeding pairs) and Kransberg (>600 breeding pairs) in the Limpopo Province, and several colonies (>300 breeding pairs) in the Magaliesberg Mountains (Benson *et al.* 1990; Whittington-Jones *et al.* 2011; Wolter *et al.* 2013). This area of the North West and Limpopo Provinces was also intensively used by GPS-tracked immature African white-backed vultures (Phipps *et al.* 2013a), and is already considered to be particularly important for the persistence of vulture populations in the region (Mundy *et al.* 1992; Boshoff and Anderson 2007). Given that the vultures foraged mainly on unprotected farmland in this region, it will be important to target conservation measures beyond protected area boundaries by raising awareness among the farming community and limiting the illegal use of poisons (Pfeiffer *et al.* 2014).

The cross-border movements and extensive ranges traversed by the immature vultures illustrate that it is vital to establish conservation measures in key areas across southern Africa and not simply on a national basis or in close proximity to breeding colonies. Although the intensive use of Northern Cape farmland by several immature vultures in South Africa was unexpected based on historical records, the area is known to be important for other vulture species (Anderson 2000; Murn *et al.* 2002; Murn and Anderson 2008). In the same way, although only one of the immature vultures travelled to south-east South Africa it spent extended periods in areas known to be important for Cape vultures in the Eastern Cape and Kwazulu-Natal Provinces where populations are under threat from poisoning and the expanding network of power lines and wind farms (Pfeiffer *et al.* 2014; Rushworth and Krueger 2014; Krueger *et al.* 2015). Both regions should therefore continue to receive targeted conservation action, particularly along transmission lines frequently used for perching or where poisoning incidents are known to occur (Boshoff *et al.* 2011; Pfeiffer *et al.* 2014; Krueger *et al.* 2015). Similarly, the repeated seasonal movements between south-east Namibia and south-east Botswana by the immature vulture tracked in Chapter 3 potentially reflect the use of those areas by other vultures in response to fluctuating carrion abundance. Further research is needed to investigate the importance of both areas for vultures, particularly as two of the reintroduced vultures visited the same area of Namibia and similar long-distance movements to south-east Namibia and Botswana have recently been recorded by other species (Phipps *et al.* 2013a) and in ongoing tracking studies (John Mendelsohn and Peter Hancock, personal communication). The survival of immature individuals to breeding age is essential for the persistence of vulture populations (Piper *et al.* 1999) and the findings of this study illustrate the importance of establishing effective monitoring and conservation measures in key areas across southern Africa and not only within the breeding range of the species.

It is critical to assess the level of protection afforded to threatened species by the existing protected area network in order to allow effective conservation strategies to be implemented at the landscape scale, which is particularly important for highly mobile species such as vultures (Boyd *et al.* 2008; Runge *et al.* 2014). Our findings demonstrate that while officially protected areas play an important role in protecting Cape vulture breeding colonies, the tracked vultures foraged most frequently outside protected area boundaries in unprotected farmland and privately managed conservancies, as seen in other vulture species in the region (Murn and Anderson 2008; Phipps *et al.* 2013a). Consequently, vultures are likely to be regularly exposed to threats such as illegal poisoning and fatal interactions with power lines which are inherently more prevalent outside protected areas in southern Africa (St John *et al.* 2012; Thorn *et al.* 2013; Pfeiffer *et al.* 2014; Krueger *et al.* 2015). It will therefore be essential to target conservation measures towards private landowners through increased public awareness campaigns and more stringent enforcement of wildlife protection laws (Ogada 2014; Pfeiffer *et al.* 2014; Krueger *et al.* 2015). Although biodiversity conservation on private land in southern Africa faces many challenges (Trimble and van Aarde 2014), a co-ordinated effort to reduce the impact of human-wildlife conflict might present an important opportunity for the conservation of vultures and other carnivores on private land in the region (Beale *et al.* 2013; Lindsey *et al.* 2013b; Balme *et al.* 2014).

This study has illustrated the ability of GPS tracking data to identify important drivers of animal movement patterns (Cooke 2008). In Chapter 2 it was demonstrated that the extent of the home ranges of the tracked vultures in South Africa was closely associated with the distribution of transmission lines which they regularly used for perching and roosting. Although the construction of transmission lines might have allowed Cape vultures to forage in areas that otherwise lack suitable perches, as originally suggested by Mundy and colleagues (1992), it remains unclear whether the potential benefits to the population are outweighed by the risk of injuries or fatalities caused by collisions with overhead cables. Since fatal interactions with power lines are known to threaten Cape vulture populations with extinction in some regions of South Africa (Boshoff *et al.* 2011; Rushworth and Krueger 2014), our findings confirm that further related research would be valuable and necessary to inform additional investment into mitigation measures along targeted sections of frequently used sections of power line. For example, the high degree of overlap between the core ranges of the tracked vultures and the recorded locations of vulture-power line interactions (Fig. 2.1) illustrates the value of GPS tracking data for identifying areas of high collision or electrocution risk.

The ecological niche modelling (ENM) analyses carried out in Chapter 4 provided a first estimation of the environmental characteristics of the spatial niche of Cape vultures. The models indicated that bioclimatic variables such as precipitation seasonality were the most important factors in determining the probability of space use of the tracked vultures, which corresponds with similar studies on other raptors (Gschweng *et al.* 2012; Liminana *et al.* 2014). The close links between rainfall patterns, vegetation productivity and ungulate mortality rates are intrinsic to savannah ecosystem dynamics (Owen-Smith *et al.* 2005; Owen-Smith and Goodall 2014), and they have recently been demonstrated to influence vulture movement patterns as they track rainfall-mediated ungulate mortality patterns across the Serengeti-Mara ecosystem in East Africa (Kendall *et al.* 2014). Our findings that the tracked vultures were most likely to occur in relatively productive savannah grassland or sparse woodland habitats, mainly in regions with distinct wet and dry seasons and corresponding temperature fluctuations, provide further evidence to suggest that vulture distributions are driven by the interactions between climatic conditions, vegetation characteristics and ultimately seasonal ungulate mortality rates (Houston 1974b; Kendall *et al.* 2014). However, despite some evidence that the tracked vultures favoured more open habitats, the influence of vegetation characteristics, such as tree density, on the foraging activity of Cape vultures remains unclear and requires further investigation, particularly in the face of widespread bush encroachment in the region (Bamford *et al.* 2009a).

The importance of bioclimatic variables in influencing the distribution of the Cape vultures tracked in this study provides some of the first evidence to support the suggestion of Simmons and Jenkins (2007) that climate change might have played a role in the abandonment of breeding colonies in the north of their range in Namibia and Zimbabwe. Many bird species in South Africa have already exhibited significant range shifts (Walther and van Niekerk 2015) and it seems likely that the changing climate will affect vultures through a series of complex interactions between changing rainfall patterns, vegetation characteristics and productivity, and ultimately carrion availability through changing ungulate mortality rates. It is also possible that changes to local weather conditions will affect Cape vulture flight patterns, breeding success and overall survival rates (Virani *et al.* 2012; Lambertucci and Ruggiero 2013; Duriez *et al.* 2014). Although ENM methods can only provide a best estimation of the potential effects of changing conditions on the distribution of a species (Guillera-Arroita *et al.* 2015), and factors such as poisoning pose a more immediate threat to Cape vultures (Krueger *et al.* 2015), the loss of suitable environmental conditions in the main Cape vulture breeding range in northern South Africa predicted in this study indicates that climate change is a potentially serious threat and merits further investigation.

The priorities for Cape vulture conservation are to protect existing breeding sites, provide a sufficient and uncontaminated supply of carrion, and to reduce or eliminate poisoning incidents and fatal interactions with power lines (Boshoff and Anderson 2007; BirdLife International 2015). Although some conservation measures have reduced Cape vulture mortality rates in some parts of their range (Piper *et al.* 1999; Whittington-Jones *et al.* 2011), the overall population continues to decline and augmentation by introducing captive-bred individuals remains a possible conservation strategy (BirdLife International 2015), with the first ten individuals having been released in South Africa in recent months (Hirschauer 2015).

