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Spatial patterns of land-use by Immature African white-backed vultures (*Gyps africanus*) captured in the North-West Province, South Africa

by

William Louis Phipps

Submitted in partial fulfilment of the requirements for the degree of Magister Scientiae (Veterinary Science) in the Department of Paraclinical Sciences, Faculty of Veterinary Science, University of Pretoria

2011

Supervisor: **Prof V Naidoo**

Department of Paraclinical Sciences, University of Pretoria

Co-supervisor: **Dr S G Willis**

Institute of Ecosystem Science, Durham University, UK

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DECLARATION

I declare that this dissertation, which I hereby submit for the degree of Magister Scientiae (Veterinary Science) at the University of Pretoria, is my own work and has not previously been submitted by me for a degree at this or any other tertiary institution.

Signed: ____

William Louis Phipps

Date: ____

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TABLE OF CONTENTS

CHAPTER 3 MATERIALS AND METHODS 33

CHAPTER 4 RESULTS 58

FORAGING RANGES OF IMMATURE AFRICAN WHITE-BACKED VULTURES (*GYPS AFRICANUS*) AND THEIR USE OF PROTECTED AREAS IN SOUTHERN AFRICA

LIST OF TABLES

LIST OF FIGURES

ABBREVIATIONS

DEM	Digital elevation model
E_i	Ivlev's electivity index
GCR	Grid cell range
GIS	Geographical information system
GPS	Global positioning system
GR	Game Reserve
GSM	Global system for mobile communications
h	KDE bandwidth
ha	Hectares
h_{ref}	KDE reference bandwidth
HRT	Home range tools
IUA	Intensively used area
IUCN	International Union for the Conservation of Nature
KDE	Kernel density estimation
m	Metres
MCP	Minimum convex polygon
MWR	Mankwe Wildlife Reserve
n	Sample size
Non-PA	Unprotected area
NP	National Park
NSAID	Non-steroidal anti-inflammatory drug
PA	Protected area
PDOP	Positional dilution of precision
PNP	Pilanesberg National Park
r_s	Spearman's correlation coefficient
RSF	Resource selection function
SD	Standard deviation
SE	Standard error
TFCA	Trans-frontier conservation area
UTM	Universal Transverse Mercator

SUMMARY

Spatial patterns of land-use by immature African white-backed vultures (*Gyps africanus*) captured in the North-West Province, South Africa

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Degree:	MSc (Veterinary Science)

As obligate scavengers *Gyps* vultures provide an important ecosystem service as the main consumers of ungulate carcasses in African savannas. Throughout the continent, however, multiple threats are causing vulture populations to decline, especially outside protected areas. Although the African white-backed vulture *Gyps africanus* is the most numerous and widely distributed *Gyps* species in Africa, its foraging ecology and land use preferences remain poorly understood. Furthermore, while protected areas are known to be important for vultures in East and West Africa, their role in South Africa has not been fully investigated.

This study uses GPS-GSM tracking units to investigate the movement and land-use patterns of six immature African white-backed vultures that were caught at Mankwe Wildlife Reserve in the North West Province of South Africa. Immature individuals were chosen because they were expected to travel extensively and be exposed to the full range of threats. The tracking units recorded the GPS location, speed, altitude and direction of travel three times per day. The size and extent of the vultures' foraging ranges were estimated using three methods: minimum convex polygons (MCPs), fixed kernel density estimation (KDE) and grid cell range (GCR) estimation. The vultures' use of protected areas and areas of different cattle densities (zero, low, medium and high) was assessed to determine whether they were visited more or less than expected based on the area they occupied within the vultures' foraging ranges. The distances travelled by the vultures and their flight speeds and altitudes were also calculated, as well as the amount of time that they spent in the vicinity of supplementary feeding sites.

The vultures were tracked for between 101 and 313 days and the GPS tracking units acquired 99.44% of expected GPS locations. The vultures ranged extensively and generally travelled in a nomadic manner. While three individuals occupied foraging ranges (mean 95% KDE contour area = 106,282.33 km^2) either side of the South African borders between Botswana and Zimbabwe, the other three travelled more extensively through southern Africa, entering six different countries (mean 95% KDE contour area = 563,564.67 km^2). The vultures rarely visited protected areas in South Africa but two of the vultures regularly used protected areas in northern Botswana and Zimbabwe. Areas of high cattle density were used less than expected by all vultures, but not at a significant level, while two of the vultures used areas with zero cattle density more than expected due to their regular use of supplementary feeding sites in those areas. Areas of medium cattle density were the most regularly used, containing an average of 30.72% of each vulture's stationary GPS locations. The vultures travelled an average of 33 km/day and a maximum of 267 km/day, flying at an average of 50 km/h (maximum = 107 km/h) at 561 m above ground level (maximum = 2,267 m).

This study provides the first description of movement and land-use patterns of immature African white-backed vultures tracked continuously from South Africa. Their extensive foraging ranges and limited use of protected areas implies that the vultures could potentially encounter the full range of threats in the region, and it is clear that their future conservation will depend upon conservation strategies that extend across international borders.

CHAPTER 1

INTRODUCTION

1.1. Project background

Gyps vulture populations are declining globally, largely as a result of reduced food availability, habitat loss and persecution (Johnson et al., 2006; Pain et al., 2008). A serious threat to *Gyps* vultures has recently been identified following the loss of more than 99% of individual birds in some parts of Asia since the 1990s (Pain et al., 2008; Prakash et al., 2007). Those declines were caused primarily by accidental poisoning of vultures when they fed on dead livestock that had previously been treated with the non-steroidal anti-inflammatory drug (NSAID) diclofenac (Green et al., 2004; Oaks et al., 2004).

Recent research has shown that African *Gyps* vulture species are at least as sensitive to NSAID toxicity as Asian *Gyps* species (Naidoo & Swan, 2009; Naidoo et al., 2010). As diclofenac is now being imported into Africa (Anderson, Piper & Swan, 2005) and recent satellite telemetry studies have shown that *Gyps* vultures regularly cross international borders over their extensive foraging range (Bamford et al., 2007), the widespread use of diclofenac and other NSAIDs in any southern African country potentially poses a significant threat to *Gyps* vultures across the entire region (Naidoo et al., 2010). It is important, therefore, that we improve our knowledge of *Gyps* vulture movement patterns and foraging ecology so that we can assess the risk of exposure not only to veterinary drugs but also to the many other threats present on the continent (Anderson et al., 2005; Virani, Kendall, Njoroge & Thomsett, 2011).

While the global population of African white-backed vultures (*Gyps africanus*) is estimated at 270,000 individuals (BirdLife International, 2010a), the species has been identified as a species of concern due to recent declines recorded in different parts of Africa, prompting suggestions that its conservation status should be upgraded from Near Threatened to Vulnerable on the IUCN Red List (IUCN, 2010; Thiollay, 2007; Virani et al., 2011). The widespread distribution of the species makes it susceptible to the full range of threats on the continent, particularly outside protected areas where habitat loss, declines in wild ungulate populations and direct persecution are more severe than within protected reserves (Thiollay, 2007; Virani et al., 2011). The more extensive foraging ranges of immature vultures and their inexperience compared to adults make them particularly vulnerable to multiple threats across their range (Mundy, Butchart, Ledger & Piper, 1992).

Research into African white-backed vulture movement patterns, habitat use and foraging behaviour has been identified as a priority to aid the planning and implementation of effective conservation strategies (Virani et al., 2011). Recent advances in GPS tracking technology have facilitated the research of wide-ranging bird species and data from such studies have provided valuable information for conservation purposes (Kie et al., 2010). In this study GPS tracking technology is used to investigate the movement patterns of immature African white-backed vultures, the size and extent of their foraging ranges, their relative use of protected and unprotected areas and areas of different cattle densities, and how frequently they visited supplementary feeding sites.

1.2. Hypotheses

- Immature African white-backed vultures traverse extensive foraging ranges
- Immature African white-backed vultures do not use officially protected or unprotected areas disproportionately based on their availability within their foraging ranges
- A variation in cattle density does not influence the foraging behaviour of immature African white-backed vultures
- Supplementary feeding sites do not influence the movement patterns of immature African white-backed vultures

1.3. Objectives

The primary objective of the project was to fit GPS tracking devices to six immature African white-backed vultures in the North West Province of South Africa to investigate their movements and patterns of land use for the first time in the region.

CHAPTER 2

LITERATURE REVIEW

2.1. *Gyps* vultures: an introduction

The history of vultures in the fossil record spans more than 50 million years (Rich, 1983). The 22 species of vultures that occur in the world today are split into two groups, namely the New World (Cathartidae) vultures (including condors) comprising seven species, and Old World (Accipitridae) vultures of which there are 15 species (Feduccia, 1996). The two groups are not closely related taxonomically, with the New World species sharing distant ancestry with storks and the Old World vultures descending from ancestral eagles (Wink, 1995). Despite their independent ancestry, New and Old World vultures share morphological characteristics and are both members of the scavenging guild: they therefore represent a classic example of convergent evolution (Hertel, 1994; Wink, 1995).

Africa holds the highest diversity of vultures globally, with 11 of the 15 Old World species occurring on the continent (Mundy et al., 1992). The *Gyps* genus of vultures shows the highest degree of speciation, with eight species occurring globally and four of these so-called ‘griffon’ vultures occurring in sub-Saharan Africa: Eurasian griffon vulture (*G. fulvus*), Rüppell’s vulture (*G. rueppellii*), Cape vulture (*G. coprotheres*) and African white-backed vulture (*G. africanus*) (Johnson, Lerner, Rasmussen, & Mindell, 2006). *Gyps* vultures are characterized by a large body size, long, almost featherless necks and heads, they are generally brown or creamy in colour, and they usually breed and feed gregariously (Houston, 1983; Mundy et al., 1992).

Gyps vultures are the only extant vertebrates that survive by locating and feeding exclusively from dead animals, and are therefore regarded as obligate scavengers (Houston, 1974c, 2001; Ruxton & Houston, 2004). Due to the unpredictable spatial and temporal occurrence of their food source (Houston, 1974a), and the competition that they face at carcasses (Kruuk, 1967), *Gyps* vultures have developed several physical adaptations specialised for consuming soft muscle and visceral tissues of ungulate carcasses as efficiently as possible (König, 1983; Kruuk, 1967).

- The most striking of those adaptations is the **almost featherless, elongated "periscope"-like neck** (Mundy et al., 1992) that allows the birds to reach deep inside a carcass (König, 1983). Although the lack of feathers on the head and neck is commonly believed to be an adaptation to prevent accumulation of soiled material during typically unclean feeding conditions (Mundy et al., 1992), it has been suggested that the areas of bare skin also play an important role in thermoregulation (Ward, McCafferty, Houston, & Ruxton, 2008), and during dominance and courtship displays (König, 1983; Mundy et al., 1992).

- The **large, strongly curved and sharp-edged bill** of a *Gyps* vulture is specialised for efficient feeding at a carcass and, together with the muscular neck, allows meat to be pulled quickly from a carcass (Houston & Cooper, 1975; König, 1983). Furthermore, the *Gyps* vulture's tongue is strongly grooved with serrated edges that aids removal of tissues and pushes food quickly through the mouth (Houston & Cooper 1975).

- Another characteristic feature of *Gyps* vultures is the presence of a **large crop** (a pouch-like enlargement of the oesophagus (Mundy et al., 1992)) that protrudes from the base of the neck when filled with food (Houston, 1976; Mundy, Morris, & Haxen, 1983). The crop can be filled with food weighing as much as 20% of the vulture's normal body weight (Houston & Cooper, 1975; Mundy et al., 1983), which is suggested to be sufficient to maintain an individual for up to four days (Houston & Cooper, 1975). During the breeding season the crop is also used by adult vultures to deliver food to the chick, which is fed by regurgitation (Houston, 1976).

These physical features, together with the vultures' highly efficient digestive system (Houston & Cooper, 1975), allow them to exploit an irregular and unpredictable food supply by gaining as much energy as possible during each feeding event (Houston, 1975; Ruxton & Houston, 2004).

2.2. The role of *Gyps* vultures as obligate scavengers in Africa

Scavengers fulfil a vital ecological function by consuming carrion and consequently maintaining energy transfer through ecosystems (DeVault, Rhodes, & Shivik, 2003). Avian scavengers, and vultures in particular, are the main consumers of carrion in many ecosystems owing to their efficiency in locating and consuming carcasses (Houston, 1979), and their role in providing an essential ecosystem service has been established (Sekercioglu, 2006).

Vultures reduce the length of time that a carcass remains in the environment, decreasing the likelihood that diseases will develop or spread to the surrounding environment (DeVault et al., 2003; Sekercioglu, 2006). For example, although vultures have been implicated in the mechanical transmission of anthrax (*Bacillus anthracis*) (Hugh-Jones & Blackburn, 2009), it has been suggested that they are also likely to curtail the spread of the disease by rapidly consuming contaminated carcasses and preventing the development and transmission of infective spores (De Vos, 1974; Houston & Cooper, 1975; Hugh-Jones & de Vos, 2002; Turnbull et al., 2008). Furthermore, the highly acidic digestive tract of the African white-backed vulture has the ability to destroy all but the most resistant bacterial organisms, thereby reducing sources of infection in the environment (Houston & Cooper, 1975).

A stark illustration of the importance of vultures filling the role of “nature’s incinerators” (Kanaujia & Kushwaha, 2009) has recently become clear in Asia. Recent declines in vulture numbers have led to increases in the populations of disease-carrying feral dogs and rats, resulting in a rise in the incidence of human cases of rabies (Markandya et al., 2008). It is suggested that the incidence of livestock diseases such as brucellosis, tuberculosis and anthrax may also increase (Kanaujia & Kushwaha, 2009; Mudur, 2001; Pain et al., 2008; Sekercioglu, 2006).

Vultures obtain food from a variety of sources in Africa, and the relative importance of those different sources has changed over the last few centuries as the continent has undergone significant social and economic development (Benson, Plug, & Dobbs, 2004; Biggs et al., 2008). South Africa has experienced some of the fastest and most advanced economic development on the continent (Biggs et al., 2008), with corresponding changes in the agricultural sector. Between the 18th and 20th centuries, the vast majority of wild herbivorous mammals were removed from most

South African land to make way for livestock and arable farming practices, and vultures were forced to alter their regular diet from wild, often migratory ungulates to livestock carcasses (Boshoff & Vernon, 1980; Mundy et al., 1992). It is suspected that the change to livestock farming, and the associated improvement in animal husbandry, led to a decrease in the number of carcasses available to vultures, and contributed significantly to observed population declines (Boshoff & Vernon, 1980; Dean, 2004; Friedman & Mundy, 1983).

In the latter half of the 20th Century, the farming of ‘game’ animals became a popular and profitable business, and many farmers restocked their properties with wild ungulates, often alongside existing livestock herds (Dean, 2004; Mundy et al., 1992; Murn & Anderson, 2008; Van der Merwe & Saayman, 2005). Significant changes in land use have taken place elsewhere in Africa (Herremans & Herremans-Tonnoeyr, 2000; Mendelsohn, 2006; Thiollay, 2006a, 2006b, 2007), and today’s vulture populations have adapted to feed on whatever carcasses are available within their foraging range (Benson et al., 2004; Donázar, Cortés-Avizanda, & Carrete, 2010; Lambertucci, Di Martino, Sánchez-Zapata, Donázar, & Hiraldo, 2009; Mundy et al., 1992), varying from an exclusive diet of livestock carcasses (Boshoff, Robertson, & Norton, 1984) to a mixture of domestic livestock and wild ungulates (Benson et al., 2004; Ogada & Keesing, 2010; Schultz, 2007). A further change has followed the introduction of supplementary feeding stations, or “vulture restaurants”, where carcasses (mostly livestock) are placed at specific locations in an attempt to stabilize declining vulture populations (Brown & Jones, 1989; Friedman & Mundy, 1983).

The Serengeti ecosystem in Tanzania, where vultures obtain most of their food from wild ungulates (Houston, 1974c), has been suggested as an appropriate model for African conditions prior to modern development (Benson et al., 2004). It has been the location of detailed studies that form the basis of our knowledge of the ecology of *Gyps* vultures (Houston, 1974a, 1974c, 1976, 1979; Hunter, Durant, & Caro, 2006). Vultures in the Serengeti obtained most of their food from wild ungulates that died from causes other than predation, such as old age, disease, malnutrition or accidents (Houston, 1974c). Although mammalian predators such as lions (*Panthera leo*) and cheetahs (*Acinonyx jubatus*) do provide vultures with some food, they also directly compete with vultures at a carcass and often prevent them from feeding (Houston, 1974c, 1979; Hunter et al., 2006; Kruuk, 1967). Houston (1974c) suggests that the carcasses which the mammalian carnivores cannot utilize form the basic food supply for *Gyps* vultures in the Serengeti savannah ecosystem, and Benson and colleagues (2004) propose that this is also the case in southern Africa.

The vultures' food supply is unpredictable and irregularly distributed through space and time (Ruxton & Houston, 2004), often with seasonal fluctuations of high and low carcass availability (Houston, 1974c; Sinclair & Norton-Griffiths, 1979). *Gyps* vultures have developed several morphological and ecological features designed to successfully exploit the ephemeral supply of carcasses and overcome competition from other scavengers (DeVault et al., 2003; Houston, 1979; König, 1983).

One physical adaptation to the scavenging lifestyle is the *Gyps* vulture's large body size, with Cape vultures and African white-backed vultures having average body masses of 8 kg and 5.3 kg respectively (König, 1983). *Gyps* vultures are therefore among the heaviest flying birds in Africa (Mundy et al., 1992), and Houston (1975) suggested that evolutionary development has caused them to attain this high body mass. Ruxton and Houston (2004) demonstrated that there is a clear evolutionary pressure towards large body size for scavenging vertebrates because large-bodied animals can consume more food from each carcass, and accumulate greater body reserves than small ones. This is important when considering the unpredictable nature of their food source, and it allows *Gyps* vultures to go for long periods (at least 14 days) without feeding (Mundy et al., 1992). It has been suggested that vultures rely on stored energy reserves to sustain them through periods of low food availability, particularly during the breeding season when adult birds must also provide sufficient food for chicks (Houston, 1976; Komen & Brown, 1993). Large body size is also advantageous when attempting to feed at carcasses where there is usually a high level of inter- and intra-specific competition (Hiraldo, Blanco, & Bustamante, 1991; König, 1983; Kruuk, 1967; Wallace & Temple, 1987).

The large body size and high wing loading of *Gyps* vultures (e.g. 112 N/m^2 for Cape vultures) are features designed for soaring flight, allowing them to make use of surrounding air movements and thermals to cover large distances with relatively little energy expenditure (Pennycuick, 1972). A larger body mass allows greater flight speeds, and so heavier birds can forage over a larger area each day, increasing the efficiency of locating a carcass that could be situated more than 150 km from the nest or roost site (Houston, 1976; Pennycuick, 1972, 1979). Pennycuick (1972) estimated an average cross-country speed of 47 km/h for *Gyps* vultures, and recorded an African white-backed vulture travelling at an average speed of 75 km/h, with another study recording speeds of 69 km/h in a Cape vulture (Boshoff et al., 1984). Tucker (1988) recorded a maximum speed of a descending African white-backed vulture at an impressive 141 km/h, illustrating their ability to reach high flight speeds. A scavenger must detect and reach a carcass before it has been fully consumed by its competitors, and the ability of vultures to travel quickly over large areas gives them an advantage over less mobile terrestrial mammalian scavengers that expend more energy when searching for carcasses (Pennycuick, 1972, 1979).

While some New World vultures (Houston, 1986) and most mammalian scavengers rely mainly on their sense of smell to detect carcasses (König, 1983; Mills, 1984), olfaction plays no role in carcass detection in Old World vultures (Houston, 1974a). *Gyps* vultures use sight alone to search directly for food, relying on their high visual acuity (Fischer, 1969) to detect carcasses from distances of at least 4 km (Houston, 1974a; Pennycuick, 1972). In addition to using vision to look directly for carcasses, vultures improve foraging efficiency by monitoring the movements of other soaring vultures (Kruuk, 1967), and immediately move towards any bird that they observe descending rapidly towards the ground (Pennycuick, 1972). A single vulture descending towards a carcass triggers a “chain reaction” of many birds arriving from increasing distances, even though only one vulture may have directly located the carcass (Houston, 1974a). Houston (1974a) suggests that vultures are attracted to a carcass in this way from a distance of at least 35 km, drawn from an area of *ca* 4,000 km^2. This process of social facilitation partially explains the gregarious feeding and breeding habits of vultures, whereby “information transfer” between foraging vultures plays a key role in locating food (Houston, 1974a; Jackson, Ruxton, & Houston, 2008; Newton, 1979).

This combination of their relatively fast and energy-efficient soaring flight (Pennycuick, 1972), their extensive foraging network (Houston, 1974a), and the unimpeded view of the ground below, gives vultures a significant advantage over terrestrial mammalian scavengers when searching for carcasses (Houston, 1974a; Ruxton & Houston, 2004). However, vultures are limited to flying only when air movements and thermals provide sufficient lift (Pennycuick, 1972), giving mammalian carnivores the opportunity to consume carcasses without competition from vultures at night or immediately after dawn (Houston, 1974c; König, 1983; Kruuk, 1967). Moreover, the longer that it takes for vultures to locate a carcass, the greater the chance that a mammalian scavenger, such as a spotted hyaena (*Crocuta crocuta*) or lion (*Panthera leo*) will find it first and actively defend it, preventing the vultures from feeding (Houston, 1974c; Hunter et al., 2006).

There is therefore a limited time period for vultures to locate a carcass and feed successfully, and this is reflected in the speed at which vultures fill their crops once they arrive at a carcass (Houston, 1974c). For example, it has been estimated that 65% of the gross body mass of a 60 kg impala will be edible to vultures, providing enough soft tissue for 39 African white-backed vultures to fill their crops within approximately 10 minutes (Houston, 1974c; Mundy et al., 1992; Mundy et al., 1983). Despite the competition that mammalian scavengers present to vultures, they also increase the availability of certain resources through a facilitatory process by revealing the soft tissues of thick skinned animals such as elephants and buffalo (König, 1983; Kruuk, 1967). Their role in providing an essential source of calcium in the form of bone fragments has also been discussed (Benson et al., 2004; Mundy & Ledger, 1976; Richardson, Mundy, & Plug, 1986).

In summary, *Gyps* vultures are the only true obligate scavengers among extant vertebrates in the Old World (Donázar et al., 2010), and they exhibit morphological and ecological traits that allow them to compete with terrestrial mammals and other scavenging species (DeVault et al., 2003; Ruxton & Houston, 2004; Sekercioglu, 2006). Nevertheless, due to potential competition with mammalian scavengers and predators we might expect *Gyps* vultures to forage more frequently outside of protected areas harbouring such mammalian communities. This, in turn, may render them more vulnerable to changes in the wider environment and less easy to conserve using the traditional approach of maintaining protected areas. This is discussed in more detail in Section 2.5 of this chapter.

2.3. *Gyps* vultures: their place in southern Africa

Southern Africa is one of the few regions on the continent where the distributions of two species of *Gyps* vultures overlap (Mundy et al., 1992). The African white-backed vulture is distributed widely through sub-Saharan Africa over a range of 11.3 million km^2 (Figure 2.1), and is the most numerous vulture species on the continent, numbering approximately 270,000 individuals (BirdLife International, 2010a). In contrast, the Cape vulture has a much smaller population of 8,000 - 10,000 individuals occurring over a smaller range (860,000 km^2) restricted to southern Africa (BirdLife International, 2010b). In the IUCN Red List of Threatened Species the African white-backed vulture and the Cape vulture are listed as *'Near Threatened'* and *'Vulnerable'* respectively (IUCN, 2010). The key ecological difference between the two species is their nesting requirements, Cape vultures breeding exclusively on cliffs (Borello & Borello, 2002; Mundy et al., 1992), while African white-backed vultures nest in trees (Houston, 1976; Kemp & Kemp, 1975).

Several species of vulture may occur in the same region or at the same carcass, but their different morphological and behavioural adaptations allow them to coexist through facilitatory and competitive processes (Donázar et al., 2010; Kruuk, 1967; Wallace & Temple, 1987). For example, the compact skulls and powerful beaks of lappet-faced (*Aegypius tracheliotos*) and white-headed (*Aegypius occipitalis*) vultures are specialised for removing tough and coarse body parts (e.g. tendons) from ungulate carcasses (König, 1983), often opening them up and providing *Gyps* vultures the opportunity to gain access to the soft internal tissues on which they depend (i.e. a facilitatory process - Hertel, 1994; König, 1983; Kruuk, 1967; Mundy et al., 1992). In areas where two species of *Gyps* vultures overlap, however, their similar morphologies and behaviours force them to compete for the same food supply (Hertel, 1994; König, 1983; Mundy et al., 1992).

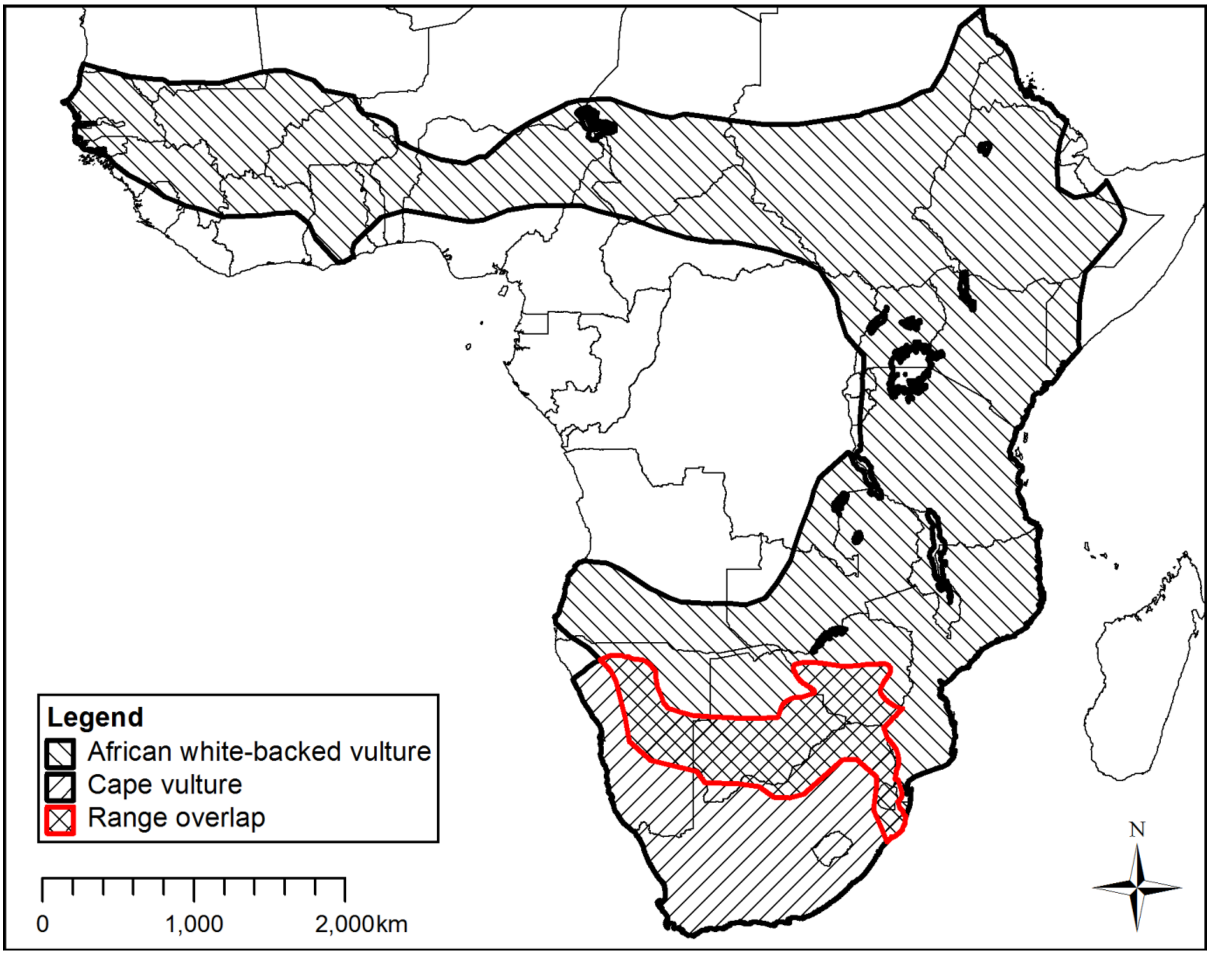

Figure 2.1. Species distribution map for the Cape and African white-backed vulture, and the area of overlap between their ranges. The map was produced using data supplied by BirdLife International (2011).

The most significant physical difference between Cape and African white-backed vultures is their size, with the former having an average body mass of 8.0 - 9.35 kg (König, 1983; Mundy et al., 1992), compared to 5.46 kg for the latter (Mundy et al., 1992). When competing at a carcass the larger Cape vultures generally dominate African white-backed vultures (Houston, 1974c; Kruuk, 1967; Mundy et al., 1992), although the level of hunger and the relative number of each species are also important in determining the dominance hierarchy at any given carcass (König, 1983; Kruuk, 1967). König (1983) suggests that the "power" of a relatively large group of hungry African white-backed vultures often allows them to maintain their place at a carcass during challenges from larger vultures, and even some mammal species. Carrete et al. (2010) found a similar case in New World vultures, when observations of feeding events showed that highly gregarious black vultures (*Coragyps atratus*) were able to out-compete the much larger but less abundant Andean condors (*Vultur gryphus*). It has been demonstrated, however, that when large, more dominant species occur in high numbers they are able to monopolise food resources to the detriment of smaller competitors (Mönkkönen, Forsman, & Thomson, 2004), particularly if those resources are sparsely distributed (Cortés-Avizanda, Carrete, & Donázar, 2010).

The African white-backed vulture has a lower wing-loading (76 N/m^2) than the larger Cape vulture (112 N/m^2), and so can make use of much weaker air currents and thermals for foraging flights (Pennycuick, 1972). Houston (1975) suggested that these differences explain why the smaller African white-backed vulture is generally found more in lowland, wooded savannas, compared to the larger *Gyps* species that are more restricted to mountainous areas with stronger air currents and cliffs for roosting and breeding. Similarly, Carrete et al. (2010) also found that while the smaller New World black vulture is able to exploit carcasses in both mountainous and plains habitat, the much larger Andean condor is mainly restricted to mountainous areas. It has also been demonstrated that African white-backed vultures are more likely to land and feed at carcasses in more treed areas than are Cape vultures (Bamford, Monadjem, & Hardy, 2009a), supporting previous suggestions that African white-backed vultures are able to exploit carcasses in a wider range of habitats than the larger species (Houston, 1974a, 1974c).

Despite a degree of spatial segregation or “habitat partitioning” between the two species (i.e. mountainous areas versus flat savannah - Houston, 1975; Kruuk, 1967), African white-backed and Cape vulture foraging ranges do overlap in large areas of southern Africa, and consequently they directly compete for the same food supply (Hertel, 1994; König, 1983; Mundy et al., 1992). This is especially true in the Limpopo and North West Provinces of South Africa, where breeding sites of both species are well within each other’s foraging ranges (Benson, 1997; Benson, Tarboton, Allan, & Dobbs, 1990; Tarboton & Allan, 1984).

Due to their typically large numbers at a carcass, African white-backed vultures also have to contend with intra-specific competition, as well as competing with other avian and mammalian scavengers. In fact, out of all aggressive interactions at carcasses, African white-backed vultures engaged in intra-specific competition (as opposed to inter-specific) on 86 - 88% of occasions (König, 1983; Kruuk, 1967). The African white-backed vulture is thought to be the most aggressive species in terms of the number of competitive interactions in which it engages (König, 1983; Mundy et al., 1992). Mundy *et al*. (1992) attribute this to the pressure for an African white-backed vulture to gain and retain a place at a carcass because it is easily displaced by larger vultures, or by large numbers of conspecifics.

While some authors have stated that age has little influence on the hierarchy of a group of *Gyps* vultures (König, 1983), others have found that older birds won aggressive encounters against younger birds more frequently than *vice versa* (Houston, 1976), and that the youngest birds are often the last to gain access to a carcass (Mundy et al., 1992). Possibly as a result of this, the Cape vulture has an estimated survival rate of only 17 - 50% in the first year, which is much lower than survival of older age groups (Houston, 1974b; Piper, Boshoff, & Scott, 1999). The relative survival rates for African white-backed vultures are thought to be similar (Mundy et al., 1992). Adult *Gyps* vultures also often struggle to meet the food requirements to sustain themselves and their nestling during the breeding season and are forced to use stored energy reserves during this period (Houston, 1976; Komen & Brown, 1993). While breeding vultures are restricted to a foraging range within a certain distance of the nest (Houston, 1976), movements of over 1,200 km from their natal origin have been recorded for immature or non-breeding birds (Houston, 1974b; Oschadleus, 2002), with a foraging range of over 480,000 km^2

recorded in an 8 month period for an immature Cape vulture in southern Africa (Bamford et al., 2007).

This widespread dispersal of juvenile and immature African white-backed vultures is thought to be a life-history strategy to reduce intra-specific competition for the same food supply (Houston, 1976; Mundy et al., 1992). Immature vultures have also been observed to spend prolonged periods at locations with an abundant food supply, such as abattoirs (Houston, 1976), or following heavy mortalities among ungulate populations (Houston, 1974a, 1974c). Immature vultures are therefore thought to track the food supply, moving to "nursery" areas with less competition from breeding birds (Houston, 1976; Mundy et al., 1992), resulting in a reduction of immature mortality rates that might otherwise be much higher (Mundy et al., 1992). Such "nomadic" movement patterns whereby a bird travels "from one area to another, residing for a time wherever food is temporarily plentiful" are common among immature raptors, particularly for gregarious species that rely on an unpredictable food supply (Newton, 1979).

2.4. Trends in *Gyps* vulture populations and associated threats: global and African perspectives

Populations of vultures in the *Gyps* genus are declining across the globe (IUCN, 2010; Johnson et al., 2006; Pain et al., 2008). The four species of Asian *Gyps* vultures, *G. bengalensis, G. indicus, G. tenuirostris* and *G. himalayensis,* have exhibited the most dramatic declines over recent decades (Pain et al., 2008). For example, in 1985 *G. bengalensis* was referred to as "possibly the most abundant large bird of prey in the world" (Houston, 1985), occurring in such high numbers around human settlements that they were considered a serious hazard to aircraft (Satheesan & Satheesan, 2000; Singh, 1999). Between 1992 and 2007 the Indian population of *G. bengalensis* experienced a dramatic decline of up to 99.9% in some regions and, together with *G. indicus* and *G. tenuirostris,* is currently at severe risk of extinction (Prakash et al., 2007). In Pakistan decreases of 25% per year and 50% per year were also recorded for *G. indicus* and *G. bengalensis* respectively, with the extirpation of several large breeding colonies (Gilbert et al., 2006; Pain et al., 2008). Consequently, the conservation status of those three species was upgraded in 2000 from '*Lower Risk'* to '*Critically Endangered'* (IUCN, 2010). Although the status of *G. himalayensis* is currently considered as '*Least Concern'* (IUCN, 2010) recent declines of 70% have been recorded in Nepal, with an 84% reduction in the number of active nests (Acharya, Cuthbert, Baral, & Shah, 2009), prompting calls for a reassessment of its conservation status. For these long-lived raptor species that would usually be expected to have annual adult survival rates of over 95% (Newton, 1979; Sarrazin, Bagnolini, Pinna, Danchin, & Clobert, 1994), the observed decreases were unprecedented (Pain et al., 2008).

Initially the suspected causes of the precipitous population declines included a reduction in a previously predictable food source following over-hunting and changes in livestock husbandry (Kushwaha & Kanaujia, 2010; Pain et al., 2003), direct persecution and poisoning (Satheesan, 2000; Thewlis, Timmins, Evans, & Duckworth, 1998), and infectious disease (Cunningham et al., 2003; Pain et al., 2003). However, through a combined effort of many studies throughout the region including necropsies of vultures (Gilbert et al., 2006; Oaks et al., 2004; Shultz et al., 2004), sampling of tissues from livestock carcasses (Taggart et al., 2006; 2007), and modelling methods (Green et al., 2004; 2006; 2007), the sole cause of the decline was attributed to vultures consuming dead livestock previously treated with the non-steroidal anti-inflammatory drug (NSAID) diclofenac (Oaks et al., 2004; Pain et al., 2008). Clinical trials determined that residues of diclofenac present in carcasses from treated livestock were of sufficiently high concentrations to cause visceral gout and subsequent kidney failure and death of *Gyps* vultures within 48 hours of a feeding event (Naidoo & Swan, 2009; Oaks et al., 2004; Swan, Cuthbert et al., 2006).

Diclofenac, the veterinary "drug of choice" in the region used to reduce pain, inflammation and fever in livestock, became widely available from the 1990s when the vulture numbers started to fall rapidly (Pain et al., 2008; Taggart et al., 2006). Furthermore, and largely due to the sociality of *Gyps* vultures, it was determined that the observed declines could be explained by diclofenac residues being present in less than 1% of available carcasses (Green et al., 2004). Following recommendations from international conservation organizations, and the identification of meloxicam as a safe and effective alternative NSAID to diclofenac (Naidoo et al., 2008; Swan, Naidoo, et al., 2006), the governments of India, Nepal and Pakistan banned the manufacture of diclofenac in 2006 (Pain et al., 2008). However, the effects of the Asian vulture decline have been far reaching, with serious ecological, social and economic implications: an increase in human cases of rabies following the rise in number of feral dogs after reduced competition from vultures; an expected increase in cases of bacterial diseases such as anthrax; and the loss of vultures as an important feature of various religious communities (Markandya et al., 2008; Pain et al., 2003).

African species of *Gyps* vultures are known to be at least as sensitive to diclofenac toxicity as Asian vultures (Naidoo & Swan, 2009; Swan, Cuthbert, et al., 2006), and concern has been expressed that vultures in Africa may face a similar fate to their Asian counterparts (Anderson, Piper, & Swan, 2005), especially as the drug is now available for purchase in 15 African countries (BirdLife International, 2007, 2008). Although diclofenac is not available for veterinary use in southern Africa, other NSAIDs (e.g. ketoprofen) that are used to treat livestock in the region are now known to be equally as toxic to *Gyps* vultures and other birds (Cuthbert, Parry-Jones, Green, & Pain, 2007; Naidoo et al., 2010). Exposure to harmful NSAIDs could worsen the current trends of declining vulture populations in Africa (Anderson et al., 2005).

Some of the most dramatic declines in vulture populations on the continent have occurred in West Africa, with African white-backed and Rüppell's vultures declining by up to 98% over a 35 year period (Rondeau & Thiollay, 2004; Thiollay, 2006a, 2006b, 2007). Similarly, numbers of scavenging raptors observed in Kenya declined by approximately 50% per year, and by a total of 70% over a three-year study period (Ogada & Keesing, 2010). Recent comparisons of data from road transect surveys conducted in Kenya's Masai Mara ecosystem indicate that *Gyps* vultures have declined by 52% over a 30-year period, with the highest declines recorded outside the protected reserve (Virani, Kendall, Njoroge, & Thomsett, 2011). The declines in the formerly widespread African white-backed vulture population led to the upgrade of its global conservation status from '*Least Concern'* to '*Near Threatened'* in 2007 (IUCN, 2010), and there have been recent recommendations to further up-list the species to '*Vulnerable*' (Virani et al., 2011).

The species is also declining in southern Africa, and may have lost 10% of its population in the previous three generations, qualifying it as '*Vulnerable*' in a regional assessment of its conservation status (Anderson, 2000a). The range of the African white-backed vulture is thought to have decreased markedly in the former Transvaal region of South Africa (today's North West and Limpopo Provinces) (Tarboton & Allan, 1984). The Cape vulture has the smallest distribution of all Old World vultures (Mundy et al., 1992) and has experienced severe decreases across southern Africa, possibly losing 20% of its total population in the last three generations, qualifying it as globally and regionally '*Vulnerable*' (Anderson, 2000b; IUCN, 2010). The most dramatic declines have occurred in Namibia, where the population declined from around 2000 birds in the 1950s (Brown, 1985), to being regionally extinct as a breeding population with only 25 remaining birds in 2006 (BirdLife International, 2010b; Koenig, 2006). Declines in Cape vulture populations have also been seen in Botswana (Borello & Borello, 2002), Zimbabwe (Mundy et al., 1992), and South Africa (Boshoff, Piper, & Michael, 2010; Piper, 2004a), including within its core breeding and foraging range in the former Transvaal (Benson et al., 1990).

The factors leading to the vulture population declines observed in Africa are multi-faceted, dynamic and widespread. Cape and African white-backed vultures face similar threats in southern Africa due to their overlapping foraging ranges and exploitation of the same food supply (Mundy et al., 1992). Specifically, these threats include the following:

- **Changing land-use patterns and agricultural practices** are thought to have contributed significantly to vulture declines in southern Africa (Anderson, 2000a, 2000b). Over-hunting led to the extinction of wild ungulates in many parts of Africa, and their replacement with domestic livestock was concurrent (Dean, 2004; Du Toit & Cumming, 1999; Thiollay, 2006a). Coupled with improved livestock husbandry techniques over time, this led to a decrease in the number of carcasses available to vultures and corresponding population declines (Boshoff & Vernon, 1980; Dean, 2004; Robertson & Boshoff, 1986; Tarboton & Allan, 1984). In East Africa recent land use changes and declines in ungulate numbers due to poaching (Ogutu, Bhola, & Reid, 2005; 2009) have also been implicated in the decline of vultures through reduced food availability (Virani et al., 2011).

- **Poisoning** has been one of the most significant causes of vulture mortalities since the early 20th Century and has affected vulture populations across Africa (Brown & Piper, 1988; Finch-Davies, 1920; Mundy et al., 1992; Thiollay, 2006a, 2006b; Virani et al., 2011). Following the expansion of commercial farming practices in Africa there was an increase in the level of persecution directed at animals perceived as predators of livestock, and therefore a potential threat to economic stability (Blaum, Tietjen, & Rossmanith, 2009; Holmern, Nyahongo, & Roskaft, 2007; Kissui, 2008; Thiollay, 2006a). Inadvertent, or secondary poisoning caused many vulture fatalities throughout the 20th century, after they either consumed carcasses laced with poisons (e.g. strychnine, carbofuran, other systemic insecticides) aimed at killing mammalian carnivores (e.g. black-backed jackal *Canis mesomelas;* caracal *Felis caracal*), or they consumed the carcasses of the poisoned carnivores themselves (Brown & Piper, 1988; Mundy et al., 1992). Vultures were also intentionally persecuted due to suspicions of them predating new born lambs and fouling livestock water supplies during bathing activity (Brown & Piper, 1988; Finch-Davies, 1920; Mundy et al., 1992). Mundy et al. (1992) compiled a list of 33 poisoning events over a 12-year period that accounted for the deaths of about 1,250 vultures in southern Africa. Two of the worst cases resulted in the deaths of 89 African white-backed vultures in Kruger National Park in 1987 (Van Jaarsveld, 1987) and 126 African white-backed vultures in Wedza, Zimbabwe in 1992 (Mundy et al., 1992). Although legislation regarding the use of poisons may have reduced the numbers of vultures being poisoned, it is still regarded as a major threat and regular mass poisoning events occur throughout the continent (Anderson, 1994; Ogada & Keesing, 2010; Otieno et al., 2010; Thiollay, 2006b; Van Wyk et al., 2001). Virani *et al.* (2011) suggest that carbofuran poisoning aimed at livestock predators is the most significant cause of vulture declines in East Africa, with the deaths of as many as 187 vultures recorded at a single poisoned carcass.

- **The expanding power line network** poses a serious and increasing threat to vultures across southern Africa, with electrocutions and collisions causing a high number of fatalities since the mid 20th Century (Jenkins, Smallie, & Diamond, 2010; Markus, 1972; Nikolaus, 1984). For example, between 1970 and 1977, 300 vultures were killed due to fatal interactions with power-lines in the eastern region of the North West Province (Ledger & Annegarn, 1981). While Cape vultures use pylons for roosting (Ledger & Annegarn, 1981), African white-backed vultures have been recorded nesting on the structures (Anderson & Hohne, 2007; Ledger & Hobbs, 1985), and it is these activities that cause both species to be among the most likely species to suffer fatal collisions and electrocutions (Janss, 2000; Jenkins et al., 2010).

- **Habitat transformation and land degradation** in southern Africa have reduced the potential foraging range of vultures, as well as directly reducing the availability of breeding sites (Anderson, 2000a, 2000b; Mundy et al., 1992). For example, shrub encroachment caused by over-grazing has led to dramatic changes in the global savannah landscape with associated changes in biodiversity (Blaum, Rossmanith, Schwager, & Jeltsch, 2007; Sirami, Seymour, Midgley, & Barnard, 2009). Shrub encroachment negatively affects vultures by reducing the detectability of carcasses, and their high wing-loading and large size deters them from landing and taking off in areas of high tree density, and has thus been implicated in the near extinction of Cape vultures from Namibia (Bamford, Monadjem & Hardy, 2009a; Schultz, 2007).

- **The illegal harvesting of vultures** in southern Africa for traditional superstitious or medicinal beliefs is an increasingly severe threat, with estimates that both Cape and African white-backed vultures could be over-harvested to extinction within 15 years in certain parts of South Africa (Hengari, Cunningham, & Adank, 2004; Koenig, 2006; McKean, 2004; Whiting, Williams, & Hibbitts, 2011).

Additional threats to vultures in southern Africa include heavy metal poisoning (e.g. ingestion of lead bullets from hunting practices - Fisher, Pain, & Thomas, 2006; Garcia-Fernandez et al., 2005; Hunt et al., 2006; Van Wyk, van der Bank, Verdoorn, & Hofmann, 2001); osteodystrophy and calcium deficiency due to a reduction in the number of bone fragments available for consumption (Mundy & Ledger, 1976; Richardson et al., 1986); ingestion of man-made non-food items resulting in nestling mortality (Benson et al., 2004; Houston, Mee, & McGrady, 2007); drowning in farm reservoirs (Anderson, 2000c); intense competition from an increasing feral dog population (Butler & du Toit, 2002); and disturbance and loss of nest sites due to human and elephant activity (Bamford, Monadjem, & Hardy, 2009b; Benson, 1997; Borello & Borello, 2002; Monadjem & Garcelon, 2005). Furthermore, climate change could also be implicated in past and continuing declines of vultures in southern Africa (Simmons & Jenkins, 2007).

2.5. The role of protected areas for conserving vultures in Africa

With current rates of human population growth and global change, officially protected areas are playing an increasingly important role in the conservation of biodiversity (Biggs et al., 2008). The protected area network that covers 12% of the Earth's terrestrial surface, however, is not evenly distributed, and the effectiveness of protected areas in conserving biodiversity varies regionally (Jenkins & Joppa, 2009; Loucks et al. 2008). This is particularly true in Africa. For example, Botswana has protected areas covering 18.2% of its land surface, with a further 23% as wildlife management areas (CBD, 2010a). By comparison, South Africa's protected area network consists of 508 relatively small terrestrial protected areas covering only 6.2% of its land surface (CBD, 2010b).

The relative importance of protected and unprotected areas for vultures also varies regionally in Africa, although the majority of studies suggest that protected areas will play a critical role in the future conservation of vultures on the continent (e.g. (Thiollay, 2006a; Virani et al., 2011)). Declines in vulture populations in East and West Africa caused largely by food shortages and poisoning have led to their complete absence in unprotected areas in many areas, while they persist in protected areas in much lower numbers than previously (Rondeau & Thiollay, 2004; Thiollay, 2006a, 2006b, 2007; Virani et al., 2011). In Guinea, however, Rondeau et al. (2008) failed to record a single vulture inside a protected area during 3,635km of road transect surveys, while they were regularly observed in unprotected areas.

In Botswana, vultures were encountered most often and in the largest numbers at the interface between conservation areas and unprotected land, and were better represented away from conservation areas than inside them (Herremans & Herremans-Tonnoeyr, 2000). It was suggested that vultures are able to exploit the "best of both worlds" by using the security of conservation areas for roosting and breeding activity, while livestock carcasses on the periphery of those areas provide a regular food supply in addition to the wild species inside the reserves (Herremans & Herremans-Tonnoeyr, 2000). Furthermore, by foraging outside protected areas vultures are perhaps more likely to feed successfully at a carcass without competition from large mammalian carnivores that rely on the protection of conservation areas (Bauer & Van der Merwe, 2004; Houston, 1974c; Hunter et al., 2006; Kruuk, 1967).

Several studies have suggested that African white-backed vultures show a preference to nest within protected areas in southern Africa due to reduced levels of human disturbance and increased food availability (Bamford et al. 2009a; Bamford et al., 2009b; Monadjem & Garcelon, 2005). In certain areas of South Africa, however, the majority of African white-backed vulture nests are located on private land outside protected areas (Anderson & Maritz, 1997; Benson, 1997; Murn, Anderson, & Anthony, 2002). Furthermore, in many regions of southern Africa vultures regularly feed, sometimes exclusively, on livestock carcasses outside protected areas (Murn & Anderson, 2008; Robertson & Boshoff, 1986). Murn and Anderson (2008) found that vultures in the Kimberley area of South Africa's Northern Cape favoured mixed cattle and game farms for feeding, roosting and breeding activity, mainly due to the higher food availability on those properties. In addition, they found a positive relationship between vulture activity and hunting and culling activity (Murn & Anderson, 2008), supporting suggestions made in Europe that hunting activity increases food availability for *Gyps* vultures, and influences their spatiotemporal distribution (Mateo-Tomás & Olea, 2010). Communal grazing land is also thought to be an important source of food for vulture populations in the Limpopo Province of South Africa due to high stock mortalities relative to commercial farms (Benson et al., 2004; Benson et al., 1990). In contrast, however, vultures fitted with satellite tracking devices in Namibia avoided communal land and fed most regularly on private livestock farmland (Bamford et al., 2007).

The establishment of relatively new protected areas such as Pilanesberg National Park and Madikwe Game Reserve in the North West Province of South Africa was expected to benefit vulture populations by providing a safe source of food and security from anthropogenic threats (Anderson, 2000a; Benson, 1997; Mundy et al., 1992). In contrast to other southern African countries, however, South Africa's protected area network consists mainly of medium- or small-sized reserves that are completely fenced and isolated, with ungulate populations often limited by high densities of predators (CBD, 2010b; Hayward, O'Brien, & Kerley, 2007; Newmark, 2008). Increasing isolation of protected areas in Africa has led to a number of negative ecological impacts (Newmark, 2008). Where ungulate populations undergo seasonal migrations, predators do not play an important regulatory role, and other factors (e.g. lack of food, disease) account for the majority of mortalities (Mills & Shenk, 1992; Sinclair, Dublin, & Borner, 1985). In enclosed reserves, however, where prey species are forced to be sedentary, predators regulate and often reduce ungulate populations (Harrington et al., 1999; Power, 2002; Smuts, 1978). For example, in Pilanesberg National Park, populations of several ungulate species declined by up to 76% between 1997 and 2002, due to high levels of lion predation and a high ratio of lions to prey species (Hayward, O'Brien, & Kerley, 2007; Tambling & du Toit, 2005).

The high levels of ungulate predation in isolated protected areas would result in a reduction in carcasses available to vultures and high levels of competition from mammalian carnivores such as lions and hyaena (Hunter et al., 2006; Kruuk, 1967). This is likely to reduce the ability of vultures to exploit carcasses in isolated protected areas that contain a full complement of mammalian carnivores (Houston, 1974c). For instance, Houston (1974c) cites the Ngorongoro Crater in Tanzania as an example of an isolated reserve where vultures "are rarely seen feeding" due to intense competition from unusually high numbers of mammalian carnivores. Fenced reserves in southern Africa often exceed their carrying capacity for large predators (Hayward et al., 2007), but the resultant effects on vultures have not been studied. Furthermore, fenced reserves in southern Africa often introduce elephants, with severe impacts on vegetation structure (Boundja & Midgley, 2010; Duffy et al., 2002), and damage to trees has been implicated in the decline or absence of nesting African white-backed vultures in those areas (Monadjem & Garcelon, 2005).

Protected areas do play a critical role in conserving vulture populations, particularly during the breeding season (Bamford, Monadjem, & Hardy, 2009b; Monadjem & Garcelon, 2005; Thiollay, 2006a). It is clear, however, that there is a high degree of spatial variation of land use preferences exhibited by vultures in Africa, and it is likely that food availability is the main factor that determines the level of vulture activity in an area (Mundy et al., 1992; Murn & Anderson, 2008). The ability of vultures to fly long distances and cover extensive foraging ranges in a short period of time (Pennycuick, 1972), coupled with the ephemeral nature of their food supply (Houston, 1974a), make it necessary for them to exploit resources across a range of land-use types and under varying levels of protection (Murn & Anderson, 2008).