While populations of some vulture species have been successfully re-established or increased through reintroductions and supplementations (Le Gouar *et al.* 2008a; Rivers *et al.* 2014), it is essential to gain a thorough understanding of potential dispersal patterns of introduced individuals before undertaking a large scale reintroduction project (Le Gouar *et al.* 2008c; Margalida *et al.* 2013). Although the sample size was very small for this study, the large post-release dispersal distances of the three individual vultures released in Namibia suggest that dispersal patterns of introduced Cape vultures still need to be fully assessed, and their natal origins carefully considered as with other species (Margalida *et al.* 2013). Moreover, it will be essential to reduce or eliminate existing and widespread threats such as poisoning before an effective reintroduction strategy can be implemented (Khan and

Murn 2011; Prakash *et al.* 2012). Although further pilot vulture release projects could be justified, the use of limited conservation funds for reducing severe threats such as mass poisonings is likely to be the most effective conservation strategy in the short term (Krueger *et al.* 2015).

The use of feeding sites to supply an uncontaminated source of supplementary carrion has been proposed as a useful vulture conservation tool, and many vulture "restaurants" now exist in South Africa (Piper *et al.* 1999; Kane *et al.* 2014). A full assessment of the use of supplementary feeding sites by the tracked vultures was beyond the scope of this study, although the analyses conducted in Chapter 3 indicated that the wild vultures did not make regular use of the two available sites in north-central Namibia. However, it has been demonstrated that providing supplementary carrion in fixed locations can significantly alter the movement patterns and foraging ecology of vultures (Deygout *et al.* 2009; Monsarrat *et al.* 2013; Phipps *et al.* 2013a) and other scavenging species (Orros and Fellowes 2015; Yarnell *et al.* 2015). Considering the potentially detrimental effects that artificially altering the spatial and temporal distribution of carrion can have on wider ecosystem dynamics, the use of supplementary feeding sites for vulture conservation in southern Africa should be fully assessed (Cortes-Avizanda *et al.* 2010; Yarnell *et al.* 2015).

In summary, the findings of this study demonstrate that Cape vultures are likely to regularly encounter multiple threats when foraging, and that a range of conservation measures must be co-ordinated across southern Africa to ensure the persistence of Cape vulture populations in the future. In order to inform the planning and implementation of effective conservation strategies in key areas, further research activities are proposed in the following section.

5.3. Limitations and further research

This study presents a first insight into the patterns of space use by Cape vultures and although the results of this study are novel and have already been used to inform conservation measures (Phipps *et al.* 2010), a number of limitations should be considered when interpreting the findings.

Firstly, the sample size of vultures that were tracked during this study (total = 19 Cape vultures) was relatively small due to financial constraints when tracking technology was more expensive and less advanced than it is today. Although basic comparisons between the ranging patterns of adult and immature, and wild and released vultures were made, the limited sample size restricted any in-depth analysis. Moreover, although the gregarious nature of Cape vultures means that the tracking data from one individual probably represent the movements of other vultures (Jackson *et al.* 2008b), high levels of variation in space use patterns between individuals are likely which means that population-level inferences must be treated with some caution in tracking studies with relatively small sample sizes (Lindberg and Walker 2007; Thomas *et al.* 2011). Even so, limited financial budgets are common in threatened species research and the data provided by even a small number of tracked individuals often provides valuable information to inform conservation decisions and stimulate further research (Cooke 2008). The initial findings of this study, and others previously (Bamford *et al.* 2007; Phipps *et al.* 2013a), have stimulated several recent vulture tracking projects in southern Africa which will increase the overall sample size of tracked individuals and allow firmer conclusions to be made in the future.

A further limitation was the lack of ability to definitively confirm the activity of the vultures when they were recorded as stationary due to the long distances travelled between consecutive stationary GPS locations. Although this was initially carried out for a number of ground locations recorded over a short period for the vultures tracked in Namibia, which proved useful in identifying food sources and effects of vegetation characteristics on foraging behaviour (Schultz 2007), it was not possible to continuously follow the vultures to assess their activity, despite initial attempts to do so. It was therefore not possible to identify the exact sources of carrion that the vultures were feeding upon, which was made more difficult by the lack of available accurate data relating to stocking rates of wild and domestic ungulates in southern Africa (Balme *et al.* 2014). It was also not possible to assess inter- and intraspecific competition (or facilitation) that the vultures faced when foraging, and consequently their lack of use of protected areas containing large mammalian predators remains poorly understood and requires further study. However, field visits in Namibia did prove useful for identifying roost sites on private farmland and on the former breeding cliffs of the Waterberg Plateau Park, and visits to frequently used transmission lines confirmed the location of vulture roost sites in South Africa (Fig. 1.4). Despite visiting the breeding cliffs of the Kransberg colony in South Africa, where some of the adult vultures frequently roosted, no breeding attempts could be confirmed by myself or the colony monitor (Pat Benson, personal communication), which constrained any comparisons between breeding and non-breeding individuals. Similarly, although some breeding attempts by the Cape vultures in Namibia were observed initially, the monitoring was not continuous throughout the tracking periods. Despite these limitations, the combination of the tracking data and digital spatial datasets relating to environmental characteristics have allowed the identification of several key factors that influenced the movement patterns of the tracked vultures (Cooke 2008).

The limitations and benefits of ecological niche modelling (ENM) methods have been widely reviewed and are deemed useful for assessing patterns of space use and to provide first approximations of the potential impacts of climate change on species distributions (Pearson and Dawson 2003; Guisan *et al.* 2013; Porfirio *et al.* 2014;

Guillera-Arroita *et al.* 2015). However, although the results from this study provide a useful first description of the spatial niche occupied by the tracked vultures, the limited sample size of individuals and the caveats associated with ENM techniques mean that the range changes predicted under climate change in Chapter 4 should not be regarded as definitive. It is still unclear how Cape vultures will respond to climate change, and it is possible that they will be relatively resilient, as predicted for other large species that are able to forage and disperse over large distances (Simmons *et al.* 2004; Dodge *et al.* 2014). Even so, given the severity of existing threats in the region it is likely that any negative impacts of climate change will have an additive effect on population declines, and so should be investigated further (Krueger *et al.* 2015).

Despite these limitations the findings from this study provide a firm basis for further investigation of the ranging patterns and foraging ecology of Cape vultures, and the relative importance of different threats within their range. A summary of the recommendations for future research is as follows:

- Additional tracking studies on larger samples of Cape vultures caught from the wild throughout their range should be carried out to allow population level inferences to be confidently made and to further assess differences between breeding and non-breeding individuals.

- The collation and analysis of existing tracking datasets from past and current studies on Cape vultures and other vulture species should be performed to identify key areas for vulture conservation in the region (e.g. south-east Namibia).
- Ground surveys for evidence of fatal interactions beneath regularly used lengths of transmission line would allow a more comprehensive assessment of collision risks and mortality rates. Similar studies should also investigate the use of smaller distribution lines for vulture roosting and perching activity, and assess the associated risks.
- Further research is required to investigate why vultures rarely forage in officially protected areas in South Africa despite regularly foraging in surrounding unprotected farmland (Phipps *et al.* 2013a). It would be useful to compare the availability of carrion inside and outside protected areas, and the levels of inter- and intraspecific competition that vultures face at carcasses in both scenarios.
- The role of supplementary feeding sites for vulture conservation and their potential impacts on the wider ecosystem in southern Africa should be fully assessed (Yarnell *et al.* 2015)
- Additional research is required to confirm whether bush encroachment is likely to lead to a reduction in suitable

foraging habitat for Cape vultures and other species, particularly in Namibia where the problem is widespread.