The relative importance of protected and unprotected areas for vulture activity is still not fully understood (Murn & Anderson, 2008), and has been recognised as a priority research area of particular importance for the future conservation of vultures, especially when considering existing and emerging threats, such as the exposure to harmful veterinary drugs (Anderson et al., 2005; Boshoff & Anderson, 2006). The use of GPS tracking technology has been advocated as the most efficient and accurate method to study vulture foraging activity (Boshoff & Anderson, 2006; Urbano et al., 2010) and is discussed in the following section.

2.6. Tracking technology and ranging studies

Tracking technology is able to produce data that are often unattainable using other methods, and telemetry studies are regarded as valuable tools for the conservation of endangered species, particularly for species that occupy large ranges or undertake large-scale movements (Cooke, 2008). Telemetry was first used to study raptor movement and ecology in the 1960s using Very High Frequency (VHF) radio-tracking equipment (Southern, 1964), and since then rapid advances in technology have led to increased use of biotelemetry for a wide variety of ecological studies (Hebblewhite & Haydon, 2010). Terrestrial mammal species studied by such tracking techniques range from African elephants (Douglas-Hamilton, Krink, & Vollrath, 2005; Loarie, van Aarde, & Pimm, 2009) to short-snouted elephant shrews (*Elephantulus brachyrhynchus*) (Yarnell et al., 2008). Owing to their high mobility and large ranges, tracking technology has been used extensively on a variety of raptor species to study migration, home ranges, habitat preferences, dispersal, movement patterns and survival (Lindberg & Walker, 2007; Meyburg & Fuller, 2007). New technology has led to the “miniaturisation” of tracking devices (Tomkiewicz, Fuller, Kie, & Bates, 2010) which has allowed studies to be carried out on much smaller species such as

Eleonora's falcon *Falco eleonorae* (López- López, Liminana, Mellone, & Urios, 2010), compared to earlier studies that focussed on larger species (e.g. Bald eagles *Haliaeetus leucocephalus* (Mabie, Merendino, & Reid, 1994)).

The incorporation of GPS technology into tracking methods has increased the efficiency and accuracy of collecting positional data for a diverse array of ecological studies (Hebblewhite & Haydon, 2010). Locations recorded by GPS tracking units are consistently accurate to within 10-28 m, compared to 200-600 m for locations acquired via triangulation and homing using VHF devices (Frair et al., 2010). An additional advantage of GPS and satellite tracking systems over earlier VHF technology is that data can be collected remotely without the need for a field researcher to determine locations of the study animal on the ground (Hebblewhite & Haydon, 2010; Rodgers, Rempel, & Abraham, 1996). The data can be downloaded via a range of communication networks, such as the Argos satellite network and the Global System for Mobile communications (GSM) network (Tomkiewicz et al., 2010). The main disadvantage of GPS tracking technology is that the cost per unit (US$ 2000 - 8000) is often an order of magnitude greater than for a VHF device, leading to smaller sample sizes and potentially limited statistical rigour (Hebblewhite & Haydon, 2010; Lindberg & Walker, 2007).

There are many methods for the analysis of location data from telemetry studies, and the method chosen depends on the aims of the study and the nature of the data (Hebblewhite & Haydon, 2010; Urbano et al., 2010). In an extensive review, Hebblewhite and Haydon (2010) suggest that the most important data from a conservation point of view have frequently arisen from simplistic but clearly presented analyses. While stochastic modelling techniques are being used more frequently for the interpretation of movement processes, particularly at the population level (Morales, Haydon, Frair, Holsinger, & Fryxell, 2004), home range estimation methods remain popular (Kie et al., 2010; Laver & Kelly, 2008).

Burt (1943) describes an animal's home range as "that area traversed by the individual in its normal activities of food gathering, mating and caring for young". An animal's home range is essentially a spatial expression of the link between its movements and the distribution of the resources necessary for its survival and reproduction (Börger, Dalziel, & Fryxell, 2008). The accurate estimation of animals' home ranges provides important information about a species' spatial and behavioural ecology (Harris et al., 1990), and is important for the planning and implementation of effective conservation and management strategies (Boyle, Lourenco, da Silva, & Smith, 2009; Caro, 1998). There are a large variety of home range estimation methods and software packages that have been extensively reviewed (Kie et al., 2010; Laver & Kelly, 2008; Seaman & Powell, 1996), but the most commonly used techniques involve minimum convex polygon analysis and kernel density estimation (Börger et al., 2008; Kie et al., 2010; Laver & Kelly, 2008).

The minimum convex polygon (MCP) method involves the creation of polygons by connecting adjacent peripheral locations, with all internal angles being less than 180 degrees (Mohr, 1947), including all fixes or a subset of these (Harris et al., 1990). Due to its widespread use, MCP analysis has been suggested to provide comparability between studies (Harris et al., 1990). However, the method has a number of disadvantages: MCPs provide only a crude outline of an animal's range; they assume uniform space use within the range boundary; and estimates are highly sensitive to variations in sample size, sampling regime and outlying locations, resulting in the inclusion of large areas that were never visited by the animal (Börger et al., 2006; Burgman & Fox, 2003; Downs & Horner, 2008; Laver & Kelly, 2008; Worton, 1987). Laver and Kelly (2008) suggested that MCP analysis should only be used to identify forays outside of the home range (Burt, 1943), and should be used in addition to other more robust methods (Kie et al., 2010).

Kernel density estimation (KDE) of home ranges has become the method of choice for the majority of studies (Kie et al., 2010; Laver & Kelly, 2008) due to its greater ability to exclude large proportions of unused areas and account for multiple centres of activity, resulting in more accurate depictions of space use (Hemson et al., 2005; Kenward, 2001; Worton, 1989). KDE creates contours of different intensities of utilisation (isopleths) across a home range by calculating the mean influence of GPS locations at a series of grid intersections (Hemson et al., 2005; Worton, 1989). To achieve this, a kernel (i.e. a probability density) is placed over each GPS location and a grid is superimposed on the data (Seaman & Powell, 1996). The average of the densities of all of the kernels that overlap at each grid intersection is then calculated to produce an estimated kernel density at that point, with areas with many GPS locations producing higher density estimates than those with few (Seaman &

Powell, 1996; Worton, 1989). The resulting isopleths contain a fixed percentage of the utilization density corresponding to the amount of time that the study animal spent in the area within that contour (Hemson et al., 2005; Wartmann, Purves, & van Schaik, 2010; Wauters, Preatoni, Molinari, & Tosi, 2007). The overall home range is most frequently represented by the 95% contour, while core areas are normally delineated by 50% contours (Kie et al., 2010; Laver & Kelly, 2008). The spatial distribution of the different contours is termed a “utilisation distribution” (Worton, 1989), and each contour essentially describes the probability of being reasonably close to the study animal when stood in a given place (Kie et al., 2010).

The critical issue during KDE is the selection of the width of the kernel, also termed the smoothing parameter, bandwidth, or ‘*h*’ (Seaman & Powell, 1996; Silverman, 1986; Worton, 1989). The size of the kernel is the distance over which a data point (i.e. GPS location) influences the grid intersections, with smaller bandwidths resulting in nearby locations having the greatest influence on density estimates, and larger values allowing more distant locations to have a greater influence (Seaman & Powell, 1996). Large bandwidths tend to produce larger and less detailed home range contours, while smaller bandwidths reveal the internal structure of a home range at a finer scale but can produce discontinuous outer contours (Hemson et al., 2005; Seaman & Powell, 1996; Wauters et al., 2007).

A number of methods exist for bandwidth selection, each of which tend to select different *h* values and therefore produce home range estimates of different sizes and shapes (Hemson et al., 2005). The reference bandwidth (h_{ref}) is frequently used and is calculated as the square root of the mean variance in the x and y co-ordinates divided by the sixth root of the number of GPS locations (Rodgers & Kie, 2010; Worton, 1989, 1995). This method of bandwidth selection assumes, however, that the GPS locations are normally distributed in bivariate space (Worton, 1995), which is unlikely due to the irregular manner in which most animals use their home ranges, often occupying multiple centres of activity (Kie et al., 2010; Seaman & Powell, 1996). Consequently, the reference bandwidth is often too large, particularly when animal locations are clumped, resulting in over-smoothed outer contours and over-estimated home range areas (Kie et al., 2010; Seaman & Powell, 1996; Wauters et al., 2007; Worton, 1989).

A regularly used alternative to the reference bandwidth method is least-squared cross-validation (LSCV - Seaman & Powell, 1996; Silverman, 1986). LSCV examines different bandwidths and selects the one (h_{lscv}) that minimises the estimated error score between the true density function and the kernel density estimate (Seaman & Powell, 1996; Silverman, 1986). Although LSCV has been shown to reduce the problem of over-smoothing associated with the use of the reference bandwidth (Seaman & Powell, 1996; Worton, 1989), it often results in under-smoothing when used to analyse a large number of GPS locations distributed in numerous small clusters, producing small isolated contours around individual locations (Boyle et al., 2009; Hemson et al., 2005; Kie et al., 2010). Furthermore, the LSCV method often fails to select an alternative bandwidth to the reference bandwidth if there are numerous GPS locations very close together when the study animal intensively uses core areas or displays high levels of site fidelity (Hemson et al., 2005).

A compromise between using h_{ref} or h_{lscv} is to reduce the reference bandwidth by a fixed proportion (e.g. 0.75) to produce an “adjusted” bandwidth, h_{adj} (Kie et al., 2010; Wauters et al., 2007). Similarly, the *ad hoc* method of bandwidth selection involves selecting the smallest increment of the reference bandwidth (e.g. $h_{ref} \times 0.80$) that results in a contiguous outer home-range boundary (e.g. 95% isopleth) (K. M. Berger & Gese, 2007; Jacques, Jenks, & Klaver, 2009; Kie et al., 2010). Both methods have proved to be successful at reducing the effects of over- or under-smoothing of kernel contours associated with h_{ref} or h_{lscv} selected bandwidths (Berger & Gese, 2007; Jacques et al., 2009; Kie et al., 2010; Wauters et al., 2007). There is no single best method for bandwidth selection, and it is recognised that the final choice will depend on the aims of the analysis and a degree of subjectivity (Kie et al., 2010; Worton, 1989).

One of the original approaches to studying animal movement patterns is the method of overlaying grid cells onto animal locations (Adams & Davis, 1967; Siniff & Tester, 1965), and it has been especially well utilised for studies of primate ranging patterns (Chapman & Wrangham, 1993; Grueter, Dayong, Ren, & Wei, 2009; Herbinger, Boesch, & Rothe, 2001; Li, Chen, Ji, & Ren, 2000; Robbins & McNeilage, 2003), as well as for other taxonomic groups including bears (Horner & Powell, 1990), elephants (Douglas-Hamilton et al., 2005) and dolphins (Frère et al., 2010). An estimate of the size of an animal’s range is derived by summing the area of the grid cells containing positional records, or through which the animal is assumed to have travelled (Chapman & Wrangham, 1993; Douglas-Hamilton et al., 2005; White & Garrott, 1990). Identification of core areas is achieved by the selection of grid cells containing a certain proportion of locations (e.g. 50% (Horner & Powell, 1990); 75 % (Frère et al., 2010; Robbins & McNeilage, 2003)), or that contain more than the mean number of locations per cell (Horner & Powell, 1990). Although the size of the estimates produced using the grid cell method are highly sensitive to the size of the grid cells used (Grueter et al., 2009; Kool & Croft, 1992) and range sizes are often under-estimated, the inclusion of unvisited areas within the range boundaries is reduced compared to other methods (Grueter et al., 2009; Sterling, Nguyen, & Fashing, 2000).

Due to the non-random manner in which animals tend to move and the fixed time intervals at which locations are recorded, GPS tracking datasets often consist of locations that are not independent of each other and are therefore strongly autocorrelated (De Solla, Bonduriansky, & Brooks, 1999; Fieberg, Matthiopoulos, Hebblewhite, Boyce, & Frair, 2010). While some authors suggest subsampling locations to achieve independence of observations to produce unbiased estimates during range analysis (Swihart & Slade, 1985), others recommend maximising the number of locations using constant time intervals to increase the accuracy of range estimates (De Solla et al., 1999). Recently the issue of autocorrelation when applied to tracking data has been considered to be a potential “red herring”, with the subsampling of data often reducing the accuracy of the home range estimates due to the removal of biological meaningful data (De Solla et al., 1999; Fieberg, 2007; Fieberg et al., 2010). Laver and Kelly (2008) do, however, recommend that the degree of autocorrelation in tracking data is assessed and reported.

It is generally agreed that the methods chosen for home range estimation will largely depend on the data available and the research questions posed (Boyle et al., 2009; Harris et al., 1990; Kie et al., 2010; Laver & Kelly, 2008; Wauters et al., 2007). Kernel density estimation has been widely advocated as an appropriate method for home range analysis (Börger et al., 2006; Laver & Kelly, 2008), particularly when combined with additional information such as habitat and other environmental variables (Fieberg et al., 2010; Kie et al., 2010). Due to the large number and variability of different techniques for home range estimation, full reporting of the methods used and parameters set are essential (Boyle et al., 2009; Laver & Kelly, 2008). Furthermore, the use of multiple methods when analysing ranging patterns has been regularly promoted (Boyle et al., 2009; Harris et al., 1990; Kie et al., 2010).

2.7. *Gyps* vultures as subjects of tracking studies

One of the first studies of *Gyps* vulture movement patterns using tracking methods was carried out on an adult Cape vulture at the Potberg nesting colony in the south-western Cape Province of South Africa (Boshoff et al., 1984). A VHF transmitter was fitted to a rehabilitated vulture using a nylon ‘backpack’ harness, and the vulture’s locations were determined by triangulation on 32 days (Boshoff et al., 1984). Using the tracking data in conjunction with a questionnaire survey, the authors estimated that the vultures from the Potberg colony foraged in an area of 1,940 km^2, and fed exclusively on livestock carcasses (Boshoff et al., 1984; Robertson & Boshoff, 1986). Flying speeds were estimated between 26 and 69 km/h, and foraging distances from the colony were greater in the summer than winter (Boshoff et al., 1984). There were significant limitations of the study, however, mainly due to the limited range (50 km from the observer) and potential inaccuracy of the VHF system (Boshoff et al., 1984). Brown and Piper (1988) estimated a much larger foraging range of 9,200 km^2 for Cape vultures in the Drakensberg Mountains of South Africa, using re-sightings of individuals marked with colour leg rings.

A recent study used GPS-satellite tracking units to study the movements of five adult and one immature Cape vulture and one immature African white-backed vulture in the Waterberg area of Namibia (Bamford et al., 2007). The vultures were caught at a vulture restaurant using a walk-in cage trap (Bamford, Monadjem, Diekmann, & Hardy, 2009), and the units were fitted using a Teflon ribbon backpack harness, a stronger alternative to nylon (Diekmann, Scott, Scott, & Diekmann, 2004). The tracking devices recorded hourly daytime locations accurate to within 10 m (Bamford et al., 2007) and their ability to collect continuous and highly accurate data provided previously unknown information about vulture activity, with emphasis on the much larger foraging ranges compared to previous studies. Home range analyses generated combined MCPs of 38,327 km^2 for the five adult Cape vultures and a mean MCP of 482,276 km^2 for the two immature vultures, supporting the suggestion that immature vultures range much more widely than adults, regularly crossing international borders (Mundy et al., 1992). The data also indicated that the vultures foraged almost exclusively on private farmland, where the risk of inadvertent poisoning was likely to be higher than in protected areas, and that they regularly used a number of vulture restaurants (Bamford et al., 2007).

Additional tracking studies on *Gyps* vultures in Africa are limited, but include the use of GPS-GSM devices to study the movements and survival of rehabilitated vultures in the Magaliesberg area of South Africa (Bartels, van't Foort, & Wolter, 2007). Studies on *Gyps* vultures using tracking technology outside of Africa include a VHF tracking study used to investigate foraging behaviour and flight characteristics of Eurasian griffon vultures (Xirouchakis & Andreou, 2009); a satellite tracking study to follow the migratory route of a Eurasian griffon vulture in Spain (Berthold, Griesinger, Nowak, & Querner, 1991); and the use of GPS-satellite devices to investigate the foraging patterns of Oriental white-backed vultures in Pakistan (Gilbert, Watson, Ahmed, Asim, & Johnson, 2007).

Non-*Gyps* species of both Old and New World vultures studied using tracking technology include Egyptian vultures (*Neophron percnopterus*) (Garcia-Ripolles, Lopez-Lopez, & Urios, 2010; Meyburg, Gallardo, Meyburg, & Dimitrova, 2004), cinereous vultures (*Aegypius monachus*) (Carrete & Donázar, 2005), and black vultures (*Coragyps atratus*) and turkey vultures (*Cathartes aura*) in North America (Coleman & Fraser, 1989; Mandel, Bildstein, Bohrer, & Winkler, 2008). A recent GPS tracking study investigated the foraging range and land use preferences of a juvenile bearded vulture (*Gypaetus barbatus meridionalis*) in South Africa (Urios, Lopez-Lopez, Liminana, & Godino, 2010). Continued use of tracking technology to gain information about vulture behaviour, land use preferences and potential threats is encouraged as a valuable conservation tool (Boshoff & Anderson, 2006; Virani et al., 2011).

2.8. Dissertation objectives and structure

Given the lack of detailed studies on landscape utilisation by *Gyps* vultures and the declining status of many species, there is an urgent need to increase our knowledge of their movement patterns in order to assess likely drivers of population changes. Moreover, the recent discovery that certain veterinary drugs are toxic to *Gyps* vultures emphasises the importance of investigating their foraging ecology and identifying their key foraging areas in order to assess the potential risk of poisoning.

In this dissertation I use GPS telemetry to investigate the ranging patterns of African white-backed vultures caught from the wild in the North West Province of South Africa, and also quantify their use of protected areas. I focus on immature vultures because they are believed to range widely and are therefore more likely to be exposed to the full range of threats that operate in the wider landscape. While studies on adult vultures are also crucial, the number of GPS tracking units available for this study was limited and the focus was therefore on a sample of similar-aged birds.

The remainder of the dissertation is divided into three general chapters consisting of Methods, Results and Discussion, and a final chapter in the format of an article for submission to a peer reviewed journal.

Chapter 3 provides details of the methods used to investigate the following topics:

- **Foraging range analysis**

  Three methods were used to provide estimates of the size and extent of the foraging ranges used by the vultures during their total tracking periods:

  - Minimum convex polygons
  - Fixed kernel density estimation
  - Grid cell range estimates

  Grid cell range estimates were also calculated for individual months for each vulture to identify temporal patterns of range use.

- **Use of protected areas and areas of varying cattle density**

  The amount of time that the vultures spent inside protected areas and areas of different cattle densities was calculated to determine whether they were used in proportion to their availability in the vultures' overall foraging ranges.

- **Flight characteristics**

  Three features of the tracked vultures' flight patterns were investigated:

  - Distances travelled
  - Flight speeds
  - Flight altitudes above ground level

- **Use of supplementary feeding sites**

  The amount of time that the vultures spent in the vicinity of supplementary feeding sites for scavengers was estimated and their influence on the vultures' movement patterns was examined.

The results of the different sections of analysis are presented and discussed in Chapters 4 and 5, respectively. The key findings have been compiled into an article prepared for submission to a peer-reviewed journal, presented in Chapter 6.

CHAPTER 3

MATERIALS AND METHODS

3.1. Study site

A supplementary feeding site for mammalian and avian scavengers was established in 2008 at Mankwe Wildlife Reserve (MWR) in the North West Province of South Africa (25°13'S, 27°18'E). MWR is a privately managed game reserve covering an area of 47 km^2 approximately 4 km east of Pilanesberg National Park (PNP; 25°14'S, 27 °05'E; Figure 3.1). The Pilanesberg area is located within the transition zone between Bushveld in the east and the drier Kalahari Thornveld in the west (Acocks, 1988). The habitat consists mainly of savannah ranging from *Acacia* and *Dichrostachys* thickets to open grassland. Climate is sub-arid, with annual rainfall of approximately 650 mm falling in the summer months from October until April, and mean daily temperatures ranging from 11°C in July to 23°C in December (Yarnell et al., 2008).

Food was delivered to the scavenger feeding site approximately twice per week in the form of intact ungulate carcasses and waste products (e.g. offal, heads) from hunting activity conducted on MWR. The majority of the carcasses, however, were of domestic ungulates such as cattle (*Bos taurus*), donkeys (*Equus asinus*) and sheep (*Ovis aries*) collected from local farmers, as well as wild ungulates that died from natural causes on MWR. The scavenging species that regularly used the feeding site included Cape, lappet-faced and African white-backed vultures, pied crows (*Corvus albus*), black-backed jackals (*Canis mesomelas*), brown hyaena (*Hyaena brunnea*) and bushpigs (*Potamochoerus larvatus*).

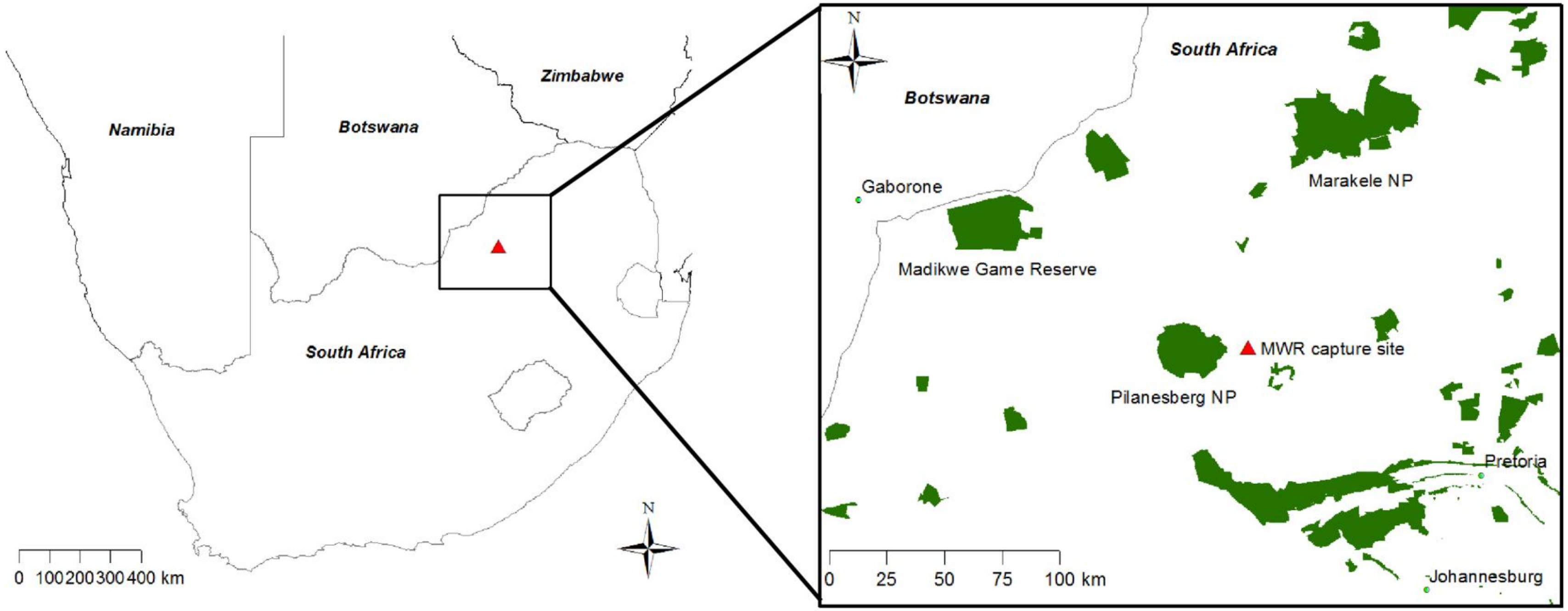

Figure 3.1. Maps showing the location of the Mankwe Wildlife Reserve vulture capture site (red triangle) in relation to Pilanesberg National Park, Marakele National Park and Madikwe Game Reserve in South Africa. Green polygons represent protected areas (IUCN & UNEP, 2010).

3.2. Study subjects

The population status and distribution of African white-backed vultures were described in the previous chapter (Section 2.3.). Only immature African white-backed vultures less than five years of age were required for this study. They were differentiated from Cape vultures by their smaller size, darker brown plumage and black, rather than pale eyes (Figure 3.2 - Mundy et al., 1992). Immature white-backed vultures also lack the characteristic white patch present on the back of adult birds, tend to be darker in colour and have longer feathers at the base of the neck, forming a feathery ‘ruff’ (Mundy et al., 1992). These features were used to identify the immature African white-backed vultures targeted for capture.

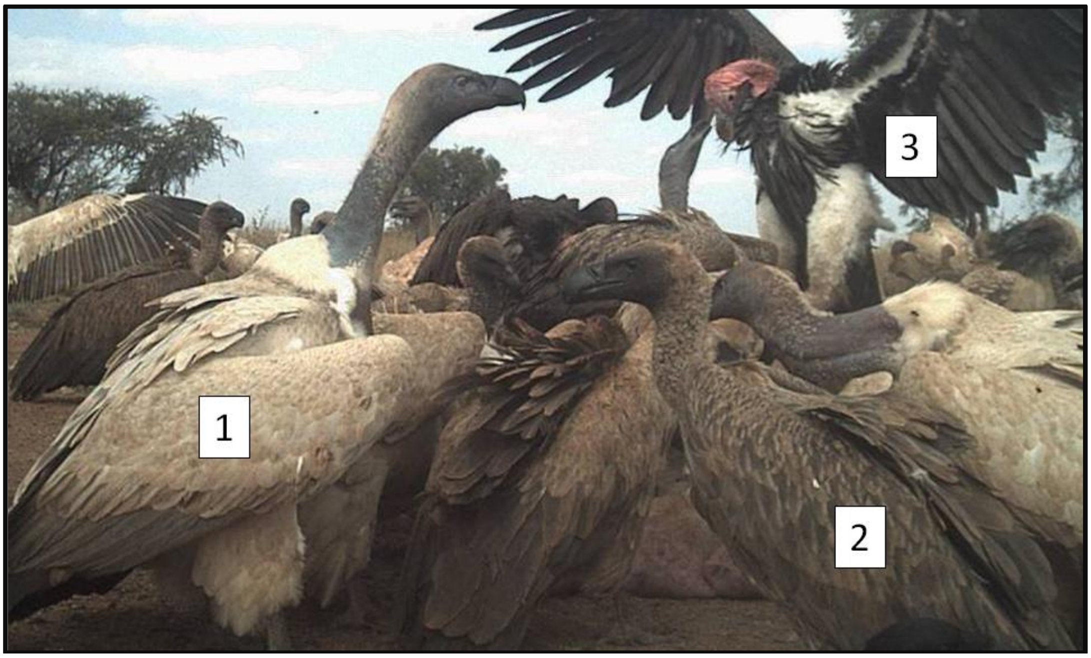

Figure 3.2. Photograph of (1) an adult Cape vulture, (2) an immature African white-backed vulture and (3) an adult lappet-faced vulture at a carcass at Mankwe Wildlife Reserve scavenger feeding site.

3.3. Capture method

A walk-in cage trap (6 x 3 x 3 m) constructed from a lightweight steel frame overlaid with 50 x 25 mm wire mesh was used to catch the vultures at the feeding site (Figure 3.3). The top of the cage was covered with plastic netting. The cage was closed by pulling a steel cable attached to the bottom of a plastic curtain across an entrance opening (3 x 2 m) at one end of the trap from a small observation hide concealed 30 metres away beneath a tree. Large branches from dead trees were placed around the cage (~2 m away) to act as perches for the vultures, to prevent resident white rhinoceroses (*Ceratotherium simum*) from damaging the steel frame and to provide anchor points to which the cage was attached with guy-cables. The trap was specifically designed to be portable and could be made ready for capture within four hours by a team of five people.

For at least two days prior to attempted captures, carcasses were placed in and around the cage to attract vultures to the area and allow them to become accustomed to feeding at the site. A carcass was placed inside the cage on the evening before a capture, with a small amount of meat left outside to encourage the vultures to land and feed. All captures were undertaken in the early morning to coincide with the vultures' normal feeding behaviour and to avoid heat stress. Once the target vulture(s) had entered far enough into the cage, the cable was pulled from the hide to close the curtain.

Figure 3.3. Photograph of a heifer carcass inside the walk-in capture cage at Mankwe Wildlife Reserve. The curtain was closed by pulling a cable attached to the bottom corner after the target vulture(s) had entered the cage.

3.4. Processing of captured vultures

Captured vultures were removed from the cage by hand and lightly restrained on a table without sedation for a general examination and fitting of patagial tags, a metal leg ring and the GPS tracking unit. One person held the vulture by the head and neck while a second held the legs and wings. Each vulture's body condition was examined by feeling the size of the pectoral muscles either side of the sternum, with poorer condition being indicated by reduced muscle size and a protruding breastbone. Only vultures with normal muscle condition were fitted with tracking devices.

3.4.1. Fitting of patagial tags and metal leg rings

Patagial tags were fitted to both wings of the captured vultures. The tags were the same as livestock ear-tags and were attached to the wing through the patagium at the leading edge of the wing, sightly distal to the elbow joint (Varland, Smallwood, Young, & Kochert, 2007). The tags were yellow with a unique four-character code etched in black comprising a letter indicating the tagging location and three numbers representing the vulture's identification number (e.g. B308). This allowed identification of the marked vultures from a reasonable distance after release. A G-size metal SAFRING (South African Bird Ringing Unit, University of Cape Town) ring with a unique identification code was also fitted to one leg of each captured vulture. The rings and patagial tags were fitted by SAFRING-certified vulture ringers (K. Wolter, SAFRING number: 1394; W.L. Phipps, SAFRING number: 1534) in accordance with a regional vulture mark-resighting study co-ordinated by SAFRING and the Endangered Wildlife Trust of South Africa (Botha, 2007).

3.4.2. Fitting of GPS tracking units

The tracking devices deployed in this study were Hawk105 GPS-GSM units manufactured by Africa Wildlife Tracking Ltd, Pretoria, South Africa (www.awt.co.za). Each device weighed 170g (*c.* 3.1% of the mean mass of an African white-backed vulture (Mundy et al., 1992)), and measured 35 x 70 x 25 mm. The casing was made from specially designed hardened resin for protection and waterproofing, with three protruding metal rings used to attach the harness. The units were powered by three AA lithium batteries and recorded the vultures' GPS location to an accuracy of 10 metres, as well as the altitude above sea level, speed and direction of travel, date, time and ambient temperature. The tracking units also recorded a positional dilution of precision (PDOP) value to measure the accuracy of each GPS location. PDOP is a geometric measurement dependent on the number and relative position of the satellites that transmit the signals to the GPS receiver in the tracking unit required to calculate the vulture's position, with more satellites and larger distances between them resulting in increased accuracy of GPS readings and lower PDOP values (D'Eon & Delparte, 2005; Tsui, 2000).

The tracking units were programmed to record data three times per day at 7h00, 11h00 and 15h00 (UTC+02). These times were chosen to provide information about the vultures' movement patterns throughout the day. At 7h00 the vultures were expected to be perched or feeding near ground level due to the lack of thermals necessary for soaring, while the 11h00 and 15h00 readings were likely to record both moving and stationary GPS locations (Mundy et al., 1992; Pennycuick, 1972) The data were stored in each unit's non-volatile memory before being sent once daily by short message service (SMS) to a secure online database via the Global System for Mobile communications (GSM) network. When a vulture was located in an area without GSM coverage, up to 20,000 data points could be stored on the unit and transmitted when it returned to an area with coverage. Based on the selected sampling regime, the manufacturer estimated that a unit would record and transmit data for approximately one year.

The tracking units were secured to the backs of each vulture using a Teflon® 'backpack' harness enclosed in flexible plastic tubing to prevent skin abrasions (Figure 3.4) (Bartels et al., 2007; Diekmann et al., 2004). From the metal ring on the back of the unit, the harness was looped between the legs, along the breastbone and over the 'shoulders' of the vulture. The two ends of the harness were then tied together after passing through both of the metal rings on the front corners of the device and secured with dental cord and super-glue (Meyburg & Fuller, 2007). Excess lengths of harness were removed using scissors. The tightness of the harness was checked and adjusted throughout the process, and two metal rings were closed around the harness near the tail-bone and breast-bone to ensure that it was held in position after releasing the vulture. The vultures were examined to ensure that they were able to move freely and normally before being released a suitable distance (*c.* 100 m) from the capture cage, and were monitored until they left MWR.

This study was approved by the Animal Use and Care Committee of the University of Pretoria (Protocol: V033-09). 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).

Figure 3.4. Photograph showing an immature African white-backed vulture (AG350) being fitted with a GPS-GSM tracking device with a Teflon® backpack harness. The patagial tag (code B345) is visible on the vulture’s right wing.

3.5. Data Analysis

Data from six GPS-GSM tracking units deployed on immature African white-backed vultures were used to investigate:

- Foraging ranges of individuals
- The utilisation of protected areas and areas of different cattle densities
- Characteristics of flight patterns e.g. distance travelled, speed, altitude
- The influence of supplementary feeding sites on movement patterns.

3.5.1. Foraging range estimation

As the tracked vultures were immature individuals rather than adults, it was not deemed appropriate to term their ranges as *home* ranges based on Burt's (1943) definition because it was assumed that the primary factor determining the vultures' movements was that of "food gathering" rather than "mating, and caring for young" (Burt, 1943). The areas in which the vultures were present during the study are therefore termed *foraging* ranges.

The aim of the foraging range analysis was to quantify the extent of the area over which the vultures travelled during the study period, and to identify the relative intensity of utilisation of different areas within their overall ranges.

Three methods were used to estimate the size and extent of the foraging ranges traversed by the vultures: minimum convex polygon (MCP) (Mohr, 1947), fixed kernel density estimation (KDE) (Worton, 1989) and grid cell range estimates (GCR) (Chapman & Wrangham, 1993; Harris et al., 1990). While all three methods were used to estimate the foraging ranges using the data obtained from the total tracking periods for each vulture, only GCR estimates were calculated separately for individual complete months (i.e. months with GPS locations recorded on at least 90% of days in that month).

Home Range Tools (HRT version 1.1.; (Rodgers, Carr, Beyer, Smith, & Kie, 2007)) extension for ArcGIS (version 9.3; Environmental Systems Research Institute (ESRI, 2008), Redlands, California, USA) was used for all range estimation methods unless otherwise stated. GPS locations were converted to the Universal Tranverse Mercator

(UTM) coordinate system (WGS 1984 UTM Zone 35S) using Franson CoordTrans software (Version 2.3; Franson Technology).

(i) Minimum Convex Polygon (MCP) analysis.

Foraging ranges delineated by MCPs were calculated for total tracking periods to allow for comparisons to be made with previous studies of *Gyps* vulture ranges in southern Africa (e.g. Bamford et al., 2007).

Home Range Tools extension (Rodgers et al., 2007) for ArcGIS (ESRI, 2008) generated MCPs by connecting the outermost GPS locations to form an enclosed polygon with no internal angles exceeding 180 degrees (Mohr, 1947; Worton, 1989). All fixes were used to produce a total, or 100% MCP that represented the total area that could *potentially* have been exploited by the vultures (Harris et al., 1990).

(ii) Kernel Density Estimation (KDE).

A description of kernel density estimation and associated procedures used in this study is provided in section 2.6 of Chapter 2.

KDE was performed using the Home Range Tools (Rodgers et al., 2007) extension for ArcGIS (ESRI, 2008) to calculate the vultures' foraging ranges for the total tracking periods. The kernel width (i.e. bandwidth) used for KDE was selected by using incrementally smaller multiples (in steps of 0.05) of the reference bandwidth (H_{ref}) until the 95% kernel isopleth became contiguous with no internal lacunae. That is, the H_{ref} value was multiplied by 0.95, 0.90, 0.85, 0.80 etc until the 95% isopleth became discontinuous following KDE, at which point the previous H_{ref}*multiple value was selected as the "*ad hoc"* bandwidth, H_{adhoc} (K. M. Berger & Gese, 2007; Jacques et al., 2009; Rodgers & Kie, 2010). The fixed-kernel method was used rather than the adaptive-kernel method (Seaman & Powell, 1996; Worton, 1989).

Home Range Tools (Rodgers et al., 2007) generated polygon shapefiles of the KDE contours which were then imported into ArcGIS (ESRI, 2008) to calculate their areas. The area of the 95% and 50% KDE contours provided estimates of the size of the overall and core foraging ranges, respectively (Laver & Kelly, 2008; Seaman & Powell, 1996). The contours represented an estimate of the probability of finding the vulture inside the area delineated by that contour boundary (Hemson et al., 2005; Kernohan, Gitzen, & Millspaugh, 2001; Wauters et al., 2007).

For each dataset, if the ratio of the standard deviations of the x and y coordinates deviated significantly from a value of 1.0 (i.e. <0.5 or >1.5), data were rescaled with a unit variance (i.e. each value of x and y was divided by its respective standard deviation (Seaman & Powell, 1996) before proceeding with KDE analysis (Rodgers & Kie, 2010; Wartmann et al., 2010). This process was automated in the HRT programme. The raster cell size on which the KDE contours were created was set at 1000 x 1000 m. A smaller cell size was not used because the large area over which the locations were distributed and the correspondingly large bandwidths resulted in excessive calculation times (Rodgers & Kie, 2010; Wartmann et al., 2010).

(iii) Grid cell range (GCR) estimation.

A grid consisting of 10 x 10 km cells was generated in ArcMap (version 9.3; ESRI 2008) under a projected UTM coordinate system (WGS 1984 UTM Zone 35S) using the *'create vector grid'* tool in Hawth's Analysis Tools version 3.27 (Beyer, 2009). The cell size was selected based on the mean distance between all consecutive locations for all vultures (11.17 ± 1.47 km; n = 6) (White & Garrott, 1990) and to produce a grid consisting of appropriate units from a conservation management perspective. Grid cell ranges were calculated using two approaches using ArcMap (ESRI, 2008):

- Path GCR: a shapefile of a continuous line between all consecutive GPS locations was created for each individual in ArcMap (version 9.3 - ESRI, 2008) using the '*convert locations to paths'* tool in Hawth's Analysis Tools version 3.27 (Beyer, 2009) to represent the minimum assumed path traversed between consecutive locations. Summing the area of the grid cells that were intersected by the line provided the overall foraging range estimate, or path GCR (Chapman & Wrangham, 1993; Douglas-Hamilton et al., 2005).

- Point GCR: summing the area of all grid cells that contained any GPS locations (Chapman & Wrangham, 1993; White & Garrott, 1990) provided conservative estimates to represent the *known* foraging ranges of the vultures and were only calculated for monthly ranges for overlap analysis.

The number of GPS locations in each grid cell was counted using the '*spatial join*' function of ArcMap (ESRI, 2008) to provide an estimate of relative intensity of use throughout the range (Horner & Powell, 1990; Robbins & McNeilage, 2003). Core GCR areas were determined by identifying the cells in which the number of GPS locations (moving and stationary) was greater than the mean number per cell across the range (Horner & Powell, 1990). The group of cells collectively containing the top 25% of all locations was selected to indicate the most intensively utilized areas (Douglas-Hamilton et al., 2005; Horner & Powell, 1990), termed IUAs. Cells containing the same number of locations as the grid cell containing the smallest number of locations in the collective top 25% group were all assigned to the IUA. Therefore the IUAs may have included more than 25% of all locations.

An index of dispersion, or clumping, of the GPS locations recorded in each tracking period was calculated to describe the pattern of use throughout the grid cell ranges (Chapman & Wrangham, 1993; Herbinger et al., 2001; Horner & Powell, 1990). The index of clumping was a modification of the variance-to-mean ratio of the number of locations per cell (or coefficient of dispersion - Chapman & Wrangham, 1993), with calculated values >0 indicating a clumped distribution of locations, and maximum clumping indicated by the total number of locations minus 1 (Table 3.1. - Green, 1966; Herbinger et al., 2001; Horner & Powell, 1990).

Table 3.1. Formula and explanation of index of clumping values calculated for grid cell range estimates. (Modified from Herbinger *et al*. (2001))

		Index value		
	Formula	**Maximum uniformity**	**Random**	**Maximum clumping value**
Index of clumping	$\delta^2/\bar{x} - 1$	-1	0	$n - 1$

Key: δ^2 = variance in the number of locations per grid cell; $\bar{x}$ = mean number of locations per grid cell; n = total number of locations in foraging range.

Path and core GCR estimates were calculated for the total and monthly tracking periods. Point GCR estimates were calculated for individual months only for overlap analysis. IUAs were not calculated for individual monthly ranges. Indices of clumping were calculated for all range estimates.

(iv) Incremental area analysis.

Incremental area analysis was carried out in Ranges7 version 2.7 (South, Kenward, & Walls, 2008) to investigate how the size of the vultures' foraging ranges changed during the total tracking period. For each individual, foraging ranges were estimated by sequentially adding consecutive GPS locations to produce 100% MCPs (Harris et al., 1990; Mohr, 1947) until all GPS locations were used to produce the range estimate for the total tracking period (Harris et al., 1990; South et al., 2008). A foraging range area curve was produced by plotting the estimated foraging range size (i.e. area of 100% MCP) on the y-axis and number of GPS locations used to generate the estimate on the x-axis (Harris et al., 1990; Kernohan et al., 2001).

After calculating the percentage change in range estimates between consecutive GPS locations, asymptotes were identified both visually and when adding consecutive GPS locations produced less than a 1% change in foraging range size for 42 consecutive locations (approximately 14 tracking days) (Odum & Kuenzler, 1955). The number and temporal position of asymptotes indicated the effect of the length of the tracking period on foraging range size, as well as the movement patterns of the vultures over time (Wartmann et al., 2010).

3.5.2. Analysis of foraging range overlap

The amount of overlap between individual vultures' overall and core ranges was calculated to provide an estimate of potential exploitation of the same resources, and to identify areas that were regularly used by more than one vulture (Fieberg & Kochanny, 2005; Millspaugh, Gitzen, Kernohan, Larson, & Clay, 2004). Overlap between individual vultures' foraging ranges was calculated (Equation 1) for the total tracking periods, and for coinciding monthly ranges. The following range estimates were used to calculate overlap *between* vultures for each time period:

- *Total tracking period*: 95% and 50% KDE isopleths; path GCRs and core GCRs.
- *Coinciding monthly ranges*: overlap of point GCRs for complete months only.

The amount of overlap between consecutive monthly foraging ranges for individual vultures was also calculated to indicate spatial shifts in overall (path GCRs) and core (core GCRs) foraging ranges over time, and to identify repeated use of specific areas (i.e. site fidelity (Jacques et al., 2009; Kelly et al., 2010; Olson et al., 2010)).

Overlap analyses were performed in ArcMap (version 9.3; ESRI, 2008) using the '*clip'* tool to create shapefiles of the overlapping portions of the foraging ranges. The areas of the overlapping portions were then calculated from their attribute tables in ArcMap (version 9.3; ESRI, 2008) and were used in Equation 1 to calculate an index of average overlap between the two ranges.

Equation 1: Calculation of an index of average percentage overlap between two foraging ranges ($HR_{1,2}$). $AO_{1,2}$ is the area of overlap, and A_1 and A_2 are the foraging range estimates (i.e. areas) of vultures 1 and 2 (Fieberg & Kochanny, 2005; Kernohan et al., 2001).

$$HR_{1,2} = \left(\frac{\left((AO_{1,2}/A_1) + (AO_{1,2}/A_2) \right)}{2} \right) \times 100$$

3.5.3. Statistical tests for autocorrelation

Analysis of the degree of autocorrelation of each set of GPS locations was performed using HRT (version 1.1.; (Rodgers et al., 2007)) extension for ArcGIS (version 9.3; ESRI, 2008) which automatically calculated a Schoener's (1981) index value (*V*). Departures from independence of observations were detected using

Schoener's (1981) value by calculating the ratio of the mean squared distance between successive observations (t^2) and the mean squared distance of all observations from the arithmetic mean centre of activity (r^2; Rooney, Wolfe, & Hayden, 1998). A Schoener's value of 2 indicated fully independent locations (Swihart & Slade, 1985) and significant deviations from 2 indicated significant positive ($V < 1.6$) or negative ($V > 2.4$) autocorrelation of GPS locations (Rodgers & Kie, 2010; Rooney et al., 1998; Schoener, 1981). Subsampling of GPS locations to reduce autocorrelation was not performed in order to avoid the elimination of biologically meaningful data (De Solla et al., 1999; Fieberg, 2007; Fieberg et al., 2010). GPS locations were recorded at regular intervals to ensure an unbiased temporal coverage of the vultures' movements, thereby reducing the negative effects of autocorrelation (Kie et al., 2010; Otis & White, 1999).

3.5.4. Utilisation of protected areas and areas of different cattle densities

An individual's use of a habitat or defined area is indicated by the proportion of time spent in that area, and use of that area is considered to be selective if it is used disproportionately to its availability (Beyer et al., 2010; Johnson, 1980; McClean, Rumble, King, & Baker, 1998). Utilisation and selection of protected areas and areas of different cattle densities was investigated separately at two scales within the overall foraging range of each vulture (i.e. third order scale of selection - Johnson, 1980; Thomas & Taylor, 2006). Analyses were carried out separately for each vulture to avoid invalid inferences being made from the pooling of data from a small sample size with variation between individuals (Aebischer, Robertson, & Kenward, 1993; Alldredge & Griswold, 2006; Thomas & Taylor, 2006).

Protected area data:

Preparation of data and spatial analyses of land use availability and utilisation were performed in ArcMap (version 9.3; (ESRI, 2008)). Firstly, the landscape was split into two categories based on protected area status, *viz* formally protected areas and non-protected areas.The spatial distribution of protected areas in southern Africa was represented by a polygon shapefile created using data from the 2010 World Database on Protected Areas (WDPA) containing all IUCN category I-VI protected areas (IUCN & UNEP, 2010) and 'national other areas' (i.e. protected areas uncategorized by IUCN) polygons from the 2003 WDPA (IUCN & UNEP, 2003). The two datasets were merged and dissolved into a single polygon shapefile in ArcMap (version 9.3 - ESRI, 2008). All areas outside the protected areas polygon were designated as non-protected areas.

Cattle density data:

A raster dataset representing the density of cattle at a grid cell resolution of 3 minutes of arc (approximately 5 x 5 km at the Equator) was obtained from the Food and Agriculture Organization's (FAO) Gridded Livestock of the World (GLW) dataset (FAO, 2007; www.fao.org/geonetwork). The raster cell values were of cattle densities per square kilometre derived from official census and survey data and subsequently adjusted to account for the area of land modelled to be suitable for livestock production based on empirical relationships between cattle densities and environmental variables in similar areas (Robinson, Franceschini, & Wint, 2007). Cells were assigned a value of zero cattle per kilometre if the area was modelled to be unsuitable for livestock based on environmental variables (e.g. grazing capacity; elevation; slope) and where land use practices would prohibit the presence of livestock, such as in urban areas and most protected areas (Robinson et al., 2007). The dataset used in this study was the modelled dataset corrected to match FAO official national livestock statistics for the year 2005 (FAO, 2007).

The raster was projected to a UTM coordinate system (WGS 1984 UTM Zone 35S), extracted for the southern African region and then converted to polygons in ArcMap (version 9.3 - ESRI, 2008). For each individual vulture a circular polygon was then created which was centred at the mean centre of all GPS locations recorded during that vulture's total tracking period, with a radius equal to the distance to the furthest location from the mean centre plus a 10 km buffer (Gervais, Rosenberg, & Anthony, 2004; Thomas & Taylor, 2006). The five circular polygons were then merged into a single polygon that was used to clip the cattle density polygons to represent the cattle densities available to the vultures at a regional scale. All polygon cells with a value of zero cattle per kilometre were then extracted from the overall grid within the combined study sites to produce a separate polygon representing all areas with zero cattle. The remaining cells contained a minimum value of one cow per square kilometre, and these cells were classified into three categories using the quantile method (i.e. approximately equal numbers of features are placed in each class) in ArcMap (version 9.3 - ESRI, 2008). This produced three categories of the following ranges of cattle density values that were extracted to create separate polygon shapefiles representing ‘low’, ‘medium’ and ‘high’ cattle densities respectively: 1 – 6, 7 – 15 and 16 – 1383[1] cattle per square kilometre.

Determination of availability and utilisation of protected areas and cattle density categories:

(i) Overall foraging range scale:

The relative proportions of protected versus non-protected areas or each cattle density category within each vulture’s 95% KDE contour represented the availability of each land use category within the vultures’ overall foraging ranges. This was determined by clipping the polygons of each category by the 95% KDE contour boundary, calculating the total area occupied by each category and dividing by the total area of the 95% KDE contour. Therefore, the proportions of each land use category available in the 95% KDE contour always summed to 1 (protected versus non-protected areas, and cattle density categories were analysed separately).

Use of an individual land use category was represented by the proportion of stationary (i.e. <10 km/h) GPS locations within the 95% KDE contour that were recorded in that category. The proportions of GPS locations recorded in each land use category always summed to one. Moving locations were not included in this analysis because it was impossible to confirm whether the vultures were directly utilising the area beneath them, or simply travelling over the area from one point to another.

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[1] The high value of 1383 cattle per kilometre in the ‘high’ category was due to the presence of a single grid cell with an unusually high reported number of cattle from national statistics (T. Robinson, personal communication).

Definitions of availability and use at the overall foraging range scale:

- ***Availability*****:** the relative proportions of each category within the 95% KDE contour.
  Calculation: proportional availability (A) of category "i" was calculated by dividing the area of category "i" within the 95% KDE contour by the total area of the 95% KDE contour.
- ***Use*****:** the relative proportion of stationary GPS locations recorded within each category within the 95% KDE contour.
  Calculation: proportional use (U) of category "i" was calculated by dividing the number of stationary locations in category "i" within the 95% KDE contour by the total number of stationary locations within the 95% KDE contour.

(ii) Core foraging range scale:

At the core foraging range scale availability was defined in the same way as at the overall foraging range scale: the relative proportions of protected and non-protected areas or each cattle density category within the 95% KDE contour of each vulture. The relative use of each category was represented by the proportions of each vulture's 50% KDE contours that were occupied by each individual category (Beasley, DeVault, Retamosa, & Rhodes, 2007). The availability and use of all categories always summed to 1 for each vulture (protected versus non-protected areas, and cattle density categories were analysed separately).

Definitions of availability and use at the core foraging range scale:

- ***Availability*****:** the relative proportions of each category within the 95% KDE contour.
  Calculation: proportional availability (A) of category "i" was calculated by dividing the area of category "i" within the 95% KDE contour by the total area of the 95% KDE contour.

- ***Use***: the relative proportions of each category within the 50% KDE contours. *Calculation:* proportional use (U) of category “i” was calculated by dividing the area of category “i” within the 50% KDE contour by the total area of the 50% KDE contour.

Selection analysis.

The following calculations were performed to determine whether or not the vultures used the different land use categories in proportion to their availablity. The analyses were carried out separately for individual vultures, rather than grouping the data, and followed the principles of use-availability designed studies (Alldredge & Griswold, 2006; Beyer et al., 2010; Thomas & Taylor, 2006).

Firstly, the Ivlev’s electivity index (E_i) was calculated (Equation 2) to determine whether each category (i) was used in proportion to its availability by the vultures at both overall and core foraging range scales (Ivlev, 1961).

Equation 2: Ivlev’s electivity index (E_i) calculation for each category (i). A_i is the proportional availability of category i; U_i is the proportional use of category i (explained above) (Manly, McDonald, Thomas, McDonald, & Erickson, 2002):

$$E_i = (U_i - A_i)/(U_i + A_i)$$

Ivlev’s electivity index produced a value ranging from -1 to +1, with zero indicating that use of a resource category was equal to its availability, while positive and negative values indicated use more and less than expected based on availability, respectively (Manly et al., 2002).

Secondly, selection ratios for each category of land use and cattle density were calculated (Equation 3) as a basis for generating resource selection functions (RSFs; see below) (Manly et al., 2002). Selection ratios indicated whether selection or avoidance was exhibited by an individual vulture based on deviations from proportionality between use and availability of a land use category (Manly et al., 2002). Values greater than 1 indicated some degree of selection, equal to 1 indicated proportional use and less than 1 some degree of avoidance (Aarts, MacKenzie, McConnell, Fedak, & Matthiopoulos, 2008; Manly et al., 2002).

Equation 3: Selection ratio (w_i) calculation for each category (i). A_i is the proportional availability of category i; U_i is the proportional use of category i (explained above) (Manly et al., 2002):

$$w_i = U_i / A_i$$

The selection ratios were further standardized into resource selection functions (RSF; Equation 4) (Manly et al., 2002; McLoughlin, Walton, Cluff, Paquet, & Ramsay, 2004). Each category's calculated RSF value (B_i) can be interpreted as the probability that the individual would select land use category "i" over all others, assuming that all categories are available in equal proportion (Boyce, Vernier, Nielson, & Schmiegelow, 2002; Manly et al., 2002; McLoughlin et al., 2004). Therefore, the RSF values of all categories always summed to 1. If an individual used all categories in proportion to their availability, the RSF values were expected to be equal for each category. For example, if a vulture used all four categories of cattle density in proportion to their availability within the foraging range, each category would have an RSF value (B_i) of 0.25.