- Increased attention should be given to the potential impacts of climate change on Cape vulture distribution patterns. Studies should not only investigate the direct effects of changing climate on the vultures themselves (Chaudhry 2007), but also potential changes to foraging habitat and carrion availability through climate-mediated ungulate mortality rates.
- Continued monitoring of the status and demography of the population throughout their range will be essential to detect population declines and evaluate the success of conservation measures. It will be particularly important to detect declines of breeding populations in the northern colonies which might be more at risk from climate change.

Overall, in order to identify and implement vulture conservation priorities in southern Africa, continued research is required to investigate the relative impacts and interactions of multiple mortality factors on current and future vulture population dynamics.

5.4. Conclusions

This study has provided a valuable first insight into patterns of space use by Cape vultures in their core breeding range in northern South Africa and in northern Namibia where a small, isolated population no longer breeds. The findings have demonstrated the ability of GPS tracking data to identify important areas for vulture conservation and the results have been used to identify potentially high risk areas for fatal interactions with power lines. The foraging patterns of the vultures tracked in this study show the importance of unprotected farmland and private conservancies for vultures in southern Africa and confirm that conservation measures must be implemented beyond protected areas boundaries. The wide ranging movements recorded for the immature individuals demonstrate that conservation measures must be co-ordinated across international borders, far beyond the core breeding range of the species. In addition to confirming that Cape vultures are likely to be regularly exposed to recognised threats such as poisoning and collisions with power lines, the findings of this study indicate that climate change might also play a role in their decline.

This research is timely in an era when the widespread decline of vulture populations is widely recognised as one of the most serious issues facing avian conservation, particularly in Africa. I hope that the findings from this thesis will stimulate further research to inform effective conservation strategies to allow future generations to benefit from the impressive sight of vultures circling overhead and the valuable ecosystem services that they provide.

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Appendices

Appendix 1. Photograph of walk-in cage trap

Figure A1. Walk-in cage trap at Mankwe Wildlife Reserve vulture research and capture site, North West Province, South Africa. Once vultures had entered through the door and started feeding on the bait the curtain was closed by pulling an attached cable from an observation hide approximately 30 metres to the left of the photograph. The branches are positioned to prevent the resident white rhinos from damaging the trap. The trap was baited with livestock or wild ungulate carcasses. Marabou storks and vultures can be seen behind and to the left of the trap.

Appendix 2. Photograph of GPS tracking unit

Figure A2. Immature Cape vulture with patagial identification tags and Hawk105 GPS-GSM tracking unit (Africa Wildlife Tracking Ltd., Pretoria, South Africa) attached by Teflon backpack harness with integrated weak point for eventual release.

Appendix 3. Published version of Chapter 2

Phipps WL, Wolter K, Michael MD, MacTavish LM, Yarnell RW (2013). Do Power Lines and Protected Areas Present a Catch-22 Situation for Cape Vultures (*Gyps coprotheres*)? PLoS ONE 8(10): e76794. doi:10.1371/journal.pone.0076794

Do Power Lines and Protected Areas Present a Catch-22 Situation for Cape Vultures (*Gyps coprotheres*)?

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Abstract

Cape vulture *Gyps coprotheres* populations have declined across their range due to multiple anthropogenic threats. Their susceptibility to fatal collisions with the expanding power line network and the prevalence of carcasses contaminated with illegal poisons and other threats outside protected areas are thought to be the primary drivers of declines in southern Africa. We used GPS-GSM units to track the movements and delineate the home ranges of five adult (mean ±SD minimum convex polygon area = 121,655±90,845 km^2) and four immature (mean ±SD minimum convex polygon area = 492,300±259,427 km^2) Cape vultures to investigate the influence of power lines and their use of protected areas. The vultures travelled more than 1,000 km from the capture site and collectively entered five different countries in southern Africa. Their movement patterns and core foraging ranges were closely associated with the spatial distribution of transmission power lines and we present evidence that the construction of power lines has allowed the species to extend its range to areas previously devoid of suitable perches. The distribution of locations of known Cape vulture mortalities caused by interactions with power lines corresponded to the core ranges of the tracked vultures. Although some of the vultures regularly roosted at breeding colonies located inside protected areas the majority of foraging activity took place on unprotected farmland. Their ability to travel vast distances very quickly and the high proportion of time they spend in the vicinity of power lines and outside protected areas make Cape vultures especially vulnerable to negative interactions with the expanding power line network and the full range of threats across the region. Co-ordinated cross-border conservation strategies beyond the protected area network will therefore be necessary to ensure the future survival of threatened vultures in Africa.

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Introduction

Vultures in the *Gyps* genus are obligate scavengers of vertebrate carcasses and provide vital ecosystem services by recycling carrion, thereby limiting the development and spread of disease and maintaining energy transfer through food webs [1,2]. Their longevity, delayed maturity and low reproductive rates mean that even minimal reductions in adult survival rates or the proportion of immatures reaching breeding age could result in population declines [3,4]. As a consequence all eight species of *Gyps* vultures found globally are declining [5] because of multiple threats such as reduced food availability [6,7], illegal poisoning [8], and collisions with wind turbines [3,9] and power lines [10]. The recent collapse of *Gyps* vulture populations in Asia caused by accidental contamination of their food supply [11] has resulted in major changes to scavenger community dynamics and a wide range of human health and socio-economic impacts in the region [12]. The urgency to prevent similar ecological catastrophes from occurring elsewhere is widely acknowledged [5,11].

African vulture populations have also declined considerably, with land use change and illegal poisoning identified as widespread mortality factors [13–15]. For example, a 52% decline in *Gyps* vulture numbers in the Masai Mara region of Kenya over a 30 year period was largely attributed to secondary poisoning after they fed on carcasses illegally laced with poisons to kill livestock predators [15]. Electrocutions and collisions with the expanding power line network are also frequent causes of vulture mortality and injury in Africa [16,17]. *Gyps* vultures are especially prone to fatal interactions with power lines in southern Africa due to their frequent use of power line towers for perching and roosting [4,18]. For example, in the Eastern Cape Province of South Africa it is conservatively estimated that fatal interactions with power lines kill *ca.* 4% of the local population of Cape vultures *G. coprotheres* per year, with the possibility of rapid local extinctions in some high risk areas [16]. Despite this vultures might have derived some benefits from the presence of power lines. For example, African white-backed vultures *G. africanus* nest on pylons [19] and it has even been suggested that some areas previously devoid of suitable perches might become newly accessible as vultures utilise power line towers as roost sites and vantage points [4]. Under the current rate of expansion of the power line network it is important to investigate the relationship between power lines and vultures in southern Africa, particularly in a spatial context to allow mitigation measures to be implemented in key areas [10,16].

Vultures and other raptors in Africa are thought to be increasingly restricted to protected areas where they are less exposed to multiple threats that persist in the wider landscape [13–15]. For example, in several African countries increasing prevalence of anthropogenic mortality factors such as illegal poisoning have led to higher vulture mortality rates and population declines outside compared to inside protected areas [14,15,20]. While protected areas often provide safe breeding and roosting sites for vultures [15,21–23], they frequently forage far beyond protected area boundaries, leaving them exposed to numerous threats [20,24]. The role and effectiveness of protected areas for vulture ecology and conservation remains unclear, therefore, and merits further investigation.

In this study we use Global Positioning System (GPS) telemetry techniques to provide a first insight into the size and extent of Cape vulture home ranges in relation to the network of power lines and protected areas in southern Africa. The Cape vulture is endemic to southern Africa and is listed as Vulnerable on the IUCN Red List due to declines across its range [25]. It is a gregarious cliff-nesting species with a global population estimated at 8,000–10,000 individuals (*ca.* 4,000 breeding pairs) [25]. The largest remaining breeding colonies are located in the north-eastern provinces of South Africa [4,23,25,26], where increasing urbanisation and land use change has caused habitat loss, food shortages and an increasing incidence of negative vulture-power line interactions [17]. We hypothesize that frequent use of transmission line pylons as perching and roosting sites by Cape vultures will influence the extent of their home ranges and the location of their core foraging areas. We also assess the ability of GPS tracking data to identify potentially high risk areas of vulture-power line interactions in order to inform future mitigation strategies. We predict that Cape vultures regularly roost and forage outside protected areas, but expect adults to traverse smaller home ranges in closer proximity to protected breeding colonies compared to the less restricted movements of immature individuals [27].

Methods

Vulture Captures and GPS Tracking

A walk-in cage trap (6×3×3 m) baited with ungulate carcasses was used to catch vultures at a supplementary feeding site for vultures at Mankwe Wildlife Reserve (MWR; 25°13'S, 27 °18'E) in the North West Province of South Africa (Fig. 1) [24]. Ten Cape vultures were caught between November 2009 and June 2010 during seven separate captures. Owing to the difficulty in ageing *Gyps* vultures individuals could only be identified as adults (>5 years), immatures (2–5 years) or juveniles (first year) based on characteristic plumage traits and eye colouration [28]. For statistical analyses juveniles ($n = 1$) were pooled with immatures. The genders of vultures were not confirmed by molecular analysis as blood or feather samples were not taken from each individual and *Gyps* vultures exhibit no obvious sexual dimorphism in plumage or body characteristics [29]. Furthermore, Bosé *et al.* [29] found no difference in male or female life history or movement patterns in a closely related species and so this was not investigated during this study. Teflon® ribbon backpack-style harnesses were used to secure Hawk105 GPS-GSM (Global System for Mobile communications) tracking units (Africa Wildlife Tracking Ltd., Pretoria, South Africa; www.awt.co.za) onto the back of each vulture [24,30]. Each unit recorded GPS locations (~10 m accuracy, verified by a positional dilution of precision (PDOP) measure of accuracy [31]), altitude above sea level, speed, direction of travel, date, time and temperature three times per day at 07:00, 11:00 and 15:00 Central Africa Time (CAT). One additional data point was recorded per day at 13:00 CAT for three adult vultures (AG314, AG349 and AG355) to account for foraging trips from cliff roosts between the 11:00 and 15:00 readings. The units were expected to record and transmit data for approximately one year. Patagial tags with unique numeric codes were attached to both wings of each vulture to allow identification of individuals following release.

Ethics Statement

The procedures were approved by the ethical review committee of the School of Animal, Rural and Environmental Science, Nottingham Trent University. Permits for the capture and handling of vultures and the fitting of tracking units were granted by the Department of Agriculture, Conservation, Environment and Rural Development, North West Provincial Government, Republic of South Africa (Permit: 000085 NW-09). All procedures were carried out by South African Bird Ringing Unit permit holders (KW and WLP). All necessary measures were taken to minimise any potential discomfort to the birds. Each tracking unit weighed 170g which is *c.* 1.8% of the mean mass of an adult Cape vulture [4], and less than the 3% recommended for flying birds. A weak point was included on each harness to allow it to eventually fall off, releasing the tracking unit from the bird.

Data Analysis

GPS locations were projected to the Universal Transverse Mercator (UTM) coordinate system for all spatial analyses. Stationary and moving GPS locations were defined as all those recorded with a speed $<$ or $\geq$ 10 $\text{km}\cdot\text{h}^{-1}$, respectively. Distances travelled between consecutive GPS locations were calculated for each vulture. Two methods were used to delineate the home ranges of each vulture.

Firstly, Minimum Convex Polygons (MCPs) were created using the Home Range Tools extension [32] for ArcGIS® using all recorded GPS locations to allow comparisons to be made with other *Gyps* vulture tracking studies [27,33]. Incremental area analysis was performed for each vulture by creating MCPs using sequentially added consecutive GPS locations until all locations were used to create an MCP for the total tracking period. Home range area curves were then plotted to identify whether the home range areas reached asymptotes by the end of the tracking period [33]. Secondly, fixed kernel density estimation (KDE) was carried out using the Geospatial Modelling Environment (GME) program [34] to delineate 99% and 50% contours to represent the overall and core foraging ranges, respectively [35]. The plug-in method of bandwidth selection was used following preliminary analyses that indicated that the least-squares cross-validation (LSCV) method failed to select a bandwidth due to numerous identical GPS locations and use of the reference bandwidth resulted in over-smoothed home range boundaries [36]. A 1 km^2 cell size was used for KDE calculations. The 99% KDE contours were used instead of the 95% contours to represent the overall home ranges as the latter generally produced undersmoothed and more fragmented outer contours. The size of the 99% KDE contours and MCPs of the adult and immature vultures were compared using Mann-Whitney tests. The spatial extent of the home ranges were compared to the IUCN Cape vulture species distribution map [37]