Equation 4: Resource selection function (B_i) calculation for each category (i). The resource selection function (B_i) of category "i" is calculated by dividing its selection ratio (w_i) by the sum of the selection ratios of all categories, where H is the number of categories (Manly et al., 2002):

$$B_i = \frac{w_i}{\sum_{i=1}^{H} w_i}$$

To test if the the RSF values for protected areas and non-protected areas differed significantly from proportional use (expected RSF value for random use of two resource categories = 0.50), an exact binomial test of goodness-of-fit was performed. To test whether the RSF values for the four categories of cattle density differed significantly from proportional use (expected RSF value for random use of four resource categories = 0.25) a chi-squared goodness-of-fit test was used (Neu, Byers, & Peek, 1974; Thomas & Taylor, 2006). The confidence level was set at 0.00625 following Bonferroni corrections (Neu et al., 1974), whereby the initial significance level ($\alpha =$ 0.05) was divided by the number of resource categories multiplied by 2 (i.e. $\alpha =$ 0.05 / 8 = 0.00625).

If significant deviations from proportional use were found for an individual's use of protected versus non-protected areas or the different cattle density categories, the category used least proportionately to its availability was identified as the one whose Ivlev's electivity index value (E_i) was furthest from zero (i.e. proportional use). The analyses were repeated at both overall and core foraging range scales.

3.5.5. Distances travelled

The distance between consecutive GPS locations was calculated using Ranges7 (Version 2.7 - South et al., 2008) for the total tracking period and each complete month for all vultures. The total distances travelled per day were calculated by summing the distances between the 07:00h and 11:00h GPS locations, the 11:00h and 15:00h GPS locations and the 15:00h and 07:00h (of the following day) GPS locations each day. For each time period analysed, the total distance travelled, the mean distance between consecutive locations, and the mean and maximum total distance travelled per day were calculated.

The proportion of days on which vultures travelled more than 10 km was also calculated for each tracking period to provide an indication of the movement patterns exhibited during that time (e.g. settled versus exploratory movements - Morales et al., 2004). The distance of 10 km was chosen to differentiate between assumed foraging or dispersal movements and short-distance movements in the general vicinity of an exploited resource (e.g. a feeding or roosting site). The mean distance travelled on each day that the vulture moved more than 10 km and the proportion of the total distance travelled on days when more than 10 km was moved (= total distance travelled on days when >10km was moved / total distance travelled during tracking period) were also calculated for each tracking period to provide information about characteristics of foraging flights.

3.5.6. Flight speeds and altitudes

Analysis of flight speeds and altitudes was carried out to describe the flight characteristics of the vultures during regular foraging flights and cross-country flights. This allowed comparisons to be made with estimates derived from direct observations in East Africa (e.g. Pennycuick, 1972). The data presented here are the first to be obtained using tracking devices on a sample of African white-backed vultures.

In order to provide a basic estimate of daily flight patterns, the relative proportion of moving GPS locations and stationary GPS locations was calculated separately for 07:00h, 11:00h and 15:00h locations during the total tracking period for each vulture. The locations were defined as moving when the vulture's recorded speed was at least 10 km/h. This speed was selected to differentiate between foraging or dispersal movements and low-level flights, or even terrestrial movements, in the vicinity of an exploited resource (Gilbert et al., 2007).

Each GPS location was assigned a ground-level elevation corresponsing to the ground elevation above sea level directly below the recorded grid-reference of each fix by using ArcMap (version 9.3 - ESRI, 2008) to join each location to the Shuttle Radar Topography Mission digital elevation model (SRTM DEM - downloaded from the WorldClim website http://www.worldclim.org/download; USGS, 2004) consisting of 30-arc second (~1 x 1km) grid cells with aggregated elevation values. All altitudes were rounded to the nearest metre. The altitude of each GPS location above ground level was then determined by calculating the difference between the altitude reading recorded by the tracking device and the elevation of the ground at that location indicated by the DEM. If negative values were generated they were changed to 1 metre altitude above ground level.

A frequency histogram of 100 metre altitudinal intervals plotted against the number of moving GPS locations recorded within each interval for all vultures was used to identify the altitudinal range at which the vultures travelled most frequently. To test for a relationship between altitude above ground and flight speed, a Pearson's product-moment correlation coefficient was calculated for all moving GPS locations for all vultures in a pooled dataset. For this analysis all speeds and altitudes were rounded to the nearest kilometre per hour and metre respectively.

3.5.7. Utilisation of supplementary feeding sites

In order to provide an estimate of the frequency that each vulture used sites that provided supplementary food for vultures and other scavengers, the proportion of stationary (i.e. < 10km/h) GPS locations recorded within 5 km of known feeding sites in southern Africa (n = 147) were selected and counted separately using ArcMap (version 9.3 - ESRI, 2008) for each individual. The supplementary feeding sites were identified from a combination of databases compiled during questionnaire surveys between 2000 and 2010 (Piper, 2004b; Wolter, unpublished data), and enquiries made to landowners and other interested parties during this study. Of these, 142 sites were in South Africa, two each in both Namibia and Zimbabwe, and one in Botswana. Only supplementary feeding sites assumed to be active during the tracking period and with known GPS coordinates were selected for the analysis, and their locations were plotted as points in an ArcMap (version 9.3 - ESRI, 2008) shape file.

An assumption made during this analysis is that the presence of stationary GPS locations within 5 km of a feeding site indicated a vulture's direct use of that site. This was not necessarily the case and this analysis rather provides an estimate of how frequently the vultures' were in the proximity of supplementary feeding sites, and therefore *potentially* using them. The analysis was conducted for the total tracking periods and for each complete month for all vultures, to estimate the potential contribution to the vultures' food supply made by supplementary feeding sites.

In order to investigate the effect of supplementary feeding sites on the vultures' movement patterns, Spearman's rank correlation coefficients were calculated to test for associations between the proportion of stationary GPS locations recorded within 5km of feeding sites and the size of path and core GCR estimates, and the mean distance between consecutive locations for each complete month. The data were pooled across vultures and analysed as one dataset, and only months during which at least one stationary GPS locations was recorded within 5 km of a feeding site were included in the dataset. Spearman's rank correlation coefficients between the same variables were also calculated separately for two vultures that visited supplementary feeding sites at least once every month.

3.5.8. Statistical analyses and presentation of results

All statistical analyses were performed in SPSS Statistics version 17.0 (SPSS Inc, 2008) or Microsoft Excel (2007). Significance levels were set at $\alpha = 0.05$ unless otherwise stated. Standard errors are provided with all mean average values. Some statistical tests were described in the relevant methods sections above, others are described below.

Comparison of foraging range estimation methods.

The 100% MCP, 95% KDE and path GCR estimates of the overall foraging ranges for all vultures were tested for significant differences in size using Wilcoxon signed-rank tests.

Seasonal differences in monthly foraging range estimates and distances travelled.

The tracking periods were divided into summer and winter based on the typical rainfall patterns in the study region where the majority of rain falls between November and April, and the months of May to September are usually dry (Reason, Hachigonta, & Phaladi, 2005). The rationale behind this temporal split is derived from the seasonal mortality patterns of ungulates, and therefore the number of carcasses available to vultures, which is closely related to the regional rainfall regime (Houston 1974; Fynn & O'Connor, 2001; Cronje, Reilly & MacFadyen, 2002).

The means of the summer (December to April) and winter (May to September) monthly path GCR estimates were calculated for each vulture and a Wilcoxon signed-rank test was performed to test whether there was a significant difference between the mean summer and winter estimates across all vultures.

The means of the total distance travelled per day during the summer and winter periods were calculated for each vulture and a Wilcoxon signed-rank test was used to test whether there was a significant difference in the mean total distance travelled per day between summer and winter across all vultures.

CHAPTER 4

RESULTS

4.1. Capture information

Vulture captures using the walk-in capture enclosure were successful and efficient, with successful capture attempts usually occurring on the second or third day after a carcass had been placed at the trap. This method facilitated the capture of target individuals as soon as they had entered the cage. The presence of other species such as pied crows (*Corvus albus*) and marabou storks (*Leptoptilos crumeniferus*) feeding inside the cage appeared to encourage the vultures to enter. Once they were left undisturbed inside the closed trap, the vultures soon became calm and often continued to feed.

Six immature African white-backed vultures were caught and fitted with GPS-GSM tracking units (Table 4.1). Three of the four units deployed in November and December 2009 continued to record data beyond a 10-month period, and one unit deployed in February 2010 was also still functioning in October 2010. One unit recorded and transmitted data for a 7-month period in 2009, after which transmission ceased for reasons unknown. This latter vulture (AG032) was identified from its patagial tags 10 months after its capture with the tracking unit still attached, suggesting that it had malfunctioned or the batteries had lost charge (M. Haupt [Africa Wildlife Tracking Ltd.], personal communication). One vulture (AG332) was tracked for just over 3 months before the tracking device ceased to transmit data in March 2010. A visit to the site of the last recorded GPS location in south east Namibia resulted in the discovery of the remains of a domestic livestock carcass and partially buried remains of at least one black-backed jackal (*Canis mesomelas*) nearby (K. Wolter, personal communication). It is possible that AG332 was fatally poisoned after consuming meat from the livestock carcass that might have been laced with poison to kill mammalian carnivores (K. Wolter, personal communication). Firm evidence is lacking, however, and it is plausible that the tracking unit malfunctioned or became detached from the vulture in an area without GSM coverage.

A summary of each vulture's patagial tag codes, capture dates, estimated age at time of capture, total tracking period, the number of locations recorded by each device, and the mean accuracy of each reading indicated by the PDOP (positional dilution of precision) scale is provided in Table 4.1. The six tracking units recorded a mean of 99.44 ± 0.25% of expected GPS locations, with a mean accuracy of 2.4 ± 0.02 PDOP (n = 4,326 locations).

Table 4.1. Capture information for six immature African white-backed vultures: patagial tag codes, capture date, estimated age at time of capture, sex, length of total tracking period, the number of GPS locations that were recorded, and the mean accuracy of each location on the PDOP scale.

Vulture ID	Patagial tag code	Estimated age at capture	Sex	Capture date	Tracking period (Days)	Number of GPS locations	Mean (±SE) PDOP per location
AG032	B299	1st year	Male	18/03/09	206	616	2.72 ± 0.06
AG330	B344	2nd year	Male	03/12/09	301	896	2.14 ± 0.04
AG331	B308	2nd year	Male	21/11/09	313	935	3.21 ± 0.05
AG332	B309	3rd year	Female	21/11/09	101	301	2.56 ± 0.07
AG350	B345	2nd year	Female	03/12/09	300	898	2.06 ± 0.04
AG356	B394	2nd/3rd year	Male	13/02/10	226	680	1.77 ± 0.04

* Values of < 3 PDOP indicate very high positional accuracy (D'Eon & Delparte, 2005).

Foraging ranges and distances travelled were calculated for the total tracking periods and complete individual months for all six vultures.

The relatively short tracking period for AG332 restricted the amount of analysis that could be applied to the data because it is likely that the vulture would have continued to expand its range if it was tracked for a similar period to the other vultures. The data from AG332 were not included in any between-individual overlap analysis or any land use selection analysis.

4.2. Foraging range estimation

4.2.1. Foraging ranges for total tracking periods

Estimates of the overall and core foraging ranges for the total tracking periods of all vultures are presented in Table 4.2. Figure 4.1 shows the path grid cell ranges (GCRs) for all vultures, illustrating the extent of their movements across southern Africa. Figure 4.2a-f shows the overall and core foraging ranges for the total tracking periods of all vultures estimated from fixed kernel density estimation (KDE). Figure 4.3a-f shows the overall foraging ranges for the total tracking period of all vultures represented by 100% minimum convex polygons (MCPs) and path GCRs. Figure 4.4a-f shows the core foraging ranges for the total tracking period of all vultures represented by 50% KDE contours, core GCRs and Intensively Used Areas (IUAs). The 100% MCP (median = 243,876 km^2) and 95% KDE (median = 244,133 km^2) estimates were not significantly different (Z = -0.314, p = 0.753), but the path GCR estimates (median = 52,150 km^2) were significantly smaller than 100% MCPs (Z = -2.201, p = 0.028) and 95% KDEs (Z = -2.201, p = 0.028).

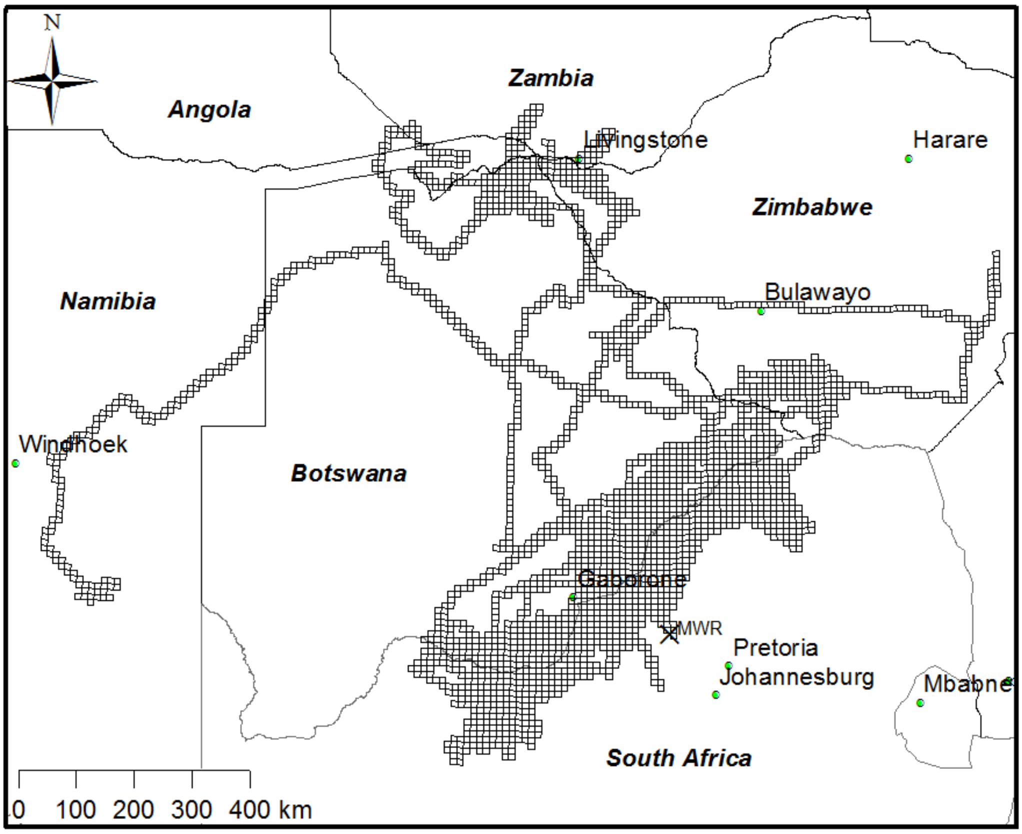


Figure 4.1. Path GCRs for the total tracking periods of all vultures combined. Path GCRs represent 100km^2 grid cells entered or travelled through by the vultures. Mankwe Wildlife Reserve capture site is marked "X MWR".

Three vultures (AG330, AG331 and AG350) spent the majority of their tracking periods in the Limpopo and North West Provinces of South Africa, and in south-east Botswana. The mean (± SE) area of their overall and core foraging ranges represented by 95% and 50% KDE contours was 106,282 ± 30,133 km^2 and 22,194 ± 6,702 km^2, respectively. Figures 4.2a-c show that their overall foraging ranges were approximately aligned with, and intersected by, the political border between Botswana and South Africa. This is particularly clear for AG330 and AG331 as they spent the majority of their time either side of the Limpopo and Molopo Rivers that demarcate the border. 56.4%, 56.7% and 49.0% of all tracking locations were inside South Africa for AG330, AG331 and AG350 respectively, the remainder being in southern Botswana apart from AG330 which spent several weeks in south-west Zimbabwe.

KDE analysis of locations from AG330 identified three core foraging areas covering 29,714 km^2 (Figure 4.2a). The largest area was located either side of the Limpopo River international border between Botswana and South Africa, north west of Lephalale (Ellisras). The second area stretched approximately 200 km from Lobatse in southern Botswana to north-west of Madikwe Game Reserve in South Africa. The third core foraging area was in south-west Zimbabwe. Seven of the nine grid cells (900 km^2) comprising the Intensively Used Areas (IUAs) for AG330 were located inside the 50% KDE contour north west of Lephalale, while the remaining two were in the south western core area (Figure 4.4a).

AG331 spent the majority of its tracking period in two core foraging areas covering 28,044 km^2 (Figure 4.2b). The largest area was located north of Vryburg and west of Mafikeng in the North West Province, extending into southern Botswana, and the second area was located east of Grobler's Bridge border post extending across the Limpopo River into Botswana. The majority (61%) of AG331's IUA grid cells were within its south-western core foraging area (Figure 4.4b). Both AG330 and AG331 travelled regularly between their core foraging areas.

AG350's two core foraging areas covered 8,825 km^2 and were located south east of Gaborone and north-west of Madikwe Game Reserve (Figure 4.2c). Both areas were intersected by the Botswana-South Africa border. AG350 occupied only two IUA grid cells, one of which contained a supplementary feeding site (Section 4.8) south east of Gaborone, Botswana (Figure 4.4c). Over a two-week period in August 2010, AG350 travelled in a loop from the Limpopo Province of South Africa to the eastern Makgadikgadi Pans area of Botswana before returning to its core foraging area near Gaborone in September (Figure 4.3c).

Two vultures (AG032 and AG356) ranged extensively across southern Africa, regularly crossing international borders and entering five different countries outside South Africa (Botswana, Zimbabwe, Namibia, Angola and Zambia). The mean (± SE) area of their overall and core foraging ranges represented by 95% and 50% KDE contours was 460,578 ± 128,127 km^2 and 78,716 ± 43,749 km^2, respectively. AG032 left South Africa after approximately 3.5 months spent foraging in the North West and Limpopo Provinces, and travelled north into Zimbabwe and Botswana (64% of all locations were outside South Africa), while AG356 left South Africa four days after being fitted with the tracking unit and had not returned by the end of the tracking period (98% of stationary GPS locations were outside South Africa).

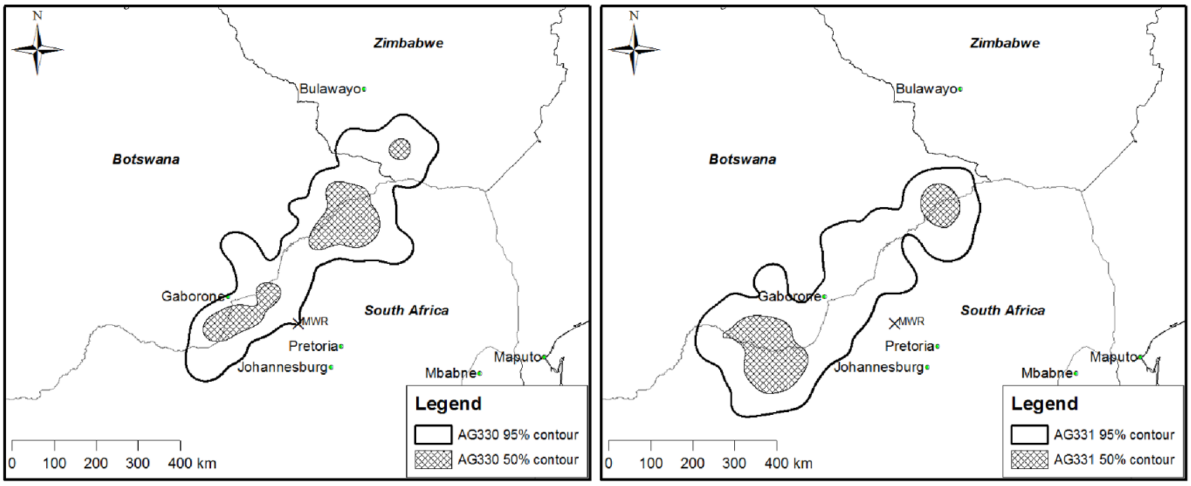
AG032's core foraging range (Figure 4.2e) was delineated by three 50% KDE contours covering 122,465 km^2. Two contours spanned the Botswana-South Africa border in the Mafikeng and Lephalale regions, and the third extended across several international borders in the Chobe region of northern Botswana. AG032 used seven IUA grid cells, with six located inside the three 50% KDE contours, and one in eastern Zimbabwe (Figure 4.4e). AG356 used a single core foraging range covering 132,662 km^2 that also crossed international borders in the Victoria Falls area of Zimbabwe (Figure 4.2d). Only two grid cells were included in AG356's IUA, both of which were located in the Victoria Falls area and contained supplementary feeding sites (Section 4.8; Figure 4.4d).

AG332 travelled extensively before the tracking unit stopped transmitting data, flying over 800 km through Botswana to the Okavango Delta, and another 800 km to south-east Namibia, all within a 7 week period (Figure 4.3f). The limited tracking period for AG332 resulted in unrealistically large estimates of its overall foraging range calculated by KDE analysis (765,483 km^2), but the vulture spent almost half of its total tracking period in a relatively small area east of Mariental in south east Namibia (Figure 4.2f) before the tracking unit stopped transmitting data. Four out of five of its IUA grid cells were located in that area, with a single IUA grid cell located at Mankwe Wildlife Reserve after the vulture remained in the area for several days immediately after its release (Figure 4.4f).

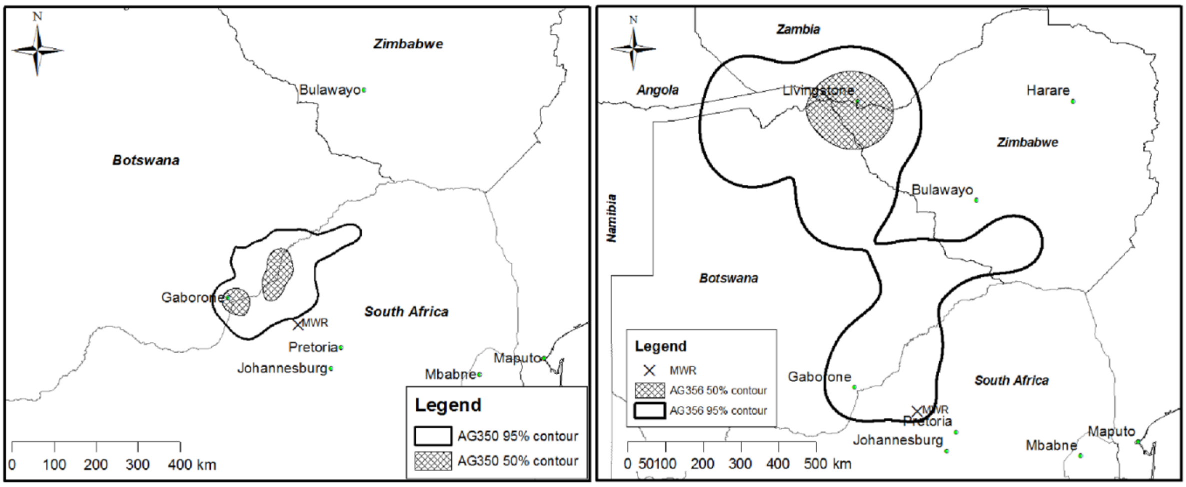
The kernel bandwidths selected for KDE analysis using the *ad hoc* method of bandwidth selection are presented in Appendix A. The multiples of the reference bandwidths (H_{ref}) used during KDE for the total tracking periods varied between individuals from 0.50 to 0.95, with associated bandwidths ranging from 17.28 km to 95.16 km (Mean = 47.13 ± 12.85 km; n = 6).

Table 4.2. Overall and core foraging range estimates for total tracking periods of all vultures, represented by 100% minimum convex polygon (MCP); 95% and 50% contours from kernel density estimation (KDE); path and core grid cell ranges (GCR), and intensively used areas of the grid cell ranges. The tracking period and number of GPS locations recorded for each vulture are also shown.

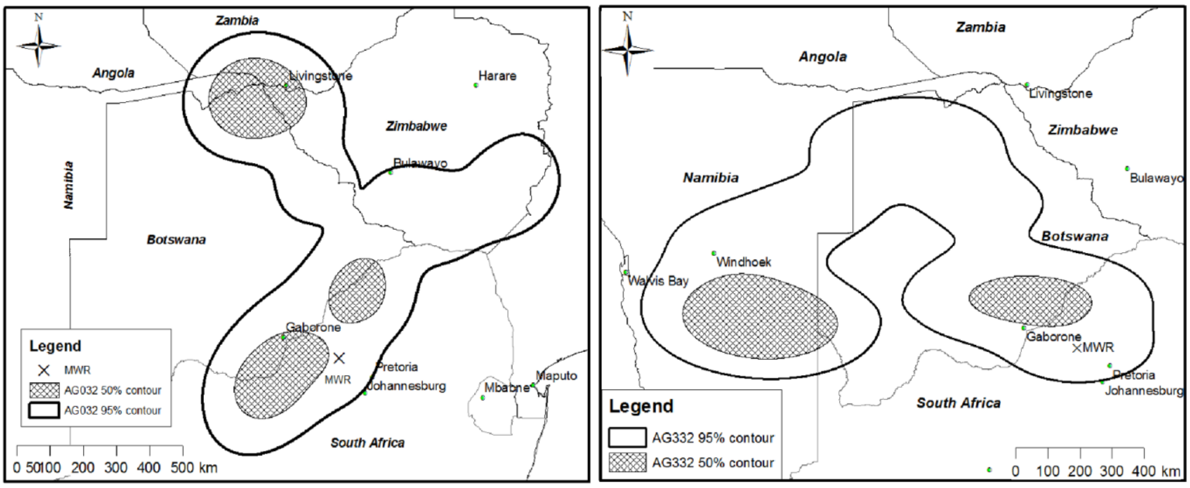
			Foraging range areas (km^2)					
Vulture ID	**Tracking period (days)**	**Locations**	**100% MCP**	**95% KDE**	**50% KDE**	**Path GCR**	**Core GCR**	**Intensively Used Areas - GCR**
AG330	301	896	144,568	125,861	29,714	59,400	5,700	900
AG331	313	935	155,301	145,854	28,044	89,800	11,400	2,300
AG350	300	898	124,492	47,132	8,825	43,100	4,200	200
AG356	226	680	332,451	342,413	34,967	44,900	2,300	200
AG032	206	616	588,705	582,795	122,465	74,500	4,000	700
AG332	101	301	439,520	765,483	132,662	28,400	2,700	500



(a). AG330 (b). AG331

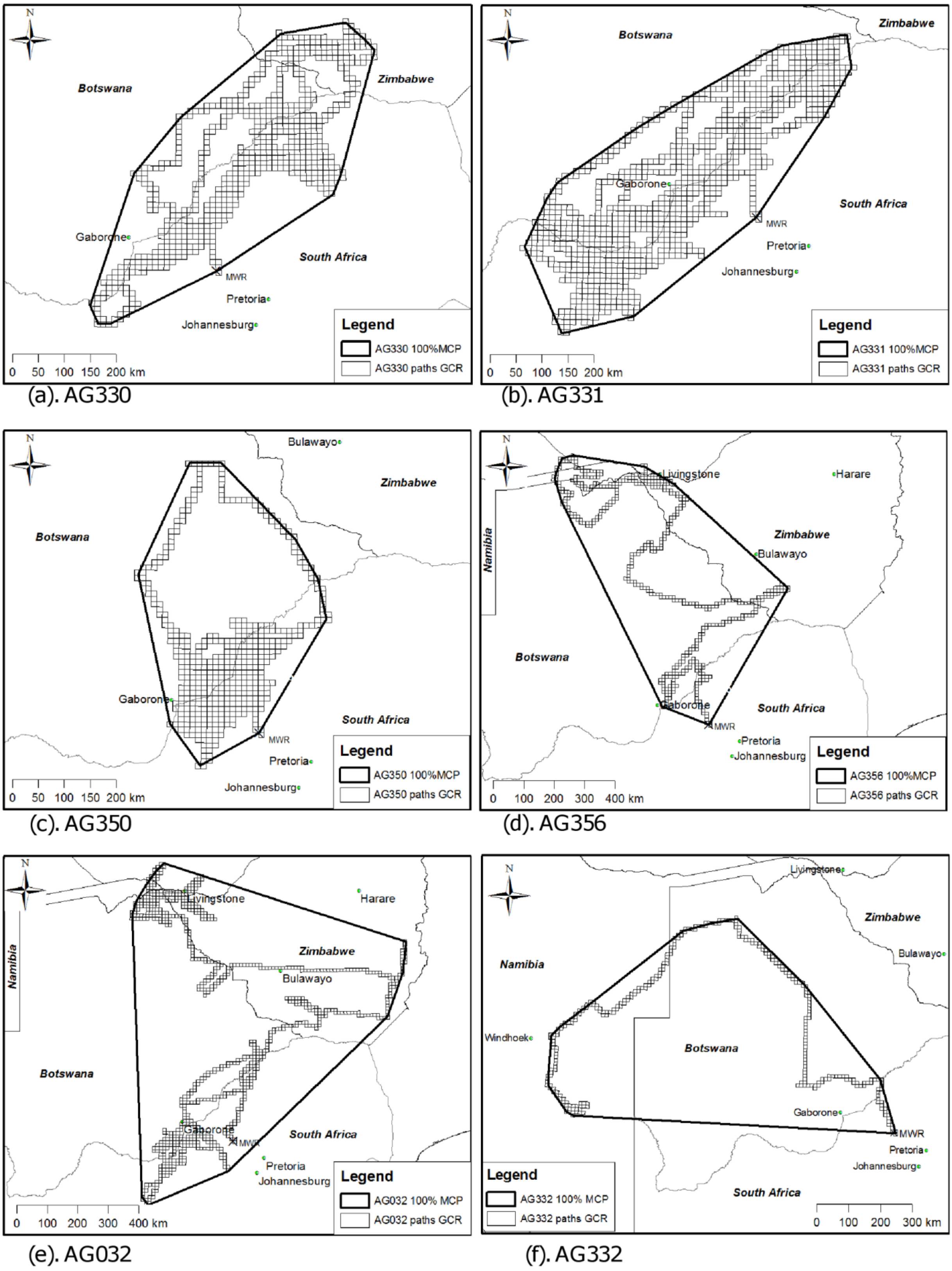


(c). AG350 (d). AG356



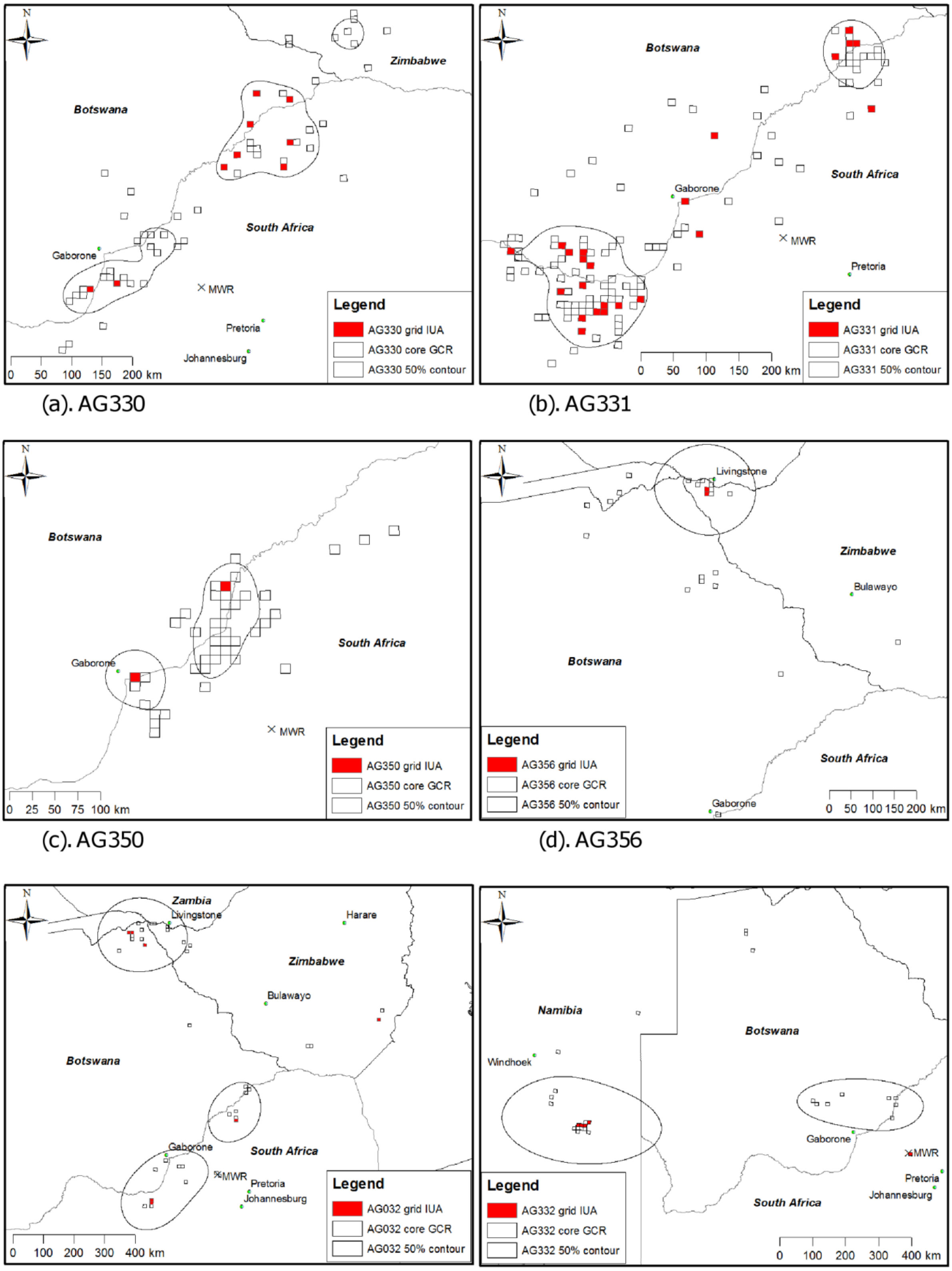
(e). AG032 (f). AG332

Figure 4.2a-f. Overall and core foraging ranges for the total tracking periods of all vultures represented by 95% (solid black line) and 50% (cross-hatched area) KDE contours respectively. Mankwe Wildlife Reserve is indicated by ‘X MWR’.



(a). AG330
(b). AG331
(c). AG350
(d). AG356
(e). AG032
(f). AG332

Figure 4.3a-f. Overall foraging ranges for the total tracking periods of all vultures represented by 100% MCPs (solid black line) and path GCRs (hollow grid squares). Mankwe Wildlife Reserve is indicated by ‘X MWR’.


(a). AG330

(b). AG331

(c). AG350

(d). AG356

(e). AG032

(f). AG332

Figure 4.4a-f. Core foraging ranges for the total tracking periods of all vultures represented by core GCRs (hollow grid squares), IUAs (red grid squares) and 50% KDE contours (hollow polygons). Mankwe Wildlife Reserve is indicated by ‘X MWR’.

4.2.2. Incremental area analysis

Foraging range area curves reached asymptotes for all vultures following incremental area analysis (Figures 4.5a-f). The numbers of asymptotes per vulture (mean = 3.3 ± 0.88; n = 6) and their approximate durations are presented in Table 4.3. The general pattern of foraging range use was for 'settled' periods lasting at least 14 days (i.e. asymptotes) to be followed by 'exploratory' movements during which the foraging range would increase in size before becoming stable during another settled period. The first asymptote was reached by each vulture after between 25 and 70 days (mean = 53.67 ± 6.79 days), and each asymptote lasted between 14 and 137 days (mean = 45.70 ± 7.34 days; n = 20). The number of days between consecutive asymptotes averaged 14.62 ± 4.03 days (n = 14).

Table 4.3. The number of foraging range asymptotes identified for each vulture by incremental area analysis using 100% MCPs, the approximate duration of each asymptote, and the number of days since the start of the tracking period on which the asymptote was reached.

Vulture ID	Asymptote	Days since start of tracking period	Duration (~Days)
AG330	A	68	20
AG330	B	107	137
AG330	C	276	≥ 22
AG331	A	52	32
AG331	B	94	30
AG331	C	129	50
AG331	D	179	14
AG331	E	221	40
AG331	F	262	≥ 50
AG350	A	25	21
AG350	B	69	68
AG350	C	139	64
AG350	D	203	41
AG350	E	246	16
AG350	F	272	≥ 27
AG356	A	60	121
AG356	B	205	≥ 21
AG032	A	47	49
AG032	B	145	≥ 60
AG332	A	70	≥31

Asymptotes marked with "≥"for duration denote an asymptote at the end of the total tracking period.

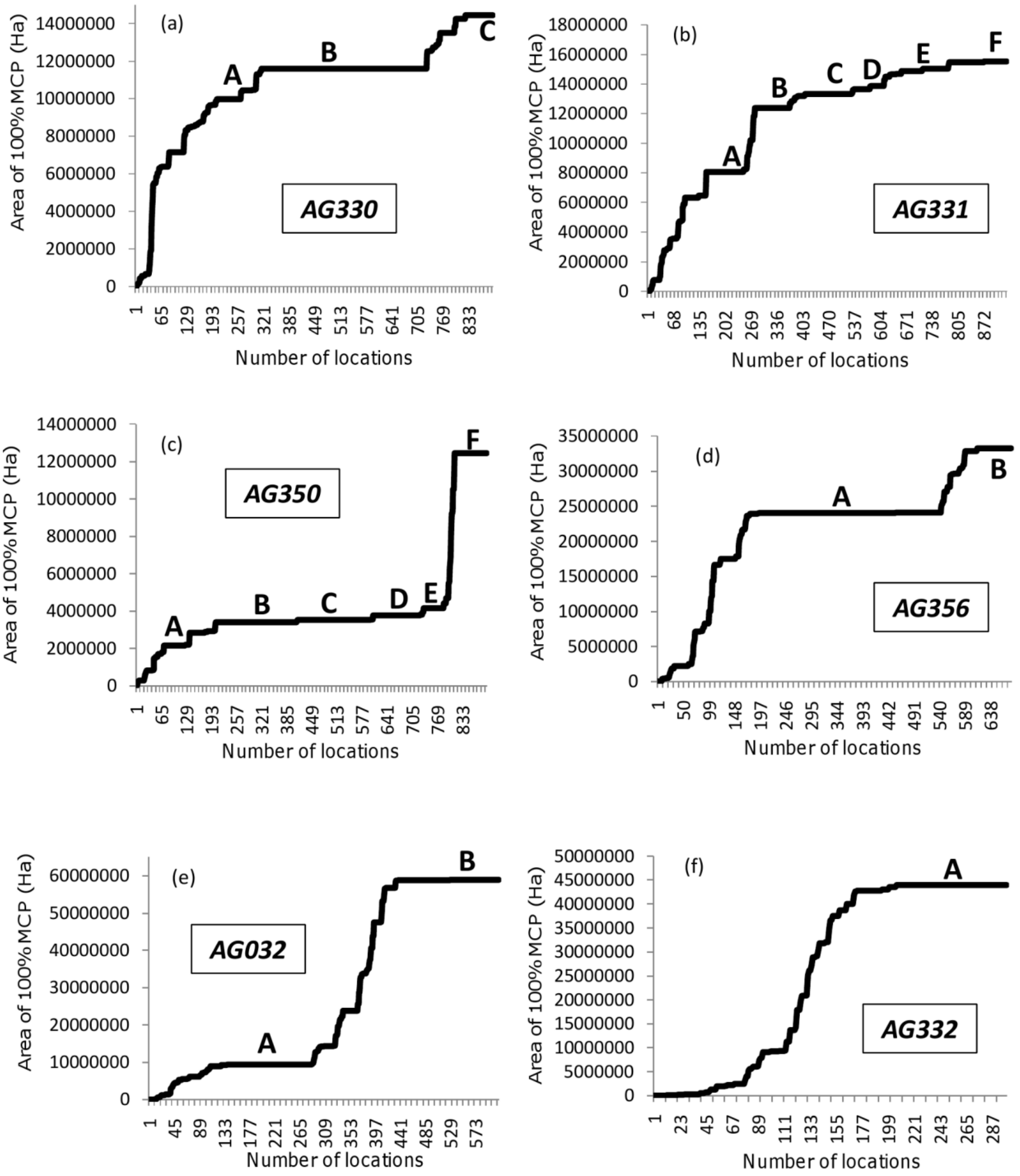


Figure 4.5a–f. Foraging range area curves for all vultures obtained from incremental area analysis. The number of locations used for each 100% MCP is plotted against the area of each 100% MCP. Asymptotes are labelled with letters corresponding to Table 4.3.

4.2.3. Monthly foraging ranges

Path and core GCR estimates for complete months (n = 46) ranged from 600 to 22,200 km^2 (mean = 9,878.26 ± 846.37 km^2) and 100 to 2,300 km^2 (mean = 923.91 ± 77.60 km^2) respectively (Table 4.4). AG331 occupied the largest monthly path (mean = 14,210 ± 1,891.29 km^2; n = 10 months) and core GCRs (mean = 1,400 ± 182.57 km^2; n = 10 months). AG356 occupied the smallest monthly path (mean = 6,100 ± 2,234.60 km^2; n = 7 months) and core GCRs (mean = 600 ± 95.12 km^2; n = 7 months).

Figures 4.6 and 4.7 show the path and core GCR estimates averaged across individual vultures for each complete month during which they were tracked. For three out of five vultures the smallest path GCR estimates were recorded in May, while the smallest path GCRs for the other two vultures were recorded during April and August. Figures 4.8a-f and 4.9a-c show the spatial patterns of the monthly path GCRs of five vultures.

The five vultures that were tracked during both the summer (December to April) and winter (May to September) periods occupied significantly larger average monthly path GCRs during summer months (mean = 12,162.00 ± 1,216.55 km^2; n = 5 vultures) compared to winter months (mean = 8,874.00 ± 1,720.00 km^2; n = 5 vultures), $Z = -2.2023$, $p = 0.043$.

Table 4.4. Monthly path and core grid cell range (GCR) estimates for complete months for all vultures.

	Monthly path and core GCR areas (km^2)											
Month	***AG330***		***AG331***		***AG350***		***AG356***		***AG032***		***AG332***	
	Paths GCR	*Core GCR*	*Paths GCR*	*Core GCR*	*Paths GCR*	*Core GCR*	*Paths GCR*	*Core GCR*	*Paths GCR*	*Core GCR*	*Paths GCR*	*Core GCR*
December	13,700	1,200	12,000	1,000	12,000	900	-	-	-	-	13,000	1,300
January	11,500	1,200	9,000	1,400	8,900	1,000	-	-	-	-	12,700	1,000
February	12,400	1,300	20,600	1,900	15,000	2,300	-	-	-	-	1,300	500
March	10,700	600	18,600	2,100	6,100	1,000	17,000	1,000	-	-	-	-
April	2,100	300	12,600	700	4,100	600	6,100	700	15,400	1,000	-	-
May	1,900	500	5,200	600	4,600	300	600	300	8,300	600	-	-
June	4,600	600	17,100	1,800	7,200	700	700	500	8,100	400	-	-
July	2,800	500	6,600	800	6,800	200	1,600	300	19,100	1,000	-	-
August	11,300	1,300	18,200	2,000	19,100	1,200	9,100	700	7,200	500	-	-
September	11,100	1,100	22,200	1,700	7,800	100	7,600	700	10,800	1,100	-	-
Mean	*8,210.00*	*860.00*	*14,210.00*	*1,400.00*	*9,160.00*	*830.00*	*6,100.00*	*600.00*	*11,483.33*	*766.67*	*9,000.00*	*933.33*
± SE	*1,498.40*	*124.01*	*1,891.29*	*182.57*	*1,520.47*	*201.14*	*2,234.58*	*95.12*	*1,947.21*	*122.93*	*3,850.97*	*233.33*

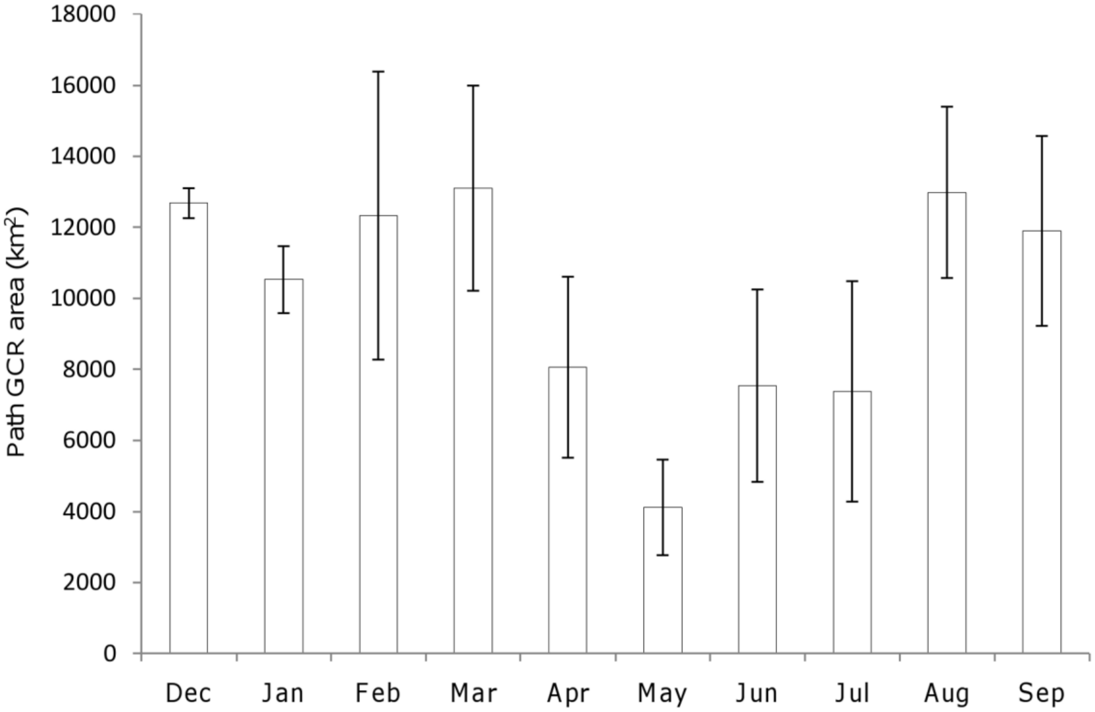


Figure 4.6. Mean (± SE) path GCR estimates for complete months for all vultures. Due to differences between tracking periods estimates were calculated for four vultures for December to March, and five vultures from April to September, inclusive. Refer to Table 4.4 for foraging ranges of individuals.

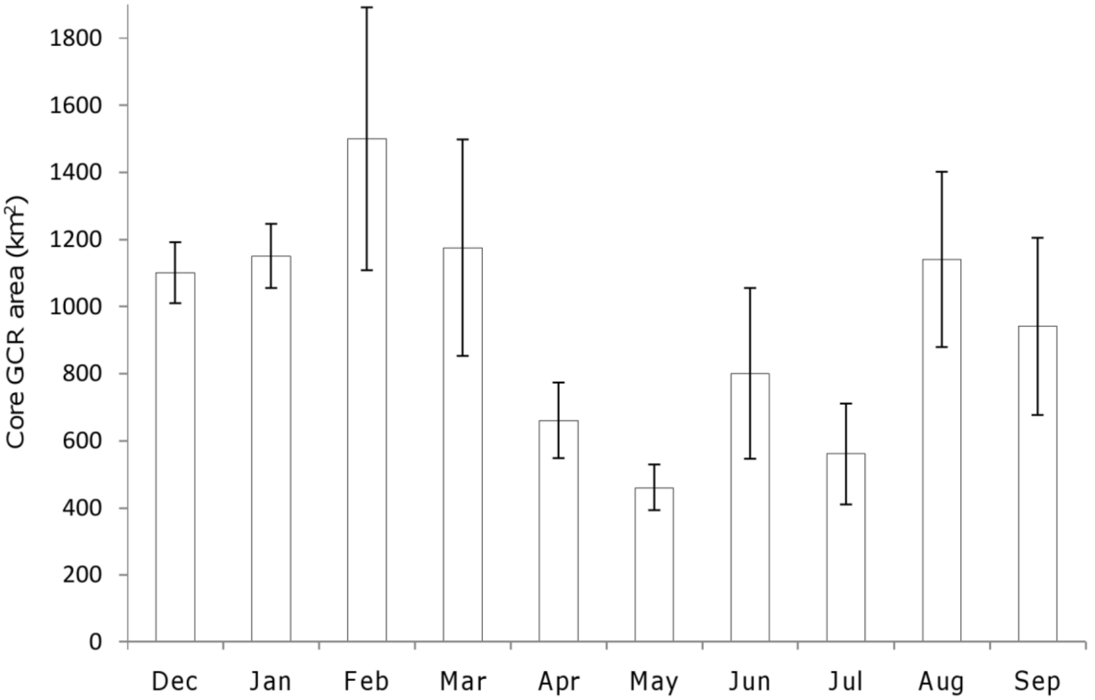
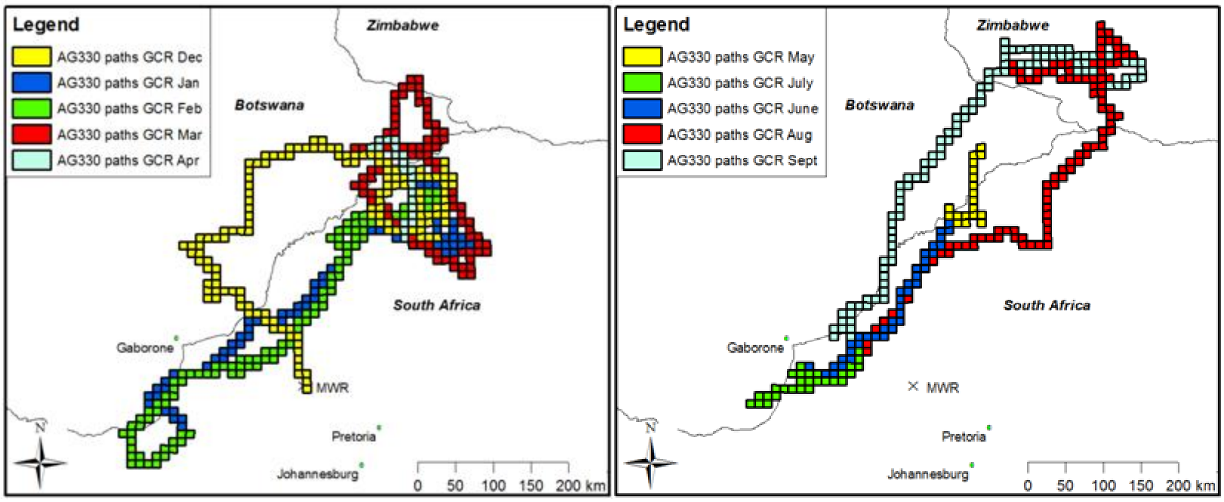
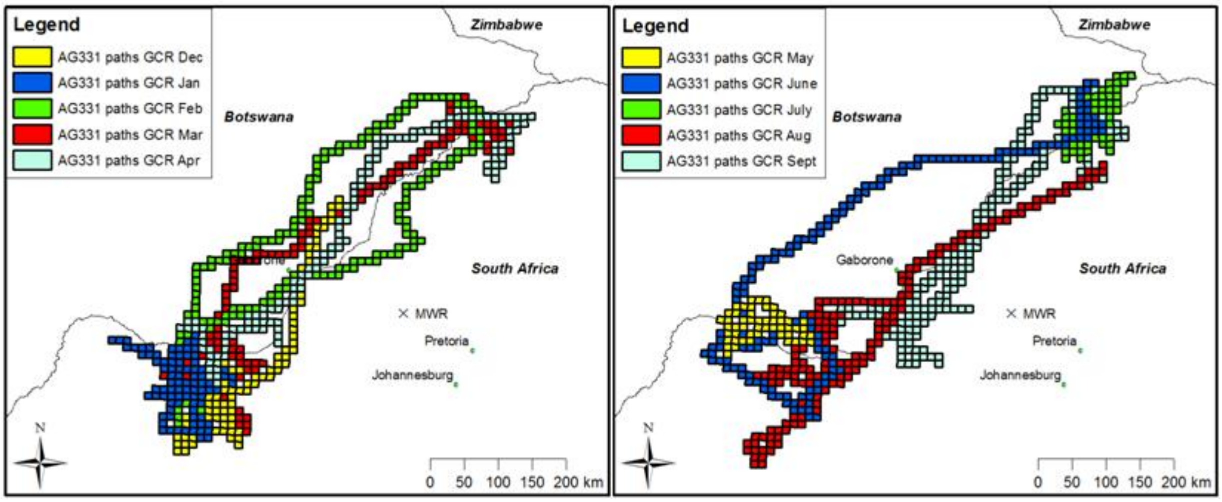


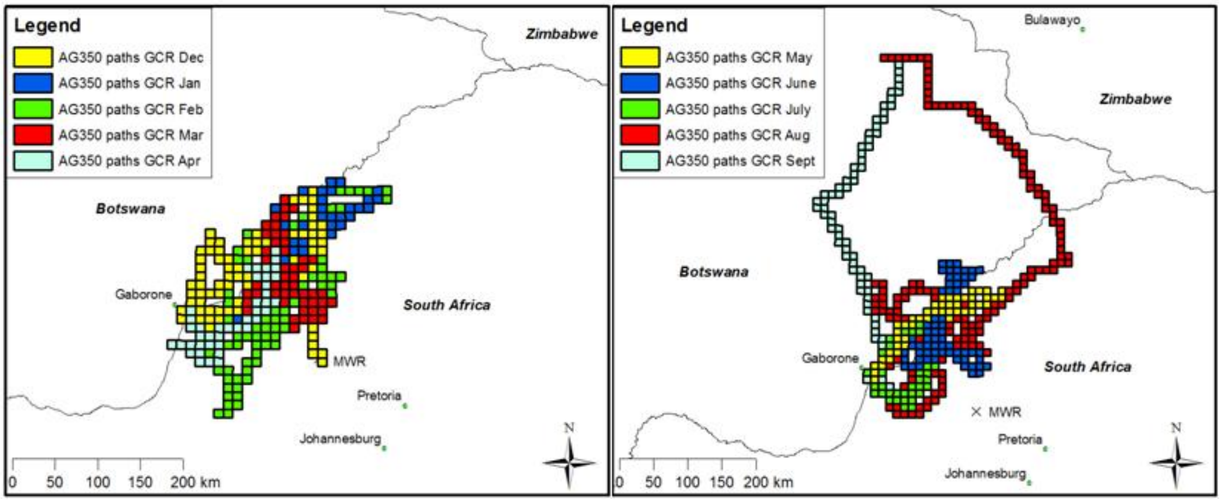
Figure 4.7. Mean (± SE) core GCR estimates for complete months for all vultures. Due to differences between tracking periods estimates were calculated for four vultures for December to March, and five vultures from April to September, inclusive. Refer to Table 4.4 for foraging ranges of individuals.