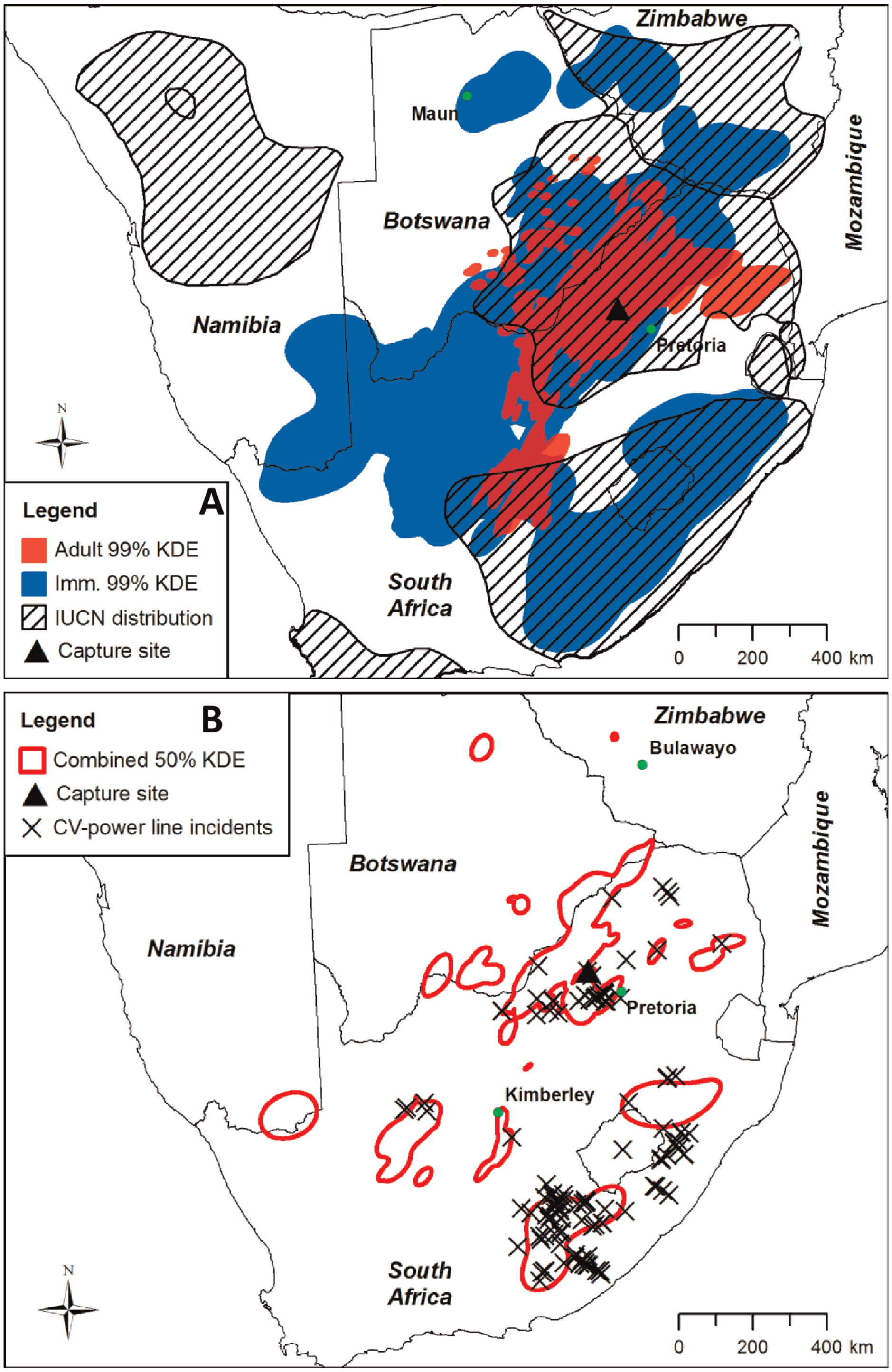

Figure 1. Home ranges of nine Cape vultures with species distribution map and Cape vulture-power line incidents. (A) Shaded red and dark blue polygons represent the combined 99% kernel density estimated (KDE) contours of all adult and immature vultures, respectively. The diagonal line shaded polygons represent the extent of the Cape vulture species distribution according to BirdLife International [37]. The capture site is indicated by a black triangle. (B) The hollow red polygons represent the combined 50% KDE contours of all nine vultures. Black crosses show locations of Cape vulture-power line incidents recorded in the Central Incident Register of the EWT-Eskom strategic partnership [39].
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and the proportion of GPS locations recorded within the IUCN distribution were compared between adults and immatures using Mann-Whitney tests to determine whether either age class travelled beyond the known species distribution more or less frequently than the other.

The use of transmission power lines and associated stuctures for perching and roosting by vultures was estimated by calculating the proportion of stationary (i.e. $< 10\ \mathrm{km{\cdot}h^{-1}}$) GPS locations recorded within 50 m of transmission power lines within each vulture's home range. Analyses were performed in ArcMap v9.3

[38] and spatial data for transmission power lines were sourced from Eskom (South Africa), the Africa Infrastructure Knowledge Program (Botswana and Zimbabwe; http://www.infrastructureafrica.org) and the Environmental Information Service (Namibia; http://www.the-eis.com). We assumed that if a vulture was recorded as being stationary within 50 m of a transmission line or pylon it was likely to be using it as a roost or perch site. To test whether vulture perching or roosting activity was more closely associated with transmission line corridors than other features in the wider landscape the density of stationary GPS locations within a 50 m buffer each side of the transmission line network was compared with the density of stationary GPS locations in the overall home range (i.e. 99% KDE contour) for each vulture. The density of stationary GPS locations within the 50 m transmission line buffer inside each vulture's core area (i.e. 50% KDE contour) was also compared to the density inside the total core area to identify whether stationary locations were concentrated in the vicinity of power lines inside core areas. Wilcoxon signed-rank tests were used to identify significant differences in GPS location densities at the different scales with each vulture considered as a sampling unit. The proportion of stationary GPS locations recorded within 50 m of transmission lines was compared between adult and immature vultures using a Mann-Whitney test. To assess the potential for GPS tracking data to identify possible high risk areas of vulture-power line interactions the proportion of locations of Cape vulture-power line incidents with known GPS co-ordinates (437 mortalities at 126 locations) recorded in the Central Incident Register (CIR) of the Endangered Wildlife Trust (EWT) and Eskom (the main electricity distributor in the country) between May 1996 and July 2012 [16,18,39] that overlapped with the vultures' core foraging ranges was calculated.

To assess vulture use of protected areas a polygon shapefile was created comprising all IUCN category I-VI protected areas and 'national other areas' (i.e. protected areas uncategorized by IUCN) polygons from the 2010 and 2003 World Database on Protected Areas (WDPA) [40,41]. Each vulture's use (U_i) of protected areas was then estimated as the proportion of stationary (< 10 km·h^{-1}) GPS locations recorded inside the protected area polygons. The availability of protected areas (A_i) to each vulture was defined as the proportion of the 99% KDE contour covered by the protected areas polygons. Wilcoxon signed-rank tests were used to identify differences between U_i and A_i with each vulture considered as a sampling unit. Ivlev's electivity index (E_i) was then calculated as a measure of whether protected areas were visited more frequently than expected based on their availability at the overall home range scale: $E_i = (U_i - A_i)/(U_i + A_i)$ [42]. A value of zero indicated that use of protected areas was proportional to their availability, while positive (maximum = +1) and negative (minimum = -1) values indicated greater and lesser use of protected areas than expected, respectively. Use of protected areas was also assessed in the same way at the core range scale by defining U_i as the proportion of the 50% KDE contour covered by the protected areas. Adult and immature vulture use (U_i) of protected areas were compared using a Mann-Whitney test. The values reported in the Results section correspond to mean ± standard deviation unless stated otherwise.

Results

Ten Cape vultures, five adults, four immatures and one juvenile (hereafter considered as an immature) were captured and tracked using GPS-GSM tracking units for 300±178 days from November 2009 to August 2011 (Table 1). The average number of GPS locations recorded per individual was 1,052±578 with 78.35±9.47% recorded as stationary (< 10 km·h^{-1}) (Table 1). The mean and maximum speed of all moving (≥ 10 km·h^{-1}) locations ($n = 2319$) was 54.54±16.93 km·h^{-1} and 115 km·h^{-1}, respectively. Mean accuracy of all GPS locations on the PDOP scale was high at 2.17±1.97 ($n = 9468$). Tracking units stopped transmitting data prematurely (i.e. < 1 year) for five vultures for unknown reasons. The tracking unit on an immature vulture (AG351) stopped transmitting after only 12 days and the data were excluded from the analyses. Another immature vulture (AG352) travelled north through eastern Zimbabwe before heading west to an area 40 km east of Maun, Botswana, where its tracking unit ceased transmitting data. An adult vulture (AG382) was tracked for a month to an area west of the Kruger National Park *ca.* 400 km from the capture site, where its remains were found and the tracking unit recovered. The cause of death was unconfirmed. Tracking units on two adults functioned properly for more than 8 months before data transmission ceased.

Size and Extent of Home Ranges

The nine vultures occupied large home ranges (mean 99% KDE = 223,132±227,256 km^2; mean 50% KDE contour = 25,851±28,473 km^2; Table 1) and long distance cross-border movements were not unusual with a total of five countries (Namibia, Botswana, Zimbabwe, Lesotho and South Africa) entered by different vultures (Fig. 1A). The mean maximum distance recorded between two consecutive GPS locations for all vultures was 178±46 km (maximum = 254 km; Table 1). Some individuals were recorded more than 1000 km straight-line distance from the capture site. Incremental area analysis indicated that the home range areas of most of the vultures had become stable by the end of their tracking periods (Fig. S1). The most intensively used areas, as indicated by the 50% KDE contours (Fig 1B), were located in the north-western Limpopo Province and north-eastern North West Provinces of South Africa, extending north into southern Botswana either side of the Limpopo River, and south to the Magaliesberg Mountains and Mafikeng district in North West Province, South Africa (Fig. 2). The 99% KDE contours (median = 353,717 km^2) and the MCPs (median = 413,722 km^2) of the four immature vultures were significantly larger than the 99% KDE contours (median = 69,254 km^2; $Z = -2.45$, $p = 0.014$) and MCPs (median = 92,092 km^2; $Z = -2.45$, $p = 0.014$) of the five adult vultures (Table 1, Fig. S2).

The combined 99% KDE contours for all individuals covered 1,052,467 km^2, of which 36% was located outside the extent of the IUCN distribution for the species, largely due to the movements of several individuals into the Northern Cape Province of South Africa and southern Namibia (Fig. 1A). A significantly higher proportion of GPS locations were recorded inside the extent of the IUCN Cape vulture distribution for adults (median = 98.41%) compared to immatures (median = 67.53%; $Z = -2.21$, $p = 0.027$; Fig. 1A), indicating that immatures travelled beyond the known distribution for the species more frequently than adults.