(a). AG330 summer months. (b). AG330 winter months.



(c). AG331 summer months. (d). AG331 winter months.



(e). AG350 summer months. (f). AG350 winter months.

Figure 4.8a-f. Monthly path grid cell ranges (GCRs) for the summer (December - April; a, c, e) and winter (May - September; b, d, f) periods for AG330, AG331 and AG350. Mankwe Wildlife Reserve is marked 'X MWR'.

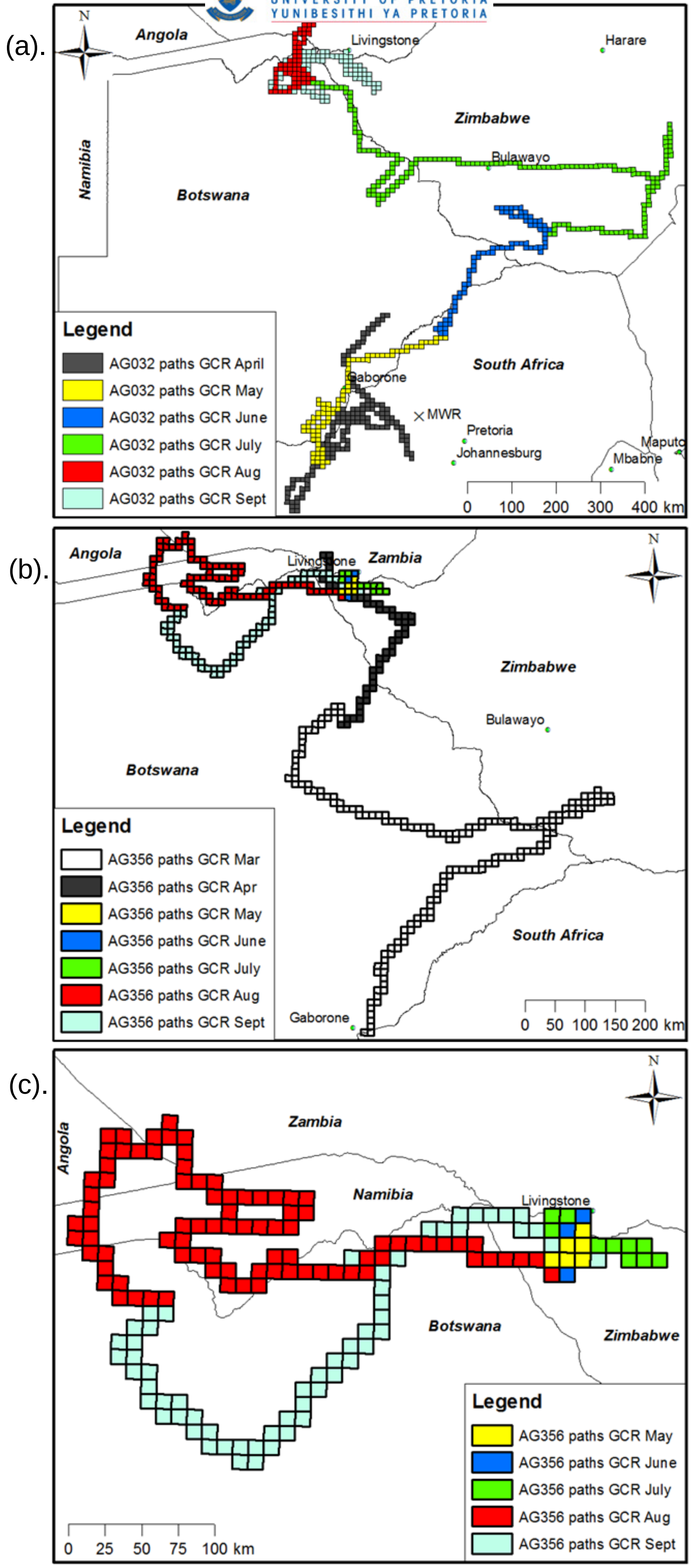


Figure 4.9a-c. Path grid cell ranges (GCRs) for all complete months for AG032 (a) and AG356 (b), and path GCRs for May – September for AG356 (c).

4.3. Overlap of foraging ranges

4.3.1. Overlap of total tracking period foraging ranges between individual vultures

AG332 was not tracked for a sufficient period of time to provide a representative estimate of its foraging range, and so data from this bird were not included in the analysis of the amount of overlap between different vultures' foraging ranges. The foraging ranges of the remaining five vultures potentially overlapped with four other individuals, providing a total of ten between-vulture overlap pairings (Table 4.5). Figure 4.10a-b shows the vultures' overlapping 95% and 50% KDE contours for their total tracking periods.

The average percentage overlap between pairs of vultures' overall foraging ranges for their total tracking periods (Table 4.5) represented by 95% KDE contours and path GCRs ranged from 27.79% to 65.85% (mean = 53.29 ± 3.52%; n = 10) and 11.19% to 35.71% (mean = 22.97 ± 2.89%; n = 10), respectively. The average percentage overlap between pairs of vultures' core foraging ranges ranged from 0.00% to 50.28% (mean = 17.89 ± 5.75%; n=10) for 50% KDE contours, and from 0.00% to 10.27% (mean = 5.18 ± 1.15%; n=10) for core GCRs. The highest values of average percentage overlap of pairs of path GCRs were between the three vultures that occupied foraging ranges either side of the Botswana-South Africa border (AG330, AG331 and AG350; mean overlap = 34.99 ± 0.50%).

Table 4.5. Average percentage overlap of overall and core foraging ranges between pairs of vultures. Overall foraging ranges were represented by 95% contours from kernel density estimation (KDE) and path grid cell ranges (GCR). Core foraging ranges were represented by 50% KDE contours and core GCRs.

		Average percentage overlap (%)			
		KDE		**GCR**	
Vulture A	**Vulture B**	**95% contour**	**50% contour**	**Paths**	**Core**
AG330	***AG331***	59.74	23.12	35.24	9.21
AG330	***AG350***	59.59	14.75	34.03	6.20
AG330	***AG356***	40.67	0.00	13.69	0.00
AG330	***AG032***	59.62	37.88	21.03	8.51
AG331	***AG350***	56.04	0.00	35.71	6.52
AG331	***AG356***	27.79	0.00	11.19	2.61
AG331	***AG032***	57.47	31.89	25.30	5.07
AG350	***AG356***	52.12	0.00	17.05	3.36
AG350	***AG032***	54.04	21.00	17.76	0.00
AG356	***AG032***	65.85	50.28	18.74	10.27

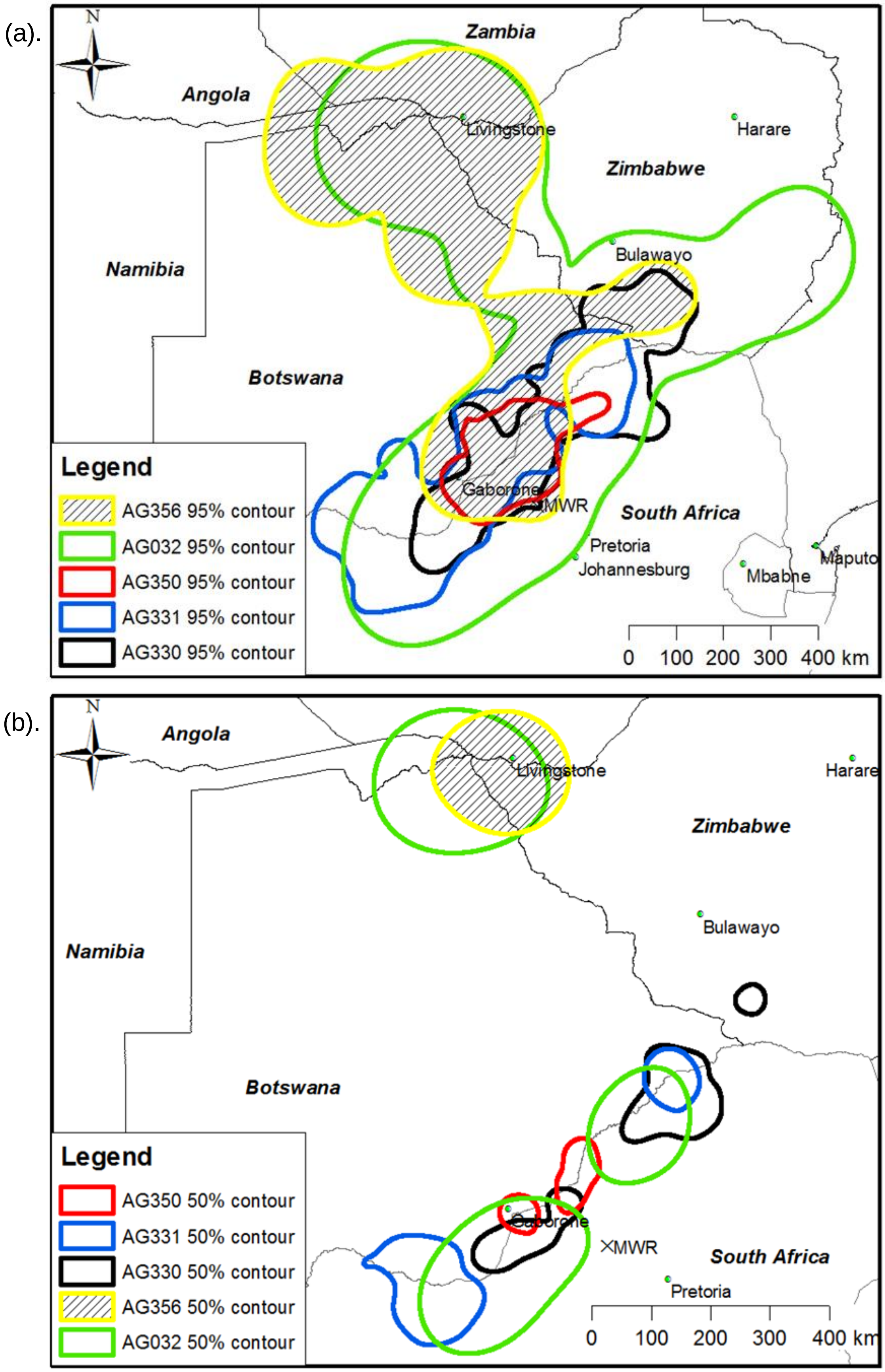


Figure 4.10a-b. Map to illustrate the overlap between five vultures' 95% (a) and 50% (b) KDE contours for their total tracking periods.

4.3.2. Overlap of coinciding monthly foraging ranges between vultures

Four vultures (AG330, AG331, AG350 and AG356) were tracked for a sufficient number of coinciding months for the calculation of the average percentage overlap of their point GCRs. Results are shown for three vultures that were tracked for 10 complete months in Table 4.6. Overlap of point GCRs occurred in 4 out of 10 months between AG330 and AG331, as well as between AG330 and AG350. Monthly point GCRs for AG331 and AG350 overlapped in five out of 10 months. For all months in which overlap of point GCRs occurred for those three vultures (n = 13), the mean (± SE) average percentage overlap was only 6.65 ± 1.79%. Figure 4.11a-b illustrates the complete absence of overlap between the three vultures' point GCRs in May and June.

For complete monthly point GCRs, only AG330 overlapped with AG356 by 3.11% (i.e. 1 grid cell) in March 2010. The point GCRs of AG331 and AG350 overlapped with AG356 in February by 3.47% and 3.42% (i.e. 1 grid cell for both) respectively, but February was not a *complete* month for AG356. Overlap with the point GCR of AG356 did not occur in any other months.

Table 4.6. Average percentage overlap of coinciding monthly point grid cell ranges (GCRs) between pairs of vultures (AG330, AG331 and AG350).

	Average percentage overlap of point GCRs (%)		
Month	**AG330 ∩ AG331**	**AG330 ∩ AG350**	**AG331 ∩ AG350**
December	*0.00*	2.57	2.47
January	*0.00*	8.03	*0.00*
February	2.48	9.40	*0.00*
March	5.34	*0.00*	2.41
April	25.60	*0.00*	8.04
May	*0.00*	*0.00*	*0.00*
June	*0.00*	*0.00*	*0.00*
July	*0.00*	10.71	*0.00*
August	*0.00*	*0.00*	2.03
September	2.35	*0.00*	5.00

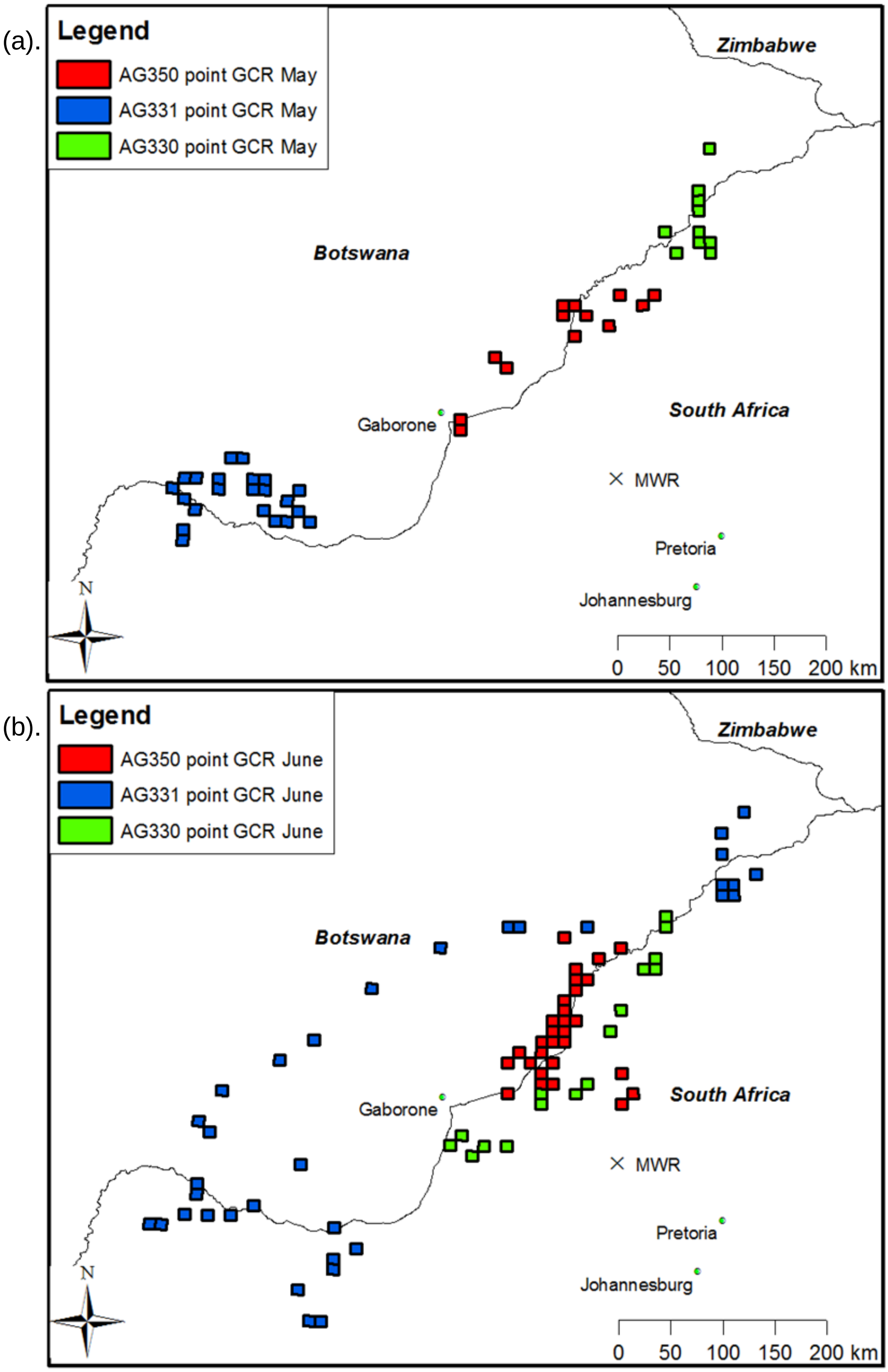


Figure 4.11a-b. Map to illustrate the complete absence of overlap of point GCRs for the months of May (a) and June (b) for AG330, AG331 and A350. AG356 was not present in the mapped area during that time.

4.3.3. Overlap of foraging ranges between consecutive months for individual vultures

For five vultures considered separately, mean (± SE) average percentage overlap of foraging ranges between consecutive months ranged from 10.53 ± 7.13% (AG032) to 32.65 ± 11.04% (AG356) for path GCRs and 2.16 ± 1.44% (AG331) to 45.71 ± 12.82% (AG356) for core GCRs (Table 4.7). The spatial patterns of the five vultures' monthly path GCRs are shown in Figures 4.8a-f and 4.9a-c. Data were recorded for only three complete months for AG332, and so were not included in this analysis.

Only two out of 10 pairs of consecutive monthly core GCRs overlapped for AG330 and AG331, compared to four out of 10 for AG350, five out of six for AG356 and three out of five for AG032 (Table 4.7).

Table 4.7. Average percentage overlap of overall (path GCR) and core (core GCR) foraging ranges between complete consecutive months for five vultures. The mean (± SE) average percentage overlap for each vulture is also shown.

		Average percentage overlap (%) between foraging ranges of consecutive months									
Method	**Vulture ID**	**Dec∩Jan**	**Jan∩Feb**	**Feb∩Mar**	**Mar∩Apr**	**Apr∩May**	**May∩June**	**June∩July**	**July∩Aug**	**Aug∩Sep**	**Mean ± SE**
Paths GCR	**AG330**	17.59	27.65	10.45	25.63	5.01	7.44	20.11	2.23	10.72	***14.09 ± 3.02***
	AG331	31.11	32.73	15.86	17.31	8.15	22.57	19.95	0.00	15.50	***18.13 ± 3.43***
	AG350	48.92	40.28	47.27	24.47	4.61	16.03	22.88	28.92	4.51	***26.43 ± 5.55***
	AG356	-	-	-	1.11	45.77	61.90	61.61	11.02	14.49	***32.65±11.04***
	AG032	-	-	-	-	10.20	2.44	0.88	0.96	38.19	***10.53 ± 7.13***
Core GCR	**AG330**	8.33	16.03	0.00	0.00	0.00	0.00	0.00	0.00	0.00	***2.71 ± 1.90***
	AG331	8.57	0.00	0.00	0.00	0.00	0.00	0.00	0.00	10.88	***2.16 ± 1.44***
	AG350	21.11	0.00	7.17	0.00	25.00	47.62	0.00	0.00	0.00	***11.21 ± 5.60***
	AG356	-	-	-	0.00	23.81	80.00	80.00	47.62	42.86	***45.71±12.82***
	AG032	-	-	-	-	13.33	20.83	0.00	0.00	29.09	***12.65 ± 5.73***

4.4. Autocorrelation and clumping

GPS locations in all datasets used for the calculation of foraging ranges were significantly autocorrelated, with a mean (± SE) Schoener's value (*V*) of 0.019 ± 0.011 for the total tracking periods of all six vultures (Table 4.8). GPS locations recorded during the total tracking periods of all six vultures had clumped distributions, with index of clumping values ranging from 2.90 for AG331 to 52.50 for AG350, at an average (± SE) of 17.68 ± 8.58 (Table 4.8).

GPS locations were significantly autocorrelated for all complete months for all vultures, with a mean (± SE) Schoener's *V* of 0.102 ± 0.017 (n = 46 complete months; Table 4.9). Index of clumping values (Table 4.9) indicated that GPS locations from 39 out of 46 complete months were clumped, with a mean (± SE) of 5.01 ± 1.30, ranging from -0.46 to 55.44. Five out of the seven months for which the index of clumping values were negative (i.e. dispersed locations) were calculated from locations recorded by AG331's tracking unit. Locations recorded each month for AG350 were the most clumped, with a mean clumping index value of 10.69 ± 5.46.

Table 4.8. Autocorrelation (Schoener's *V*) and clumping index values of GPS locations from total tracking periods of all vultures.

Vulture ID	**Tracking period (days)**	**Locations (*n*)**	**Schoener's *V***	**Index of clumping**
AG330	301	896	0.010	6.53
AG331	313	935	0.018	2.90
AG350	300	898	0.070	52.50
AG356	226	680	0.005	35.11
AG032	206	616	0.005	5.76
AG332	101	301	0.003	3.27

Schoener's values of <1.6 and >2.4 indicate significant autocorrelation (Rodgers & Kie, 2010; Schoener, 1981). Index of clumping values of >0 indicate clumping of GPS locations with maximum clumping indicated by a value of *n*-1 (Chapman & Wrangham, 1993; Green, 1966).

Table 4.9. Autocorrelation (Schoener's *V*) and clumping index values of GPS locations from complete months for all vultures. Mean (± SE) Schoener's and clumping index values for each vulture are presented, as well as the mean (± SE) number of locations recorded per month.

Vulture ID	Mean±SE locations (*n*) per month	Index	Dec	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	*Mean ± SE*
AG330	89.20 ±1.27	**Schoener's**	0.027	0.019	0.019	0.133	0.030	0.061	0.013	0.054	0.031	0.012	***0.040±0.012***
		Clumping	0.38	2.95	0.84	5.56	13.28	4.10	4.47	4.35	0.37	0.90	***3.72±1.22***
AG331	90.20 ±1.18	**Schoener's**	0.057	0.370	0.028	0.021	0.014	0.132	0.021	0.510	0.075	0.060	***0.129±0.054***
		Clumping	0.26	3.32	- 0.23	- 0.13	3.98	7.09	- 0.04	4.00	- 0.32	- 0.11	***1.78±0.83***
AG350	89.80 ±1.07	**Schoener's**	0.134	0.133	0.157	0.214	0.056	0.033	0.178	0.204	0.046	0.102	***0.126±0.021***
		Clumping	1.52	2.10	- 0.46	1.75	7.21	18.54	1.88	18.49	0.46	55.44	***10.69±5.46***
AG356	90.29 ±1.80	**Schoener's**	-	-	-	0.021	0.028	0.320	0.300	0.201	0.025	0.024	***0.131±0.052***
		Clumping	-	-	-	2.33	4.62	10.79	2.64	8.29	2.75	2.32	***4.82±1.28***
AG032	91.50 ±0.92	**Schoener's**	-	-	-	-	0.075	0.037	0.024	0.019	0.364	0.149	***0.111±0.054***
		Clumping	-	-	-	-	- 0.16	4.10	11.74	1.72	7.50	2.87	***4.63±1.77***
AG332	90.67 ±1.86	**Schoener's**	0.010	0.022	0.150	-	-	-	-	-	-	-	***0.061±0.045***
		Clumping	0.92	1.28	4.75	-	-	-	-	-	-	-	***2.32±1.22***

Schoener's values of <1.6 and >2.4 indicate significant autocorrelation (Rodgers & Kie, 2010; Schoener, 1981). Index of clumping values of >0 indicate clumping of GPS locations with maximum clumping indicated by a value of *n*-1 (Chapman & Wrangham, 1993; Green, 1966).

4.5. Utilisation of protected areas and areas of different cattle densities

4.5.1. Utilisation of protected areas

Figure 4.12 compares the proportion of stationary GPS locations recorded inside protected and non-protected areas (i.e. use) by five vultures relative to their availability in the vultures' foraging ranges. Due to the short period over which AG332 was tracked, insufficient data were collected for inclusion in the analysis. Protected areas occupied a mean of 4.33 ± 1.50% of the 95% KDE contours of the three vultures that spent the majority of their tracking periods either side of the South Africa-Botswana border (AG330, AG331 and AG350), compared to 32.22 ± 9.75% of the 95% KDE contours of the two vultures that travelled north through southern Africa (AG356 and AG032). A mean of 5.21 ± 0.88% of stationary GPS locations within the 95% KDE contours of AG330, AG331 and AG350 were inside protected areas, compared to 35.30 ± 1.13% for AG356 and AG032.

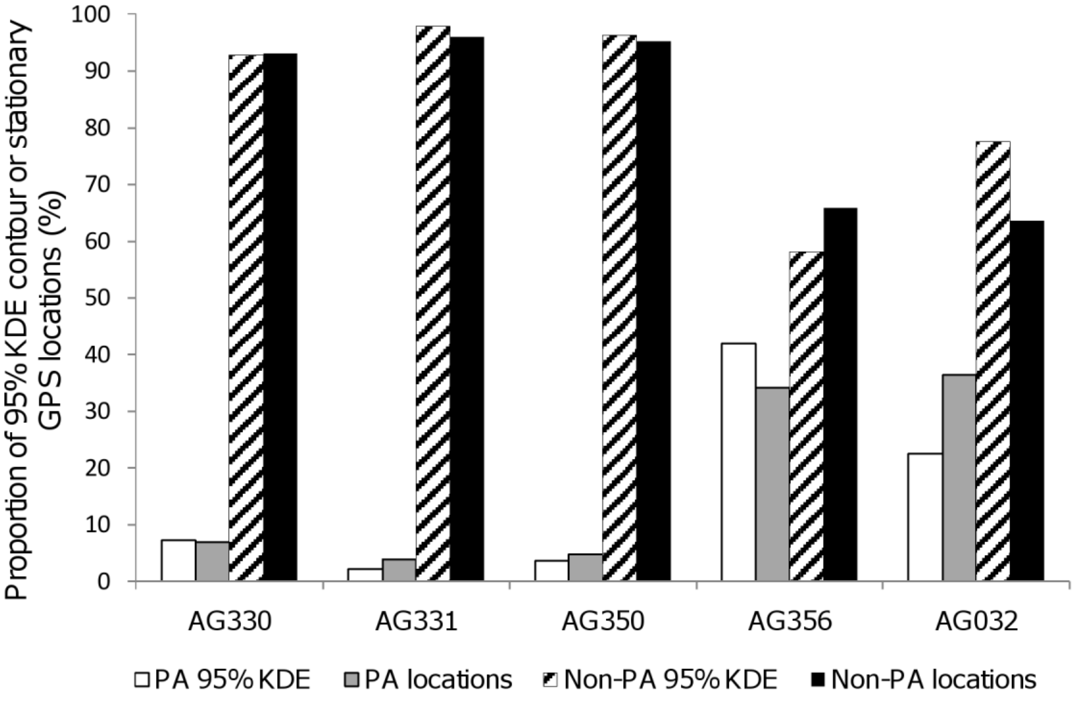


Figure 4.12. Use versus availability of protected (PA) and unprotected (Non-PA) areas at the overall foraging range scale. The relative proportions of PAs and non-PAs in each vulture's 95% KDE contour represent availability, and the proportion of stationary GPS locations recorded in PAs and non-PAs represent use.

Protected areas occupied a mean of 3.15 ± 1.58% of the 50% KDE contours of AG330, AG331 and AG350, compared to 38.62 ± 11.63% for AG356 and AG032 (Figure 4.13). Protected areas were completely absent from the 50% KDE contours of AG331.

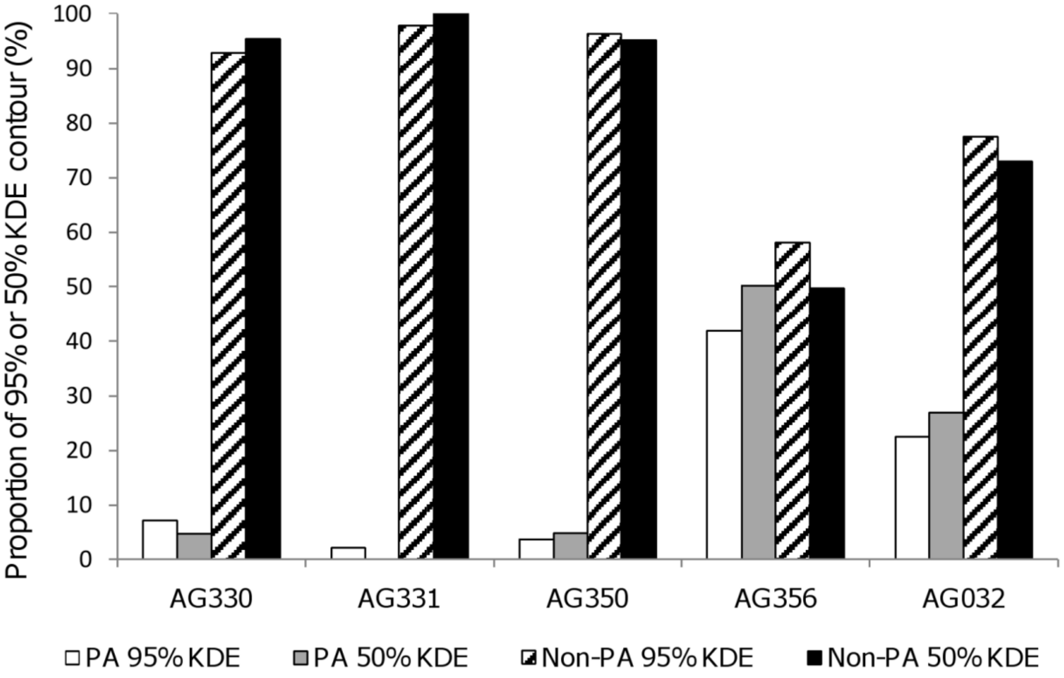


Figure 4.13. Use versus availability of protected (PA) and unprotected (Non-PA) areas at the core foraging range scale. The relative proportions of PAs and non-PAs in each vulture's 95% and 50% KDE contours represent availability and use, respectively.

At the overall foraging range scale RSF values (Table 4.10) were significantly different from proportional use for AG331 (Exact binomial goodness-of-fit test, *p* = 0.0018) and AG032 (Exact binomial goodness-of-fit test, *p* = 0.0009). Ivlev's electivity index values (Figure 4.14) indicated that a higher proportion of stationary GPS locations were recorded within protected areas than expected based on their availability within the 95% KDE contours of both vultures. Use of protected and non-protected areas was not significantly disproportionate for any other vultures, although Ivlev's electivity index values (Figure 4.14) indicated a degree of avoidance of protected areas by AG330 and AG356, and a degree of positive selection for protected areas by AG350.

At the core foraging range scale Ivlev's electivity index values (Figure 4.15) and RSF values (Table 4.10) indicated that the relative proportions of protected and non-protected areas in the 50% KDE contours were not significantly different from the 95% KDE contours for AG350, AG356 or AG032. RSF values were significantly different from proportional use for AG330 (Exact binomial goodness-of-fit test, p = 0.021), indicating lower than expected proportions of protected areas in the 50% KDE contours. Protected areas were totally absent from the 50% KDE contours for AG331, resulting in a significant difference from proportional use (Exact binomial goodness-of-fit test, $p < 0.0005$) and an Ivlev's electivity index value for protected areas of -1.00 (maximum avoidance). Figures 4.18a-b show the 50% KDE contours of the vultures in relation to the distribution of protected areas.

Table 4.10. Selection of protected (PA) and unprotected (Non-PA) areas at the overall and core foraging range scales: resource selection functions (RSFs) and significance (*p*) of disproportionate use determined by exact binomial tests for goodness-of-fit ("*" = significantly disproportionate use at 0.05 level). Availability was represented by the relative proportions of PAs and non-PAs in 95% KDE contours. At the overall foraging range scale use was represented by the relative proportions of each vulture's stationary GPS locations recorded in PAs and non-PAs. At the core foraging range scale use was represented by the relative proportions of PAs and non-PAs in the 50% KDE contours.

	RSF values[(a)] indicating selection/avoidance of PAs and non-PAs					
	95% KDE (available) vs stationary GPS locations (use)			***95% KDE (available) vs 50% KDE (use)***		
Vulture ID	***PA***	***Non-PA***	***Sig.(p)***	***PA***	***Non-PA***	***Sig.(p)***
AG330	0.488	0.512	0.764	0.385	0.615	0.021*
AG331	0.656	0.344	0.0018*	0.000	1.000	< 0.0005*
AG350	0.568	0.432	0.193	0.571	0.429	0.133
AG356	0.418	0.582	0.089	0.583	0.417	0.089
AG032	0.664	0.336	0.0009*	0.560	0.440	0.193

(a) RSF values of 0.50 indicate use of a category in proportion to its availability, RSF values >0.50 indicate use more than expected based on availability (maximum = 1.00) and RSF values <0.50 indicate use less than expected based on availability (maximum avoidance = 0.00).

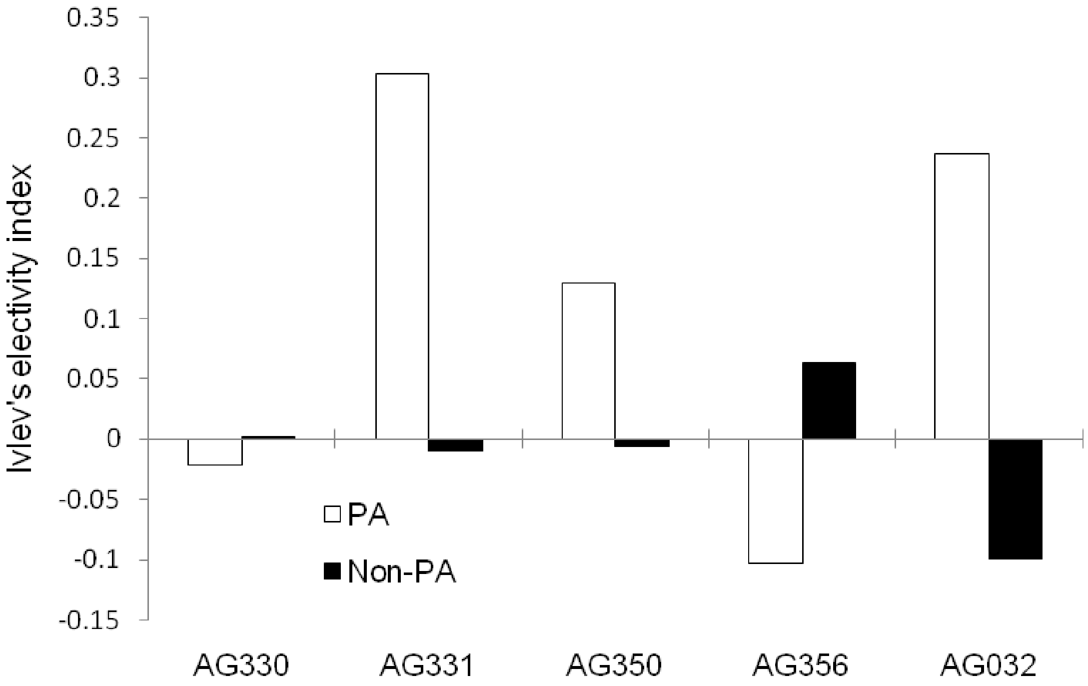


Figure 4.14. Ivlev's electivity index values for protected (PA) and unprotected (Non-PA) areas at the overall foraging range scale. Availability was represented by the relative proportions of PAs and non-PAs in each vulture's 95% KDE contour, and use was represented by the proportion of stationary GPS locations recorded inside PAs and non-PAs. Negative Ivlev's electivity index values indicate avoidance (maximum avoidance = -1), positive values indicate positive selection (maximum = 1) and values of zero indicate use in proportion to availability.

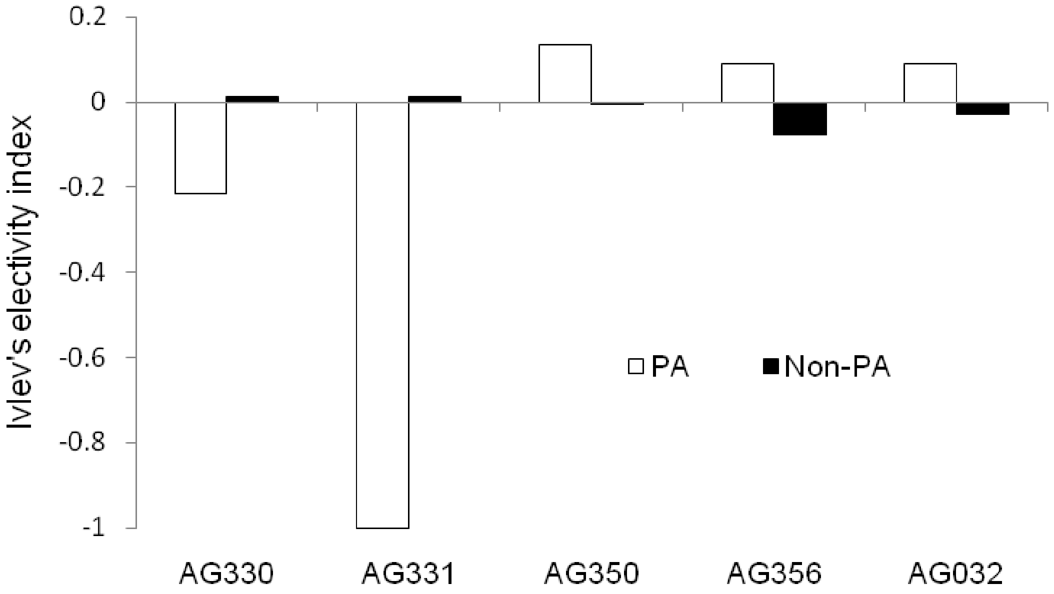


Figure 4.15. Ivlev's electivity index values for protected (PA) and unprotected (Non-PA) areas at the core foraging range scale. Availability and use were represented by the relative proportions of PAs and non-PAs in each vulture's 95% and 50% KDE contours, respectively. Negative Ivlev's electivity index values indicate avoidance (maximum avoidance = -1), positive values indicate positive selection (maximum = 1) and values of zero indicate use in poportion to availability.

The three vultures that spent the majority of their time in northern South Africa or southern Botswana did not regularly utilise protected areas (Figures 4.16, 4.18a). Atherstone Nature Reserve (24°32' S, 26°47'E) was visited most regularly by AG350 (98% of AG350's stationary GPS locations recorded inside PAs (i.e. 4.67% of all of its stationary locations) were at Atherstone NR) compared to other protected areas, which only tended to be visited for relatively short periods (e.g. Wonderkop NR, 23°24' S, 28°37'E). Pilanesberg NP (25°14'S, 27°05'E), Welgevonden (24°18'S, 27°49'E), Lapalala (23°51'S, 28°15'E), Moepel NR (23°42'S, 28°27'E), Kwalata (23°53'S, 28°07'E) and other conservation areas in the Waterberg Biosphere Reserve were never visited by any of the vultures, while only 2 and 5 stationary locations (both from AG331) were inside Madikwe GR (24°45'S, 26°14'E) and Marakele NP (24°24'S, 27°35'E) respectively. 18 (2.33%) stationary GPS locations from AG330 were inside the Shashe-Limpopo Transfrontier Conservation Areas in south-western Zimbabwe (21°34'S, 29 °18'E).

Stationary GPS locations from AG032 and AG356 were never recorded inside South African protected areas (Figure 3.17), despite 38% of AG032's stationary locations being recorded inside South Africa's borders. The protected areas utilized most frequently by AG032 and AG356 were in the Kavango-Zambezi Transfrontier Conservation Area, including Chobe NP (18°08'S, 24 °43'E) and associated wildlife management areas (WMAs) in northern Botswana, and the Matetsi safari area (17°57'S, 25°28'E), Zambezi NP (17°54'S, 25°46'E) and Hwange NP (18°39'S, 26°32'E) in north-west Zimbabwe (Figures 3.17, 3.18b). AG032 also visited Gonarezhou NP (21°35'S, 31°50'E) and the Save Conservancy (20°13'S, 32°18'E) in south-eastern Zimbabwe, with 25 (4.7%) stationary GPS locations inside the latter. The majority of AG032's stationary GPS locations that were recorded within protected areas were inside Chobe NP and surrounding WMAs (24% of all of its stationary locations). The southernmost protected area visited by AG356 was a WMA south of the Makgadikgadi Pans National Park in Botswana (20°55'S, 24 °55'E). AG356 also travelled through protected areas in the Caprivi Strip (Namibia) and entered Sioma Ngwezi NP in Zambia (17°17'S, 23°18'E), Luiana NP in Angola (17°29'S, 23°06'E) and Moremi Game Reserve in the Okavango Delta of Botswana (18°45'S, 23°01'E) over a four week period.

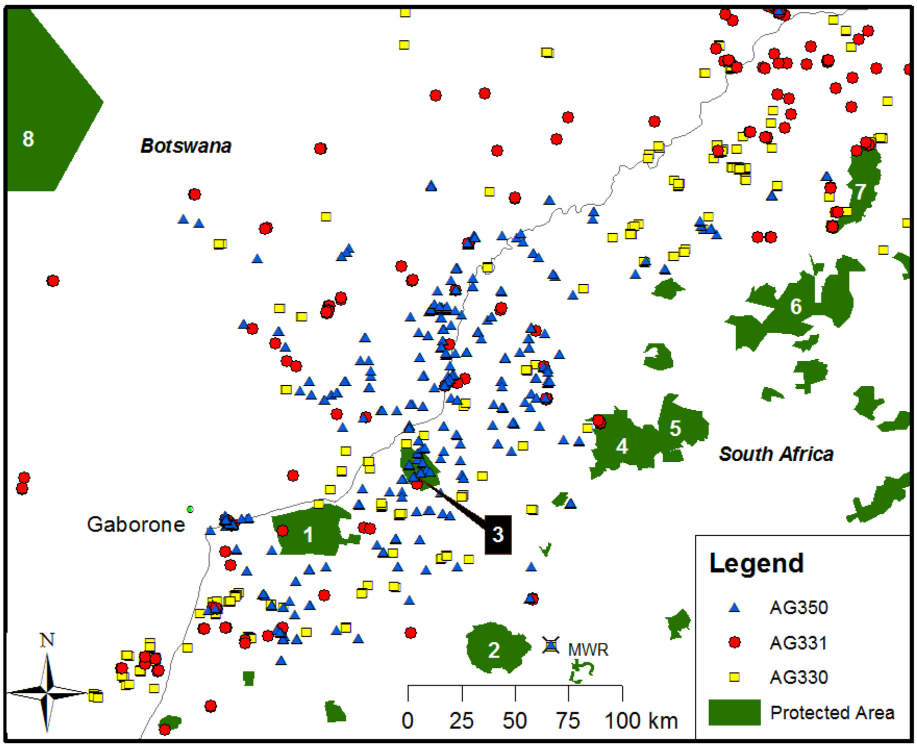


Figure 4.16. Stationary GPS locations from AG330 (squares), AG331 (circles) and AG350 (triangles), and the distribution of protected areas in the south-western Limpopo and north-eastern North West Provinces of South Africa, and south east Botswana. 1 = Madikwe GR; 2 = Pilanesberg NP; 3 = Atherstone NR; 4 = Marakele NP; 5 = Welgevonden NR; 6 = Lapalala / Moepel et al. reserves; 7 = Wonderkop NR; 8 = Central Kalahari GR; MWR = Mankwe Wildlife Reserve capture site.

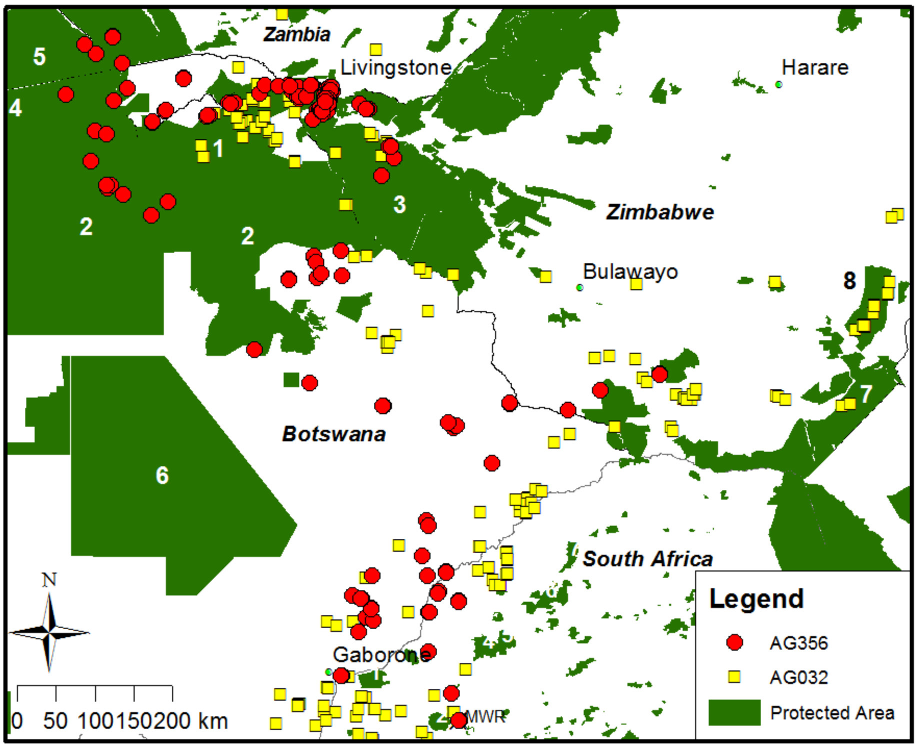


Figure 4.17. Stationary GPS locations from AG032 (squares) and AG356 (circles), and the distribution of protected areas. 1 = Chobe NP; 2 = Wildlife Management Areas (Botswana); 3 = Hwange NP; 4 = Caprivi GR; 5 = Luiana NP (Angola); 6 = Central Kalahari GR; 7 = Gonarezhou NP; 8 = Save Conservancy; MWR = Mankwe Wildlife Reserve capture site.

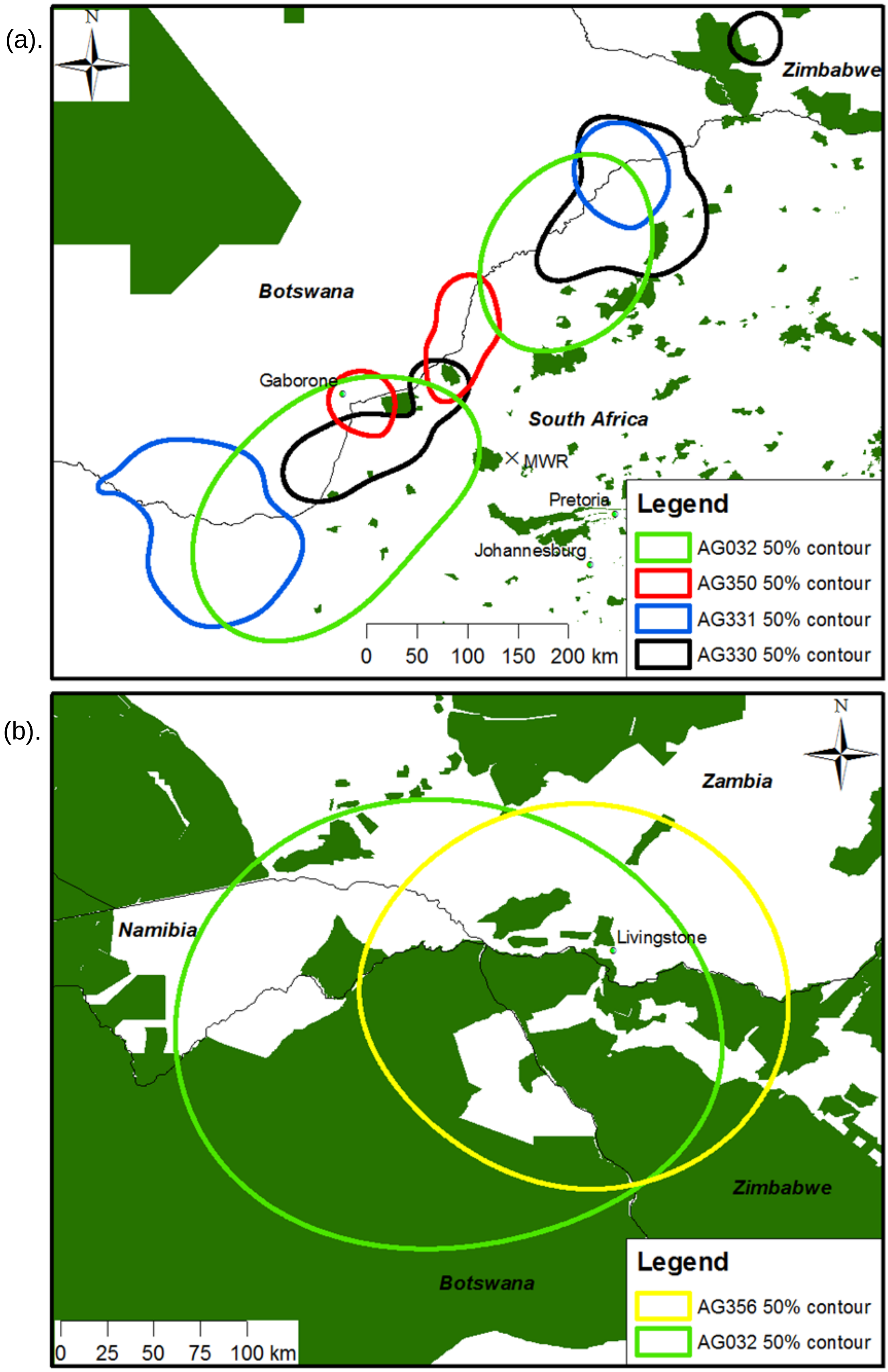


Figure 4.18a-b. Maps to show the distribution of protected areas (shaded green polygons) in relation to 50% KDE contours for AG330, AG331, AG350 (a), AG032 (a, b) and AG356 (b).

4.5.2. Utilisation of areas of different cattle densities

The relative proportions of the four different categories of cattle densities (zero = 0 cattle km^{-2}; low = 1 – 6 cattle km^{-2}; medium = 7 – 15 cattle km^{-2}; high = ≥16 cattle km^{-2}) in each vulture's 95% KDE contour are shown in Figure 4.19, and the proportions of stationary GPS locations recorded in each category are shown in Figure 4.20. The 95% KDE contours of the three vultures that spent the majority of their tracking periods either side of the South Africa-Botswana border (AG330, AG331 and AG350) contained only small proportions of the zero cattle density category (mean = 7.72 ± 0.10%) compared to the two vultures that travelled north through southern Africa (AG356 and AG032; mean = 24.92 ± 4.81%). On average the medium cattle density category occupied the largest proportion of the 95% KDE contours of AG330, AG331 and AG350 (mean = 35.87 ± 2.00%), while the low cattle density category was the most prevalent within the foraging ranges of AG032 and AG356 (mean = 31.33 ± 0.91%). The high cattle density category occupied the lowest proportion of the 95% KDE contours of AG032 and AG356 (mean = 17.95 ± 4.22%).

Averaged across the five vultures, the highest proportion of stationary GPS locations (Figure 4.20) were recorded in the medium cattle density category (mean = 30.72 ± 6.42%), followed by zero cattle density (mean = 27.68 ± 11.10%), low cattle density (mean = 22.76 ± 4.62%) and finally the high cattle density category (mean = 18.83 ± 4.71%). The zero cattle density category contained the highest proportion of a single vulture's stationary GPS locations (66.17% for AG356), while the high cattle density category contained the smallest proportion of the same vulture's stationary GPS locations (4.15%).

On average, the highest proportion of the 50% KDE contours consisted of the medium cattle density category (mean = 35.36 ± 4.35%), followed by low cattle density (mean = 31.04 ± 3.68%), high cattle density (mean = 18.15 ± 4.78%) and finally the zero cattle density category (mean = 15.44 ± 5.67%) (Figure 4.21). The medium cattle density category comprised the highest proportion of a single vulture's 50% KDE contours (46.08% for AG331), while the zero cattle density occupied the smallest proportion (2.21%) of the same vulture's 50% KDE contours.

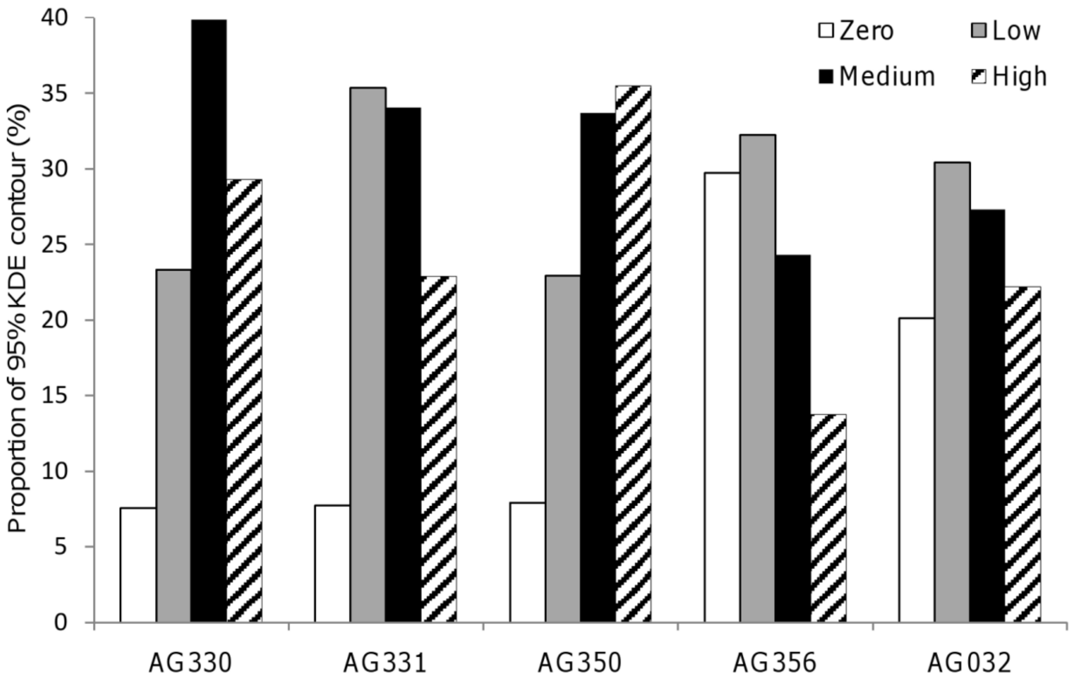


Figure 4.19. Relative proportions of areas of different cattle densities within the 95% KDE contour of each vulture. Zero = 0 cattle km^{-2}; low = 1 – 6 cattle km^{-2}; medium = 7 – 15 cattle km^{-2}; high = ≥16 – 1383 cattle km^{-2}.

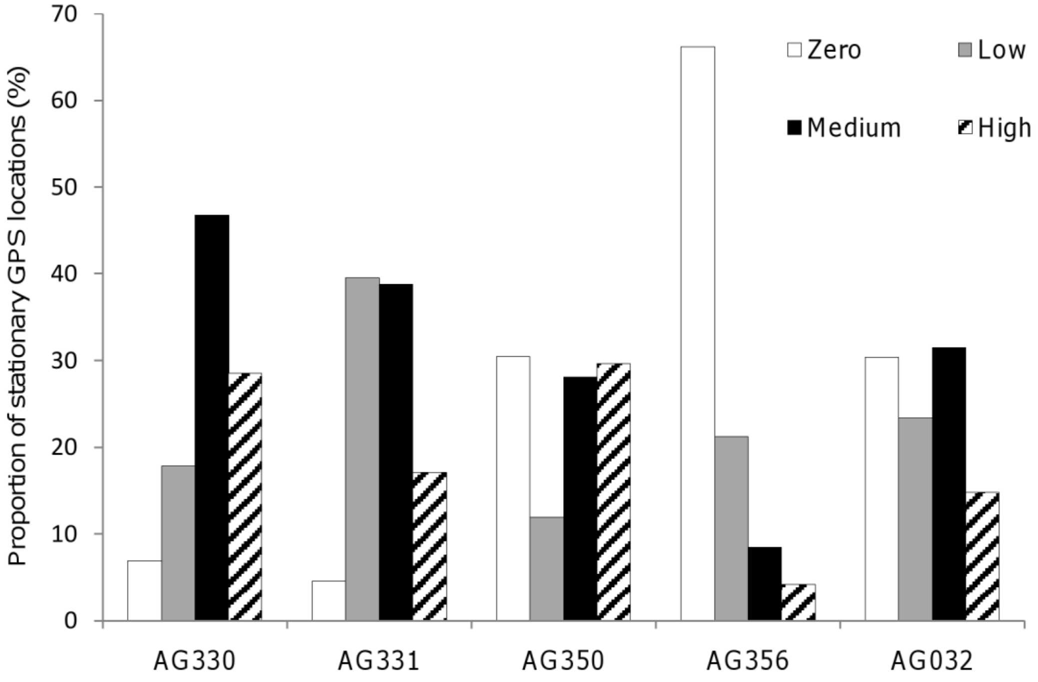


Figure 4.20. Relative proportions of stationary GPS locations within each cattle density category. Zero = 0 cattle / km^2 ; Low = 1 – 6 cattle / km^2; Medium = 7 – 15 cattle / km^2; High = 16 – 1,383 cattle / km^2.

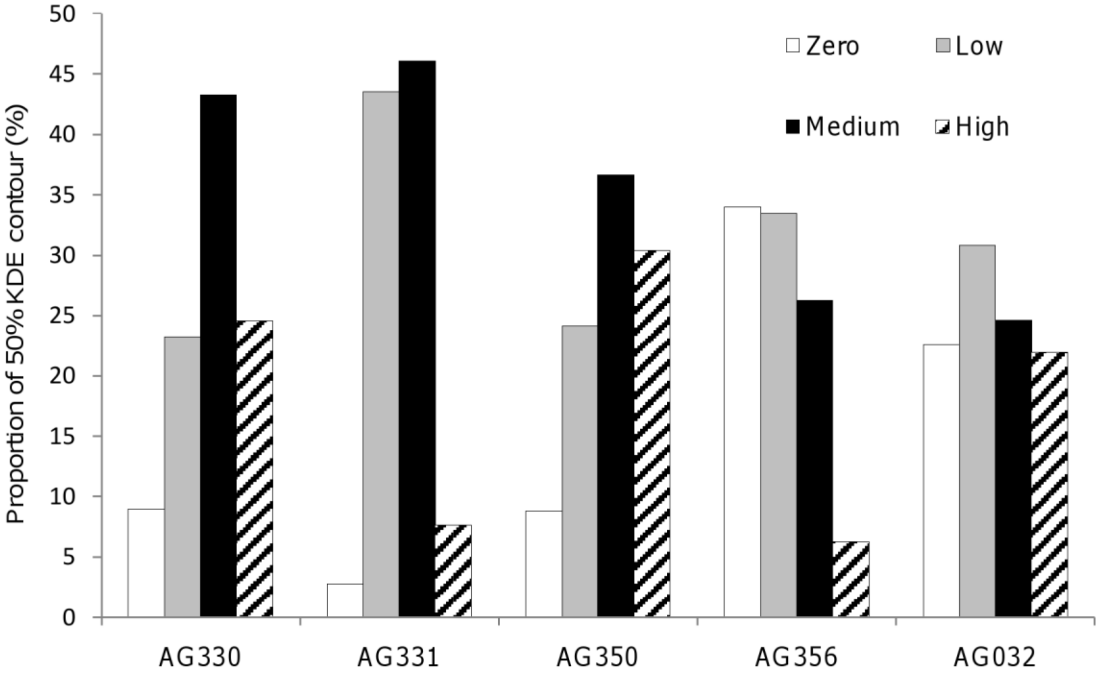


Figure 4.21. Relative proportions of areas of different cattle densities within the 50% KDE contours of each vulture. Zero = 0 cattle km^{-2}; low = 1 – 6 cattle km^{-2}; medium = 7 – 15 cattle km^{-2}; high = 16 – 1383 cattle km^{-2}.

At the overall foraging range scale, chi-squared goodness-of-fit tests (α = 0.00625 following Bonferroni adjustments (Sokal & Rohlf, 1995)) suggested that the use of the different cattle density categories (indicated by RSF values, Table 4.11) were significantly disproportionate to their availability for AG350 (χ^2 (3) = 79.95, p < 0.0005) and AG356 (χ^2 (3) = 79.65, p < 0.0005). Ivlev's electivity index values (Figure 4.22) indicated that a higher proportion of stationary GPS locations were recorded within the zero cattle density category than expected for both vultures. AG356 also showed a degree of avoidance of the medium and high cattle density categories. There was no significant difference between the RSF values for the relative proportions of stationary GPS locations recorded inside each cattle density category and proportional availability of each category for AG330 (χ^2 (3) = 2.48, p = 0.499), AG331 (χ^2 (3) = 7.28, p = 0.064) or AG032 (χ^2 (3) = 10.80, p = 0.013) (Table 4.11).

At the core foraging range scale the use of cattle density categories (i.e. the proportion of the 50% KDE contour that each cattle density category covered) was significantly disproportionate to their availability in the overall foraging range (indicated by RSF values, Table 4.11) for AG331 (χ^2 (3) = 33.84, p < 0.0005). Ivlev's electivity index values (Figure 4.23) indicated that the 50% KDE contours consisted of higher proportions of the low and medium cattle density categories than expected based on their availability in the 95% KDE contour, and lower proportions of the zero and high categories. There were no significant differences between the RSF values for the 50% KDE contours (Table 4.11) and proportional use for AG330 (χ^2 (3) = 1.727, p = 0.651), AG350 (χ^2 (3) = 0.880, p = 0.841), AG356 (χ^2 (3) = 9.20, p = 0.028) or AG032 (χ^2 (3) = 0.720, p = 0.883).

For all five vultures, at both the overall and core foraging range scales, the high cattle density category was the only one to be used less than expected based on its overall availability.

Figures 4.24-4.26 show the spatial distribution of the different cattle density categories within the 95% and 50% KDE contours of each vulture.

Table 4.11. Selection of different cattle density categories (zero = 0 cattle km^{-2}; low = 1 – 6 cattle km^{-2}; medium = 7 – 15 cattle km^{-2}; high = 16 – 1383 cattle km^{-2}) at the overall and core foraging range scales. Availability was represented by the relative proportions of the different cattle density categories in the 95% KDE contour of each vulture. At the overall foraging range scale use was represented by the relative proportions of stationary GPS locations recorded in each cattle density category. At the core foraging scale use was represented by the relative proportions of the different cattle density categories in the 50% KDE contours of each vulture. Resource selection functions (RSFs) and significance (*p*) of disproportionate use determined by chi-squared tests for goodness-of-fit (“*” = significantly disproportionate use at $p < 0.00625$) are shown.

	RSF values(a) indicating selection/avoidance of cattle density categories									
	95% KDE contour (available) versus stationary GPS locations (use)					**95% KDE contour (available) versus 50% KDE contour (use)**				
Vulture ID	***Zero***	***Low***	***Medium***	***High***	***Sig.(p)***	***Zero***	***Low***	***Medium***	***High***	***Sig.(p)***
AG330	0.239	0.200	0.307	0.255	0.499	0.288	0.243	0.264	0.204	0.651
AG331	0.164	0.311	0.317	0.209	0.064	0.110	0.375	0.413	0.102	< 0.0005*
AG350	0.639	0.086	0.138	0.138	< 0.0005*	0.272	0.256	0.264	0.208	0.841
AG356	0.630	0.186	0.098	0.085	< 0.0005*	0.308	0.279	0.290	0.123	0.028
AG032	0.368	0.187	0.282	0.163	0.013	0.279	0.251	0.224	0.246	0.883

a) RSF values of 0.25 indicate use of a category in proportion to its availability, RSF values >0.25 indicate use more than expected based on availability (maximum = 1.00) and RSF values <0.25 indicate use less than expected based on availability (maximum avoidance = 0.00).

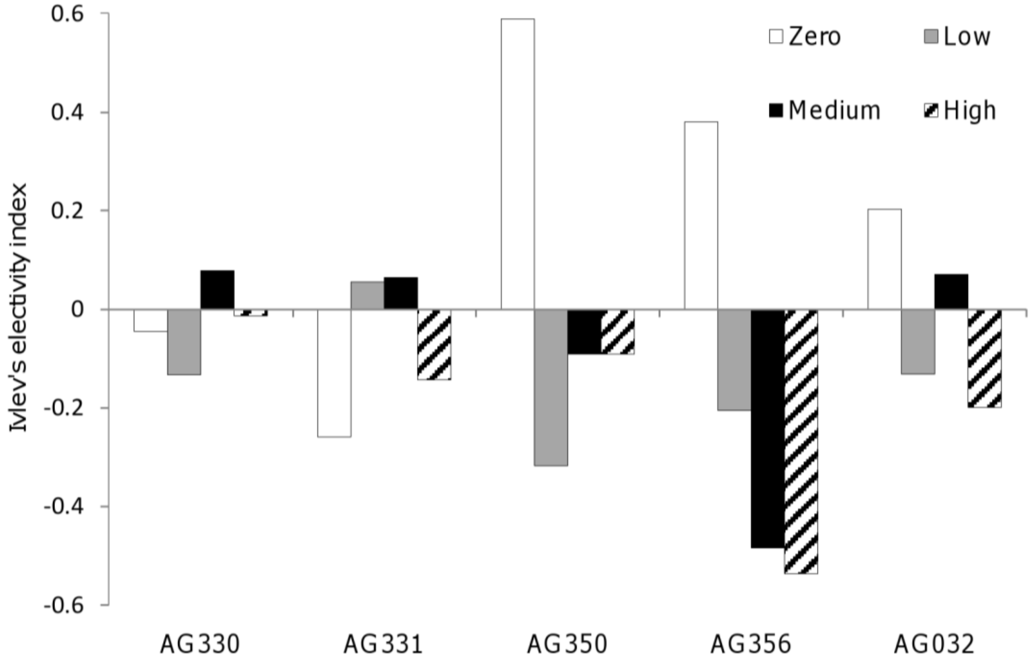


Figure 4.22. Selection of different cattle density categories (zero = 0 cattle km^{-2}; low = 1 – 6 cattle km^{-2}; medium = 7 – 15 cattle km^{-2}; high = 16 – 1383 cattle km^{-2}) by five vultures at the overall foraging range scale indicated by Ivlev's electivity indices. Availability was represented by the proportion of each cattle density category in the 95% KDE contour of each vulture, and use was represented by the proportion of stationary GPS locations recorded in each category. Negative Ivlev's electivity index values indicate avoidance (maximum avoidance = -1), positive values indicate positive selection (maximum = 1) and values of zero indicate use in proportion to availability.

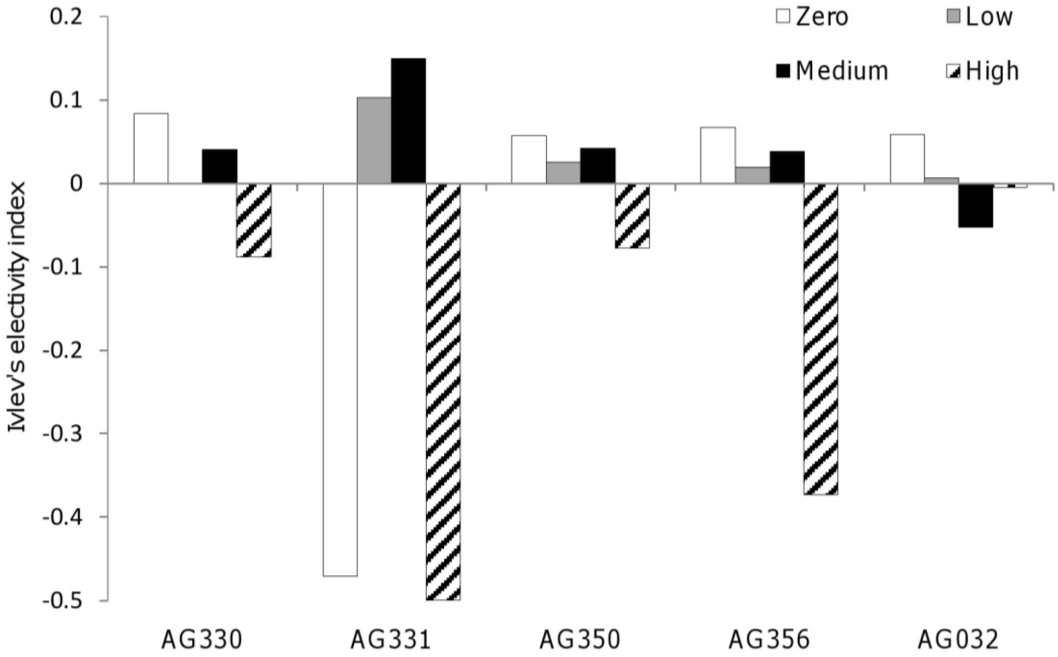


Figure 4.23. Selection of different cattle density categories (zero = 0 cattle km^{-2}; low = 1 – 6 cattle km^{-2}; medium = 7 – 15 cattle km^{-2}; high = 16 – 1383 cattle km^{-2}) by five vultures at the core foraging range scale indicated by Ivlev's electivity indices. Availability and use were represented by the proportion of each cattle density category in the 95% and 50% KDE contours of each vulture, respectively. Negative Ivlev's electivity index values indicate avoidance (maximum avoidance = -1), positive values indicate positive selection (maximum = 1) and values of zero indicate use in proportion to availability.

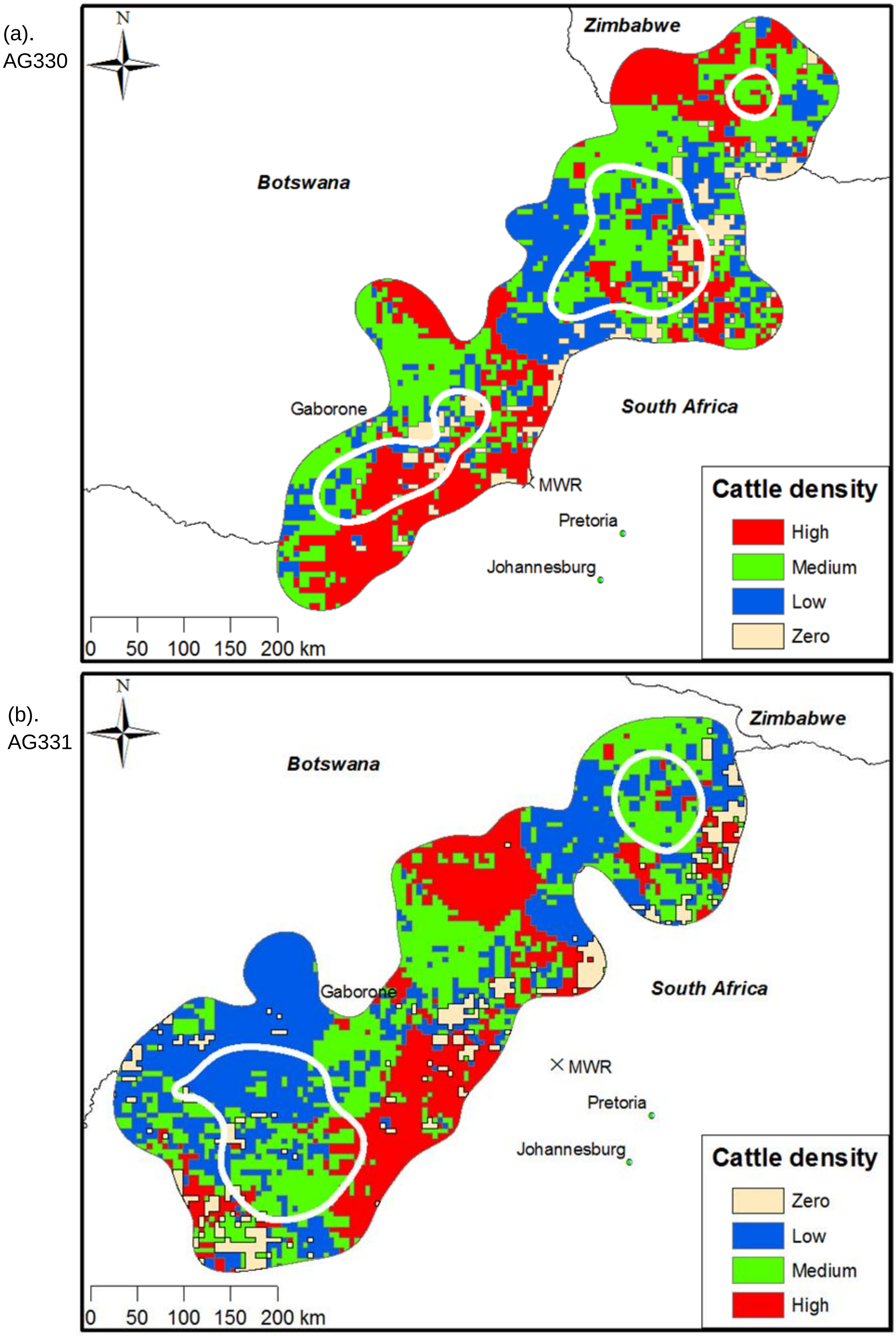


Figure 4.24a-b. Distribution of cattle density categories (zero = 0 cattle km^{-2}; low = 1 – 6 cattle km^{-2}; medium = 7 – 15 cattle km^{-2}; high = 16 – 1383 cattle km^{-2}) in the 95% and 50% (polygon with white border) KDE contours of AG330 (a) and AG331 (b).

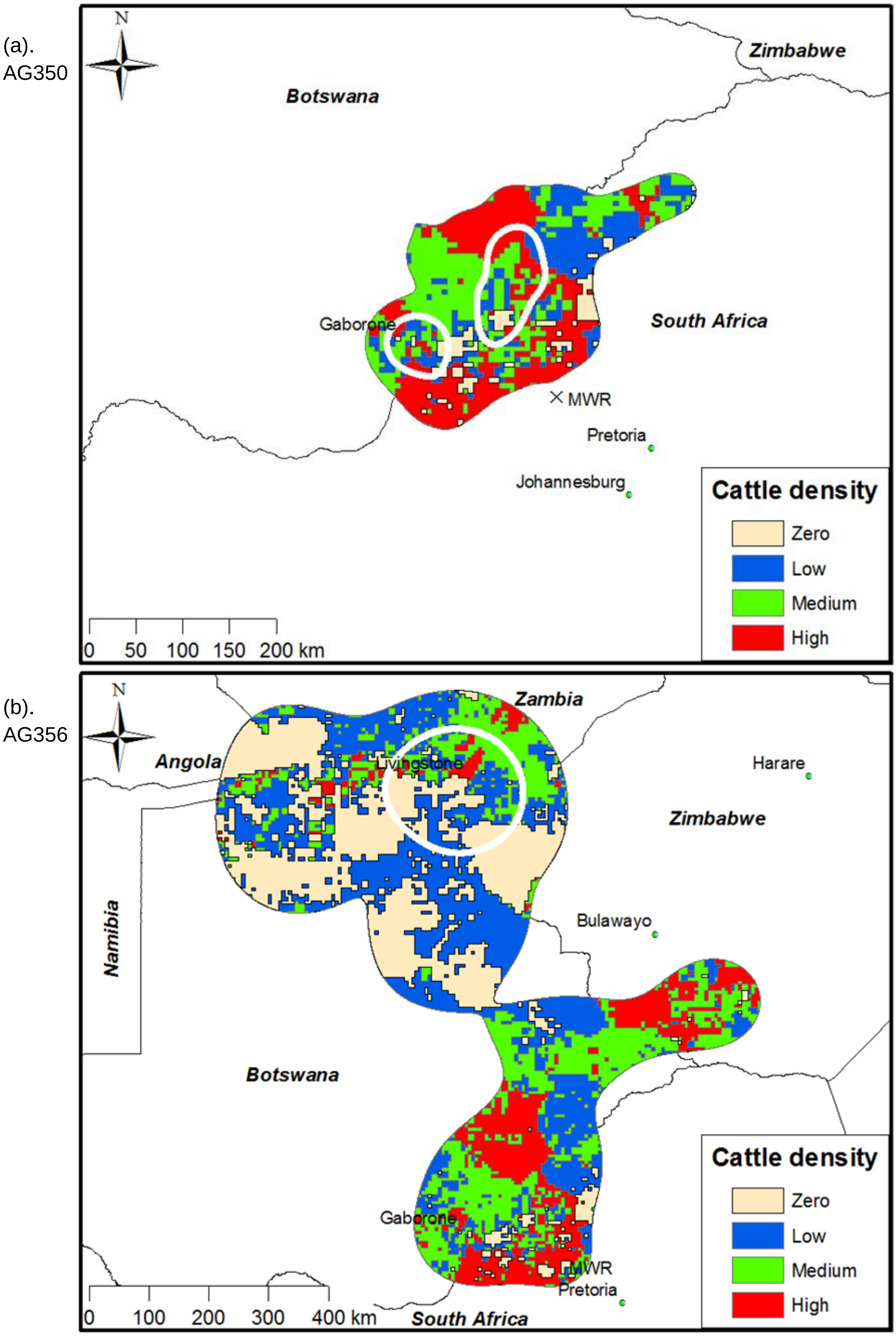


Figure 4.25a-b. Distribution of cattle density categories (zero = 0 cattle km^{-2}; low = 1 – 6 cattle km^{-2}; medium = 7 – 15 cattle km^{-2}; high = 16 – 1383 cattle km^{-2}) in the 95% and 50% (polygon with white border) KDE contours of AG350 (a) and AG356 (b).

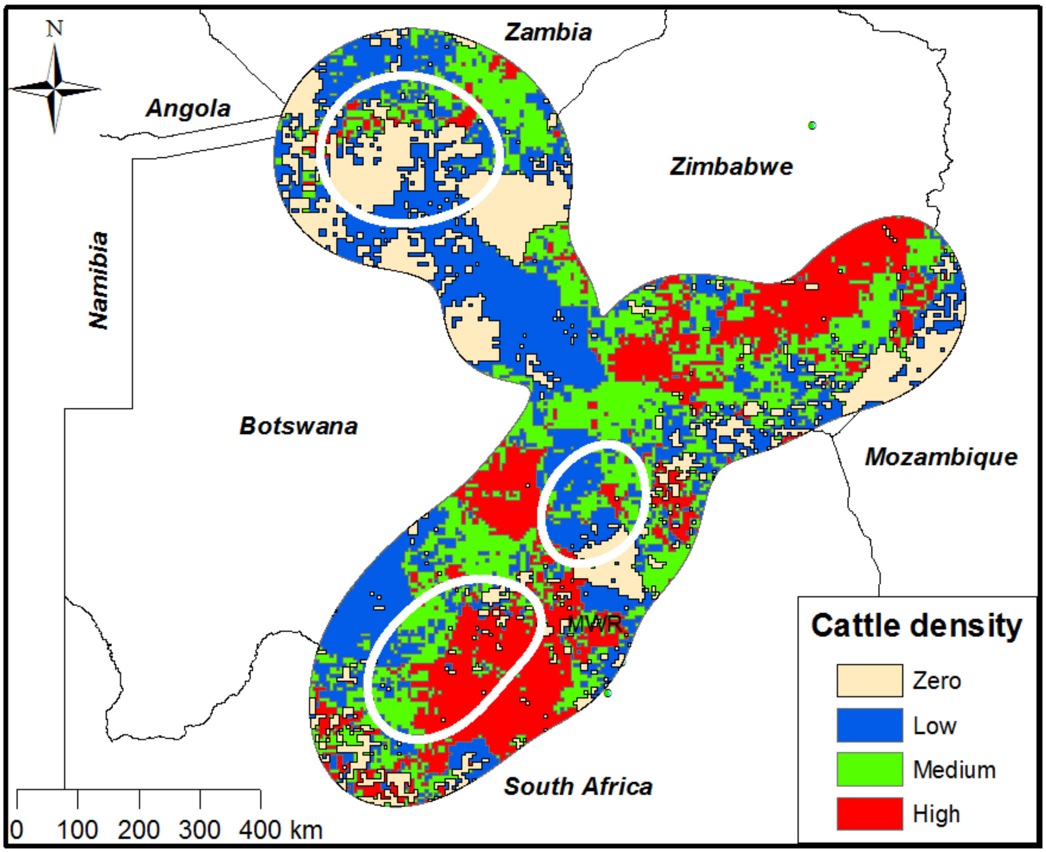


Figure 4.26. Distribution of cattle density categories (zero = 0 cattle km^{-2}; low = 1 – 6 cattle km^{-2}; medium = 7 – 15 cattle km^{-2}; high = 16 – 1383 cattle km^{-2}) in the 95% and 50% (polygon with white border) KDE contours of AG032.

4.6. Distances travelled

Excluding AG332, which travelled 2,502 km in 101 days, the total distances travelled during the vultures' total tracking periods ranged from 5,032 in 226 days by AG356 to 15,293 km in 313 days by AG331 (Table 4.12). The mean (± SE) total distances travelled per day ranged from 22.27 ± 2.13 km (AG356) to 48.86 ± 2.59 km (AG331) (mean = 33.39 ± 4.36 km), and the mean distances between consecutive GPS locations ranged from 7.41 km to 16.37 km (mean = 11.17 ± 1.47 km) (Table 4.12). The maximum distance travelled per day ranged from 160.17 km (AG332) to 267.43 km (AG331) (mean = 207.97 ± 17.44 km) (Table 4.12).

On average, the vultures travelled more than 10 km on 58.34 ± 5.02% days of their total tracking periods (Table 4.12). The mean distance travelled on days on which more than 10 km was travelled was 54.55 ± 3.45 km, and the mean proportion of the total distance travelled during the total tracking period that was travelled on days when more than 10 km was travelled was 96.97 ± 0.63% (Table 4.12).

Table 4.12. Total distances travelled during total tracking periods, mean (± SE) distance between consecutive GPS locations, maximum and mean (± SE) total distance travelled per day, the proportion of days on which more than 10 km was travelled, the proportion of the total distance travelled on days when more than 10 km was travelled, and the mean (± SE) distance travelled on days when more than 10 km was travelled.

Vulture ID	Tracking days	Total distance travelled (km)	Mean distance between consecutive fixes (km)	Maximum distance travelled / day (km)	Mean (±SE) total distance travelled / day (km)	Proportion of days > 10 km travelled (%)	Proportion of total distance travelled on days > 10 km/day (%)	Mean (±SE) distance travelled on days >10 km/day travelled (km)
AG330	301	7,699.03	8.60 ± 0.61	183.90	25.84 ± 2.04	48.18	96.04	50.65 ± 3.01
AG331	313	15,293.49	16.37 ± 0.83	267.43	48.86 ± 2.59	77.32	98.75	62.26 ± 4.31
AG350	300	11,273.75	12.57 ± 0.67	241.63	37.58 ± 2.23	66.00	98.09	55.85 ± 2.53
AG356	226	5,032.54	7.41 ± 0.62	171.22	22.27 ± 2.13	50.88	94.88	41.52 ± 3.31
AG032	206	8,453.76	13.75 ± 1.01	223.48	41.04 ± 2.95	62.14	98.10	64.79 ± 3.29
AG332	101	2,502.17	8.34 ± 1.14	160.17	24.77 ± 3.94	45.54	95.96	52.20 ± 6.70

Table 4.13 provides the minimum, maximum and mean average distances travelled and associated values for all complete months for all vultures. The total distance travelled during a complete month ranged from 176.57 km for AG332, to 2,490.10 km for AG331. The mean total distance travelled per month varied markedly between individual vultures, from 630.77 ± 157.87 km (n = 7 months) for AG356 to 1,503.76 ± 165.25 km (n = 10 months) for AG331. The proportion of days per month on which more than 10km was travelled ranged from 14.81% (AG330) to 96.77% (AG331), and the mean (± SE) distance travelled on days on which more than 10km was travelled ranged from 16.38 ± 1.70 km (AG356) to 95.66 ± 31.02 km (AG350). Figure 4.27 shows the mean total distances travelled per day for each complete month averaged across all vultures. On average the vultures moved the smallest distance per day in May (mean ± SE = 14.59 ± 3.26 km; n = 5), while they moved the furthest per day in December (mean ± SE = 48.93 ± 6.28 km; n = 4).

Four out of five vultures that were tracked during summer (December to April) and winter (May to September) months travelled further during the summer than the winter (Figure 4.28), although the difference was not significant when averaged across all five vultures (summer mean = 42.51 ± 4.34 km/day; winter mean = 30.62 ± 6.23; *Z* = -1.753, *p* = 0.080). AG332 was not tracked during the winter period and was not included in this analysis.

Some of the vultures undertook relatively long distance movements outside of their existing foraging ranges. In a one week period at the end of August, AG350 travelled in a loop of more than 850 km from the Limpopo Province (23^{o}15’S, 28^{o}28’E), north to the Makgadikgadi Pans area of Botswana (20^{o}38’S, 26^{o}17’E) before returning to its core foraging area via a route just east of the Central Kalahari NP (22^{o}29’S, 25^{o}13’E), covering more than 200 km in a single day. During a ten day period AG032 travelled over 1,000 km across Zimbabwe from the Save Conservancy in the east of the country (20^{o}24’S, 32^{o}08’E), to the Makgadikgadi Pans area of Botswana (20^{o}50’S, 26^{o}30’E) and then north to the edge of Chobe NP in northern Botswana (18^{o}29’S, 25^{o}10’E). In the first 2.5 days of this journey the vulture travelled over 520 km across the width of Zimbabwe. In March AG356 travelled over 1400 km north east from Mochudi in southern Botswana (24^{o}12’S, 26^{o}07’E) to south west Zimbabwe (21^{o}12’S, 29^{o}40’E) and then to an area north of the Makgadikgadi Pans in Botswana (19^{o}51’S, 25^{o}38’E). By mid-April the vulture had travelled more than 300 km further north to the Victoria Falls area of Zimbabwe. AG331 moved the furthest in a single month (2,490.10 km), travelling twice between its two core foraging ranges over 380 km apart in the Limpopo and North West Provinces.

Table 4.13. The minimum, maximum and mean (± SE) of the total distances travelled, mean distances between consecutive GPS locations, maximum and mean total distance travelled per day, the proportion of days on which more than 10 km was travelled, the proportion of the total distance travelled during each tracking period that was travelled on days when more than 10 km was travelled, and the mean distance travelled on days on which more than 10 km was travelled, for complete months for all vultures.

Vulture ID	Number of complete months	Statistic	Total distance travelled (km)	Mean distance between consecutive fixes (km)	Maximum distance travelled / day (km)	Mean total distance travelled / day (km)	Proportion of days > 10 km travelled (%)	Proportion of total distance travelled on days > 10 km (%)	Mean distance travelled on days >10 km travelled (%)
AG330	10	*Minimum*	198.52	2.45 ± 1.00	47.21	7.35 ± 3.56	14.81	83.35	25.65 ± 4.40
		Maximum	1196.61	13.91 ± 2.15	183.90	41.26 ± 7.55	72.41	99.19	64.88 ± 12.41
		Mean	**769.90**	**8.56**	**109.90**	**25.69**	**48.70**	**93.78**	**47.35**
		S.E.	134.71	1.50	13.32	4.49	6.62	1.62	4.38
AG331	10	*Minimum*	572.94	6.16 ± 1.39	103.48	18.48 ± 4.26	48.39	92.43	35.30 ± 6.38
		Maximum	2490.10	26.78 ± 3.47	267.43	80.33 ± 11.16	96.77	99.96	91.50 ± 11.30
		Mean	**1503.76**	**16.64**	**162.65**	**49.67**	**78.28**	**98.27**	**61.24**
		S.E.	165.25	1.80	15.65	5.37	4.69	0.70	4.68
AG350	10	*Minimum*	409.38	4.55 ± 1.17	77.07	13.65 ± 3.63	24.14	90.78	34.85 ± 5.60
		Maximum	1784.62	21.14 ± 2.52	241.63	63.41 ± 8.26	93.33	99.76	95.66 ± 31.02
		Mean	**1127.38**	**12.59**	**131.50**	**37.64**	**65.92**	**97.19**	**56.47**
		S.E.	158.80	1.80	15.85	5.39	7.98	0.94	5.88
AG356	7	*Minimum*	226.55	2.44 ± 0.51	29.68	7.31 ± 1.42	32.26	79.55	16.38 ± 1.70
		Maximum	1406.85	15.13 ± 2.87	171.22	45.38 ± 9.36	67.74	98.10	86.26 ± 10.43
		Mean	**630.77**	**7.02**	**93.05**	**21.11**	**50.28**	**90.04**	**37.42**
		S.E.	157.87	1.72	21.79	5.16	4.95	3.54	9.11
AG032	6	*Minimum*	742.31	8.17 ± 2.05	76.92	24.74 ± 5.09	45.16	92.29	45.97 ± 5.44
		Maximum	1771.03	18.84 ± 3.70	223.48	57.13 ± 10.43	83.33	99.43	91.43 ± 11.26
		Mean	**1217.24**	**13.31**	**136.75**	**39.94**	**60.79**	**97.52**	**63.12**
		S.E.	184.11	2.01	19.93	6.07	5.71	1.12	6.53
AG332	3	*Minimum*	176.57	2.09 ± 0.49	31.52	6.09 ± 1.53	27.59	80.49	17.77 ± 2.29
		Maximum	1097.00	11.92 ± 2.50	160.17	35.39 ± 8.27	58.06	97.47	66.82 ± 11.33
		Mean	**770.87**	**8.40**	**116.26**	**25.00**	**45.75**	**91.73**	**46.91**
		S.E.	297.62	3.16	42.38	9.47	9.27	5.62	14.89

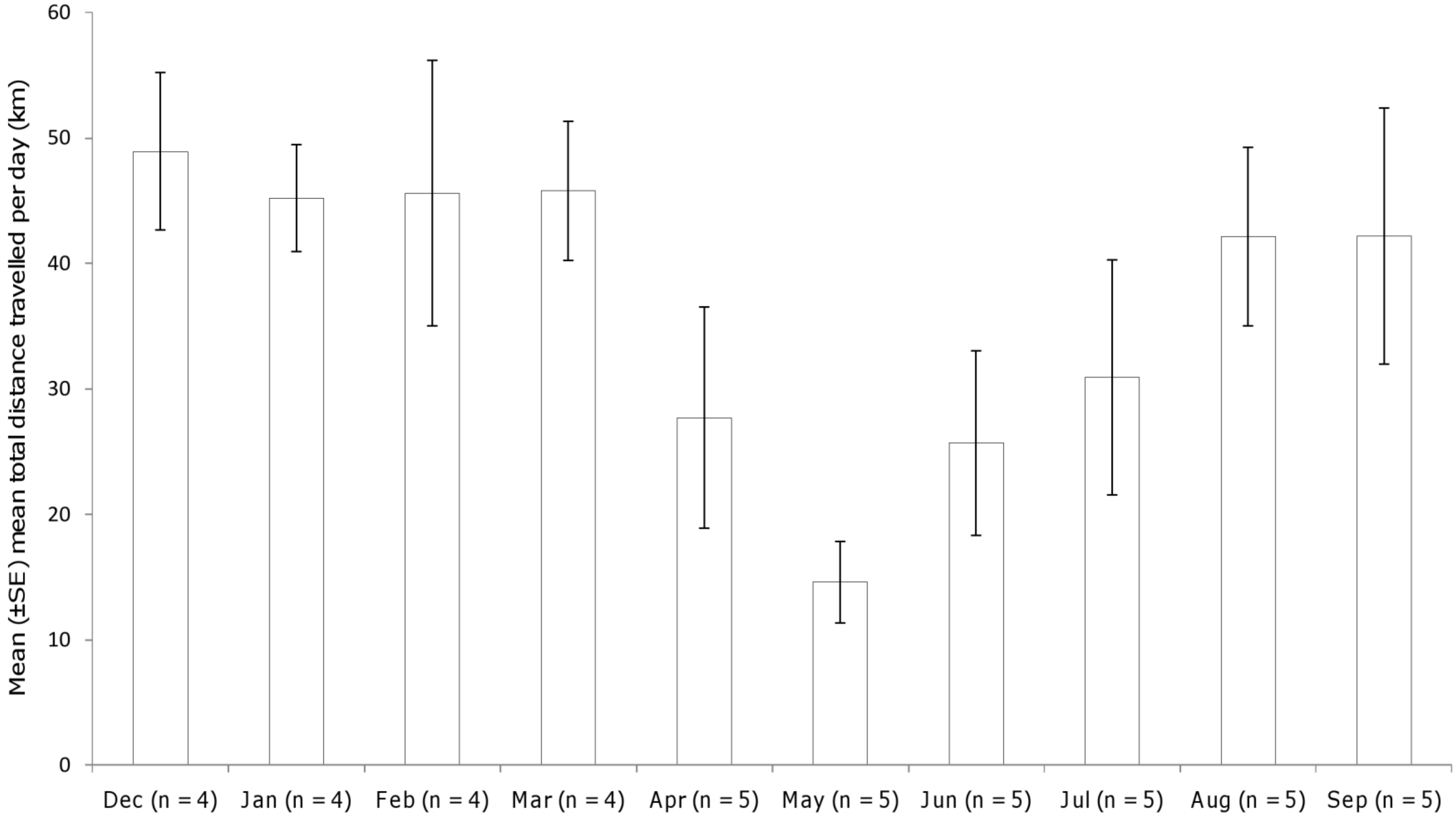


Figure 4.27. Mean total distance travelled per day during complete months averaged (± SE) across all vultures. The sample size (i.e. number of vultures) for each month is given in parentheses. Data were available for four vultures from December to February (AG330, AG331, AG350 and AG332) and March (AG330, AG331, AG350 and AG356), and five vultures from April to September (AG330, AG331, AG350, AG356 and AG032).

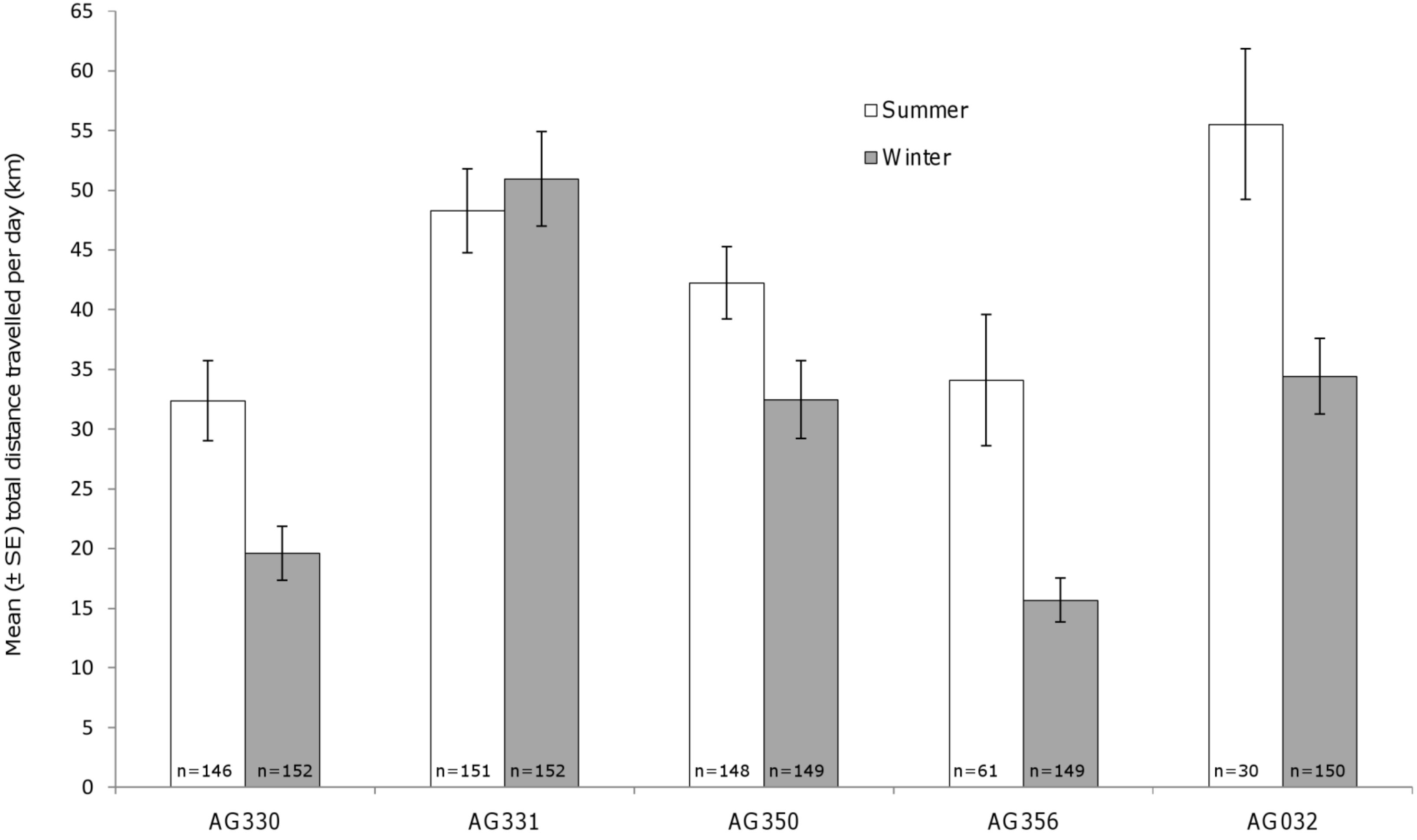


Figure 4.28. Mean (± SE) total distance travelled per day in the summer (December to April) and winter (May to September) periods for each vulture. The numbers of days for which data were available for each season are shown at the base of each bar. AG332 was not tracked during the winter period and was not included in the analysis.

4.7. Flight speeds and altitudes

For the total tracking periods of all vultures collectively, the proportion of all GPS locations that were moving (i.e. ≥10 km/h) ranged from 8.64% for AG332 to 23.61% for AG350 (mean ± SE = 15.87 ± 2.57%). Of those moving locations, a mean (± SE) of 0.42 ± 0.26 % (range: 0.00 – 1.61%) were recorded at 07:00h, 48.07 ± 4.47% (range: 32.47 – 59.09%) at 11:00h and 51.50 ± 4.51% (range: 40.91 – 67.53%) at 15:00h.

Figure 4.29 shows the proportion of GPS locations that were recorded as moving at 07:00h, 11:00h and 15:00h for all vultures. On average 0.22 ± 0.11% of all locations recorded at 07:00h were moving, 24.20 ± 5.45% of 11:00h locations were moving and 23.26 ± 2.58% of 15:00h locations were moving.

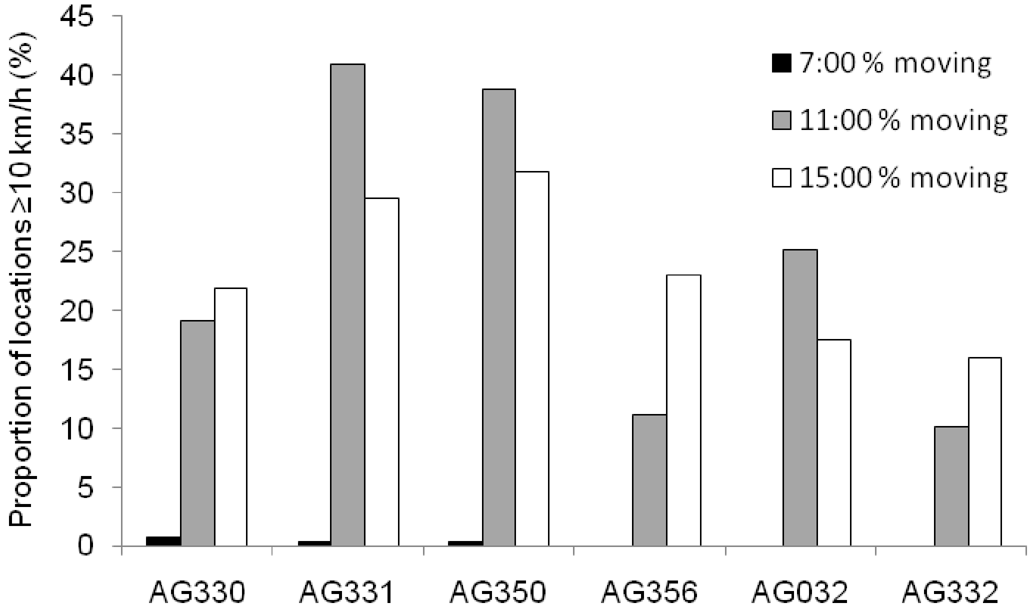


Figure 4.29. The percentage of GPS locations that were recorded as moving (≥10 km/h) at 07:00h (black column), 11:00h (grey column) and 15:00h (white column) for all vultures.

The maximum and the mean altitude above ground level (Table 4.14) ranged from 1,152 m (AG332) to 2,267 m (AG350) and 409.88 ± 17.05 m (AG331) to 653.90 ± 34.87 m (AG330), respectively. The maximum and mean speeds of moving points ranged from 76 km/h (AG332) to 107 km/h (AG331) and 47.08 ± 1.60 km/h (AG356) to 56.16 ± 1.19 km/h (AG350), respectively.

Table 4.14. The proportion of all GPS locations that were moving (i.e. ≥ 10 km/h), and the maximum and mean (± SE) altitude above ground level and speeds of travel for each vulture.

Vulture ID	**Proportion (%) of points ≥10 km/h[*]**	**Maximum altitude above ground (m)**	**Mean (± SE) altitude above ground level (m)**	**Maximum speed (km/h)**	**Mean (± SE) speed (km/h)**
AG330	13.83 (124/896)	1,855.00	653.90 ± 34.87	81.00	47.17 ± 1.24
AG331	23.53 (220/935)	1,320.00	409.88 ± 17.05	107.00	50.61 ± 1.09
AG350	23.61 (212/898)	2,267.00	532.09 ± 26.33	98.00	56.16 ± 1.19
AG356	11.32 (77/680)	1,594.00	610.43 ± 36.16	83.00	47.08 ± 1.60
AG032	14.31 (88/615)	1,749.00	642.66 ± 41.51	84.00	49.49 ± 1.54
AG332	8.64 (26/301)	1,152.00	519.08 ± 65.58	76.00	50.88 ± 3.10

[*]Figures in parentheses are the number of moving locations divided by the total number of recorded locations.

Figure 4.30 shows the proportion of all moving GPS locations in 100 metre altitude above ground level categories for all vultures collectively. The highest proportion of moving GPS locations (15.26%) was in the 301 – 400 m altitude above ground level category. 40.96% of all moving GPS locations were recorded between 200 and 500 m above ground level.

For moving GPS locations of all vultures analysed collectively, a Pearson's product-moment test for correlation identified a very strong positive correlation between altitude above ground level and speed of travel ($r = 0.278$, n = 747, $p < 0.0005$). That is, the speed of travel increased with the altitude above ground level. Figure 4.31 shows the mean speed of moving locations in each 100 metre altitude above ground level category, and the positive correlation between speed and altitude.