Utilisation of Power Lines

The vultures were frequently recorded in the vicinity of transmission power lines. The 50 m transmission line buffer area covered only 0.52±0.14% of the 99% KDE contour areas of all nine vultures but contained 20.60±12.74% of the stationary GPS locations recorded by each tracking unit (Table S1). There was no significant difference in the proportion of stationary locations recorded within 50 m of transmission lines for adults (median = 19.17%) compared to immatures (median = 14.87%; $Z = -0.490$, $p = 0.730$). The density of stationary GPS locations within the 50 m transmission line buffer in the 99% KDE contours (median

Table 1. Home range and distance estimates for nine Cape vultures tracked by GPS-GSM units.

				Home range estimates (km^2)			Distance estimates (km)		
Vulture ID	**Age**	**Tracking period (days)**	**GPS locations**	**MCP**	**99% KDE**	**50% KDE**	**Mean (± SD) distance between consecutive locations**	**Maximum distance between consecutive locations**	**Total distance travelled/tracking days**
AG314	Adult	479	1,636 (1,065)	165,337	69,254	3,056	21.34±26.49	212	73
AG329	Adult	267	793 (746)	92,092	78,847	11,113	5.17±15.58	156	15
AG349	Adult	234	752 (513)	56,152	52,385	5,998	20.07±28.63	185	64
AG355	Adult	490	1,860 (1,341)	258,294	149,687	10,071	16.70±25.35	174	63
AG382	Adult	31	84 (72)	36,401	53,589	6,691	9.35±18.22	84	25
Mean		300	1,025	121,655	80,752	7,385	14.53	162	48
SD		191	722	90,845	40,095	3,250	7.00	48	26
AG313	Imm.	315	922 (725)	273,946	161,311	10,722	13.32±25.96	254	39
AG352	Imm.	207	612 (538)	392,856	312,715	44,429	9.53±20.78	159	28
AG353	Juv.	558	1,654 (1,251)	434,588	392,719	59,927	15.25±23.71	184	45
AG383	Imm.	409	1,155 (898)	867,811	737,684	80,654	13.24±21.26	192	37
Mean		372	1,086	492,300	401,107	48,933	12.83	197	37
SD		149	439	259,427	244,042	29,481	2.39	40	7

Minimum convex polygons (MCP) including all recorded GPS locations and 99% contours from kernel density estimation (KDE) represent overall foraging ranges. 50% KDE contours represent core foraging ranges. Mean (± SD) and maximum distances between consecutive GPS locations, and the total distance travelled divided by the number of tracking days are shown. The age (adult (>5 years), immature (2–5 years) or juvenile (first year)) of each vulture, the tracking period and number of GPS locations (number of stationary ($<10\ km \cdot h^{-1}$) locations are given in parentheses) recorded are also shown.

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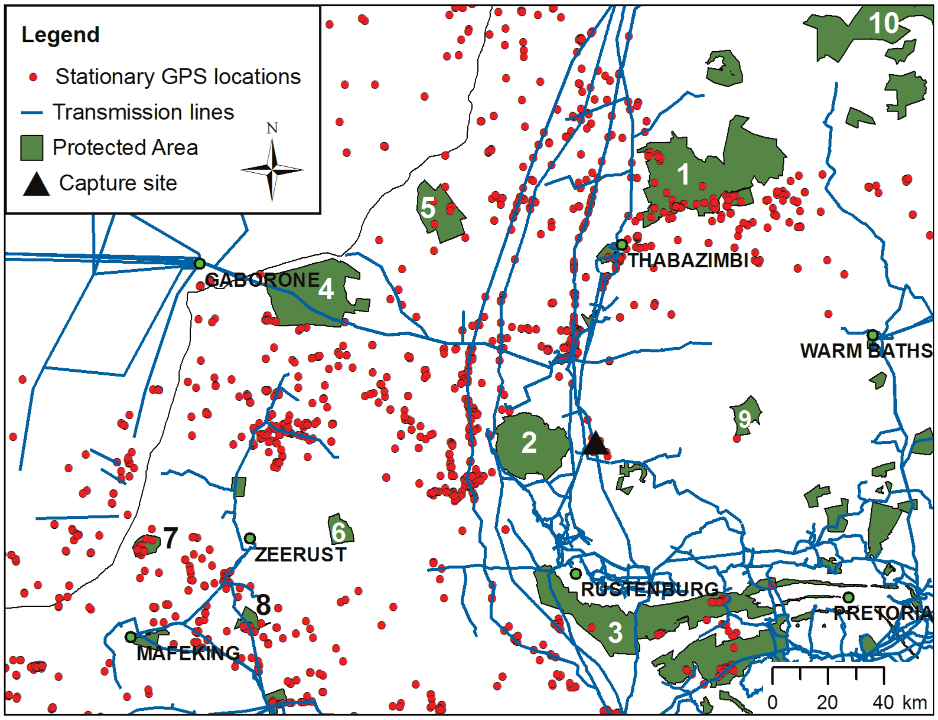

Figure 2. Stationary GPS locations in relation to protected areas and transmission power lines in the northern provinces of South Africa. Stationary GPS locations (red circles) from nine Cape vultures tracked by GPS-GSM tracking units are shown with transmission power lines (blue lines) and protected areas (green ploygons [40,41]). 1 = Marakele NP and Welgevonden NR; 2 = Pilanesberg NP; 3 = Magaliesberg NR; 4 = Madikwe GR; 5 = Atherstone NR; 6 = Marico-Bosveld NR; 7 = Botsalano GR; 8 = Oog van Malmanie GR; 9 = Borakalalo GR; 10 = Lapalala, Moepel *et al.* reserves. The capture site is indicated by a black triangle.
doi:10.1371/journal.pone.0076794.g002

= 0.267 locations·km^{-2}) was significantly higher than the density in the overall 99% KDE contours (median = 0.005 locations·km^{-2}; $Z=-2.67$, $p=0.008$; Table S1). The 50 m transmission line buffer covered significantly more of the 50% KDE contours (median = 0.80%) than the 99% KDE contours (median = 0.59%; $Z=-2.37$, $p=0.018$), and the density of stationary GPS locations within the 50 m transmission line buffer in the 50% KDE contours (median = 0.827 locations·km^{-2}) was significantly higher than in the overall 50% KDE contours (median = 0.046 locations km^{-2}; $Z=-2.67$, $p=0.008$). This indicates that the vultures were more frequently in close proximity to transmission lines when stationary compared to the wider landscape, particularly in their core foraging areas. The stationary locations within the 50 m buffer were generally clustered along certain sections of transmission line that were repeatedly visited by several different individuals (Fig. 2 and 3). Out of 126 known locations of Cape vulture-power line incidents recorded in the Eskom-EWT CIR, 120 (95%) were inside the combined 99% KDE contours of all vultures, of which 67 (56%) were recorded inside the combined 50% KDE contours (Fig. 1B).

Utilisation of Protected Areas

All vultures spent the majority of their tracking periods outside protected areas but several regularly roosted on cliffs inside national parks or nature reserves. The difference in coverage of protected areas (Table 2) was not significantly different between the 99% (median = 4.53%) and 50% KDE contours (median = 9.72%; $Z=-1.36$, $p=0.173$). Although the proportion of stationary GPS locations recorded inside protected areas (median = 27.31%) was higher than the proportion they covered of 99% KDE contours (median = 4.53%), the difference was not significant ($Z=-1.84$, $p=0.066$). Ivlev's electivity index values indicated, however, that six vultures used protected areas more than expected based on their availability in their overall home ranges (Table 2).