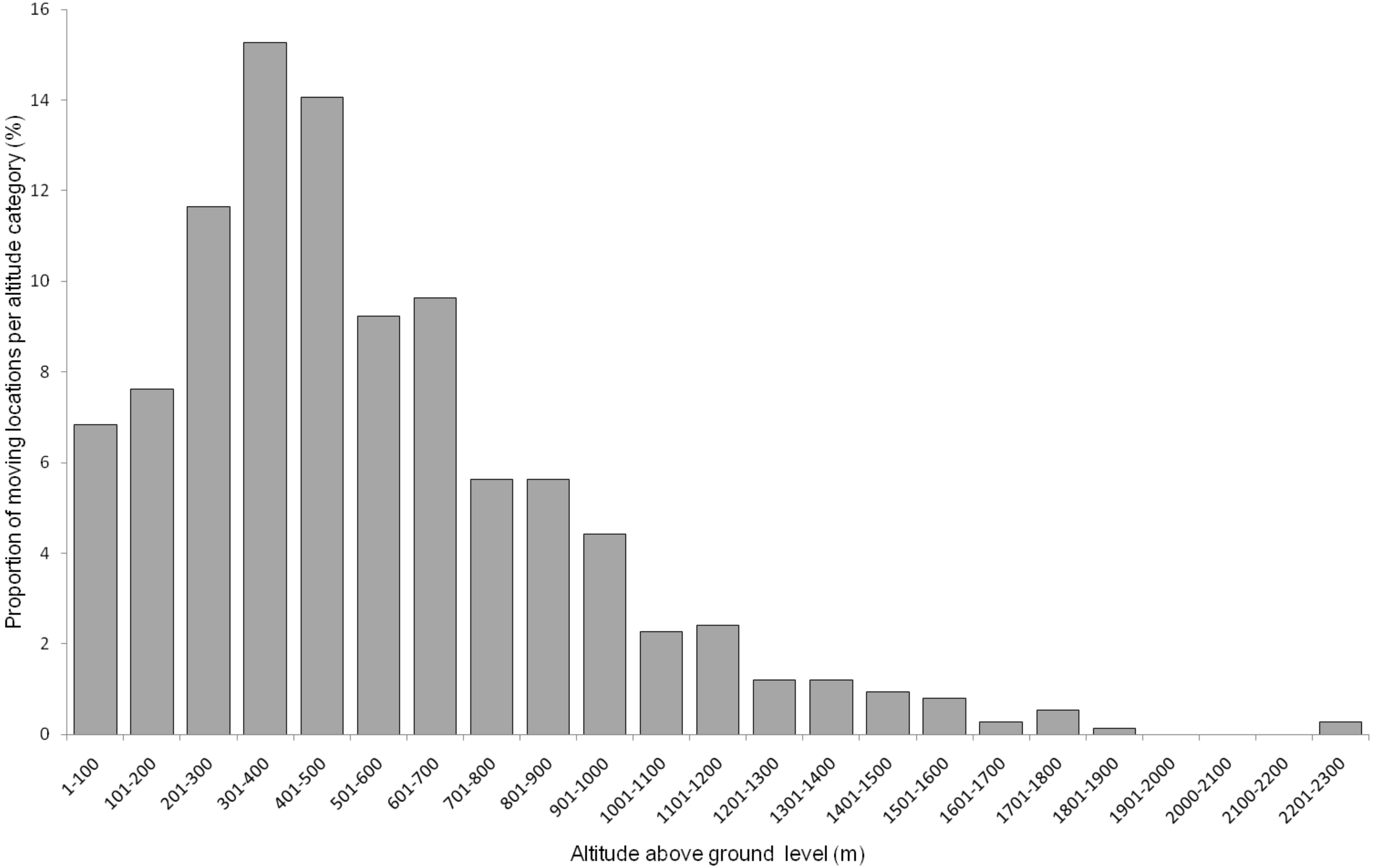


Figure 4.30. The proportion of moving GPS locations (n = 747) in 100 metre altitude above ground level categories for all vultures collectively.

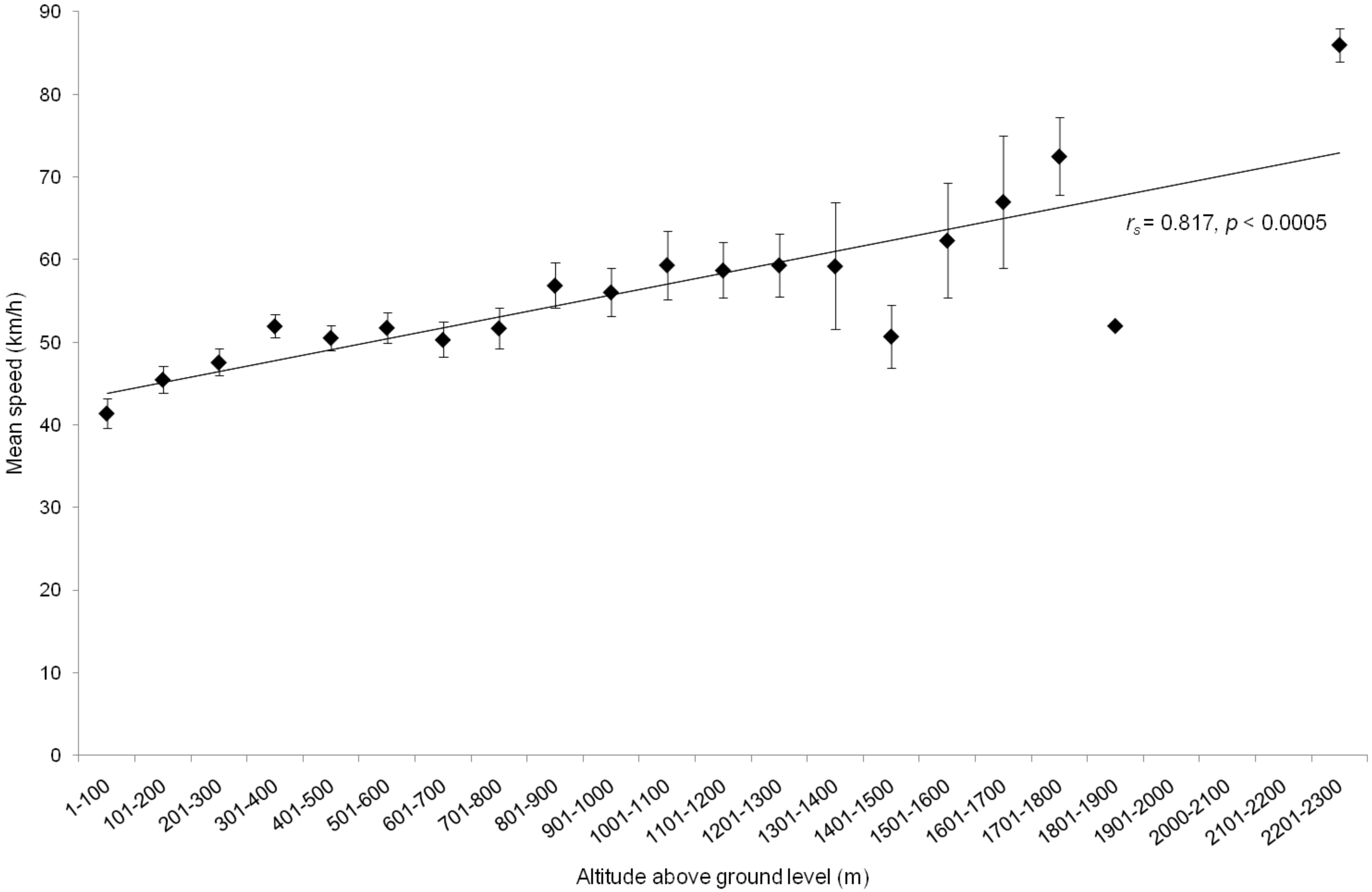


Figure 4.31. Positive correlation between mean (± SE) speed of moving GPS locations (n = 747) in 100 metre altitude above ground level categories and the altitude of each category for all vultures collectively (r_s (20)= 0.817, p < 0.0005).

4.8. Utilisation of supplementary feeding sites

Excluding AG332 which was not recorded within 5 km of a feeding site other than Mankwe Wildlife Reserve, the proportion of each vulture's stationary (< 10 km/h) GPS locations recorded within 5 km of feeding sites ranged from 2.38% for AG331 to 33.67% for AG350 (mean (± SE) = 15.91± 6.59%), and the number of feeding sites visited by each vulture ranged from 4 to 12 (mean (± SE) = 6.60 ± 1.40) (Table 4.15). At least one stationary GPS location from at least one vulture was recorded within 5 km of a total of 19 different feeding sites, including the Mankwe Wildlife Reserve capture site. Two of the sites were in the Victoria Falls region of Zimbabwe, and one was south-east of Gaborone in Botswana. The remaining 16 sites were in South Africa, 14 of which were in the western Limpopo Province and two in the North West Province. MWR capture site was never re-visited by any of the vultures fitted with tracking units after leaving the site. Figure 4.32 shows the locations of the feeding sites that were visited by the vultures.

Table 4.15. The number and proportion of stationary (< 10 km/h) GPS locations recorded within 5 km of supplementary feeding sites, and the number of supplementary feeding sites visited by each vulture.

Vulture ID	Number of stationary locations within 5km of feeding sites	Proportion of stationary locations within 5km of feeding sites (%)	Number of feeding sites visited
AG330	23	2.98	6
AG331	17	2.38	5
AG350	231	33.67	12
AG356	177	29.35	4
AG032	59	11.17	6
AG332	13	4.73	1

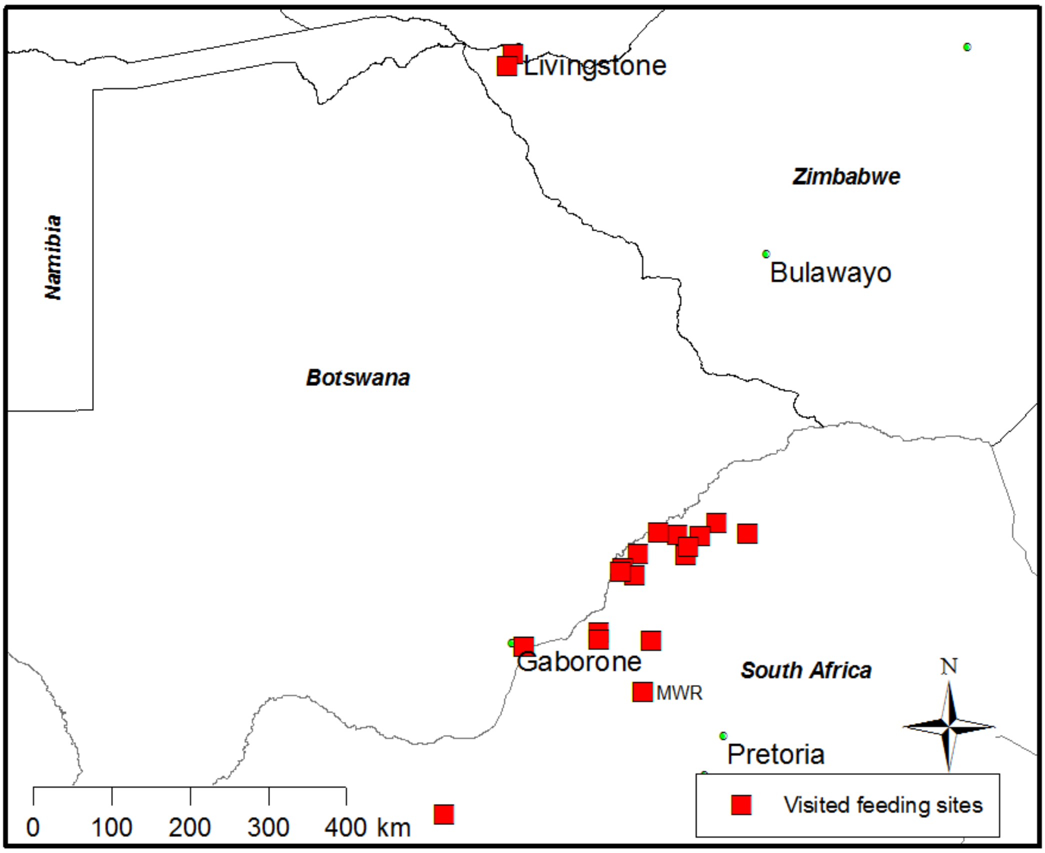


Figure 4.32. Locations of the supplementary feeding sites that were within 5 km of at least one stationary GPS location recorded by the tracking unit of at least one vulture.

At least one stationary GPS location was recorded within 5 km of supplementary feeding sites in all complete months for two vultures (AG350 and AG356), while AG330 and AG331 were recorded within 5 km of feeding sites in only 4 out of 10 months (Table 4.16). At least one stationary GPS location from AG032 was recorded within 5 km of feeding sites in 3 out of 6 complete months, and none of AG332's stationary locations during complete months were within 5 km of feeding sites. Excluding AG332, the mean proportion of stationary GPS locations within 5 km of feeding sites each month ranged from 2.24 ± 1.01 % (AG331) to 32.50 ± 8.59% (AG350) (Table 4.16).

AG350 and AG356 were recorded near feeding sites more often than the other vultures, with up to 88.73% and 58.03% of stationary GPS locations recorded within 5 km of feeding sites per month, respectively. AG350 spent extended periods at a privately managed supplementary feeding site approximately 16 km south-east of Gaborone, Botswana (24^{o}42' S, 25^{o}56'E) with 28.57% of all of its stationary locations being within 5 km of that site. From April until July AG356 regularly utilised a site approximately 16 km south-west of Victoria Falls, Zimbabwe (18^{o}02' S, 25^{o}45'E), with 18.24% of its stationary locations within 5 km of that site. An additional supplementary feeding site located several kilometres west of Victoria Falls town at Victoria Falls Safari Lodge (VFSL) (17^{o}54' S, 25^{o}48'E) was also regularly used by AG356 (8.13% of stationary locations were within 5 km of this site). AG356 was re-sighted several times by staff and visitors at VFSL, identified from its patagial tag number. AG032 was re-sighted at Ben Albert's Nature Reserve vulture feeding site near Thabazimbi, Limpopo Province, South Africa (24^{o}38' S, 27^{o}23'E) 6 weeks after the last GPS location had been transmitted. The tracking device was still attached to the vulture, and it was identified from its patagial tag number (E. Botha, personal communication).

Table 4.16. The number of complete months in which at least one stationary GPS location was recorded within 5km of supplementary feeding sites, and the mean (± SE) and range of the proportion of locations within 5 km of supplementary feeding sites each month.

Vulture ID	Number of complete months when stationary locations were within 5km of feeding sites	Mean ±SE proportion of stationary locations within 5km of feeding sites each month (%)	Range of the proportion of stationary locations within 5km of feeding sites each month (%)
AG330	4 / 10	3.43 ± 1.96	0.00 – 19.67
AG331	4 / 10	2.24 ± 1.01	0.00 – 8.48
AG350	10 / 10	32.50 ± 8.59	2.99 – 88.73
AG356	7 / 7	27.47 ± 8.20	1.33 – 58.03
AG032	3 / 6	9.63 ± 7.02	0.00 – 44.05
AG332	0 / 3	-	-

For complete months in which at least one stationary GPS location was recorded within 5 km of a feeding site for five vultures collectively (n = 28 months), a Spearman's rank test for correlation revealed significant negative correlations between the proportion of stationary GPS locations within 5 km of supplementary feeding sites each month and the size of corresponding monthly path GCRs (r_s (28) = -0.581, p = 0.001), core GCRs (r_s (28) = -0.600, p = 0.001; Figure 4.33), and the mean distance between consecutive points per month (r_s (28) = -0.459, p = 0.014). This indicates that when the vultures spent a larger proportion of their time within 5 km of feeding sites they occupied smaller foraging ranges and travelled shorter distances. When monthly data from AG350 were evaluated separately, a significant negative correlation was found between the proportion of stationary GPS locations within 5 km of feeding sites each month and the corresponding monthly core GCR areas (r_s (10) = -0.809, p = 0.005), but not with monthly path GCR areas (r_s (10) = -0.455, p = 0.187) or the mean distance between consecutive points (r_s (10) = -0.600, p = 0.067). This indicates that when AG350 spent a larger proportion of its time within 5 km of feeding sites each month it concentrated its activity in a smaller area (i.e. core area). When data from AG356 were evaluated separately there were no significant correlations between the proportion of stationary locations within 5 km of supplementary feeding sites each month and corresponding monthly path GCR areas (r_s (7) = -0.750, p = 0.052), core GCR areas (r_s (7) = -0.711, p = 0.073) or the mean distance between consecutive points per month (r_s (7) = -0.714, p = 0.071).

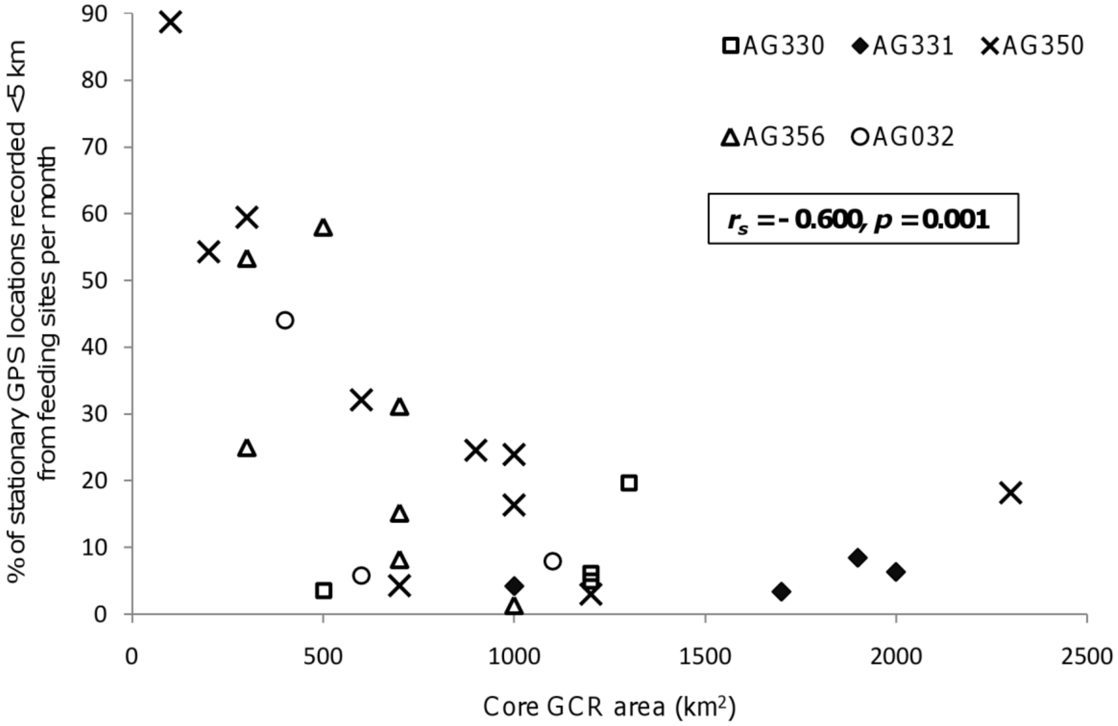


Figure 4.33. Negative correlation between the proportion of stationary GPS locations recorded within 5 km of supplementary feeding sites for each month in which at least one GPS location was recorded within 5 km of a feeding site for five vultures (n = 28 months), and the corresponding month's core GCR estimate (r_s (28) = -0.600, p = 0.001).

CHAPTER 5

DISCUSSION

5.1. Capture methods and GPS tracking unit performance

The walk-in capture enclosure proved to be a very successful and efficient method for catching vultures, particularly when a specific target individual was required, confirming previous suggestions that walk-in traps should be the favoured method for mass vulture captures (Bamford et al., 2009b). The trap used for this study was smaller than those trialled previously (6 x 3 m, by 3 m high compared to 11 x 5.5 m, by 5.5 m high - Bamford et al., 2009b), and had the added advantage of being transportable and relatively easy to erect. The main problem encountered with the captures was the sourcing of carcasses for bait, which could be mitigated if captures were carried out at a fully financed vulture feeding site with a more regular supply of carcasses.

The GPS-GSM tracking units generally functioned well and successfully acquired an average of 99.44% of expected GPS locations, which is considerably higher than similar units from the same manufacturer deployed on leopards (*Panthera pardus*), which had a location failure rate ranging from 15 – 29% (Swanepoel, Dalerum, & van Hoven, 2010). The successful location acquisition rate and high PDOP accuracy was probably due to the vultures' preference for high perching sites relative to the surrounding area (Mundy et al., 1992) and their relatively high-altitude flight patterns reducing the negative effects of topography and vegetation on GPS unit performance seen in previous studies conducted on terrestrial mammals in mountainous terrain (Cain, Krausman, Jansen, & Morgart, 2005; D'Eon & Delparte, 2005; Rempel, Rodgers, & Abraham, 1995; Swanepoel et al., 2010).

While the tracking units deployed on four of the vultures continued to function beyond the period that the data were collected for this study, two tracking units stopped transmitting data before the end of the expected tracking periods. AG032 was tracked for 207 days before its unit stopped transmitting data due to an unknown technical reason. The vulture was re-sighted at a vulture restaurant with the tracking unit still attached several weeks after the last location was received (E. Botha, personal communication). AG332 was tracked for 100 days before the tracking unit stopped transmitting data for an unknown reason. Lethal control of mammalian carnivores using livestock carcasses laced with poison is known to occur in the area where the last GPS location was recorded in south-east Namibia (J. Mendelsohn, personal communication), and it is suspected that this vulture may have died due to poisoning (K. Wolter, personal communication). Firm evidence is lacking, however, because neither the tracking unit nor the carcass of the vulture were recovered during a visit to the site of the bird's last known location.

In comparison to previous studies that experienced high numbers of tracking unit failures, the devices used during this study functioned well (Hebblewhite & Haydon, 2010; Swanepoel et al., 2010).The results from this study therefore support the use of GPS-GSM tracking units as an efficient and accurate method for studying vulture movement patterns, allowing the collection of otherwise unattainable data. For example, the opportunistic re-sighting of AG032 at the Ben Albert's NR vulture restaurant near Thabazimbi, approximately 69 km north of MWR capture site, could potentially have led to the conclusion that the vulture had remained in the surrounding area for the previous eight months since its capture. In reality, the GPS tracking data established that the vulture had travelled over 8,400 km in 200 days, ranging extensively across southern Africa.

5.2. Limitations of the study

While the tracking units provided valuable information about the vultures' movement patterns, several limitations must be considered when drawing conclusions from the data:

- **Sample size:** the number of vultures that were included in this study was limited by the high cost of the GPS tracking units (~R14 400.00), which is often the case for studies that require specialised telemetry equipment (Hebblewhite & Haydon, 2010). Nevertheless the sample size was comparable to other tracking studies on *Gyps* vultures. For example, six vultures were tracked in Pakistan (Gilbert et al., 2007), while seven vultures were tracked in both Namibia (Bamford et al., 2007) and Greece (Xirouchakis & Andreou, 2009). Although population-level inferences based on such a limited sample size should be treated with caution (Hebblewhite & Haydon, 2010; Lindberg & Walker, 2007), the information gathered during this study provides a valuable insight into the movement patterns of immature African white-backed vultures at the individual level.

- **Battery life of the tracking units:** no more than three AA batteries could be used to power each tracking unit to prevent their weight, coupled with that of the transmitter, exceeding the recommended weight of 170 g. The battery life of each unit, and therefore the tracking period for each vulture, was limited to approximately one year when recording three data points per day. Although the foraging range area curves reached asymptotes for all vultures, a longer tracking period would have provided a more complete representation of the vultures' ranging patterns (Börger et al., 2006). The much higher cost of longer-lasting solar-powered transmitters prohibited their use for this study.

- **Number of locations recorded per day:** the number of locations recorded per day was limited by the battery life of each tracking unit. Although a higher number of locations recorded per day would have increased the temporal resolution of the movement data, three locations recorded at regular intervals each day was considered sufficient to provide an accurate representation of the vultures' large-scale patterns of space use (Kie et al., 2010).

- **Limited availability of spatial land use data:** data relating to agricultural land uses and numbers of domestic livestock or wildlife were not readily available despite making many enquiries with government departments, universities and other conservation and research organizations. Although the cattle density data acted as a useful surrogate for this information, it was relatively coarse scale and the actual land use practices inside each grid cell were not identified. The results would have been greatly enhanced by being able to confirm accurately whether, for example, unprotected areas were game farms or livestock farms.

- **Difficulty ground-truthing GPS locations:** the vultures travelled large distances from the capture site, and logistical and financial constraints made it difficult to visit the majority of sites where the vultures were recorded to confirm their activity. Furthermore, it was difficult to contact landowners and gain permission to access private properties. Visits to all sites where the vultures were present for several consecutive days or returned to frequently would have provided valuable information about land use practices and the vultures' activity at those sites. Where possible, enquiries with landowners or other interested parties were made to gather information about the activity of the vultures on certain properties.

5.3. Foraging ranges

This study is the first, to my knowledge, to quantify the size and shape of the foraging ranges traversed by a sample of immature African white-backed vultures in southern Africa using continuous tracking methods. The large size of the foraging ranges occupied by the vultures supports previous suggestions that immature *Gyps* vultures travel extensively and are able to disperse large distances away from their natal origins (Houston, 1976; Mundy et al., 1992).

As expected, all of the vultures appeared to be in a state of natal dispersal characteristic of immature birds that are not restricted to foraging within a certain distance of a breeding site (Clobert, Danchin, Dhondt, & Nichols, 2001; Greenwood & Harvey, 1982; Newton, 1979). During the dispersal and settlement process, an animal is expected to use environmental and demographic cues to select areas that will maximise fitness (Matthysen, 2005; Wauters et al., 2010). One of the most important factors limiting the survival of sub-adult vultures is food availability, which is therefore a major influence on their movement patterns (Mundy et al., 1992; Piper et al., 1999). The availability and spatio-temporal predictability of a food supply are inversely related to the size of an individual's range (Maher & Lott, 2000; McLoughlin & Ferguson, 2000; Schmidt, 2008; Wauters & Dhondt, 1992). Thus, the large sizes of the foraging range estimates from this study suggest that the vultures exploited an unpredictable and sparsely distributed food source, as expected (Mundy et al., 1992).

The highly clumped distribution of the GPS locations and the exploratory nature of the vultures' movements beyond their existing range boundaries indicated by the foraging range asymptote analysis (Section 4.2.2) suggest that they mainly moved in a nomadic manner, travelling "from one area to another, residing for a time wherever food is temporarily plentiful" (Newton, 1979). Nomadic movements are common in gregarious species that rely on an unpredictable food supply (Newton, 1979) and Houston (1974c) suggested that immature *Gyps* vultures behave in this way, concentrating their foraging activity in an area with a locally abundant food supply and moving on to a different area, sometimes hundreds of kilometres away, when a new source of carcasses becomes available or when the original supply is exhausted. This might explain why settled periods of limited movement depicted by asymptotes of the foraging range area curves for all of the vultures were followed by periods of range expansion as they travelled to areas that had not been visited previously during the tracking period.

Although the immature vultures were expected to occupy large foraging ranges, the extent of their movements across southern Africa could not be predicted. The movements of three of the vultures (AG032, AG356 and AG332) across several international borders to locations more than 900 km from the capture site demonstrate their ability to travel large distances and exploit resources across an extensive range. A marked sub-adult African white-backed vulture travelled more than 900 km from its original capture site in north-west Zimbabwe to Swaziland in a six-month period, and long-distance movements of other immature African white-backed vultures have been recorded from Kimberley, South Africa, to south-east Namibia (~815 km), and from north-west Zimbabwe to the Kruger National Park, South Africa (~647 km) (Mundy, 1997; Mundy et al., 1992). The tracking data from this study confirms that immature African white-backed vultures present in any given area in southern Africa could be many hundreds of kilometres from their natal origin, and that long-distance dispersal of immatures is not unusual.

The three vultures (AG330, AG331 and AG350) that spent the majority of their tracking periods either side of the Limpopo River valley between South Africa and

Botswana also ranged over large areas, but did not travel as far from the capture site as the other three individuals. The spatial extent of their foraging ranges could indicate that those three vultures possibly originated from closer to the capture site than the three individuals that travelled further afield. However, dispersal patterns often vary between individuals of the same species from the same natal origin (Clobert et al., 2001; Greenwood & Harvey, 1982), and it is likely that multiple factors led to the observed differences in movement patterns between the individual vultures.

The overall, core and intensively used areas (IUA) of the vultures' foraging ranges followed a similar spatial pattern to the areas with the highest reporting rates for African white-backed vultures recorded during the compilation of the Southern African Bird Atlas Project (Harrison, 1992; Mundy, 1997). Similarly, the vultures' core foraging ranges corresponded with several areas identified as being important for African white-backed vulture feeding and breeding activity by Mundy et al. (1992). For example, three of the vultures' foraging ranges were positioned either side of the Limpopo River in the north-west Limpopo Province and south-east Botswana, an area with high reporting rates for African white-backed vultures (Mundy, 1997) and known to be an important breeding and foraging area for the species (Anderson, 2000a; Mundy et al., 1992; Tarboton & Allan, 1984). Similarly high reporting rates were recorded in the Victoria Falls area of Zimbabwe and the Chobe NP area of Botswana (Mundy, 1997), both areas known to have a relatively high abundance of African white-backed vultures (Bamford et al., 2009a; Herremans & Herremans-Tonnoeyr, 2000; Mundy et al., 1992), and also where the core foraging ranges of two vultures (AG032 and AG356) were located.

A combination of factors probably causes those areas to be utilised frequently by vultures. Previous studies have shown that African white-backed vultures prefer to nest in tall trees in areas away from human disturbance, generally in lowland regions with little topographic relief (Bamford et al., 2009a; Bamford et al., 2009d; Houston, 1976; Kemp & Kemp, 1975; Monadjem & Garcelon, 2005). As a result the distribution of the species coincides with woodland savannah in lowland regions with the presence of tall trees such as *Acacia* and *Ficus* species which the vultures use for roosting and breeding (Anderson, 2000a; Bamford et al., 2009a; Houston, 1976; Mundy et al., 1992). Areas with a relatively high availability of ungulate carcasses and limited human disturbance are also known to encourage vulture breeding and foraging activity (Bamford et al., 2009a; Houston, 1976; Mundy et al., 1992; Murn & Anderson, 2008).

The environmental characteristics of the north-west Limpopo Province, where several of the vultures concentrated their activity, are therefore conducive to the presence of African white-backed vultures. The dominant vegetation type is Bushveld savannah (Acocks, 1988) which consists of suitable tree species for vulture roosting and nesting activity (Tarboton & Allan, 1984), while the region also contains relatively high densities of domestic livestock and wild ungulate species (Reyers, 2004; Robinson et al., 2007; Van der Waal & Dekker, 2000). The north-west Limpopo Province is also less disturbed and degraded compared to other areas in South Africa, and is regarded as an important area from a conservation perspective due to its relatively rich biodiversity (Reyers, 2004). In the same way, the Chobe region of Botswana and the north-west region of Zimbabwe both consist of large areas of wooded savannah and contain relatively high numbers of ungulates (Booth, Jones, & Morris, 1984; Omphile & Powell, 2002; Valeix et al., 2007). In addition it has been suggested that vultures forage and breed preferentially in north-east Botswana and north-west Zimbabwe due to the presence of large areas that are designated as wildlife management areas that protect them from anthropogenic disturbance (Bamford et al., 2009a; Herremans & Herremans-Tonnoeyr, 2000).

Elevation and topography also seem to have played a role in influencing the movements of the vultures, with very few GPS locations recorded in mountainous areas. This is illustrated in Figure 5.1 which shows the vultures' combined path GCRs in relation to the ground elevation in the Limpopo and North West Provinces of South Africa. There is a conspicuous absence of path GCR grid cells in the mountainous regions of the Limpopo Province, especially the Waterberg mountain range. This apparent avoidance of mountainous areas possibly confirms that the African white-backed vulture is primarily “an inhabitant of the flat acacia savannah” (König, 1983). Although it requires further investigation, this would support suggestions that the African white-backed vulture is better adapted to foraging in flat savannah, while the larger Cape vulture is able to forage in more mountainous terrain, allowing the two species to exploit food sources in different areas where their ranges potentially overlap (Houston, 1975; König, 1983; Kruuk, 1967).

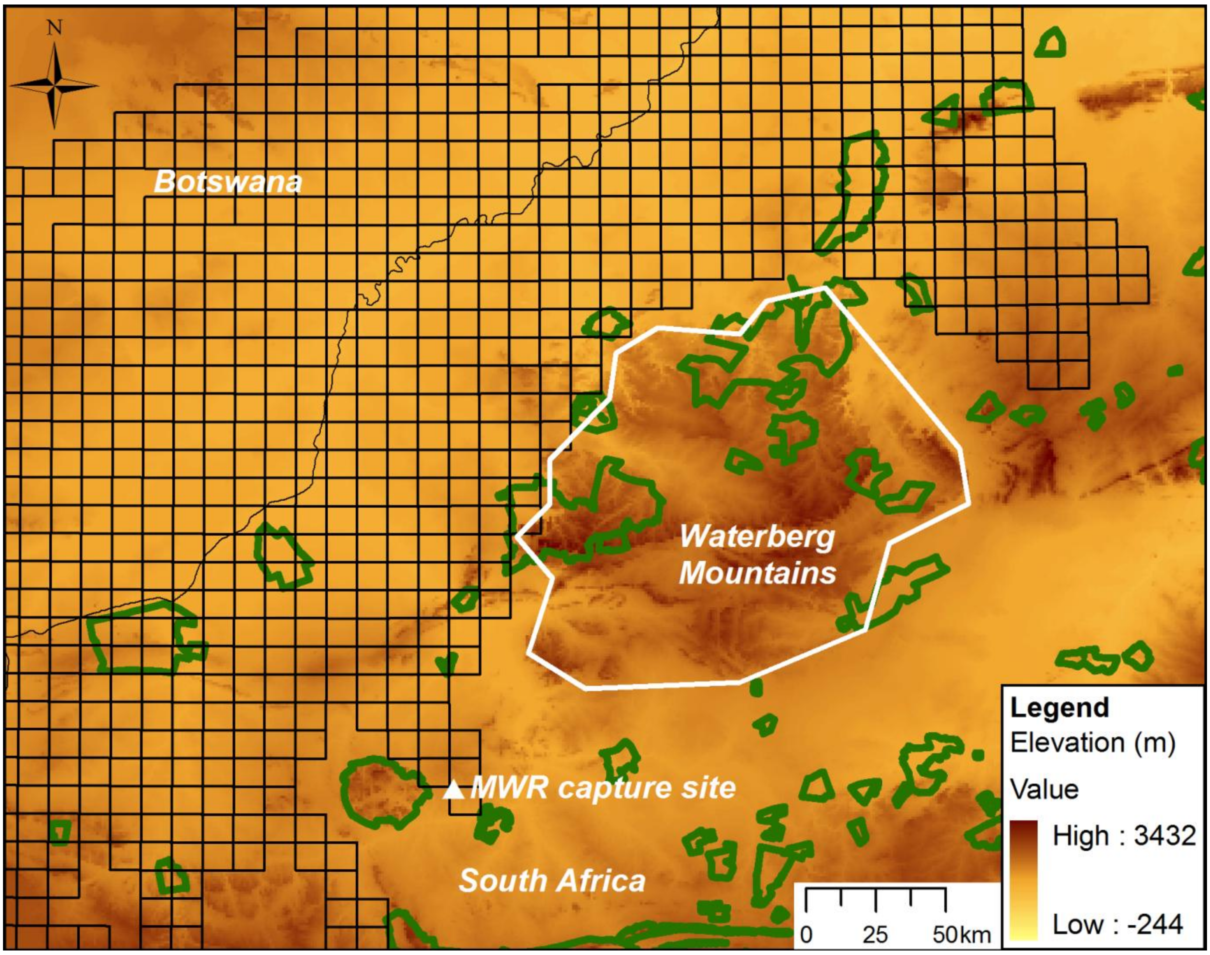


Figure 5.1. The distribution of path GCRs of all vultures in relation to elevation and protected areas (hollow polygons with green outlines). The extent of the Waterberg mountain range is approximated by a white outline. Protected area data are from (IUCN & UNEP, 2003, 2010). Elevation data are from (USGS, 2004).

There are very few, if any, studies that have quantified the size or shape of foraging ranges traversed by African white-backed vultures to allow comparisons to be made with the findings of this study. Although one study did track an immature African white-backed vulture for six months in Namibia, the authors speculated that it was potentially a hybrid between a Cape vulture and an African white-backed vulture (Bamford et al., 2007). Furthermore, the studies that have used tracking methods to follow the movements of other *Gyps* species have only used Minimum Convex

Polygons (MCPs) to delineate foraging ranges (Bamford et al., 2007; Gilbert et al., 2007) apart from one which also used kernel density estimation (Xirouchakis & Andreou, 2009). The use of MCPs for estimating the size of home or foraging ranges has been widely criticised mainly due to the inclusion of large areas that are never used by the study animal (Section 5.5 - Börger et al., 2006; Burgman & Fox, 2003; Laver & Kelly, 2008)). The MCP estimates of foraging ranges from this study are therefore used to make comparisons with other studies of *Gyps* vulture ranging patterns.

The areas of the MCPs of all vultures (mean = 297,506 ± 77,402 km^2) apart from AG032 (MCP = 588,705 km^2) were smaller than the mean estimate of 482,276 km^2 for one immature Cape vulture and one immature African white-backed vulture (mentioned above) tracked from Namibia for a six-month period (Bamford et al., 2007). Unfortunately separate MCP estimates were not provided for the individual vultures tracked in that study so it is not possible to make a direct comparison with the foraging range estimate for the juvenile African white-backed vulture. The study does mention, however, that both of the immature vultures ranged extensively, with the Cape vulture travelling from the capture site in northern Namibia into Angola and the Okavango region of Botswana, and the African white-backed vulture also making an “excursion” into Angola (Bamford et al., 2007). That study was the first to use tracking methods to confirm that immature *Gyps* vultures travel widely in southern Africa and the extensive cross-border movements of the immature African white-backed vultures tracked during this study support those findings. In addition, the MCP estimates from this study were considerably larger than those occupied by the five adult Cape vultures (mean = 21,320 km^2) from the same study, which remained relatively near the capture site and their nest sites in the Waterberg Plateau (Bamford et al., 2007). Although this supports suggestions that the movements of adult *Gyps* vultures are more restricted than non-breeding individuals due to the need to remain near a breeding colony for the majority of the year (Houston, 1976; Mundy et al., 1992), the smaller ranges recorded for the adult Cape vultures in Namibia could also be explained by a more abundant supply of carcasses at several vulture feeding sites and on the many commercial livestock and game farms in the area (Bamford et al., 2007; Mendelsohn, Jarvis, Roberts, & Robertson, 2002). Behavioural differences between Cape and African white-backed vultures, particularly between different-aged birds, make valid comparisons between their foraging ranges difficult, and the fact that the vultures tracked in Namibia were members of a very small population of a previously numerous species might also have caused unusual breeding and foraging activity (Bamford et al., 2007). It is still useful, however, to compare the findings from this study with the few ranging studies of *Gyps* vulture species available in the literature.

The foraging range estimates for the immature African white-backed vultures are substantially larger than the estimate of 1,940 km^2 for adult Cape vultures at the Potberg colony in the Western Cape Province of South Africa obtained from landowner questionnaires and a radio-tracked Cape vulture (Boshoff et al., 1984; Robertson & Boshoff, 1986), and estimates of 9,200 km^2 obtained from re-sightings of marked individuals for the Drakensberg Cape vulture population (Brown & Piper, 1988). The small ranges calculated in those early studies are probably largely due to the different methods used, as the continuous GPS tracking methods used in this study are able to provide a much more accurate and complete representation of the vultures' movement patterns (Kie et al., 2010; Tomkiewicz et al., 2010). In addition, the foraging ecology of the Cape vultures from those two colonies is likely to be very different from the immature African white-backed vultures studied here, not only because of the inherent differences between the species and the different geographical areas, but also because the populations in both of the relatively isolated Cape vulture colonies were thought to have undergone significant demographic and behavioural changes caused by high mortalities from widespread poisoning and a reduction in food availability (Boshoff & Vernon, 1980; Brown & Piper, 1988).

Additional tracking studies of *Gyps* vulture species outside Africa also produced much smaller MCP estimates of foraging ranges of 1,824 – 68,930 km^2 for six oriental white-backed vultures (*G. benegalensis*) in Pakistan (Gilbert et al., 2007) and 390 – 1,300 km^2 for seven Eurasian griffon vultures (*G. fulvus*) in Greece (Xirouchakis & Andreou, 2009). It is difficult to make valid comparisons with those estimates, however, because the environmental conditions were very different to those in southern Africa. Moreover, the study populations were very different, with the *G. benegalensis* population in Pakistan threatened with extinction due to diclofenac poisoning (Gilbert et al., 2007), and the *G. fulvus* study population being members of a colony resident on the relatively small island of Crete (Xirouchakis & Andreou, 2009).

In summary, the foraging ranges occupied by the vultures tracked during this study were large and extended across much of southern Africa, providing evidence that immature African white-backed vultures disperse widely before reaching breeding age, and are able to exploit food sources whenever and wherever they become available across the region. The data from this study confirm the suggestion by Mundy et al. (1992) that “a white-backed vulture could move over great areas of Africa should it so wish, perhaps even of the magnitude of one hundred thousand to one million square kilometres!”

5.4. Overlap of foraging ranges

5.4.1. Overlap of foraging ranges between vultures

The amount of overlap between different animals’ foraging ranges provides a measure of joint use of, and competition for resources (Millspaugh et al., 2004), and is closely linked to resource abundance, with higher amounts of overlap expected when food is scarce (Maher & Lott, 2000; McLoughlin, Ferguson, & Messier, 2000). The spatial distribution of the overlapping portions of the vultures’ core foraging ranges probably reflects the distribution of essential resources such as food (Marzluff, Millspaugh, Hurvitz, & Handcock, 2004), and could therefore be a good indicator of which areas are potentially important for African white-backed vulture activity and their conservation in the future.

The highest amount of overlap between individual vultures’ overall foraging ranges (based on path GCRs) was exhibited by the three vultures that occupied areas either side of the South African border (AG330, AG331 and AG350; mean path GCR overlap = 34.99 ± 0.50%). However, there was relatively little overlap between the same vultures’ core GCRs (mean core GCR overlap = 7.31 ± 0.95%), which indicates that while those three vultures did forage over a broadly similar overall area, they spent little time in close proximity to one another. This limited overlap of core foraging ranges suggests that those vultures were foraging and moving independently of each other, and were therefore not likely to be exploiting the same resources. This is probably not surprising given that African white-backed vultures are known to occur in large numbers in the north-eastern region of South Africa (>5,000 adults in the former Transvaal (Tarboton & Allan, 1984)), and so one would not expect all of the vultures in the region to forage in exactly the same areas throughout the year despite their gregarious nature, but rather exploit resources distributed across their ranges to reduce the level of intra-specific competition (Mundy et al., 1992).

While the overall and core foraging ranges of the vultures did overlap to some degree, the amount of overlap of coinciding monthly point GCRs was very low, with overlap between two individuals' ranges occurring in only 14 of 37 months for the four vultures that were tracked for more than three simultaneous months, at an average of only 6.40 ± 1.68% in months when overlap did occur. This indicates that although the vultures foraged over broadly similar areas at different points during their total tracking periods, they did not regularly, if at all, utilise the same resources and feed at the same carcass at the same time. This suggests that carcasses were distributed widely enough through the overall study area to allow the vultures to feed completely independently of each other, in separate foraging groups.

At this stage it is important to mention that the GPS locations recorded by the tracking units do not only represent the movements of a single vulture, but they also imply the presence of other vultures due to their gregarious foraging behaviour (Jackson et al., 2008; Mundy et al., 1992). As a result, when the simultaneous GPS locations of AG330, AG331 and AG350, for example, did not overlap at all during a particular month (e.g. May [Figure 4.11a, Section 4.3.2] and June), this suggests that enough carcasses were available to sustain different foraging groups of vultures for that period in at least three distinct areas within the overall foraging area. As a shortage of carcasses has been proposed as a major cause of the decline of vulture populations in southern Africa (Anderson, 2000a; Benson, 1997; Dean, 2004; Mundy et al., 1992; Piper, Mundy, & Ledger, 1981; Richardson et al., 1986), a higher amount of overlap of core and coinciding monthly foraging ranges might have been expected based on previous studies that have shown that animals are forced to exploit resources in similar areas when those resources are scarce or concentrated in certain areas (Maher & Lott, 2000; Marzluff et al., 2004; McLoughlin et al., 2000; Schmidt, 2008). It is plausible, however, that if a larger sample of vultures had been tracked simultaneously they would have had a higher degree of overlap between their foraging ranges, because the probability of at least some of them feeding at the same carcass would have been higher.

The relatively small amount of overlap between the foraging ranges of the three vultures that remained closer to the capture site and the two that travelled more extensively through southern Africa (mean path GCR overlap = 17.67 ± 2.06%; mean core GCR overlap = 3.26 ± 1.32%) can be explained by their different movement patterns, particularly AG356 which travelled north out of South Africa almost immediately after its release. During the three months that AG032 spent in South Africa, however, it utilised fairly similar areas to AG330 (path GCR overlap = 21.03%; core GCR overlap = 8.51%) and AG331 (path GCR overlap = 25.30%; core GCR overlap = 5.07%). The highest amount of overlap between individual vultures' core foraging ranges occurred between AG032 and AG356 (core GCR overlap = 10.27%; 50% KDE contour overlap = 50.28%), with the overlapping portions of their ranges located in the Victoria Falls area of Zimbabwe, where both vultures spent extended periods. Although the two vultures were not tracked simultaneously, the large amount of time that they spent in that area, and the high amount of overlap between their core foraging ranges there, confirms the region's importance for vulture activity (Bamford et al., 2009a; Mundy et al., 1992), and indicates that there is probably a relatively stable food supply there (Section 5.10).

5.4.2. Overlap of consecutive monthly foraging ranges for individual vultures

The relatively low amount of overlap between the vultures' consecutive monthly GCRs (mean path GCR overlap = 20.43 ± 2.73%; mean core GCR overlap = 12.69 ± 3.45%; n = 38 months) suggests that they did not regularly become settled in any one area for more than a month. This is confirmed by the fact that overlap of core GCRs between consecutive months only occurred for two pairs of months for AG330 and AG331, four for AG350, and three for AG032, showing that they did not regularly visit the same 10 x 10 km grid cells from one month to the next. The lowest amount of overlap between consecutive monthly path GCRs was recorded for AG032 (mean = 10.53 ± 7.13%), which can be explained by its long-distance movements through southern Africa in only six months. The high amount of overlap between consecutive monthly GCRs recorded for AG356 (mean path GCR overlap = 32.65 ± 11.04%; mean core GCR overlap = 45.71 ± 12.82%) was mainly due to its regular use of two supplementary feeding sites in the Victoria Falls area of Zimbabwe, where it occupied a relatively small foraging range for more than three months (Section 5.10). Similarly, AG350's regular use of a single feeding site south-east of Gaborone partially explains the higher amount of overlap between consecutive monthly ranges compared to the other vultures.

The vultures' monthly movement patterns within their overall foraging ranges appear to have been largely nomadic as they travelled from one area to another, presumably from carcass to carcass. This supports previous suggestions that the movements of immature African white-backed vultures are not restricted by having to return to regular roost sites or breeding colonies, but that they are able to move from one area with a relatively abundant food supply to another (Houston, 1976; Mundy et al., 1992).

5.5. Comparison of foraging range estimation methods

There were large variations in the size and spatial extent of foraging ranges between estimation methods (Figures 4.2 and 4.3), as seen in previous studies (Börger et al., 2006; Boyle et al., 2009; Downs & Horner, 2008). Although 100% MCP and 95% KDE estimates were not significantly different in size, they delineated the foraging range boundaries very differently, with MCPs failing to provide an accurate representation of the movement patterns of the vultures, especially for the widest ranging individuals. Both 100% MCPs and 95% KDE contours incorporated large areas that were never visited by the vultures and subsequently produced over-estimates that were on average 6.31 (SE ± 2.12) and 7.87 (SE ± 4.01) times larger than the path GCR estimates, respectively.

The findings from this study confirm suggestions that MCPs do not delineate range boundaries accurately and should only be used in conjunction with other methods (Börger et al., 2006; Burgman & Fox, 2003; Laver & Kelly, 2008). Despite this, the limited number of tracking studies performed on *Gyps* vultures to date have only used MCPs to delineate home ranges (Bamford et al., 2007; Gilbert et al., 2007), and so it was necessary to use them here to allow comparisons to be made (Harris et al., 1990). As seen previously, KDE contours were more suitable than MCPs for delineating ranges from GPS locations distributed across a large area in a concave pattern, but they still tended to include large areas that were never visited by wide-ranging individuals despite the use of the *ad hoc* method of bandwidth selection to reduce the effects of over-smoothing (K. M. Berger & Gese, 2007; Downs & Horner, 2008; Jacques et al., 2009; Kie et al., 2010). The large differences in the size of the bandwidths used for KDE influenced the size of the range estimates and should also be taken into account (Hemson et al., 2005).

The GCR method produced the most conservative foraging range estimates and most closely represented the known movements of the vultures, eliminating most of the problems associated with KDE and MCP methods. For example, the GCR method was successful at minimising the inclusion of areas that were never visited by the vultures, an advantage recognised in previous studies (Douglas-Hamilton et al., 2005; Grueter et al., 2009; Horner & Powell, 1990; Sterling et al., 2000). Although the regular sampling interval between GPS locations probably provided a sufficient representation of the “actual continuous path” (Kie et al., 2010) flown by the vultures, they were unlikely to have travelled in an exact straight line between consecutive locations (Reynolds & Laundre, 1990), meaning the path GCRs might have underestimated the actual area covered during flights (Grueter et al., 2009; Sterling et al., 2000). Nevertheless, the GCR method provided a realistic representation of the minimum area traversed by the vultures.

A further advantage of the GCR method is that the level of spatial autocorrelation does not affect the accuracy of the estimates (Ostro, Young, Silver, & Koontz, 1999) but provides biologically meaningful information about the distribution of resources and the relative intensity of use of different areas within the overall home range (De Solla et al., 1999; Fieberg, 2007; Horner & Powell, 1990; Li et al., 2000; Samuel, Pierce, & Garton, 1985). The spatial distribution of core GCRs and IUAs corresponded closely with the 50% KDE contours, which is currently the favoured method for identifying centres of activity within an animal’s home range (Börger et al., 2006; De Luca, Phillipps, Machaga, & Davenport, 2010; Laver & Kelly, 2008; Wartmann et al., 2010). Although the 50% KDE contours over-estimated the extent of the core areas for the more clumped GPS locations (e.g. AG350 and AG356) all three methods (KDE, GCR and IUA) were useful for identifying multiple centres of activity at different spatial resolutions.

The importance of selecting the most appropriate method of home range estimation is widely recognised, particularly when results might be used for planning conservation strategies (Downs, Gates, & Murray, 2008; Hebblewhite & Haydon, 2010; Hemson et al., 2005). The ability of GPS tracking technology to provide "near-perfect knowledge of an animal's movements" has raised questions about the use of traditional KDE and MCP methods that tend to include large areas never visited in the calculated ranges (Kie et al., 2010). The preliminary comparison of range estimation methods from this study indicates that a combination of KDE and GCR methods would be most appropriate for the analysis of similar vulture tracking data, given their ability to delineate accurately the internal structure of the overall range and identify core areas.

5.6. Utilisation of protected areas and areas of different cattle densities

The foraging ranges of the three vultures (AG330, AG331 and AG350) that spent the majority of their tracking periods either side of the South African border encompassed only a small proportion (mean = 4.33 ± 1.50%) of protected areas compared to the two vultures (AG032 and AG356) that travelled further north through southern Africa (mean = 32.22 ± 9.75%). This reflects the distribution and size of protected areas in those regions, with small isolated protected areas covering a small proportion of South Africa compared to larger protected areas covering a greater proportion of the total land area in northern Botswana and Zimbabwe (CBD, 2010a, 2010b; IUCN & UNEP, 2010; Newmark, 2008).

At the individual level, a significantly higher proportion of stationary GPS locations were recorded inside protected areas for AG032 and AG331. The high proportion of stationary GPS locations recorded in protected areas for AG032 (36.43%) were due to its presence in Chobe NP and the surrounding wildlife management areas in northern Botswana for several weeks, an area known to be favoured by vultures due to an abundance of wild ungulates and limited anthropogenic disturbance (Bamford et al., 2009a; Herremans & Herremans-Tonnoeyr, 2000). For AG331, only 3.97% of its stationary GPS locations were recorded inside protected areas, showing that they were not regularly visited by the vulture, despite the analysis indicating that they were used significantly more than expected based on their availability in its foraging range. This significant result should be considered with caution because it might have been due to a Type I error sometimes encountered in use-availability analyses of resource selection when the values of availability or use of a resource category are very small (<5) compared to the other categories (Bingham & Brennan, 2004; Thomas & Taylor, 2006). Furthermore, sub-sampling to achieve independence of GPS locations was not carried out, and so the high level of autocorrelation might have influenced this result (Fieberg et al., 2010). The complete absence of protected areas from the vulture's core foraging range provides further evidence that it did not visit them frequently or for extended periods. Protected areas were also present in significantly lower proportions than expected in AG330's core foraging range.

Numbers of vultures outside protected areas in many parts of Africa have declined rapidly in recent years, and their future conservation is thought to rely heavily on the ability of protected areas to reduce the effects of anthropogenic threats and provide a regular source of uncontaminated food (Herremans & Herremans-Tonnoeyr, 2000; Thiollay, 2006a, 2007; Virani et al., 2011). The expansion of the protected area network in South Africa following the establishment of relatively new reserves such as Madikwe GR, Pilanesberg NP, and Marakele NP was expected to benefit vultures greatly (Anderson, 2000a; Benson, 1997; Mundy et al., 1992). It is perhaps surprising, therefore, that the vultures tracked in this study made very little use of any of the officially protected areas in South Africa, with the exception of Atherstone NR which was visited fairly regularly by AG350, and where there is an African white-backed vulture breeding colony (Benson, 1997). In fact, despite regular movements in the surrounding area, no stationary GPS locations from any of the vultures were ever recorded inside Pilanesberg NP, and only one vulture visited Madikwe GR and Marakele NP very briefly (Figure 4.16). Possible explanations for the limited use of South African protected areas by the tracked vultures are discussed further below.