Of the 1,496 stationary GPS locations recorded inside protected areas (21% of all stationary locations), 94% were in South African reserves, of which 68% were recorded in Marakele National Park (NP) in the Limpopo Province (24°24'S, 27°35'E), and 11% were recorded in the Magaliesberg Nature Reserve (NR) (25°44'S, 27°45'E), both of which encompass large Cape vulture breeding colonies (Fig. 2) [23,26]. Marakele NP was visited by a total of seven vultures but the majority (96%) of stationary locations recorded inside the park were from three adult vultures (AG314, AG349, AG355) that frequently roosted on the breeding cliffs. 93% of stationary locations recorded inside Marakele NP were situated on the Kransberg nesting cliffs. Breeding attempts by those vultures could not be confirmed during colony observations, however, and so the influence of breeding status could not be investigated. Similarly, all stationary locations recorded in the Magaliesberg NR were situated on known breeding or roosting cliffs, the majority (87%) of which were from one immature vulture (AG313). Beyond the breeding colonies 15 other protected areas were visited in South Africa (Fig. 2), although only six contained more than 10 stationary GPS locations. Outside South Africa one immature vulture (AG383) briefly entered two protected areas in south-west Zimbabwe, another (AG353) visited the Central Kalahari GR in Botswana, while a third (AG352) entered several protected areas in eastern Zimbabwe and central Botswana. Despite the more frequent use of roost sites within protected areas by the adult vultures there was no significant difference in the

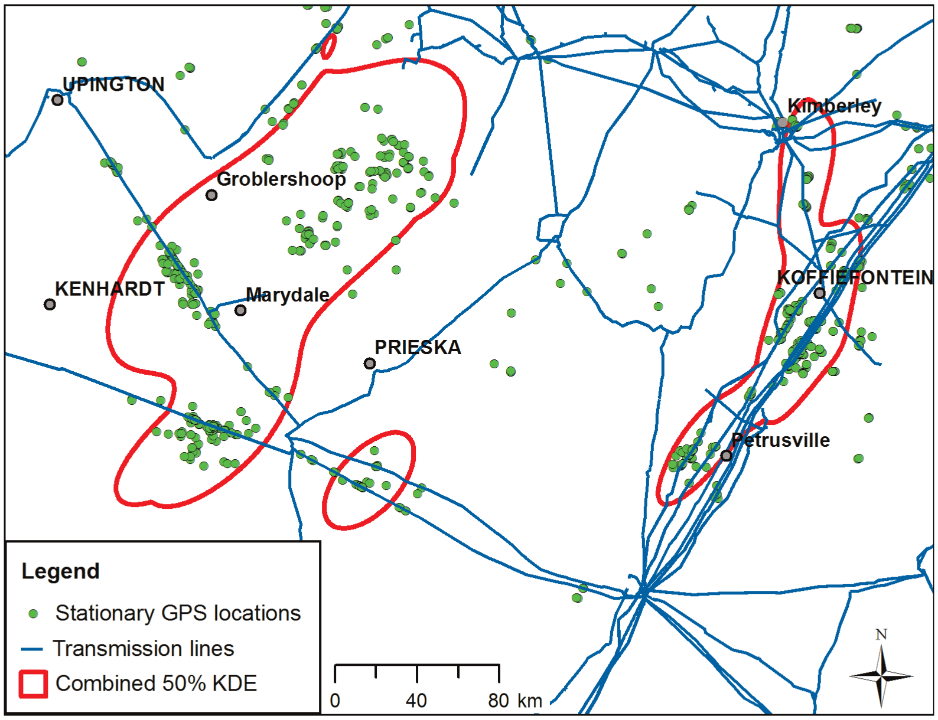

Figure 3. Stationary GPS locations and core areas in relation to transmission power lines in the Northern Cape Province, South Africa. Stationary GPS locations (green circles) and merged 50% kernel density estimated (KDE) contours (hollow red polygons) from nine Cape vultures are shown in relation to transmission power lines (blue lines).
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proportion of stationary locations recorded within protected areas for adults (median = 36.45%) compared to immatures (median = 11.71%; $Z=-1.470$, $p=0.190$).

Discussion

This study uses GPS tracking methods to provide the first description of the relationship between the power line network and ranging behaviour of Cape vultures in southern Africa, together with their use of protected areas. The vultures, particularly immature individuals, traversed large home ranges that closely followed the spatial distribution of transmission power lines. The core foraging areas overlapped with known locations of negative vulture-power line interactions. All vultures spent the majority of their tracking periods outside protected areas, although some regularly used roost sites at breeding colonies within national parks or nature reserves.

The home ranges recorded during this study are among the largest for any vulture species. Although the five adult vultures traversed larger home ranges (mean MCP = 121,655±90,845 km^2) than five adult Cape vultures tracked in Namibia (mean MCP = 21,320 km^2 [27]), such comparisons should be considered with caution because breeding attempts by the vultures from this study could not be confirmed during colony surveys. If they were non-breeding birds their foraging movements would not have been restricted by the need to return to a nest site, allowing them to range further than breeding individuals from the Namibian study [1,27]. The four immature vultures occupied similarly extensive home ranges (mean MCP = 492,300 ±259,427 km^2) to two immature vultures from the Namibian study (mean MCP = 482,276 km^2) [27]), but larger than those of six immature African white-backed vultures tracked from South Africa (mean MCP = 269,103±197,187 km^2 [24]). Compared to *Gyps* species outside Africa the home ranges recorded here exceeded those of Eurasian griffon vultures (*G. fulvus*) tracked in France (combined MCP = *c.* 1,000 km^2 (n = 28) [43]) and Spain (median MCP = 7,419 km^2 (n = 8) [44]), and Asian white-backed vultures (*G. bengalensis*) in Pakistan (mean MCP = 24,155 km^2 (n = 6) [45]). A recent study in Israel reported that while the majority of 43 tagged *G. fulvus* did not travel more than 200 km from the centre of their home range, a few individuals undertook infrequent "long-range forays" of more than 1,700 km from their home range centres [46]. Such comparisons must be considered with caution, however, as factors that determine home range characteristics such as food availability, habitat quality, topography and levels of competition are likely to vary geographically and between species [43], and could not be fully investigated here due to limited data availability. Nevertheless, the similar long-distance cross-border movements and large distances travelled on a daily basis during this study confirm that *Gyps* vultures and Cape vultures in particular, are among the widest ranging bird species probably due to their reliance on a sparsely and unpredictably distributed food source [1,47].

The high densities of stationary GPS locations recorded in close proximity to transmission lines provide strong evidence that the movement patterns of Cape vultures are closely linked to the spatial extent of the transmission power line network in southern Africa and suggest that they prefer to perch, roost and forage in the vicinity of transmission line towers rather than moving randomly throughout their home ranges as might be expected from a typical central-place forager [43]. For instance, although the spatial extent of the core ranges (Fig. 1B) corresponded with areas known to be important foraging grounds for *Gyps* vultures in southern Africa [23,24,26,48], the core area used by three immature vultures in the Marydale region of the Northern Cape

Table 2. Availability and use of protected areas by nine Cape vultures at the overall and core home range scales.

Vulture ID	PA coverage in 99% KDE (%)	PA coverage in 50% KDE (%)	Ivlev's electivity index at core range scale	Proportion of stationary locations inside PAs (%)	Ivlev's electivity index at home range scale
AG314	3.47	18.43	0.68	38.78	0.84
AG329	3.84	3.20	−0.09	3.49	−0.05
AG349	5.55	13.71	0.42	36.45	0.74
AG355	4.53	9.72	0.36	32.14	0.75
AG382	16.89	32.47	0.32	40.28	0.41
AG313	3.37	11.74	0.55	27.31	0.78
AG352	19.55	8.32	−0.40	16.54	−0.08
AG353	3.97	5.43	0.16	6.87	0.27
AG383	6.02	3.21	−0.30	4.12	−0.19
Mean	7.47	11.80	0.19	22.89	0.38
SD	6.20	9.21	0.38	15.29	0.41

The proportion of each vulture's 99% kernel density estimated (KDE) contour occupied by protected areas (PAs) defined their availability (A_i) to each vulture. At the overall home range scale use (U_i) of protected areas was defined as the proportion of stationary (i.e. < 10 km·h^{-1}) GPS locations within the 99% KDE contour that were recorded inside protected areas. The proportion of each vulture's 50% KDE contours occupied by protected areas defined their use at the core foraging range scale. Ivlev's electivity index values range from −1 to +1, with zero indicating use in proportion to availability, while positive and negative values indicate use more or less than expected, respectively.