As expected, because cattle density was assumed to be zero where protected areas prohibited the grazing of domestic livestock (Robinson et al., 2007), the distribution of cattle density categories in the vultures' foraging ranges followed a similar pattern to protected areas, with the zero cattle density category being more prevalent in the

95% KDE contours of AG032 and AG356 (mean = 24.92 ± 4.81%) than the three vultures that remained either side of the South African border (mean = 7.72 ± 0.10%). The foraging ranges of those three vultures consisted of relatively large areas of medium and high cattle densities, reflecting the more favourable environmental conditions for livestock farming and more widespread land transformation in southern Botswana and northern South Africa compared to northern Botswana and Zimbabwe where populations of wild ungulates still persist (Reyers, 2004; Robinson et al., 2007; Rogers & Randolph, 1993).

At the overall foraging range scale, two of the vultures (AG350 and AG356) used the cattle density categories significantly out of proportion to their availability. While more stationary GPS locations were recorded in the zero cattle density category for both vultures, the medium and high cattle density categories were both avoided by AG356. The observed patterns of selection can be partially explained by the large proportion of time that both vultures spent at two different feeding sites (Section 5.10), both of which were located in grid cells of zero cattle density. The feeding site that AG356 used regularly was 300 metres from the edge of an officially protected area (Zambezi National Park), in a wildlife conservation area (I. Du Preez, personal communication). The site used by AG350, however was in a grid cell of zero cattle density in an area surrounded by predominantly medium and high cattle density grid cells, and it is suspected that the majority of food deposited at the site originated from domestic animals (W. Borello, personal communication). At the core foraging range scale, AG331 was the only vulture to use the cattle density categories significantly out of proportion to their availability, with the zero and high categories both being avoided and the low and medium cattle density categories occupying nearly 90% of the core foraging range. This in part reflects the absence of protected areas from the vulture’s core foraging range.

It is clear from the vultures’ limited use of South African protected areas that they were able to meet the majority of their energy requirements by locating carcasses on unprotected farmland. Therefore, as the majority of farms in northern South Africa stock both wild ungulate species and cattle (Reyers, 2004; St John et al., 2011; Van der Waal & Dekker, 2000), it is likely that the vultures consumed carcasses of both domestic livestock and wild ungulate species, as found elsewhere in the region (Bamford et al., 2007; Benson et al., 2004; Murn & Anderson, 2008; Richardson et al., 1986). For example, vulture feeding activity was observed most frequently on mixed cattle and game farms in the Northern Cape in South Africa (Murn & Anderson, 2008), and Cape vultures from the two largest colonies in the Limpopo Province are known to feed on both domestic and wild ungulate species (Benson et al., 2004). Similarly, Cape vultures tracked in Namibia fed mainly on private farmland, with 79% of consumed carcasses being game species and the majority of the remaining 21% being cattle (Bamford et al., 2007; Schultz, 2007).

The frequency of vulture activity on private farmland is thought to be primarily determined by food availability (Murn & Anderson, 2008), which is also considered to be the most important factor influencing the movement patterns of immature vultures (Houston, 1974c). A number of factors linked to food availability could explain the limited use of officially protected areas compared to unprotected farmland by the tracked vultures in South Africa.

Firstly, large mammalian carnivores such as lions, spotted hyaena and African wild dogs (*Lycaon pictus*) have been almost completely extirpated from private farmland in South Africa, but have been reintroduced to many of the fenced, and therefore isolated (Newmark, 2008), protected areas to conserve biodiversity and to generate revenue through ecotourism (Hayward, O’Brien & Kerley, 2007; Hayward et al., 2007; Lindsey et al., 2007). While free-ranging ungulate populations are regulated primarily by food availability and other mortality factors, the sedentary and isolated ungulate populations inside fenced protected areas are regulated by predation (Höner et al., 2002; Sinclair, Mduma, & Brashares, 2003; Sinclair et al., 2007). Predation by large carnivores, mainly lions, has caused rapid declines in ungulate populations in several fenced reserves within the foraging ranges of the vultures tracked in this study (Cronje, Reilly, & MacFadyen, 2002; Power, 2002; Tambling & du Toit, 2005). For example, the reintroduction of lions to Pilanesberg NP in 1993 (Van Dyk & Slotow, 2003) resulted in declines of 45% and 65% between 1995 and 2001 in the blue wildebeest (*Connochaetes taurinus*) and greater kudu (*Tragelaphus strepsiceros*) populations, respectively (Tambling & du Toit, 2005). Lion numbers in both Pilanesberg NP and Madikwe GR have exceeded the reserves’ carrying capacities in recent years (Hayward, O’Brien & Kerley, 2007; Knoop et al., 2008; Trinkel et al., 2010), and many of the reserves in the Waterberg region also contain large numbers of lions and other large carnivores (Bauer & Van der Merwe, 2004).

As predation is likely to be the main cause of mortality in the ungulate populations inside those reserves (Höner et al., 2002; Sinclair et al., 2003), the proportion of ungulate carcasses available to vultures through non-predation related mortality would be lower in fenced reserves with a full complement of large mammalian predators than on reserves or farmland without large carnivores.

In addition to the lower availability of non-depredated ungulate carcasses for vultures in fenced reserves containing high numbers of large mammalian carnivores, the carcasses that are available will be actively defended by those mammalian carnivores (Hunter, Durant, & Caro, 2007; Kruuk, 1966; Schaller, 1972). Both lions and spotted hyaena obtain a large proportion of their food by scavenging as well as hunting and will actively defend a carcass from competitors (Mills, 1984; Packer, Scheel, & Pusey, 1990), while leopards (*Panthera pardus*) often hide their kills in dense bush or in trees (Hayward et al., 2006), and wild dogs feed as quickly as possible following a successful hunt (Carbone, du Toit, & Gordon, 1997), both strategies to minimize kleptoparasitism by vultures and other scavengers (Kruuk, 1972; Schaller, 1972). Houston (1974c) observed that vultures rarely landed at carcasses with large carnivores in attendance, while they were able to completely consume a 100 kg yearling wildebeest in 30 minutes in the absence of mammalian competitors. Furthermore, in the Ngorongoro Crater NP in Tanzania, vultures rarely feed because predation is the most significant cause of ungulate mortality and competition at carcasses is high (Höner et al., 2002; Houston, 1974c; Kruuk, 1972).

As well as lions, some of the reserves in northern South Africa also contain relatively high densities of leopards, wild dogs and brown hyaena (*Parahyaena brunnea*), while Madikwe GR also contains spotted hyaena (Hayward, O'Brien & Kerley, 2007; Kilian & du P. Bothma, 2003; Knoop et al., 2008; Swanepoel et al., 2010; Thorn et al., 2009; Trinkel et al., 2010). The high levels of competition between carnivores seen in the Ngorongoro Crater are therefore likely to be present in some reserves in the study area that have a high density of large carnivores, which might have contributed to the tracked vultures' limited use of protected areas in the region. Supporting this, the protected area that was visited most regularly in South Africa was Atherstone NR which only contains low densities of brown hyaena, leopard and cheetah, and no lions or spotted hyaena (Van der Merwe et al., 2009).

The lower numbers of large carnivores outside protected areas in South Africa not only results in reduced competition, but could also lead to meso-predator release, whereby medium-sized carnivores such as black-backed jackal (*Canis mesomelas*) and caracal (*Caracal caracal*) become the apex predators (Ritchie & Johnson, 2009), and potentially provide a source of food for the vultures from the meat they cannot consume. Caracal are known to kill adult antelope up to the size of impala and mountain reedbuck (*Redunca fulvorufula*) (Grobler, 1981; Melville, Bothma, & Mills, 2004) and black-backed jackals regularly prey on medium to large (>15 kg) ungulates in southern African reserves lacking large carnivores, particularly during the calving season when they prey primarily on juvenile antelope (Kamler, Foght, & Collins, 2010; Kaunda & Skinner, 2003; Klare et al., 2010; McKenzie, 1990). Medium-sized carnivores also occasionally prey on young cattle and other livestock (Blaum et al., 2009; Gusset et al., 2009; Holmern et al., 2007). Those medium sized predators are not able to completely consume a medium sized ungulate carcass (Grobler, 1981; Kamler et al., 2010), often leaving the remains to be consumed by vultures (Houston, 1974c, 1979; Hunter et al., 2006). It is possible, therefore, that the tracked vultures were able to feed on animals killed by medium-sized carnivores outside protected areas without having to compete with larger carnivores.

It is likely that the different land use practices employed on farms in the area also have a considerable influence on the amount of food available to scavengers. For example, vulture activity in the Northern Cape is most frequent on game farms and mixed cattle and game farms, and is positively associated with hunting and culling activity that results in wounded animals and unused animal parts becoming available to vultures (Murn & Anderson, 2008). Vultures in Namibia also feed most frequently on private farms with cattle mixed with wild ungulate species, with antelope such as kudu being consumed more often than domestic livestock (Bamford et al., 2007; Schultz, 2007). Although no spatial data were available to analyse the vulture's differential use of game, livestock or mixed farmland, the spatial extents of the vultures' core foraging ranges (excluding AG356 and AG332) correspond closely with the main concentrations of game farms in the "northern, western and bushveld sub-regions" of the Limpopo Province, where hunting activity is common (Damm, 2005; Van der Waal & Dekker, 2000). It seems likely, therefore, that the vultures might have benefitted from hunting activity either by consuming wounded animals or visiting animal waste dumps, as seen elsewhere (Mateo-Tomás & Olea, 2010; Murn & Anderson, 2008; Xirouchakis & Andreou, 2009).

Considering the amount of time that the vultures spent in areas with medium and high cattle densities, however, it is unlikely that they fed exclusively on game animals. Although the removal of livestock carcasses following improved animal husbandry techniques has been implicated in the decline of vulture populations in southern Africa (Boshoff & Vernon, 1980; Dean, 2004; Mundy et al., 1992), it is unlikely that every carcass is located by the farmer before the vultures gain access to the meat. It is more likely that the vultures tracked during this study consumed both wild ungulate species and domestic livestock, as seen previously in the study area among Cape vultures from the Kransberg and Blouberg colonies (Benson et al., 2004) and elsewhere in southern African (Murn & Anderson, 2008; Richardson et al., 1986). The vultures also spent a large proportion of their time in southern Botswana where communal and commercial cattle farming are dominant land uses, and where vultures are thought to regularly feed on domestic livestock carcasses (Benson, 1997; Benson et al., 2004; Keijsper, 1993; Mundy et al., 1992). The core foraging area of AG330 also included part of the Shashe-Limpopo Transfrontier Conservation Area, and AG032 also visited this region of south-west Zimbabwe which is now dominated by areas of communal cattle grazing with some wildlife (Cumming, 2003), and where livestock mortality rates are often high due to farming practices and over-grazing (Fynn & O’Connor, 2001; Mapiye, Chimonyo, & Dzama, 2009).

While South African protected areas were not regularly visited by the majority of tracked vultures, the two vultures that travelled to northern Botswana and Zimbabwe did use protected areas more frequently. The large size of the reserves in those areas compared to those in South Africa increased the probability that the vultures would visit them, and both vultures spent a large proportion of their time inside them (mean proportion of stationary GPS locations recorded inside protected areas = 35.30 ± 1.13%). Although AG032 never entered a protected area while in South Africa for a three-month period, the analysis indicated that it selected protected areas in preference to unprotected areas at the overall foraging range scale, illustrating the vulture’s intensive use of protected areas in northern Zimbabwe and Botswana. Furthermore, AG356 selected areas with no cattle and avoided areas with high cattle densities, spending the majority of its tracking period in the vicinity of conservation areas in the Victoria Falls region of Zimbabwe. Previous studies have shown that vultures favour protected areas in Botswana and other African countries due to lower levels of anthropogenic disturbance and higher food availability (Herremans & Herremans-Tonnoeyr, 2000; Monadjem & Garcelon, 2005; Thiollay, 2006a; Virani et al., 2011). The results from this study do indicate that the vultures used protected areas more frequently outside South Africa than inside, and some of the possible reasons are discussed below.

The relatively frequent use of protected areas in Zimbabwe by two of the vultures could have been partially caused by the declining populations of wildlife and livestock outside protected areas following political unrest and the resultant increase in the illegal bushmeat trade (Lindsey et al., 2011a, b; Mundy et al., 1992). Zimbabwean protected areas such as the Save Valley Conservancy still contain high numbers of ungulates relative to the surrounding unprotected farmland (Lindsey, Romanach, & Davies-Mostert, 2009), which might explain why AG032 travelled relatively short distances while inside the reserve but relatively far while it travelled through the rest of Zimbabwe. A shortage of food outside protected areas in Zimbabwe could also explain the concentration of activity by both AG032 and AG356 in the Zambezi National Park and the surrounding conservation areas, as well as their frequent use of supplementary feeding sites in the Victoria Falls area (Section 5.10).

The abundance of wildlife in Chobe NP, Botswana, (Omphile & Powell, 2002) and the other reserves in the Kavango-Zambezi TFCA compared to the surrounding unprotected areas (Gusset et al., 2009; Parry & Campbell, 1992) probably accounts for their frequent use by AG032 and AG356 due to a higher availability of ungulate carcasses. In addition, the unusually high elephant numbers in the region have caused significant damage to vegetation and may have increased malnutrition-related mortalities of elephants and other herbivore species, particularly during the dry season and periods of drought (Teren & Owen-Smith, 2010; Van Aarde & Jackson, 2007) when the vultures were present in the area. While both vultures spent large amounts of time in the interior of the large reserves in the Kavango-Zambezi TFCA, AG356 also spent extended periods outside but within several kilometres of protected areas such as the Zambezi NP, adding some support to previous studies that recorded vultures most frequently at the interface between protected and non-protected areas (Herremans, 1998; Herremans & Herremans-Tonnoeyr, 2000), although the presence of supplementary feeding sites in the same area is also likely to have influenced the vulture's movements.

An additional factor that may lead to persistent use or avoidance of certain protected areas by vultures arises from their social foraging strategy (Deygout, Gault, Duriez, Sarrazin, & Bessa-Gomes, 2010; Jackson et al., 2008). A recent modelling study has shown that when the spatial and temporal distribution of carcasses becomes more predictable, vultures are expected to travel directly to sites where they have fed successfully on previous occasions rather than searching for carcasses that are distributed unpredictably across the wider landscape (Deygout et al., 2010). It is possible that the reverse could also be true, causing vultures that regularly forage in northern South Africa to *avoid* protected areas with predictably low food availability caused by high numbers of large mammalian carnivores and elevated levels of competition at a carcass. Similarly, if carcasses are more regularly and predictably available in protected areas in northern Botswana and Zimbabwe, then the vultures would benefit from travelling directly to those reserves.

The geographical locations and environmental characteristics of the protected areas might have also influenced whether they were visited by the vultures. For example, Figure 5.1 shows that several of the protected areas in the study area that were visited rarely, if at all, by the vultures were located in the Waterberg Mountains. As African white-backed vultures are thought to prefer flat, lowland savannah rather than mountainous terrain (Houston, 1975; König, 1983), it is possible that the protected areas that were located in mountainous areas were avoided by the vultures due to less suitable environmental characteristics (e.g. topography, air currents, vegetation) for their foraging activity compared to lowland areas. This might also partially explain why none of the vultures ever visited the mountainous reserve of Pilanesberg NP even though they visited areas adjacent to the park. Nevertheless, this does not explain the limited use of lowland protected areas such as Madikwe GR.

An additional factor that might have influenced the vultures' movement patterns is shrub encroachment. At both the overall and core foraging range scales the only category to be used less than expected (although not significantly) based on availability by all vultures was the high cattle density category. High stocking rates often result in the transformation of grass-dominated savannah into shrub-dominated savannah (Hudak, 1999; Sankaran et al., 2005), causing a reduction in the abundance of prey for carnivores and subsequently the carnivores themselves (Blaum et al., 2007; Blaum et al., 2009). High levels of shrub encroachment caused by over-grazing have been recorded within the vultures' foraging ranges in northern South Africa (Higgins, Shackleton, & Robinson, 1999; Hudak, 1999), and it is possible that the vultures avoided areas of high cattle densities because of the increased difficulty in locating carcasses in shrub encroached areas and their reluctance to land in densely treed areas (Bamford et al., 2009c; Schultz, 2007). Shrub encroachment is also prevalent in Madikwe GR due to previous mismanagement of grazing levels (Hudak, 1999), which might have contributed to the limited use of the reserve by the tracked vultures. The vultures might also have used areas of high cattle densities less than expected if the majority of farms in those areas were intensively farmed commercial livestock properties or feed-lots, where it is more likely that dead animals would have been removed compared to more extensively farmed properties, lowering food availability (Dean, 2004; Mundy et al., 1992; Murn & Anderson, 2008).

In summary, all but one of the vultures spent extended periods in the North West and Limpopo Provinces of South Africa, and in southern Botswana, where they did not regularly visit protected areas, and very rarely entered reserves containing large carnivores. Based on the dominant farming practices in the region, it is likely that the vultures exploited a number of different food sources ranging from wild ungulate species found on the many game farms in the region, to cattle and other domestic livestock that died on communal or commercial farmland. The more regular use of protected areas *outside* South Africa is consistent with a number of recent studies that have suggested that vultures in Africa are becoming increasingly restricted to protected areas due to food shortages, changing land use practices and anthropogenic disturbance and persecution in unprotected areas (Monadjem & Garcelon, 2005; Rondeau & Thiollay, 2004; Thiollay, 2006a, 2006b, 2007; Virani et al., 2011).

5.7. Distances travelled

This study presents the first quantification of the distances travelled over a continuous period by a sample of African white-backed vultures in southern Africa. As the distances were calculated from the straight-line distances between only three GPS locations per day, they should be considered conservative estimates because the vultures may have travelled further between recorded GPS locations (De Solla et al., 1999; Reynolds & Laundre, 1990).

With movements by marked individuals of over 900 km recorded in southern Africa (Mundy et al., 1992; Oschadleus, 2002) and as members of a large, carnivorous species, the immature African white-backed vultures were expected to travel long distances during this dispersal stage of their life histories (Houston, 1974c; Mundy et al., 1992; Sutherland, Harestad, Price, & Lertzman, 2000). Nevertheless, the distances they covered during the total (mean = 8,375.79 ± 1,847.46 km) and monthly (means ranged from 630.77 ± 157.87 to 1,503.76 ± 165.25 km per month) tracking periods were surprisingly large. For instance, AG331 travelled 15,293 km in 313 days, equating to 48.86 ± 2.59 km per day. This is equivalent to travelling in a straight line from Cape Town to Tunisia, and back again, and is comparable to the movements of some migratory raptors, although the distance was covered over a longer period. For example, an Egyptian vulture (*Neophron perconopterus*) travelled 3,925 km in 51 days (= 77 km / day) from Bulgaria to Chad (Meyburg et al., 2004). Similar monthly distances to those recorded during this study were also documented for an adult female Wahlberg's eagle (*Aquila wahlbergi*) that travelled 8,816 km in 9 months (mean = 980 km/month) from its breeding range in northern Namibia to its non-breeding range in north-east Nigeria, and back again (Meyburg et al., 1995).

Exploratory movements beyond the vultures' existing foraging ranges accounted for some of the longest distances covered in the shortest periods. For example, AG032 travelled over 520 km across the width of Zimbabwe in only 2.5 days when travelling north from South Africa, and AG350 travelled in a loop of more than 850 km in one week from the Limpopo Province to the Makgadikgadi Pans area of Botswana, returning to South Africa via a route just east of the Kalahari NP. These movements illustrate the vultures' ability to forage over extensive ranges and exploit resources wherever they become available within range of their flight capabilities.

The vultures also moved extensively within their foraging ranges, illustrated by AG350, which travelled the third highest distance per tracking day (37.58 ± 2.23 km/day) of all of the vultures, even though it occupied the smallest overall range (95% KDE contour = 47,132 km^2). Similarly, although AG331 travelled the furthest (48.86 ± 2.59 km per tracking day), the vulture did not regularly travel beyond its established foraging range either side of the South Africa-Botswana border, but accumulated many kilometres by travelling frequently between its two core foraging ranges which were over 500 km apart. This indicates that the vultures were regularly undertaking relatively long distance movements within the boundaries of their overall foraging ranges, which is probably a reflection of the sparse distribution of their food supply as well as their nomadic movement patterns (Houston, 1974a).

Adult African white-backed and Rüppell's vultures were estimated to have to travel up to 80 km and 150 km, respectively, from their nests to their feeding grounds in the Serengeti (Houston, 1976). The maximum distances travelled by each tracked vulture in a single day (mean = 207.97 ± 17.44 km) verify that those estimates are well within the flight capabilities of *Gyps* vultures. It is more likely, however, that the long-distance flights recorded during this study occurred when the vultures were making cross-country or exploratory movements, rather than during regular foraging flights. The "normal foraging flights" (Mundy et al., 1992) of African white-backed vultures were estimated to measure approximately 51 km (Houston, 1974a), which corresponds closely with the average distance travelled on days on which more than 10 km was travelled by the vultures (mean = 54.55 ± 3.45 km), suggesting that the foraging movements of the vultures tracked during this study were similar to the original estimates.

The average proportion of days on which the vultures moved more than 10 km (mean = 58.34 ± 5.02% of total tracking days) suggests that they had to move fairly frequently to locate enough carcasses to sustain themselves, although not all of those flights were necessarily foraging trips. As *Gyps* vultures only need to feed every 2–4 days to meet their normal energy requirements (Green et al., 2004; Mundy et al., 1992) and immatures do not return to breeding colonies every day (Houston, 1976), the movements of more than 10 km were perhaps more frequent than expected. This is possibly an indication that even if the immature vultures located and landed at a carcass, they did not necessarily feed successfully due to competition from dominant adult conspecifics, larger Cape vultures or mammalian carnivores (Houston, 1976; König, 1983; Mundy et al., 1992; Piper et al., 1999), and were forced to move on to a different food source. An unpredictable food supply and competition from conspecifics were also proposed as probable causes of similar movement patterns recorded for a second-year bearded vulture (*Gypaetus barbatus*) in South Africa, travelling a mean (± SD) of 66.03 (± 42.44) km/day and a maximum of 221.47 km/day (Urios et al., 2010). It is difficult, however, to prove the purpose and end result of each recorded flight, and it is plausible that the vultures sometimes simply travelled from place to place without locating a carcass at all.

The high proportion of the total distance that was travelled on trips of more than 10 km (mean = 96.97 ± 0.63%) and the highly clumped distribution of the GPS locations indicates that the vultures did not move around a great deal once they had settled at a carcass or other resource, which corroborates previous observations that vultures "loaf" in an area after feeding successfully (Mundy et al., 1992). This provides further evidence for a nomadic movement pattern, whereby the vultures travelled from carcass to carcass, often over large distances, and remained in the area until the food source was depleted (Houston, 1974a; Newton, 1979).

5.8. Seasonal variations in foraging ranges and distances travelled

Examination of the foraging range estimates and distances travelled for individual months revealed a general pattern of shorter travel distances and smaller foraging ranges being traversed between April and July (Figures 4.6, 4.7 and 4.27). Although the mean total distances travelled per day were not significantly different between the wet summer (December to April) and dry winter (May to September) months, on average four out of the five vultures that were tracked during both seasons did travel further per day during the summer. In addition, the monthly path GCR estimates from the summer period (mean = 12,162.00 ± 1,216.55 km^2) were significantly larger than the winter (mean = 8,874.00 ± 1,720.00 km^2) monthly path GCR estimates ($Z = -2.2023$, $p = 0.043$) for the five vultures. Only three of the vultures were tracked for equal periods during the summer and winter periods, however, with AG032 and AG356 having been tracked for five complete winter months but only one and two complete summer months, respectively. Therefore, although there seems to be a pattern of larger foraging ranges and greater daily distances being travelled during summer, conclusions should be made cautiously due to the small sample sizes. Nevertheless, possible explanations for the differences between summer and winter movement patterns recorded during this study are discussed below.

Brown (1985) suggested that the size of a vulture's foraging range provides a measure of the ease with which it can locate food, as is the case with other vertebrate species (McLoughlin & Ferguson, 2000; Schmidt, 2008; Wauters & Dhondt, 1992). Therefore, it is possible that the vultures were able to find sufficient food in a smaller area in the winter months compared to the summer months. The movement patterns of AG331 suggest that this may have been the case, as the vulture travelled between its two core foraging areas (over 500 km apart) twice during the month of February. Five Cape vultures tracked in Namibia also ranged further in February compared to other months, but as they were adult birds this might have also been influenced by breeding behaviour (Bamford et al., 2007). Although the smallest ranges coincided with the onset of the African white-backed vulture breeding season in April and May (Mundy et al., 1992), the vultures tracked during this study were all less than four years of age and their movement patterns did not show any evidence of breeding activity. The availability and distribution of food sources is likely to be the most important factor that influenced the immature vultures' movements.

The availability of carcasses varies seasonally in African savannahs, with higher mortalities of wild ungulates expected in the dry winter months when the nutrient content of the vegetation is at its lowest (Houston, 1974c, 1979; McNaughton & Georgiadis, 1986). The majority of natural mortalities of wild ungulates occurred in the dry winter months on a game ranch in the Limpopo Province (Cronje et al., 2002), and annual records of antelope mortalities on Mankwe Wildlife Reserve show the same pattern, with up to seven times more carcasses found in May compared to February (D. MacTavish, unpublished data). This contrasts with livestock mortalities in the Northern and Eastern Cape Provinces of South Africa, however, which are more common in the summer months due to calving problems and disease (Mapiye et al., 2009; Murn & Anderson, 2008). Indigenous ungulate species are commonly farmed in the Limpopo Province (Van der Waal & Dekker, 2000) and are also relatively abundant in wild populations in northern Botswana and Zimbabwe, both areas where the vultures spent a large proportion of their time, suggesting that carcasses would have been more abundant in those areas during the winter months.

Food availability might also have been higher in the winter months due to more regular hunting activity and consequentially higher numbers of wounded animals and amounts of hunting waste being made available to the vultures (Mateo-Tomás & Olea, 2010; Mundy et al., 1992; Murn & Anderson, 2008; PHASA, 2011). A higher number of animals are wounded during the peak winter hunting season in the study region (D. MacTavish, personal communication), where game ranches cover over 26% of the Limpopo Province and hunting is a widespread industry (Van der Waal & Dekker, 2000). Longer and denser vegetation in the wet summer months also makes it more difficult for vultures to locate carcasses from the air (Bamford et al., 2009c; Mundy et al., 1992), meaning that they would probably have to travel further to successfully find a source of food. It is possible, therefore, that the vultures were able to locate carcasses more frequently and in a smaller area during the winter months, resulting in the smaller monthly ranges and distances travelled recorded during that time.

Although based on data from a small number of individuals, the observed pattern of the smallest and largest ranges and distances travelled occurring in winter and summer, respectively, could be a result of a combination of these factors affecting the area over which the vultures had to forage before they successfully located a carcass. A larger number of vultures tracked for longer periods would be more likely to reveal seasonal variations of movement patterns, and allow firmer conclusions to be made.

5.9. Flight speeds and altitudes

An average of 15.87 ± 2.57% of all GPS locations were recorded as moving (i.e. ≥10 km/h), the vast majority of which were recorded at 11h00 (mean = 48.07 ± 4.47%) and 15h00 (mean = 51.50 ± 4.51%), with very few moving locations recorded at 7h00 (mean = 0.42 ± 0.26%). This observed pattern of very little movement first thing in the morning was expected because the thermal air currents on which the vultures rely for their characteristic soaring flight do not usually develop until a few hours after dawn (Pennycuick, 1972). Approximately one quarter of both the 11h00 and 15h00 locations were recorded as moving, suggesting that the vultures travelled equally during the morning and afternoon, but were possibly airborne less than expected based on previous suggestions that *Gyps* vultures spend up to seven hours foraging each day (Pennycuick, 1972; Xirouchakis & Andreou, 2009). With only three GPS locations recorded per day, however, it was difficult to confirm the amount of time that each vulture spent flying.

A previous study found that the majority of carcasses in the Serengeti were located by vultures between 7h00 and 9h00 in the morning (Houston, 1974a), which indicates that those vultures there were probably foraging earlier than the vultures tracked in this study. The environmental conditions are very different between the two study areas, however, with vultures being widely distributed in the Serengeti and usually in relatively close proximity to the wild ungulates on which they feed, meaning that they would not have to travel far to locate a carcass (Houston, 1974a). Furthermore, the observations recorded during that study also included cliff-dwelling Rüppell’s vultures that are sometimes able to leave their roosts shortly after sunrise due to additional air currents around the cliffs (Houston, 1974a; Pennycuick, 1972), and differences in the timing of thermal development between the study regions are also likely (Pennycuick, 1972). Nevertheless, it is surprising that approximately equal proportions of moving locations were recorded at both 11h00 and 15h00, as it is generally assumed that vultures are more likely to forage in the morning when thermals and air currents are strongest, and when they are under pressure to locate a carcass before competitors (Houston, 1974a, 1974c; Mundy et al., 1992; Pennycuick, 1972).

Over 40% of the moving GPS locations were recorded between 200 and 500 metres above ground level, with the highest frequency between 301 and 400 metres altitude, and the mean for each vulture ranging from 409.88 ± 17.05 m to 653.90 ± 34.87 m. This corresponds with observations of vultures in the Serengeti, where nearly half of the vultures were recorded between 140 and 360 metres above ground level (Houston, 1974a), and another study reported that the majority of flights occurred below 800 metres (Pennycuick, 1972). Mundy et al. (1992) also proposed that the typical flight altitude for African white-backed vultures is just over 300 metres above ground level, which matches the most frequently used altitude range for this study. Mean flight altitudes for Eurasian griffon vultures were also similar, at 248 ± 112 metres (Xirouchakis & Andreou, 2009). The maximum altitude above ground level recorded for each vulture ranged from 1,320 to 2,267 metres, which is comparable to Pennycuick's (1972) and Houston's' (1974a) observations, but is lower than the maximum altitude of 3,700 metres suggested by Mundy et al. (1992).

An average flight speed of approximately 45 km/h has been estimated for *Gyps* vultures (Pennycuick, 1972; Xirouchakis & Andreou, 2009), which is very similar to the mean speed obtained for each vulture during this study, ranging from 47.17 ± 1.24 km/h to 56.16 ± 1.19 km/h. The maximum speeds achieved by the vultures (mean = 90.6 ± 5.1 km/h; range = 81 – 107 km/h) are similar to other estimates of normal inter-thermal and descending flight speeds of between 75 and 90 km/h, sometimes over 100 km/h (Mundy et al., 1992; Pennycuick, 1972; Tucker, 1988), but are not as high as Tucker's (1988) maximum recorded speed of 140 km/h for a rapidly descending African white-backed vulture. The very strong positive correlation between flight speed and altitude above ground level confirms the suggestion that vultures tend to travel faster at higher altitudes, probably during cross-country flights between thermals or to cover a larger area during direct searches for carcasses in areas of low food availability (Houston, 1974a; Mundy et al., 1992; Pennycuick, 1972). The heavy body mass and broad wing shape of vultures allows them to attain faster flight speeds by using stronger wind currents at higher altitudes to maintain their forward motion once they have exploited thermals to become airborne (Pennycuick, 1972).

5.10. Utilisation of supplementary feeding sites

Two of the vultures (AG350 and AG356) were recorded in the vicinity of supplementary feeding sites during all months throughout their tracking periods, and often remained at specific sites that were regularly used for several weeks at a time. Consequently both of their intensively used areas (IUAs) were only 200 km^2 (i.e. two 10 x 10 km grid cells) in area for the total tracking period, with an average of 31.51 ± 2.16% of their time on the ground spent in the vicinity of the feeding sites. Although the other vultures visited supplementary feeding sites less frequently and did not usually spend extended periods at any particular site, the regular use of feeding sites by two of the vultures indicates that they were able to obtain a large proportion of their daily food requirements from those sites.

During months when the vultures were in the vicinity of supplementary feeding sites for a larger proportion of time they tended to traverse smaller foraging ranges and travel shorter distances between consecutive GPS locations. This suggests that they were able to meet the majority of their energy requirements by exploiting the predictable food supply at the supplementary feeding sites, and consequently did not have to travel as extensively to locate naturally occurring carcasses that are normally distributed sparsely across the wider landscape (Houston, 1974a). The same pattern was observed in Oriental white-backed vultures tracked in Pakistan (Gilbert et al., 2007).

These findings are consistent with previous suggestions that *Gyps* vultures are opportunistic foragers and potentially alter their movement patterns to exploit more predictable and abundant food sources in preference to their unpredictable and usually scarce natural food supply (Deygout et al., 2010; Deygout, Gault, Sarrazin, & Bessa-Gomes, 2009; Houston, 1974a, 1974c). For example, Houston (1976) observed large numbers of *Gyps* vultures spending extended periods at a meat-cropping abattoir in the Serengeti, and described their behaviour at the site as follows: “[the vultures] remained perched in the area for many days, feeding whenever meat became available”. The movement patterns of AG356 indicate similar behaviour. The vulture spent a large proportion of its time during a three-month period in the vicinity of a site south of Victoria Falls, Zimbabwe, which supplied mainly skinned Nile crocodile (*Crocodylus niloticus*) carcasses from a local crocodile farm three times per week (I. Du Preez, personal communication), and at another site in the area that provided waste meat on a daily basis (G. Hudson, D. Tiran, G. Wise, personal communication).

Regular use of supplementary feeding sites by *Gyps* vultures has been recorded elsewhere. For example, Cape vultures tracked in Namibia spent up to 17.9% of their time at two feeding sites (Bamford et al., 2007); feeding sites in Pakistan were visited by six tracked Oriental white-backed vultures on 73.7% of days when food was provided (Gilbert et al., 2007); and 56% of feeding events by seven tracked Eurasian griffon vultures took place at meat waste dumps on the island of Crete (Xirouchakis & Andreou, 2009). None of the vultures tracked during this study fed exclusively at sites where supplementary food was provided, as seen elsewhere (Gilbert et al., 2007)

Although only two of the vultures made regular use of supplementary feeding sites, the findings from this study suggest that those sites might be an important source of food for some members of the African white-backed vulture population in southern Africa. Furthermore, it is possible that the vultures visited unknown feeding sites that were not included in this analysis. If the majority of the many game farms in the region (Van der Waal & Dekker, 2000) have dumping sites for waste meat and offal from hunting activity as seen elsewhere in South Africa (Murn & Anderson, 2008), then the number of sites making food available to vultures could be much higher. The estimates of the vultures' use of supplementary feeding sites during this study could, therefore, be conservative.

Immature vultures in particular are known to benefit from supplementary feeding schemes due to their inexperience at searching for carcasses and their low position in the dominance hierarchy at a carcass (Houston, 1974c; König, 1983; Mundy et al., 1992; Piper et al., 1999). Given that the efficiency of the scavenging ecosystem service provided by vultures is likely to be affected by their regular use of supplementary feeding sites (Deygout et al., 2009), a more thorough investigation of their role and importance for vultures in southern Africa is required.

5.11. Implications for vulture conservation

The extensive foraging ranges, cross-border movements and limited use of protected areas by the vultures that were tracked during this study indicate that they could potentially encounter the full range of threats in southern Africa, and that reducing the severity of those threats in a single country will not necessarily ensure their protection.

Both inadvertent and intentional poisoning of vultures are known to be more prevalent on private farmland compared to protected areas (Allan, 1989; Anderson, 1994; Robertson & Boshoff, 1986; Schumann, Watson, & Schumann, 2008; Virani et al., 2011) and the use of poisons is thought to be increasing in some parts of Africa (Otieno et al., 2010; Virani et al., 2011). A recent study that was carried out within the foraging ranges of the tracked vultures revealed that 21% of game and livestock farmers that were interviewed in the Limpopo Province of South Africa admitted to using poisons to control mammalian carnivores (St John et al., 2011). As the vultures spent the majority their time in unprotected farmland in the North West and Limpopo Provinces while they were in South Africa, they would have been at risk of feeding on livestock carcasses laced with poison or the carnivores that had been poisoned themselves. The ability of a single poisoned livestock carcass to cause the death of over 100 vultures can have significant impacts on local populations (Allan, 1989; Mundy et al., 1992) and has been suggested as a major cause of the near extinction of Cape vultures in Namibia (Brown, 1985; Brown & Jones, 1989).

Although no firm evidence is available, there is a possibility that one of the vultures (AG332) was fatally poisoned after consuming a livestock carcass that had been laced with poison in south-east Namibia (K. Wolter, personal communication). Although this is rather speculative, if AG332 was indeed poisoned after travelling 2,500 km from the capture site in 100 days, then it emphasises the serious implications of the widespread use of poisons in Namibia (Marker, Mills, & Macdonald, 2003; Schumann et al., 2008; Stein et al., 2010). Intentional poisoning of vultures for use in the traditional beliefs market is also widespread and increasing and is more likely to occur outside protected areas (McKean, 2004; Whiting et al., 2011). If the limited use of protected areas by the vultures tracked during this study is repeated across the wider population, then poisoning probably poses a significant threat to them and should be addressed through farmer awareness campaigns and more rigorous enforcement of regulations (Mundy et al., 1992; St John et al., 2011).

As the vultures spent a large proportion of their time in areas containing cattle they might also have been at risk of accidental poisoning if they had consumed carcasses of animals that had been treated with veterinary NSAIDs such as ketoprofen (Naidoo et al., 2010). It has been shown that less than 1% of livestock carcasses consumed by vultures in Asia had to be contaminated with harmful veterinary drugs to have caused the rapid and widespread population declines observed there (Green et al., 2004). If the tracked vultures' regular use of private farmland corresponds to the foraging activity of the wider population it is clear that if livestock that are treated with harmful NSAIDs die and remain available to vultures in the region, then accidental poisoning could pose a serious threat to them (Anderson et al., 2005). As veterinary drugs that are harmful to vultures are used to treat livestock in southern Africa (Naidoo et al., 2010), it is important to increase awareness of the dangers of making contaminated carcasses available to vultures and also to promote the use of safe alternative drugs such as meloxicam (Anderson et al., 2005; Cuthbert et al., 2007; Naidoo et al., 2008).

The relatively large distances travelled by the vultures within their overall foraging range boundaries might indicate a scarcely distributed food supply, although there are no earlier estimates of distances travelled by vultures in the region to compare against. If this is the case it would support suggestions that the availability of ungulate carcasses for vultures has declined both within and outside protected areas in many parts of Africa (Boshoff & Vernon, 1980; Mundy et al., 1992; Ogutu et al., 2005; Robertson & Boshoff, 1986; Tarboton & Allan, 1984; Thiollay, 2006a; Virani et al., 2011).The frequent use of supplementary feeding sites by two of the vultures also suggests that carcasses might have been distributed sparsely through their foraging ranges, resulting in it being more efficient for them to exploit the more predictable food supply at the feeding sites (Deygout et al., 2010; Donázar et al., 2010). While the provision of supplementary food could benefit vultures in times of food shortages (Piper, 2004b; Piper et al., 1999), concerns have been expressed about the possibility of carcasses containing harmful substances (e.g. NSAIDs) being placed at feeding sites and resulting in the accidental poisoning of vultures (Anderson et al., 2005; Piper, 2004b). Furthermore, it is possible that the frequent use of supplementary feeding sites by the vultures will result in a decrease in the efficiency of the ecosystem service (i.e. scavenging) that they provide under natural foraging circumstances (Deygout et al., 2009; Sekercioglu, 2006). A positive result of the vultures reducing their foraging ranges when they spent more time at feeding sites is that there would have been a reduced chance of exposure to harmful veterinary drugs or poisons in the wider landscape if safe food was provided at those sites (Brown & Jones, 1989; Mundy et al., 1992; Piper, 2004b). As with previous studies, however, the vultures also foraged away from the feeding sites, and so the threats would not be completely eliminated (Gilbert et al., 2007). The use of supplementary feeding sites by vultures in southern Africa and the potential impacts of that use require further investigation.

The planning and implementation of effective conservation strategies for wide-ranging species is often challenging due to the variability in the distribution and severity of multiple threats and the problems encountered when international cooperation is required (Berger, 2004; Gentili, Rossi, Abeli, Bedini, & Foggi, 2011; Rappole & McDonald, 1994; Thirgood et al., 2004). Although only based on a small number of individuals, the findings from this study suggest that immature African white-backed vultures are likely to be exposed to multiple threats throughout their foraging ranges in southern Africa. As the survival of immature vultures beyond their recruitment into the breeding population is essential for the maintenance of a viable population (Newton, 1979; Piper et al., 1999) it is important that conservation efforts are implemented throughout their potential foraging ranges which will require a co-ordinated international effort.

5.12. Conclusion

Although this study is based on a small number of individuals it is the first to use GPS tracking technology to record the daily movement patterns of immature African white-backed vultures captured in South Africa. The results confirm that immature vultures travel extensively and traverse large foraging ranges. While the vultures did not regularly visit protected areas in the North West and Limpopo Provinces of South Africa and spent most of their time on private farmland, protected areas in northern Botswana and Zimbabwe were used more regularly by two individuals that travelled more extensively through southern Africa. The long distance movements by the vultures and their limited use of protected areas mean that they could potentially be exposed to the full range of threats in southern Africa, and that a co-ordinated international effort will be required for their future conservation in the region.

The results from this study would not have been attainable by any other methods and demonstrate the ability of modern tracking technology to be used as a powerful tool in vulture research. While additional research is required to fully establish vulture ranging patterns and land use preferences in southern Africa, this study provides the first accurate insight into the movement patterns of immature African white-backed vultures in the region.

5.13. Suggestions for further research

The following areas of research should be investigated to build on the findings of this study and further our knowledge of *Gyps* vulture foraging ecology.

- **Additional tracking studies on immature African white-backed vultures from different regions of Africa, preferably with larger sample sizes and longer tracking periods.** Although tracking units capable of recording data at more regular intervals (e.g. hourly) and for multiple consecutive years are available (e.g. Bamford et al., 2007), they are generally very expensive which limits the potential sample size (Hebblewhite & Haydon, 2010). The costs of GPS tracking units are decreasing, however, and future studies should be able to use tracking units with more advanced capabilities (Tomkiewicz et al., 2010).

- **Tracking studies on adult African white-backed vultures.** It is important to investigate the ranging behaviour of the full range of individuals in a population to gain a representative understanding of their ecology and conservation requirements (Hebblewhite & Haydon, 2010; Laver & Kelly, 2008). As *Gyps* vulture breeding sites are becoming increasingly restricted to protected areas in Africa (Monadjem & Garcelon, 2005; Thiollay, 2006a; Virani et al., 2011) it is important to investigate their foraging ecology and identify any potential threats.

- **Tracking studies on other *Gyps* species.** Further research is required to establish the foraging ecology of other declining *Gyps* species, such as the Cape vulture.

- **Investigate the distribution of supplementary feeding sites and their potential influence on vulture movement patterns and scavenging efficiency in southern Africa.** Intensive use of supplementary feeding sites by vultures can result in both positive and negative environmental impacts (Cortés-Avizanda et al., 2010; Donázar et al., 2010; Margalida, Donázar, Carrete, & Sánchez-Zapata, 2010; Piper et al., 1999). A survey is required to establish the number of supplementary feeding sites in southern Africa, the quality of food provided at those sites and the number of vultures using them.

- **Ground surveys of vulture activity in protected areas and private farmland.** Questionnaire surveys with farmers and other landowners would provide additional information about vulture activity in relation to different land use practices and the relative importance of different threats such as poisoning (Murn & Anderson, 2008; St John et al., 2011). Such surveys are resource intensive, however, and the quality of data is often variable (Murn & Anderson, 2008; St John et al., 2011).

REFERENCES

Aarts, G., MacKenzie, M., McConnell, B., Fedak, M., & Matthiopoulos, J. (2008). Estimating space-use and habitat preference from wildlife telemetry data. *Ecography, 31*, 140-160.

Acharya, R., Cuthbert, R., Baral, H. S., & Shah, K. B. (2009). Rapid population declines of Himalayan Griffon *Gyps himalayensis* in Upper Mustang, Nepal. *Bird Conservation International, 19*, 99-107.

Acocks, J. P. H. (1988). *Veld types of South Africa. Memoirs of the Botanical Survey of South Africa*. South Africa: Botanical Research Institute, Department of Agriculture and Water Supply.

Adams, L., & Davis, S. D. (1967). The internal anatomy of home range. *Journal of Mammalogy, 48*, 529-536.

Aebischer, N. J., Robertson, P. A., & Kenward, R. E. (1993). Compositional analysis of habitat use from animal radio-tracking data. *Ecology, 74*, 1313-1325.

Allan, D. G. (1989). Strychnine poison and the conservation of avian scavengers in the Karoo, South Africa. *South African Journal of Wildlife Research, 19*, 102-105.

Alldredge, J. R., & Griswold, J. (2006). Design and analysis of resource-selection studies for categorical resource variables. *Journal of Wildlife Management, 70*, 337-346.

Anderson, M. D. (1994). Mass African white-backed poisoning in the Northern Cape. *Vulture News, 29*, 31-32.

Anderson, M. D. (2000a). African Whitebacked Vulture *Gyps africanus*. In K. N. Barnes (Ed.), *The Eskom Red Data Book of Birds of South Africa, Lesotho and Swaziland* (pp. 75-77). Johannesburg, South Africa: BirdLife South Africa.

Anderson, M. D. (2000b). Cape vulture *Gyps coprotheres*. In K. N. Barnes (Ed.), *The Eskom Red Data Book of Birds of South Africa, Lesotho and Swaziland* (pp. 73-75). Johannesburg, South Africa: BirdLife South Africa.

Anderson, M. D. (2000c). Raptor conservation in the Northern Cape, South Africa. *Ostrich, 71*, 25-32.

Anderson, M. D., & Hohne, P. (2007). African white-backed vultures nesting on electricity pylons in the Kimberley area, Northern Cape and Free State Provinces, South Africa. *Vulture News, 57*, 44-50.

Anderson, M. D., & Maritz, A. W. A. (1997). *The status and distribution of vultures in the Northern Cape Province, South Africa.* Paper presented at the Vultures in the 21st Century: Proceedings of a workshop on vulture research and conservation in southern Africa, Johannesburg.

Anderson, M. D., Piper, S. E., & Swan, G. E. (2005). Non-steroidal anti-inflammatory drug use in South Africa and possible effects on vultures. *South African Journal of Science, 101*, 112-114.

Bamford, A. J., Diekmann, M., Monadjem, A., & Mendelsohn, J. (2007). Ranging behaviour of Cape vultures *Gyps coprotheres* from an endangered population in Namibia. *Bird Conservation International, 17*, 331-339.

Bamford, A. J., Monadjem, A., Anderson, M. D., Anthony, A., Borello, W. D., Bridgeford, P., . . . Hardy, I. (2009a). Trade-offs between specificity and regional generality in habitat association models: a case study of two species of African vulture. *Journal of Applied Ecology, 46*, 852-860.

Bamford, A. J., Monadjem, A., Diekmann, M., & Hardy, I. C. W. (2009b). Development of non-explosive based methods for mass capture of vultures. *South African Journal of Wildlife Research, 39*, 202-208.

Bamford, A. J., Monadjem, A., & Hardy, I. C. W. (2009c). An effect of vegetation on carcass exploitation by vultures in an African savannah. *Ostrich, 80*, 135-137.

Bamford, A. J., Monadjem, A., & Hardy, I. C. W. (2009d). Nesting habitat preferences of the African white-backed vulture *Gyps africanus* and the effects of anthropogenic disturbance. *Ibis, 151*, 51-62.

Bartels, P., van't Foort, W., & Wolter, K. (2007). Monitoring the success of released rehabilitated vultures using cellular tracking devices and or patagial tags. *Vulture News, 57*, 73-74.

Bauer, H., & Van der Merwe, S. (2004). Inventory of free-ranging lions *Panthera leo* in Africa. *Oryx, 38*, 26-31.

Beasley, J. C., DeVault, T. L., Retamosa, M. I., & Rhodes, O. E. (2007). A hierarchical analysis of habitat selection by racoons in Northern Indiana. *The Journal of Wildlife Management, 71*, 1125-1133.

Benson, P. C. (1997). *Status of vultures in the Northern Province, South Africa.* Paper presented at the Vultures in the 21st Century: Proceedings of a workshop on vulture research and conservation in southern Africa, Johannesburg.

Benson, P. C. (2004). *The status of the Kransberg and Manutsa Cape vulture colonies Gyps coprotheres in 2003: causes of mortality, reasons for concern, research needs and recommendations.* Paper presented at the The vultures of southern Africa – Quo vadis? Proceedings of a workshop on vulture research and conservation in southern Africa Johannesburg.

Benson, P. C., Plug, I., & Dobbs, J. C. (2004). An analysis of bones and other materials collected by Cape vultures at the Kransberg and Blouberg colonies, Limpopo Province, South Africa. *Ostrich, 75*, 118-132.

Benson, P. C., Tarboton, W. R., Allan, D. G., & Dobbs, J. C. (1990). The breeding status of the Cape vulture in the Transvaal during 1980-1985. *Ostrich, 61*, 134-142.

Berger, J. (2004). The last mile: how to sustain long-distance migration in mammals. *Conservation Biology, 18*, 320-331.

Berger, K. M., & Gese, E. M. (2007). Does interference competition with wolves limit the distribution and abundance of coyotes? *Journal of Animal Ecology, 76*, 1075-1085.

Berthold, P., Griesinger, J., Nowak, E., & Querner, U. (1991). Satellite tracking of a migrating griffon vulture in Spain. *Journal fur Ornithologie, 132*, 327-329.

Beyer, H. L. (2009). Hawth's Analysis Tools for ArcGIS version 3.27 (software). URL: http://www.spatialecology.com/htools.

Beyer, H. L., Haydon, D. T., Morales, J. M., Frair, J. L., Hebblewhite, M., Mitchell, M., & Matthiopoulos, J. (2010). The interpretation of habitat preference metrics under use-availability designs. *Philosophical Transactions of the Royal Society B-Biological Sciences, 365*, 2245-2254.

Biggs, R., Simons, H., Bakkenes, M., Scholes, R. J., Eickhout, B., van Vuuren, D., & Alkemade, R. (2008). Scenarios of biodiversity loss in southern Africa in the 21st century. *Global Environmental Change, 18*, 296-309.

Bingham, R. L., & Brennan, L. A. (2004). Comparison of Type I error rates for statistical analyses of resource selection. *Journal of Wildlife Management, 68*, 206-212.

BirdLife International. (2007). Vulture-killing drug now on sale in Africa. *Downloaded from http://www.birdlife.org/news/news/2007/10/africa_diclofenac.html*.

BirdLife International. (2008). Unlicensed diclofenac still on sale in Tanzania. *Downloaded from http://www.birdlife.org/news/news/2008/06/Unlicensed_diclofenac_vulture.html*.

BirdLife International. (2010a). Species factsheet: *Gyps africanus*. *Downloaded from http://www.birdlife.org on 1/7/2010.*

BirdLife International. (2010b). Species factsheet: *Gyps coprotheres*. *Downloaded from http://www.birdlife.org on 1/7/2010.*

BirdLife International. (2011). *Distribution maps of Birds of the World*. Cambridge, UK: BirdLife International.

Blaum, N., Rossmanith, E., Schwager, M., & Jeltsch, F. (2007). Responses of mammalian carnivores to land use in arid savanna rangelands. *Basic and Applied Ecology, 8*, 552-564.

Blaum, N., Tietjen, B., & Rossmanith, E. (2009). Impact of livestock husbandry on small- and medium-sized carnivores in Kalahari savannah rangelands. *Journal of Wildlife Management, 73*, 60-67.

Booth, V. R., Jones, M. A., & Morris, N. E. (1984). Black and white rhino introductions in north-west Zimbabwe. *Oryx, 18*, 237-240.

Borello, W. D., & Borello, R. M. (2002). The breeding status and colony dynamics of Cape Vulture *Gyps coprotheres* in Botswana. *Bird Conservation International, 12*, 79-97.

Börger, L., Dalziel, B. D., & Fryxell, J. M. (2008). Are there general mechanisms of animal home range behaviour? A review and prospects for future research. *Ecology Letters, 11*, 637-650.

Börger, L., Franconi, N., De Michele, G., Gantz, A., Meschi, F., Manica, A., . . . Coulson, T. (2006). Effects of sampling regime on the mean and variance of home range estimates. *Journal of Applied Ecology, 75*, 1393-1405.

Boshoff, A. F., & Anderson, M. D. (2006). Towards a conservation plan for the Cape Griffon *Gyps coprotheres*: identifying priorities for research and conservation action (pp. Report No. 55). Port Elizabeth.

Boshoff, A. F., Piper, S. E., & Michael, M. (2010). On the distribution and breeding status of the Cape Griffon *Gyps coprotheres* in the Eastern Cape province, South Africa. *Ostrich, 80*, 85-92.