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Province (Fig. 3) extended more than 100 km west of the IUCN distribution range for the species [25]. The close association of the vultures' movements with the transmission lines in that area provides strong evidence that the construction of power line "towers have proved ideal as roosting sites.....in places devoid of cliffs", allowing the species to expand its range into new foraging areas [4]. It is possible that the construction of power lines in that area has provided a "nursery area" where immature Cape vultures forage away from the competition imposed by dominant adult vultures at carcasses nearer breeding colonies [4,49]. A similar finding was recorded in immature Spanish imperial eagles *Aquila adalberti* which frequently perched on pylons where alternative perching sites were limited in dispersal areas away from adult competition [50]. This could also partially explain why the immature vultures traversed more extensive home ranges than the adults, as seen elsewhere [27,47,49]. Although the breeding status of the adult vultures was unknown it is likely that they would have remained in closer proximity to nesting colonies in order to encounter potential breeding opportunities, compared to the immature vultures which could range further between food sources [1,49]. However, further research is required to determine the primary factors driving the long-distance movements of immature vultures.

Although power line towers provide vultures with additional roost sites and vantage points, the large proportion of time that they spend in the vicinity of overhead cables associated with the structures, in combination with their large size, susceptibility to collisions with man-made structures and their gregarious nature puts them at significant risk [51,52]. These factors explain the high and increasing number of collision-related injuries and fatalities of vultures recorded in South Africa [16,17]. In some regions it is conservatively estimated that power lines kill at least 4% of the local population of Cape vultures annually [16]. The number of vultures killed by collisions is thought to be significantly under-recorded as they rarely cause electricity supply faults and are therefore not investigated, and the vast majority of vulture carcasses are likely to be removed by terrestrial scavengers before they are detected [16,18]. If the estimate of only 2.6% of power line mortalities of blue cranes *Anthropoides paradiseus* and Denham's bustards *Neotis denhami* being recorded in part of South Africa [53] is repeated for Cape vultures, then such a prevalent unnatural mortality factor is likely to cause severe population declines [16] as witnessed in other species [54]. For example, negative interactions with power lines are a major cause of mortality in Spanish imperial eagles, particularly in sub-adults which frequently perch on electricity pylons in areas lacking suitable alternatives [50].

Although organizations such as Eskom have invested significant resources in an attempt to reduce vulture mortalities, more widespread mitigation measures are required to prevent vulture population declines caused by the expanding power line network [16,17]. For example, marking wires with bird flight diverters to increase their visibility and reduce the risk of collision has been carried out in many areas with some success [18,55]. It is a costly measure (e.g. 1,100–2,600 US\$ km^{-1} [56]), however, and it is therefore essential to target high risk areas. The ease of identifying repeatedly visited sections of power line and the relatively high degree of overlap between the vulture core ranges and the known fatalities recorded in the CIR recorded during this study demonstrate the ability of GPS tracking data to inform the implementation of such mitigation measures. For example, additional surveys for vulture carcasses could be carried out at frequently visited sections of power line to determine whether mitigation measures (e.g. bird flight diverters) are required or to assess their effectiveness after installation.

Although protected areas away from breeding colonies were rarely visited by any of the vultures during this study (Fig. 2), breeding cliffs inside two protected areas were regularly used as roost sites by three adults and one immature, confirming that protected areas are important for reducing anthropogenic disturbance at nest and roost sites [13,15,21,22,57]. The most intensively used areas by the vultures were located in a south-westerly direction from the Kransberg colony (Marakele NP) on private and communal farmland, and rarely included protected wildlife reserves. Although data relating to food availability were not available, this supports suggestions that Cape vultures from the Kransberg colony regularly feed on domestic livestock carcasses [58] and are therefore at risk of exposure to harmful veterinary drugs [59,60]. The vultures also frequently travelled to the northern Limpopo Province and elsewhere in South Africa where game farming is common [61] and so it is likely that they also consumed wild ungulate species as seen previously [62]. Consequently, during their regular foraging activity the vultures would have been afforded very little protection from widespread threats such as consuming ungulate carcasses contaminated with veterinary drugs, illegal poisons used for predator control or lead bullet fragments from hunting activity on unprotected farmland [15,61,63]. A similar pattern of limited use of protected areas was observed for immature African white-backed vultures tracked in the same area [24]. Thus these findings further emphasise the need to establish vulture monitoring and conservation measures outside protected areas.

The small sample size of tracked vultures ($n = 10$) limited by financial constraints mean that the results from this study provide a first, rather than a comprehensive insight into the movement patterns of Cape vultures and their relationship with the power line network and protected areas in southern Africa. Although the findings allow preliminary comparisons between adult and immature movement patterns, future research should aim to elucidate the influence of additional individual characteristics such as breeding status and gender on Cape vulture ranging behaviour. Moreover, the effect of food availability on vulture movement patterns was not assessed during this study because of a lack of accurate data relating to ungulate densities and mortality rates. As an important factor in determining home range characteristics [33] and the risk posed by power lines at a local scale [64], this issue should be investigated further. Nonetheless, the regular sampling intervals and highly accurate GPS location data have demonstrated the ability of GPS tracking data to delineate the home ranges of vultures and assess their exposure to potential threats in the region.

Conclusions

The findings from this study demonstrate that Cape vultures have extended their range by using transmission power line structures for roosting and perching in areas otherwise devoid of suitable perches, but must frequently face the risk of colliding with overhead wires. If the extensive movement patterns and limited use of protected areas recorded during this study are representative across the species' geographical range then it is likely that the population is regularly exposed to multiple threats such as negative interactions with power lines and poisoning from contaminated carcasses on private farmland. We suggest that co-ordinated cross-border conservation measures beyond the boundaries of the protected area network will be necessary to ensure the future survival of threatened vultures in Africa. Specifically, additional monitoring and mitigation of negative interactions with power lines will be required, as well as a concerted effort to remove contaminants from the food supply. The use of GPS tracking data to inform conservation management of other threatened species is also advocated.

Supporting Information

Figure S1 Home range area curves from incremental area analysis of GPS locations from nine Cape vultures**.** The number of GPS locations used to generate minimum convex polygons (MCPs) by adding consecutive locations until all locations were used is plotted against the area of each MCP. (A) – (I) represent different vultures (refer to Table 1).
(TIF)

Figure S2 Minimum convex polygons of five adult and four immature Cape vultures tracked by GPS-GSM tracking units. Hollow red and blue polygons represent merged minimum convex polygons (MCPs) using all locations from five adult and four immature Cape vultures tracked using GPS-GSM tracking units, respectively. The capture site is indicated by a black triangle.
(TIF)

Table S1 Association of GPS tracking locations and home ranges of nine Cape vultures with the transmission power line network. The proportion of the 99% and 50% kernel density estimated (KDE) contours covered by the 50 m transmission line (Tx) buffer, and the proportion of stationary GPS locations recorded within the Tx buffer are shown, as well as the corresponding stationary GPS location densities within the 99% and 50% contours and the Tx buffer.
(PDF)

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Author Contributions

Conceived and designed the experiments: WLP KW RWY MM LM. Performed the experiments: WLP KW LM. Analyzed the data: WLP RY. Wrote the paper: WLP RWY. Acted as the first author's study supervisor: RWY.

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“Traditionally, when a great crime such as a murder occurs, people make a great effort to apprehend the guilty party. A murder is a great grievance, but it is a minor one compared to the loss of a species, especially one that is part of a cultural and ecological web that encompasses millions of people, performs ecological services on a near global scale, and enriches the enjoyment of life not just for the living but for all generations to come.”

Prof. Bernd Heinrich, Life Everlasting – The Animal Way of Death.