Boshoff, A. F., Robertson, A. S., & Norton, P. M. (1984). A radio-tracking study of an adult Cape griffon vulture *Gyps coprotheres* in the south-western Cape Province. *South African Journal of Wildlife Research, 14*, 73-78.

Boshoff, A. F., & Vernon, C. J. (1980). The past and present distribution and status of the Cape Vulture in the Cape Province. *Ostrich, 51*, 230-250.

Botha, A. (2007). A review of colour-marking techniques used on vultures in southern Africa. *Vulture News, 56*, 52-63.

Boundja, R. P., & Midgley, J. J. (2010). Patterns of elephant impact on woody plants in the Hluhluwe-Imfolozi park, Kwazulu-Natal, South Africa. *African Journal of Ecology, 48*, 206-214.

Boyce, M. S., Vernier, P. R., Nielson, S. E., & Schmiegelow, F. K. A. (2002). Evaluating resource selection functions. *Ecological Modelling, 157*, 281-300.

Boyle, S. A., Lourenco, C, W., da Silva, L. R., & Smith, A. T. (2009). Home range estimates vary with sample size and methods. *Folia Primatologica, 80*, 33-42.

Brown, C. J. (1985). The status and conservation of the Cape Vulture in SWA/Namibia. *Vulture News, 14*, 4-15.

Brown, C. J., & Jones, S. J. (1989). A supplementary feeding scheme in the conservation of the Cape Vulture at the Waterberg, SWA/Namibia. *Madoqua, 16*, 111-119.

Brown, C. J., & Piper, S. E. (1988). Status of Cape Vultures in the Natal Drakensberg and their cliff site selection. *Ostrich, 59*, 126-136.

Burgman, M. A., & Fox, J. C. (2003). Bias in species range estimates from minimum convex polygons: implications for conservation and options for improved planning. *Animal Conservation, 6*, 19-28.

Burt, W. H. (1943). Territoriality and home range concepts as applied to mammals. *Journal of Mammalogy, 24*, 346-352.

Butler, J. R. A., & du Toit, J. T. (2002). Diet of free-ranging domestic dogs (*Canis familiaris*) in rural Zimbabwe: implications for wild scavengers on the periphery of wildlife reserves. *Animal Conservation, 5*, 29-37.

Cain, J. W., Krausman, P. R., Jansen, B. D., & Morgart, J. R. (2005). Influence of topography and GPS fix interval on GPS collar performance. *Wildlife Society Bulletin, 33*, 926-934.

Carbone, C., du Toit, J. T., & Gordon, I. J. (1997). Feeding success in African wild dogs: does kleptoparasitism by spotted hyaenas influence hunting group size? *Journal of Animal Ecology, 66*, 318-326.

Caro, T. M. (1998). The significance of behavioural ecology for conservation biology. In T. M. Caro (Ed.), *Behavioural Ecology and Conservation Biology* (pp. 3-26). New York: Oxford University Press.

Carrete, M., & Donázar, J. A. (2005). Application of central-place foraging theory shows the importance of Mediterranean dehesas for the conservation of the cinereous vulture, *Aegypius monachus*. *Biological Conservation, 126*, 582-590.

Carrete, M., Lambertucci, S. A., Speziale, K., Ceballos, O., Travaini, A., Delibes, M., . . . Donázar, J. A. (2010). Winners and losers in human-made habitats: interspecific competition outcomes in two Neotropical vultures. *Animal Conservation, 13*, 390-398.

CBD. (2010a). Country profile – Botswana. Status and trends of biodiversity. Downloaded from Convention on Biological Diversity website on 1/8/2010: http://www.cbd.int/countries/profile.shtml?country=bw.

CBD. (2010b). Country profile – South Africa. Status and trends of biodiversity. Downloaded from Convention on Biological Diversity website on 1/8/2010: http://www.cbd.int/countries/profile.shtml?country=za.

Chapman, C. A., & Wrangham, R. W. (1993). Range use of the forest chimpanzee of Kibale: implications for the understanding of chimpanzee social organization. *American Journal of Primatology, 31*, 263-273.

Clobert, J., Danchin, E., Dhondt, A. A., & Nichols, J. D. (2001). *Dispersal*. Oxford: Oxford University Press.

Coleman, J. S., & Fraser, J. D. (1989). Habitat use and home ranges of black and turkey vultures. *Journal of Wildlife Management, 53*, 782-792.

Cooke, S. J. (2008). Biotelemetry and biologging in endangered species research and animal conservation: relevance to regional, national, and IUCN Red List threat assessments. *Endangered Species Research, 4*, 165-185.

Cortés-Avizanda, A., Carrete, M., & Donázar, J. A. (2010). Managing supplementary feeding for avian scavengers: Guidelines for optimal design using ecological criteria. *Biological Conservation, 143*, 1707-1715.

Cronje, H. P., Reilly, B. K., & MacFadyen, I. D. (2002). Natural mortality among four common ungulate species on Letaba Ranch, Limpopo Province, South Africa. *Koedoe, 45*, 79-86.

Cumming, D. H. M. (2003). Report: Review of land use and resource management options in the Zimbabwe component of the proposed Shashe / Limpopo TFCA. Project title: Sustainable development and natural resource management in southern Zimbabwe (Southern Lowveld Project). Zimbabwe: CESVI & Beitbridge Rural District Councils.

Cunningham, A. A., Prakash, V., Pain, D. J., Ghalsasi, G. R., Wells, G. A. H., Kolte, G. N., . . . Rahmani, A. (2003). Indian vultures: victims of an infectious disease epidemic? *Animal Conservation, 6*, 189-197.

Cuthbert, R., Parry-Jones, J., Green, R. E., & Pain, D. J. (2007). NSAIDs and scavenging birds: potential impacts beyond Asia’s critically endangered vultures. *Biology Letters, 3*, 90-93.

D’Eon, R. G., & Delparte, D. (2005). Effects of radio-collar position and orientation on GPS radio-collar performance, and the implications of PDOP in data screening. *Journal of Applied Ecology, 42*, 383-388.

Damm, G. (2005). Hunting in South Africa: facts, risks and opportunities. *African Indaba, 3*, 1-14.

De Luca, D. W., Phillipps, G. P., Machaga, S. J., & Davenport, T. R. B. (2010). Home range, core areas and movement in the ‘critically endangered’ kipunji (*Rungwecebus kipunji*) in southwest Tanzania. *African Journal of Ecology, 48*, 895-904.

De Solla, S. R., Bonduriansky, R., & Brooks, R. J. (1999). Eliminating autocorrelation reduces biological relevance of home range estimates. *Journal of Animal Ecology, 68*, 221-234.

De Vos, V. (1974). Vultures carry yet curtail anthrax. *Journal of the South African Veterinary Medicine Association, 44*, 35.

Dean, W. R. J. (2004). *Historical changes in stocking rates: possible effects on scavenging birds.* Paper presented at the The Vultures of southern Africa – Quo Vadis? Proceedings of a workshop on vulture research and conservation in southern Africa, Johannesburg, South Africa.

DeVault, T. L., Rhodes, O. E., & Shivik, J. A. (2003). Scavenging by vertebrates: behavioural, ecological and evolutionary perspectives on an important energy transfer pathway in terrestrial ecosystems. *Oikos 102*, 225-234.

Deygout, C., Gault, A., Duriez, O., Sarrazin, F., & Bessa-Gomes, C. (2010). Impact of food predictability on social facilitation by foraging scavengers. *Behavioural Ecology, 21*, 1131-1139.

Deygout, C., Gault, A., Sarrazin, F., & Bessa-Gomes, C. (2009). Modeling the impact of feeding stations on vulture scavenging service efficiency. *Ecological Modelling, 220*, 1826-1835.

Diekmann, M., Scott, A., Scott, M., & Diekmann, J. (2004). Capture and fitting of satellite- and radio-telemetry equipment onto Cape Griffon vulture *Gyps coprotheres*, African white-backed vulture *Gyps africanus* and Lappet-faced vulture *Torgos tracheliotos* in the Waterberg area, Namibia in 2004. *Vulture News, 51*, 34-45.

Donázar, J. A., Cortés-Avizanda, A., & Carrete, M. (2010). Dietary shifts in two vultures after the demise of supplementary feeding stations: consequences of the EU sanitary legislations. *European Journal of Wildlife Research, 56*, 613-621.

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

Downs, J. A., Gates, R. J., & Murray, A. T. (2008). Estimating carrying capacity for sandhill cranes using habitat suitability and spatial optimization models. *Ecological Modelling, 214*, 284-292.

Downs, J. A., & Horner, M. W. (2008). Effects of point pattern shape on home-range estimates. *Journal of Wildlife Management, 72*, 1813-1818.

Du Toit, J. T., & Cumming, D. H. M. (1999). Functional significance of ungulate diversity in African savannahs and the ecological implications of the spread of pastoralism. *Biodiversity and Conservation, 8*, 1643-1661.

Duffy, K. J., van Os, R., Vos, S., van Aarde, J., Ellish, G., & Stretch, A. M. B. (2002). Estimating impact of reintroduced elephant on trees in a small reserve. *South African Journal of Wildlife Research, 32*, 23-29.

ESRI. (2008). ArcMap version 9.3. Environmental Systems Research Institute, Redlands, CA, USA.

FAO. (2007). Gridded livestock of the world 2007. Food and Agriculture Organization of the United Nations, Rome, Wint, G.R.W. & Robinson, T.P. Downloaded from www.fao.org/geonetwork.

Feduccia, A. (1996). *The origin and evolution of birds*. New Haven, CT, USA: Yale University Press.

Fieberg, J. (2007). Kernel density estimators of home range: smoothing and the autocorrelation red herring. *Ecology, 88*, 1059-1066.

Fieberg, J., & Kochanny, C. O. (2005). Quantifying home-range overlap: the importance of the utilization distribution. *Journal of Wildlife Management, 69*, 1346-1359.

Fieberg, J., Matthiopoulos, J., Hebblewhite, M., Boyce, M. S., & Frair, J. L. (2010). Correlation and studies of habitat selection: problem, red herring or opportunity? *Philosophical Transactions of the Royal Soceity: Biology, 365*, 2233-2244.

Finch-Davies, C. G. (1920). Notes on South African Accipitres. *Ibis, 62*, 409-438.

Fischer, A. B. (1969). *Laboratory experiments on and open-country observations of the visual acuity and behaviour of old-world vultures.* PhD, University of Muenster.

Fisher, I. J., Pain, D. J., & Thomas, V. G. (2006). A review of lead poisoning from ammunition sources in terrestrial birds. *Biological Conservation, 131*, 421-432.

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

Frère, C. H., Krützen, M., Mann, J., Watson-Capps, J. J., Tsai, Y. J., Patterson, E. M., . . . Sherwin, W. B. (2010). Home range overlap, matrilineal and biparental kinship drive female associations in bottlenose dolphins. *Animal Behaviour, 80*, 481-486.

Friedman, R., & Mundy, P. J. (1983). The use of “restaurants” for the survival of vultures in South Africa *Vulture Biology and Management* (pp. 345-355). London: University of California Press.

Fynn, R. W. S., & O'Connor, T. G. (2001). Effect of stocking rate and rainfall on rangeland dynamics and cattle performance in a semi-arid savannah, South Africa. *Journal of Applied Ecology, 37*, 491-507.

Garcia-Fernandez, A. J., Martinez-Lopez, E., Romero, D., Maria-Mojica, P., Godino, A., & Jiminez, P. (2005). High levels of blood lead in Griffon Vultures (*Gyps fulvus*) from Cazorla Natural Park (Southern Spain). *Environmental Toxicology, 20*, 459-463.

Garcia-Ripolles, C., Lopez-Lopez, P., & Urios, V. (2010). First description of migration and wintering of adult Egyptian Vultures *Neophron percnopterus* tracked by GPS satellite telemetry. *Bird Study, 57*, 261-265.

Gentili, R., Rossi, G., Abeli, T., Bedini, G., & Foggi, B. (2011). Assessing extinction risk across borders: integration of a biogeographical approach into regional IUCN assessment? *Journal for Nature Conservation, 19*, 69-71.

Gervais, J. A., Rosenberg, D. K., & Anthony, R. G. (2004). Space use and pesticide exposure risk of male burrowing owls in an agricultural landscape. *Journal of Wildlife Management, 68*, 33-50.

Gilbert, M., Watson, R. T., Ahmed, S., Asim, M., & Johnson, J. A. (2007). Vulture restaurants and their role in reducing diclofenac exposure in Pakistan. *Bird Conservation International, 17*, 63-77.

Gilbert, M., Watson, R. T., Virani, M. Z., Oaks, J. L., Ahmed, S., Chaudry, M. J. I., . . . Khan, A. A. (2006). Rapid populations declines and mortality clusters in three Oriental white-backed vulture *Gyps bengalensis* colonies in Pakistan due to diclofenac poisoning. *Oryx, 40*, 388-399.

Green, R. E., Newton, I., Shultz, S., Cunningham, A. A., Gilbert, M., Pain, D. J., & Prakash, V. (2004). Diclofenac poisoning as a cause of vulture population declines across the Indian subcontinent. *Journal of Applied Ecology, 41*, 793-800.

Green, R. E., Taggart, M. A., Das, D., Pain, D. J., Kumar, C. S., Cunningham, A. A., & Cuthbert, R. (2006). Collapse of Asian vulture populations: risk of mortality from residues of the veterinary drug diclofenac in carcasses of treated cattle. *ournal of Applied Ecology 43*, 949-956.

Green, R. E., Taggart, M. A., Senacha, K. R., Raghavan, B., Pain, D. J., Jhala, Y., & Cuthbert, R. (2007). Rate of decline of the oriental white-backed vulture population in India estimated from a survey of diclofenac residues of carcasses of ungulates. *PLoS ONE, 2*, e686 doi: doi:10.1371/journal.pone.0000686

Green, R. H. (1966). Measurement of non-randomness in spatial distributions. *Researches in Population Ecology, 8*, 1-7.

Greenwood, P. J., & Harvey, P. H. (1982). The natal and breeding dispersal of birds. *Annual Review of Ecology and Systematics, 13*, 1-21.

Grobler, J. H. (1981). Feeding behaviour of the caracal *Felis caracal* Schreber 1776 in the Mountain Zebra National Park. *South African Journal of Zoology, 16*, 259-262.

Grueter, C. C., Dayong, L., Ren, B., & Wei, F. (2009). Choice of analytical method can have dramatic effects on primate home range estimates. *Primates, 50*, 81-84.

Gusset, M., Swarner, M. J., Mponwane, L., Keletile, K., & McNutt, J. W. (2009). Human-wildlife conflict in northern Botswana: livestock predation by Endangered African wild dog *Lycaon pictus* and other carnivores. *Oryx, 43*, 67-72.

Harrington, R., Owen-Smith, N., Viljoen, P. C., Biggs, H. C., Mason, D. R., & Funston, P. (1999). Establishing the causes of the roan antelope decline in Kruger National Park, South Africa. *Biological Conservation, 90*, 69-78.

Harris, S., Cresswell, W. J., Forde, P. G., Trewhella, W. J., Woollard, T., & Wray, S. (1990). Home range analysis using radio-tracking data - a review of problems and techniques particularly as applied to the study of mammals. *Mammal Review, 20*, 97-123.

Harrison, J. A. (1992). The South African Bird Atlas Project: Five years of growth. *South African Journal of Science, 88*, 410-413.

Hayward, M. W., Adendorff, J., O'Brien, J., Sholto-Douglas, A., Bissett, C., Moolman, L. C., . . . Kerley, G. I. H. (2007). Practical considerations for the reintroduction of large, terrestrial, mammalian predators based on reintroductions to South Africa's Eastern Cape Province. *The Open Conservation Biology Journal, 1*, 1-11.

Hayward, M. W., Henschel, P., O'Brien, J., Hofmeyr, M., Balme, G., & Kerley, G. I. H. (2006). Prey preferences of the leopard (*Panthera pardus*). *Journal of Zoology, 270*, 298-313.

Hayward, M. W., O'Brien, J., & Kerley, G. I. H. (2007). Carrying capacity of large African predators: Predictions and tests. *Biological Conservation, 139*, 219-229.

Hebblewhite, M., & Haydon, D. T. (2010). Distinguishing technology from biology: a critical review of the use of GPS telemetry data in ecology. *Philosophical Transactions of the Royal Society: Biology, 365*, 2163-2176.

Hemson, G., Johnson, P., South, A., Kenward, R., Ripley, R., & Macdonald, D. (2005). Are kernels the mustard? Data from global positioning system (GPS) collars suggest problems for kernel homerange analyses with least-squares cross-validation. *Journal of Animal Ecology 74*, 455-463.

Hengari, G. M., Cunningham, P. L., & Adank, W. (2004). The use of vultures by traditional healers in Namibia. *Vulture News, 50*, 23-28.

Herbinger, I., Boesch, C., & Rothe, H. (2001). Territory characteristics among three neighbouring chimpanzee communities in the Taï National Park, Côte d'Ivoire. *International Journal of Primatology, 22*, 143-167.

Herremans, M. (1998). Conservation status of birds in Botswana in relation to land use. *Biological Conservation, 86*, 139-160.

Herremans, M., & Herremans-Tonnoeyr, D. (2000). Land use and conservation status of raptors in Botswana. *Biological Conservation, 94*, 31-41.

Hertel, F. (1994). Diversity in body size and feeding morphology within past and present vulture assemblages. *Ecology, 75*, 1074-1084.

Higgins, S. I., Shackleton, C. M., & Robinson, E. R. (1999). Changes in woody community structure and composition under contrasting landuse systems in a semi-arid savanna, South Africa. *Journal of Biogeography, 26*, 619-627.

Hiraldo, F., Blanco, J. C., & Bustamante, J. (1991). Unspecialized exploitation of small carcasses by birds. *Bird Study, 38*, 200-207.

Holmern, T., Nyahongo, J., & Roskaft, E. (2007). Livestock losses caused by predators outside the Serengeti National Park, Tanzania. *Biological Conservation, 135*, 518-526.

Höner, O. P., Wachter, B., East, M. L., & Hofer, H. (2002). The response of spotted hyaenas to long-term changes in prey populations: functional response and interspecific kleptoparasitism. *Journal of Applied Ecology, 71*, 236-246.

Horner, M. A., & Powell, R. A. (1990). Internal structure of home ranges of black bears and analyses of home-range overlap. *Journal of Mammalogy, 71*, 402-410.

Houston, D. C. (1974a). Food searching in griffon vultures. *East African Wildlife Journal 12*, 63-77.

Houston, D. C. (1974b). Mortality of the Cape vulture. *Ostrich, 45*, 57-62.

Houston, D. C. (1974c). The role of griffon vultures *Gyps africanus* and *Gyps ruppellii* as scavengers. *Journal of Zoological Society of London, 172*, 35-46.

Houston, D. C. (1975). Ecological isolation of African scavenging birds. *Ardea, 63*, 55-64.

Houston, D. C. (1976). Breeding of white-backed and Rüppell's griffon vultures, *Gyps africanus* and *Gyps rueppellii*. *Ibis, 118*, 14-43.

Houston, D. C. (1979). The adaptations of scavengers. In A. R. E. Sinclair & M. Norton-Griffiths (Eds.), *Serengeti, Dynamics of an Ecosystem* (pp. 263-286). Chicago: The University of Chicago Press.

Houston, D. C. (1983). The adaptive radiation of the griffon vultures. In S. R. Wilbur & J. A. Jackson (Eds.), *Vulture Biology and Management* (pp. 135-152). London: University of California Press.

Houston, D. C. (1985). Indian white-backed vulture (*G. bengalensis*). *Conservation studies on raptors,* 465-466.

Houston, D. C. (1986). Scavenging efficiency of Turkey Vultures in tropical forest. *The Condor, 88*, 318-323.

Houston, D. C. (2001). *Vultures and Condors*. Granton-on-Spey: Colin Baxter.

Houston, D. C., & Cooper, J. E. (1975). The digestive tract of the whiteback griffon vulture and its role in disease transmission among wild ungulates. *Journal of Wildlife Diseases 11*, 306-313.

Houston, D. C., Mee, A., & McGrady, M. (2007). Why do condors and vultures eat junk?: the implications for conservation. *Journal of Raptor Research, 41*, 235-238.

Hudak, A. T. (1999). Rangeland mismanagement in South Africa: Failure to apply ecological knowledge. *Human Ecology, 27*, 55-78.

Hugh-Jones, M. E., & Blackburn, J. (2009). The ecology of *Bacillus anthracis*. *Molecular Aspects of Medicine 30*, 356-367.

Hugh-Jones, M. E., & de Vos, V. (2002). Anthrax and wildlife. *Revista Scientifique et Technique Office Internationale des Epizooties, 21*, 359-383.

Hunt, W. G., Burnham, W., Parish, C. N., Burnham, K. K., Mutch, B., & Oaks, J. L. (2006). Bullet fragments in deer remains: implications for lead exposure in avian scavengers. *Wildlife Society Bulletin, 34*, 167-170.

Hunter, J. S., Durant, S. M., & Caro, T. M. (2006). Patterns of scavenger arrival at cheetah kills in Serengeti National Park Tanzania. *African Journal of Ecology, 45*, 275-281.

Hunter, J. S., Durant, S. M., & Caro, T. M. (2007). To flee or not flee: predator avoidance by cheetahs at kills. *Behavioural Ecology and Sociobiology, 61*, 1033-1042.

IUCN. (2010). IUCN Red List of Threatened Species. Version 2010.2., Downloaded from www.iucnredlist.org on 1st August 2010.

IUCN, & UNEP. (2003). The World Database on Protected Areas (WDPA). UNEP-WCMC. Cambridge, UK.

IUCN, & UNEP. (2010). The World Database on Protected Areas (WDPA). UNEP-WCMC. Cambridge, UK. www.protectedplanet.net.

Ivlev, V. S. (1961). *Experimental ecology of the feeding of fishes*. New Haven: Yale University Press.

Jackson, A. L., Ruxton, G. D., & Houston, D. C. (2008). The effect of social facilitation on foraging success in vultures: a modelling study. *Biology Letters, 4*, 311-313.

Jacques, C. N., Jenks, J. A., & Klaver, R. W. (2009). Seasonal movements and home-range use by female pronghorns in sagebrush-steppe communities of western South Dakota. *Journal of Mammalogy, 90*, 433-441.

Janss, G. F. E. (2000). Avian mortality from power lines: a morphologic approach of a species-specific mortality. *Biological Conservation, 95*, 353-359.

Jenkins, A. R., Smallie, J. J., & Diamond, M. (2010). Avian collisions with power lines: a global review of causes and mitigation with a South African perspective. *Bird Conservation International, 20*, 263-278 doi: doi:10.1017/S0959270910000122

Jenkins, C. N., & Joppa, L. (2009). Expansion of the global terrestrial protected area system. *Biological Conservation, 142*, 2166-2174.

Johnson, D. H. (1980). The comparison of usage and availability measurements for evaluating resource preference. *Ecology, 61*, 65-71.

Johnson, J. A., Lerner, H. R. L., Rasmussen, P. C., & Mindell, D. P. (2006). Systematics within Gyps vultures: a clade at risk. *BMC Evolutionary Biology, 6*, 65 doi: doi:10.1186/1471-2148-6-65

Kamler, J. F., Foght, J. L., & Collins, K. (2010). Single black-backed jackal (*Canis mesomelas*) kils adult impala (*Aepyceros melampus*). *African Journal of Ecology, 48*, 847-848.

Kanaujia, A., & Kushwaha, S. (2009). Vultures: nature’s incinerators. *Everyman’s Science, 44*, 160-167.

Kaunda, S. K. K., & Skinner, J. D. (2003). Black-backed jackal diet at Mokolodi Nature Reserve, Botswana. *African Journal of Ecology, 41*, 39-46.

Keijsper, V. (1993). Livestock development in Botswana – consequences for the rural poor. *Afrika Spectrum, 3*, 323-339.

Kelly, B. P., Badajos, O. H., Kunnasranta, M., Moran, J. R., Martinez-Bakker, M., Wartzok, D., & Boveng, P. (2010). Seasonal home ranges and fidelity to breeding sites among ringed seals. *Polar Biology, 33*, 1095-1109.

Kemp, A. C., & Kemp, M. I. (1975). Observations on the white-backed vulture *Gyps africanus* in the Kruger National Park, with notes on other avian scavengers. *Koedoe, 18*, 51-68.

Kenward, R. E. (2001). *A Manual for Wildlife Radiotracking*. London: Academic Press.

Kernohan, B. J., Gitzen, R. A., & Millspaugh, J. J. (2001). Analysis of animal space use and movements. In J. J. Millspaugh & J. M. Marzluff (Eds.), *Radio tracking and animal populations* (pp. 125-166). San Diego: Academic Press.

Kie, J. G., Matthiopoulos, J., Fieberg, J., Powell, R. A., Cagnacci, F., Mitchell, M. S., . . . Moorcroft, P. R. (2010). The home-range concept: are traditional estimators still relevant with modern telemetry technology? *Philosophical Transactions of the Royal Society: Biology, 365*, 2221-2231.

Kilian, P. J., & du P. Bothma, J. (2003). Notes on the social dynamics and behaviour of reintroduced lions in the Welgevonden Private Game Reserve. *South African Journal of Wildlife Research, 33*, 119-124.

Kissui, B. M. (2008). Livestock predation by lions, leopards, spotted hyaenas, and their vulnerability to retaliatory killing in the Maasai steppe, Tanazania. *Animal Conservation, 11*, 422-432.

Klare, U., Kamler, J. F., Stenkewitz, U., & MacDonald, D. W. (2010). Diet, prey selection, and predation impact off black-backed jackals in South Africa. *Journal of Wildlife Management, 74*, 1030-1042.

Knoop, M.-C., Nel, H. P., Seitlhamo, W. S., van Heerden, F. W., & Newbery, R. N. (2008). Report: animal population estimates 2008: North West Parks and Tourism Board, Ecological Services, Conservation Management Division.

Koenig, R. (2006). Vulture research soars as the scavengers' numbers decline. *Science, 312*, 1591-1592.

Komen, J., & Brown, C. J. (1993). Food requirements and the timing of breeding of a Cape Vulture colony. *Ostrich, 64*, 86-92.

König, C. (1983). Interspecific and intraspecific competition for food among Old World vultures. In S. R. Wilbur & J. A. Jackson (Eds.), *Vulture biology and management* (pp. 153-171). Berkeley: University of California Press.

Kool, K., & Croft, D. (1992). Estimators for home range areas of arboreal colobine monkeys. *Folia Primatoligica, 58*, 210-214.

Kruuk, H. (1966). Clan-system and feeding habits of spotted hyaenas (*Crocuta crocuta* Erxleben). *Nature, 209*, 1257-1258.

Kruuk, H. (1967). Competition for food between vultures in East Africa. *Ardea, 55*, 171-193.

Kruuk, H. (1972). *The spotted hyaena*. Chicago: University of Chicago Press.

Kushwaha, S., & Kanaujia, A. (2010). Ecology of vultures in and around Orcha, Madhya Pradesh. *Asian Journal of Experimental Biological Sciences, 1*, 112-118.

Lambertucci, S. A., Trejo, A, Di Martino, S., Sánchez-Zapata, J. A., Donázar, J. A., & Hiraldo, F. (2009). Spatial and temporal patterns in the diet of the Andean condor: ecological replacement of native fauna by exotic species. *Animal Conservation, 12*, 338-345.

Laver, P. N., & Kelly, M. J. (2008). A critical review of home range studies. *The Journal of Wildlife Management, 72*, 72:290-298.

Ledger, J. A., & Annegarn, H. J. (1981). Electrocution hazards to the Cape vulture *Gyps coprotheres* in South Africa. *Biological Conservation, 20*, 15-24.

Ledger, J. A., & Hobbs, J. (1985). First record of African white-backed vultures nesting on man-made structures. *Bokmakierie, 37*, 99-101.

Li, B., Chen, C., Ji, W., & Ren, B. (2000). Seasonal home range changes of the Sichuan snub-nosed monkey (*Rhinopithecus roxellana*) in the Qinling Mountains of China. *Folia Primatologica, 71*, 375-386.

Lindberg, M. S., & Walker, J. (2007). Satellite telemetry in avian research and management: sample size considerations. *The Journal of Wildlife Management, 71*(3), 1002-1009.

Lindsey, P. A., Alexander, R., Mills, M. G. L., Romanach, S., & Woodroffe, R. (2007). Wildlife viewing preferences of visitors to protected areas in South Africa: implications for the role of ecotourism in conservation. *Journal of Ecotourism, 6*, 19-33.

Lindsey, P. A., Romanach, S. S., & Davies-Mostert, H. T. (2009). The importance of conservancies for enhancing the value of game ranch land for large mammal conservation in southern Africa. *Journal of Zoology, 277*, 99-105.

Lindsey, P. A., Romanach, S. S., Matema, S., Matema, C., Mupamhadzi, I., & Muvengwi, J. (2011a). Dynamics and underlying causes of illegal bushmeat trade in Zimbabwe. *Oryx, 45*, 84-95.

Lindsey, P. A., Romanach, S. S., Tambling, C. J., Chartier, K., & Groom, R. (2011b). Ecological and financial impacts of illegal bushmeat trade in Zimbabwe. *Oryx, 45*, 96-111.

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

López- López, P., Liminana, R., Mellone, U., & Urios, V. (2010). From the Mediterranean Sea to Madagascar: Are there ecological barriers for the long-distance migrant Eleonora's falcon? *Landscape Ecology, 25*, 803-813.

Loucks, C., Ricketts, T. H., Naidoo, R., Lamoreux, J., & Hoekstra, J. (2008). Explaining the global pattern of protected area coverage: relative importance of vertebrate biodiversity, human activities and agricultural suitability. *Journal of Biogeography, 35*, 1337-1348.

Mabie, D. W., Merendino, M. T., & Reid, D. H. (1994). Dispersal of Bald Eagles fledged in Texas. *Journal of Raptor Research, 28*, 213-219.

Maher, C. R., & Lott, D. F. (2000). A review of ecological determinants of territoriality within vertebrate species. *American Midland Naturalist, 143*, 1-29.

Mandel, J. T., Bildstein, K. L., Bohrer, G., & Winkler, D. W. (2008). Movement ecology of migration in turkey vultures. *Proceedings of the National Academy of Sciences of the United States of America, 105*, 19102-19107.

Manly, B. F. J., McDonald, L. L., Thomas, D. L., McDonald, T. L., & Erickson, W. P. (2002). *Resource selection by animals: statistical design and analysis for field studies*. New York, USA: Kluwer Academic.

Mapiye, C., Chimonyo, M., & Dzama, K. (2009). Seasonal dynamics, production potential and efficiency of cattle in the sweet and sour communal rangelands in South Africa. *Journal of Arid Environments, 73*, 529-536.

Margalida, A., Donázar, J. A., Carrete, M., & Sánchez-Zapata, J. A. (2010). Sanitary versus environmental policies: fitting together two pieces of the puzzle of European vulture conservation. *Journal of Applied Ecology, 47*, 931-935.

Markandya, A., Taylor, T., Longo, A., Murty, M. N., Murty, S., & Dhavala, K. (2008). Counting the cost of vulture decline – An appraisal of the human health and other benefits of vultures in India. *Ecological Economics 67*, 194-204.

Marker, L. L., Mills, M. G. L., & Macdonald, D. W. (2003). Factors influencing perceptions of conflicts and tolerance toward cheetahs on Namibian farmlands. *Conservation Biology, 17*, 1290-1298.

Markus, M. B. (1972). Mortality of vultures caused by electrocution. *Nature, 238*, 228.

Marzluff, J. M., Millspaugh, J. J., Hurvitz, P., & Handcock, M. S. (2004). Relating resources to a probabilistic measure of space use: forest fragments and steller's jays. *Ecology, 85*, 1411-1427.

Mateo-Tomás, P., & Olea, P. P. (2010). When hunting benefits raptors: a case study of game species and vultures. *European Journal of Wildlife Research, 56*, 519-528.

Matthysen, E. (2005). Density-dependent dispersal in birds and mammals. *Ecography, 28*, 403-416.

McClean, S. A., Rumble, M. A., King, R. M., & Baker, W. L. (1998). Evaluation of resource selection methods with different definitions of availability. *Journal of Wildlife Management, 62*, 793-801.

McKean, S. (2004). *Traditional use of vultures: some persepctives.* Paper presented at the The vultures of southern Africa – Quo vadis? Proceedings of a workshop on vulture research and conservation in southern Africa, Johannesburg.

McKenzie, A. A. (1990). *Cooperative hunting in the black-backed jackal Canis mesomelas, Schreber. .* University of Pretoria, Pretoria, South Africa.

McLoughlin, P. D., & Ferguson, S. H. (2000). A hierarchical sequence of limiting factors may help explain variation in home range size. *Ecoscience, 7*, 123-130.

McLoughlin, P. D., Ferguson, S. H., & Messier, F. (2000). Intraspecific variation in home range overlap with habitat quality: a comparison among brown bear populations. *Evolutionary Ecology, 14*, 39-60.

McLoughlin, P. D., Walton, L. R., Cluff, H. D., Paquet, P. C., & Ramsay, M. A. (2004). Hierarchical habitat selection by tundra wolves. *Journal of Mammalogy, 85*, 576-580.

McNaughton, S. J., & Georgiadis, N. J. (1986). Ecology of African grazing and browsing mammals. *Annual Review of Ecology and Systematics, 17*, 39-65.

Melville, H. I. A. S., Bothma, J. D. P., & Mills, M. G. L. (2004). Prey selection by caracal in the Kgalagadi Transfrontier Park. *South African Journal of Wildlife Research, 34*, 67-75.

Mendelsohn, J. (2006). *Farming Systems in Namibia.* Windhoek, Namibia: RAISON.

Mendelsohn, J., Jarvis, A., Roberts, C., & Robertson, T. (2002). *The atlas of Namibia: a portrait of the land and its people*. Cape Town: David Phillip Publishers.

Meyburg, B.-U., & Fuller, M. R. (2007). Satellite tracking *Raptor Research and Management Techniques* (pp. 242-248). Surrey, Canada: Hancock House Publishers.

Meyburg, B.-U., Gallardo, M., Meyburg, C., & Dimitrova, E. (2004). Migrations and sojourn in Africa of Egyptian vultures (*Neophron percnopterus*) tracked by satellite. *Journal of Ornithology, 145*, 273-280.

Meyburg, B.-U., Mendelsohn, J. M., Ellis, D. H., Smith, D. G., Meyburg, C., & Kemp, A. C. (1995). Year-round movements of a Wahlberg's Eagle *Aquila wahlbergi* tracked by satellite. *Ostrich, 66*, 153-140.

Mills, M. G. L. (1984). The comparative behavioural ecology of the brown hyaena *Hyaena brunnea* and the spotted hyaena *Crocuta crocuta* in the southern Kalahari. *Koedoe, 27*, 237-247.

Mills, M. G. L., & Shenk, T. M. (1992). Predator-prey relationships: the impact of lion predation on wildebeest and zebra populations. *Journal of Animal Ecology, 61*, 693-702.

Millspaugh, J. J., Gitzen, R. A., Kernohan, B. J., Larson, M. A., & Clay, C. L. (2004). Comparability of three analytical techniques to assess joint space use. *Wildlife Society Bulletin, 32*, 148-157.

Mohr, C. O. (1947). Table of equivalent populations of North American small mammals. *American Midland Naturalist, 37*, 223-249.

Monadjem, A., & Garcelon, D. K. (2005). Nesting distribution of vultures in relation to land use in Swaziland. *Biodiversity and Conservation, 14*, 2079-2093.

Mönkkönen, M., Forsman, J. T., & Thomson, R. L. (2004). Qualitative geographical variation in interspecific interactions. *Ecography, 27*, 112-118.

Morales, J. M., Haydon, D. T., Frair, J., Holsinger, K. E., & Fryxell, J. M. (2004). Extracting more out of relocation data: building movement models as mixtures of random walks. *Ecology, 85*, 2436-2445.

Mudur, G. (2001). Human anthrax in India may be linked to vulture decline. *British Medical Journal, 322*, 320.

Mundy, P. J. (1997). Whitebacked vulture Gyps africanus. In J. A. Harrison, D. A. Allan, L. G. Underhill, M. Herremans, A. J. Tree, V. Parker & C. J. Brown (Eds.), *The atlas of southern African Birds* (pp. 160-161). Johannesburg: BirdLife South Africa.

Mundy, P. J., Butchart, D., Ledger, J. A., & Piper, S. E. (1992). *The vultures of Africa*. London: Academic Press.

Mundy, P. J., & Ledger, J. A. (1976). Griffon vultures, carnivores and bones. *South African Journal of Science, 72*, 106-110.

Mundy, P. J., Morris, A., & Haxen, C. M. (1983). The proportions of an impala edible to vultures. *African Journal of Ecology, 21*, 75-76.

Murn, C., & Anderson, M. D. (2008). Activity patterns of African White-backed Vultures *Gyps africanus* in relation to different land-use practices and food availability. *Ostrich, 79*, 191-198.

Murn, C., Anderson, M. D., & Anthony, A. (2002). Aerial survey of African white-backed vulture colonies around Kimberley, Northern Cape and Free State Provinces, South Africa. *South African Journal of Wildlife Research, 32*, 145-152.

Naidoo, V., & Swan, G. E. (2009). Diclofenac toxicity in Gyps vulture is associated with decreased uric acid excretion and not renal portal vasoconstriction. *Comparative Biochemistry and Physiology, 149*, 269-274.

Naidoo, V., Wolter, K., Cromarty, A. D., Bartels, P., Bekker, L., McGaw, L., . . . Swan, G. E. (2008). The pharmacokinetics of meloxicam in vultures. *Journal of Veterinary Pharmacology and Therapeutics, 31*, 128-134.

Naidoo, V., Wolter, K., Cromarty, D., Diekmann, M., Duncan, N., Meharg, A. A., . . . Cuthbert, R. (2010). Toxicity of non-steroidal anti-inflammatory drugs to Gyps vultures: a new threat from Ketoprofen. *Biology Letters, 6*, 339-341.

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

Newmark, W. D. (2008). Isolation of African protected areas. *Frontiers of Ecology and Evolution, 6*, 321-328.

Newton, I. (1979). *Population ecology of raptors*. Berkhamsted, UK: Poyser.

Nikolaus, G. (1984). Large numbers of birds killed by electric power line. *Scopus, 8*, 42.

Oaks, J. L., Gilbert, M., Virani, M. Z., Watson, R. T., Meteyer, C. U., Rideout, B., . . . Khan, A. A. (2004). Diclofenac residues as the cause of vulture population declines in Pakistan. *Nature, 427*, 630-633.

Odum, E. P., & Kuenzler, E. J. (1955). Measurement of territory and home range size in birds. *Auk, 72*, 128-137.

Ogada, D. L., & Keesing, F. (2010). Decline of raptors over a three-year period in Laikipia, central Kenya. *Journal of Raptor Research, 44*, 129-135.

Ogutu, J. O., Bhola, N., & Reid, R. (2005). The effects of pastoralism and protection on the density and distribution of carnivores and their prey in the Mara ecosystem of Kenya. *Journal of Zoology, 265*, 281-293.

Ogutu, J. O., Piepho, H. P., Dublin, H. T., Bhola, N., & Reid, R. (2009). Dynamics of Mara-Serengeti ungulates in relation to land-use changes. *Journal of Zoology, 278*, 1-14.

Olson, K. A., Fuller, T. K., Mueller, T., Murray, M. G., Nicolson, C., Odonkhuu, D., . . . Schaller, G. B. (2010). Annual movements of Mongolian gazelles: Nomads in the Eastern Steppe. *Journal of Arid Environments, 74*, 1435-1442.

Omphile, U. J., & Powell, J. (2002). Large ungulate habitat preference in Chobe National Park. *Journal of Range Management, 55*, 341-349.

Oschadleus, D. (2002). Report on southern African vulture recoveries. *Vulture News, 46*, 16-18.

Ostro, L. E., Young, T. P., Silver, S. C., & Koontz, F. W. (1999). A geographic information system method for estimating home range size. *Journal of Wildlife Management, 63*, 748-755.

Otieno, P. O., Lalah, J. O., Virani, M., Jondiko, I. O., & Schramm, K.-W. (2010). Carbofuran and its toxic metabolites provide forensic evidence for furadan exposure in vultures (*Gyps africanus*) in Kenya. *Bulletin of Environmental Contamination and Toxicology 84*, 536-544.

Otis, D. L., & White, G. C. (1999). Autocorrelation of location estimates and the analysis of radiotracking data. *Journal of Wildlife Management, 63*, 1039-1044.

Packer, C., Scheel, D., & Pusey, A. E. (1990). Why lions form groups: food is not enough. *The American Naturalist, 136*, 1-19.

Pain, D. J., Bowden, C. G. R., Cunningham, A. A., Cuthbert, R., Das, D., Gilbert, M., . . . Swarup, D. (2008). The race to prevent the extinction of South Asian vultures. *Bird Conservation International, 18*, S30-S48.

Pain, D. J., Cunningham, A. A., Donald, P. F., Duckworth, J. W., Houston, D. C., Katzner, T., . . . Timmins, R. (2003). Causes and effects of temporospatial declines of *Gyps* vultures in Asia. *Conservation Biology, 17*, 661-671.

Parry, D., & Campbell, B. (1992). Attitudes of rural communities to animal wildlife and its utilization in Chobe Enclave and Mababe Depression, Botswana. *Environmental Conservation, 19*, 245-252.

Pennycuick, C. J. (1972). Soaring behaviour and performance of some East African birds, observed from a motor-glider. *Ibis, 114*, 178-218.

Pennycuick, C. J. (1979). Energy costs of locomotion and the concept of foraging radius *Serengeti: Dynamics of an ecosystem* (pp. 164-184). Chicago: The University of Chicago Press.

PHASA. (2011). Professional Hunters' Association of South Africa web-page: "Hunting Season". Accessed February 1st 2011. http://www.phasa.co.za/hunting-information/section-table.html.

Piper, S. E. (2004a). *Status of vulture species in southern Africa: the Cape Griffon Gyps coprotheres.* Paper presented at the The vultures of southern Africa – Quo Vadis? Proceedings of a workshop on vulture research and conservation in southern Africa, Johannesburg, South Africa.

Piper, S. E. (2004b). *Vulture restaurants.* Paper presented at the The vultures of southern Africa – Quo vadis? Proceedings of a workshop on vulture research and conservation in southern Africa, Johannesburg, South Africa.

Piper, S. E., Boshoff, A. F., & Scott, H. A. (1999). Modelling survival rates in the Cape Griffon *Gyps coprotheres*, with emphasis on the effects of supplementary feeding. *Bird Study, 46*, S230-238.

Piper, S. E., Mundy, P. J., & Ledger, J. A. (1981). Estimates of survival in the Cape Vulture *Gyps coprotheres*. *Journal of Animal Ecology, 50*, 815-825.

Power, R. J. (2002). Prey selection of lions *Panthera leo* in a small, enclosed reserve. *Koedoe, 45*, 67-75.

Prakash, V., Green, R. E., Pain, D. J., Ranade, S. P., Saravanan, S., Prakash, N., . . . Cunningham, A. A. (2007). Recent changes in populations of resident *Gyps* vultures in India. *Journal of the Bombay Natural History Society, 104*, 129-135.

Rappole, J. H., & McDonald, M. V. (1994). Cause and effect in population declines of migratory birds. *Auk, 111*, 652-660.

Reason, C. J. C., Hachigonta, S., & Phaladi, R. F. (2005). Interannual variability in rainy season characteristics over the Limpopo region of southern Africa. *International Journal of Climatology, 25*, 1835-1853.

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

Reyers, B. (2004). Incorporating anthropogenic threats into evaluations of regional biodiversity and prioritisation of conservation areas in the Limpopo Province, South Africa. *Biological Conservation, 118*, 521-531.

Reynolds, T. D., & Laundre, J. W. (1990). Time intervals for estimating pronghorn and coyote home ranges and daily movements. *Journal of Wildlife Management, 54*, 316-322.

Rich, P. V. (1983). The fossil history of vultures: A World perspective. In S. R. Wilbur & J. A. Jackson (Eds.), *Vulture Biology and Management*. London: University Of California Press.

Richardson, P. R. K., Mundy, P. J., & Plug, I. (1986). Bone crushing carnivores and their significance to osteodystrophy in griffon vulture chicks. *Journal of Zoology, 210*, 23-43.

Ritchie, E. G., & Johnson, C. N. (2009). Predator interactions, mesopredator release and biodiversity conservation. *Ecology Letters, 12*, 982-998.

Robbins, M. M., & McNeilage, A. (2003). Home range and frugivory patterns of mountain gorillas in Bwindi Impenetrable National Park, Uganda. *International Journal of Primatology, 24*, 467-491.

Robertson, A. S., & Boshoff, A. F. (1986). The feeding ecology of Cape Vultures *Gyps coprotheres* in a stock farming area. *Biological Conservation, 35*, 63-86.

Robinson, T. P., Franceschini, G., & Wint, W. (2007). The Food and Agriculture Organization’s Gridded Livestock of the World. *Veterinaria Italiana, 43*, 745-751.

Rodgers, A. R., Carr, A. P., Beyer, H. L., Smith, L., & Kie, J. G. (2007). Home Range Tools (HRT) for ArcGIS. Version 1.1. Ontario Ministry of Natural Resources, Centre for Northern Forestry Ecosystem Research, Thunder Bay, Ontario, Canada.

Rodgers, A. R., & Kie, J. G. (2010). HRT: Home Range Tools for ArcGIS. User’s Manual. Ontario Ministry of Natural Resources, Centre for Northern Forestry Ecosystem Research, Thunder Bay, Ontario, Canada.

Rodgers, A. R., Rempel, R. S., & Abraham, K. E. (1996). A GPS-based telemetry system. *Wildlife Society Bulletin, 24*, 559-566.

Rogers, D. J., & Randolph, S. E. (1993). Distribution of tsetse and ticks in Africa: Past, present and future. *Parasitology Today, 9*, 266-271.

Rondeau, G., Condeé, M. M., Ahon, B., Diallo, O., & Pouakouyou, D. (2008). Survey of the occurrence and relative abundance of raptors in Guinea subject to international trade: JNCC.

Rondeau, G., & Thiollay, J. M. (2004). West African vulture decline. *Vulture News, 51*, 13-33.

Rooney, S. M., Wolfe, A., & Hayden, T. J. (1998). Autocorrelated data in telemetry studies: time to independence and the problem of behavioural effects. *Mammal Review, 28*, 89-98.

Ruxton, G. D., & Houston, D. C. (2004). Obligate vertebrate scavengers must be large soaring fliers. *Journal of Theoretical Biology, 228*, 431-436.

Samuel, M. D., Pierce, D. J., & Garton, E. O. (1985). Identifying areas of concentrated use within the home range. *Journal of Animal Ecology, 54*, 711-719.

Sankaran, M., Hanan, N. P., Scholes, R. J., Ratnam, J., Augustine, D. J., Cade, B. S., . . . Zambatis, N. (2005). Determinants of woody cover in African savannahs. *Nature, 438*, 846-849.

Sarrazin, F., Bagnolini, C., Pinna, J. L., Danchin, E., & Clobert, J. (1994). High survival estimates of griffon vultures (*Gyps fulvus fulvus*) in a reintroduced population. *Auk, 111*, 853-862.

Satheesan, S. M. (2000). The role of poisons in the Indian vulture crash. *Vulture News, 42*, 4.

Satheesan, S. M., & Satheesan, M. (2000). Serious vulture-hits to aircraft over the world (pp. 113-126). Amsterdam: International Bird Strike Committee.

Schaller, G. B. (1972). *The Serengeti lion*. Chicago: University of Chicago Press.

Schmidt, K. (2008). Behavioural and spatial adaptation of the Eurasian lynx to a decline in prey availability. *Acta Theriologica, 53*, 1-16.

Schoener, T. W. (1981). An empirically based estimate of home range. *Theoretical Population Biology, 20*, 281-325.

Schultz, P. (2007). *Does bush encroachment impact foraging success of the critically endangered Namibian population of the Cape Vulture Gyps coprotheres?* MSc, University of Cape Town.

Schumann, M., Watson, L. H., & Schumann, B. D. (2008). Attitudes of Namibian commercial farmers toward large carnivores: the influence of conservancy membership. *South African Journal of Wildlife Research, 38*, 123-132.

Seaman, D. E., & Powell, R. A. (1996). An evaluation of the accuracy of kernel density estimators for home range analysis. *Ecology, 77*, 2075-2085.

Sekercioglu, C. H. (2006). Increasing awareness of avian ecological function. *Trends in Ecology and Evolution, 21*, 464-471.

Shultz, S., Baral, H. S., Charman, S., Cunningham, A. A., Das, D., Ghalsasi, G. R., . . . Prakash, V. (2004). Diclofenac poisoning is widespread in declining vulture populations across the Indian subcontinent *Proceedings of the Royal Society of London B - Biological Sciences, 271*, S458-S460.

Silverman, B. W. (1986). *Density estimation for statistics and data analysis*. London: Chapman & Hall.

Simmons, R. E., & Jenkins, A. R. (2007). Is climate change influencing the decline of Cape and bearded vultures in southern Africa? *Vulture News, 56*, 41-51.

Sinclair, A. R. E., Dublin, H. T., & Borner, M. (1985). Population regulation of Serengeti wildebeest: a test of the food hypothesis. *Oecologia, 65*, 266-268.

Sinclair, A. R. E., Mduma, S. A. R., & Brashares, J. S. (2003). Patterns of predation in a diverse predator-prey system. *Nature, 425*, 288-290.

Sinclair, A. R. E., Mduma, S. A. R., Hopcraft, J. G. C., Fryxell, J. M., Hilborn, R., & Thirgood, S. (2007). Long-term ecosystem dynamics of the Serengeti: lessons for conservation. *Conservation Biology, 21*, 580-590.

Sinclair, A. R. E., & Norton-Griffiths, M. (1979). *Serengeti: Dynamics of an ecosystem*. Chicago: The University of Chicago Press.

Singh, R. B. (1999). Ecological strategy to prevent vulture menace to aircraft in India. *Defence Science Journal, 49*, 117-121.

Siniff, D. B., & Tester, J. R. (1965). Computer analysis of animal movement data obtained by telemetry. *Bioscience, 15*, 104-108.

Sirami, C., Seymour, C., Midgley, G., & Barnard, P. (2009). The impact of shrub encroachment on savanna bird diversity from local to regional scale. *Diversity and Distributions, 15*, 948-957.

Smuts, G. L. (1978). Interrelations between predators, prey, and their environment. *Bioscience, 28*, 316-320.

Sokal, R. R., & Rohlf, F. J. (1995). *Biometry*. New York: W.H. Freeman.

South, A. B., Kenward, R. E., & Walls, S. S. (2008). Ranges7: for the analysis of tracking and location data. Online manual. Anatrack Ltd. Wareham, Dorset.

Southern, W. E. (1964). Additional observations on winter bald eagle populations: including remarks on biotelemetry techniques and immature plumages. *Wilson Bulletin, 76*, 222-237.

SPSS Inc. (2008). SPSS for Windows, Release 17.0.0, 2008. Chicago: SPSS, Inc.

St John, F. A. V., Keane, A. M., Edwards-Jones, G., Jones, L., Yarnell, R. W., & Jones, J. P. G. (2011). Identifying indicators of illegal behaviour: carnivore killing in human-managed landscapes. *Proceedings of the Royal Society B - Biological Sciences*. doi: 10.1098/rspb.2011.1228

Stein, A. B., Fuller, T. K., Damery, D. T., Sievert, L., & Marker, L. L. (2010). Farm management and economic analyses of leopard conservation in north-central Namibia. *Animal Conservation, 13*, 419-427.

Sterling, E., Nguyen, N., & Fashing, P. (2000). Spatial patterning in nocturnal prosimians: a review of methods and relevance to studies of sociality. *American Journal of Primatology, 51*, 3-19.

Sutherland, G. D., Harestad, A. S., Price, K., & Lertzman, K. P. (2000). Scaling of natal dispersal distances in terrestrial birds and mammals. *Conservation Ecology, 4*, 16.

Swan, G. E., Cuthbert, R., Quevedo, M., Green, R. E., Pain, D. J., Bartels, P., . . . Wolter, K. (2006). Toxicity of diclofenac to Gyps vultures. *Biology Letters, 2*, 279-282.

Swan, G. E., Naidoo, V., Cuthbert, R., Green, R. E., Pain, D. J., Swarup, D., . . . Wolter, K. (2006). Removing the threat of diclofenac to Critically Endangered Asian vultures. . *Plos Biology 4*, e66 doi: doi:10.1371/journal.pbio.0040066

Swanepoel, L. H., Dalerum, F., & van Hoven, W. (2010). Factors affecting location failure of GPS collars fitted to African leopards (*Panthera pardus*). *South African Journal of Wildlife Research, 40*, 10-15.

Swihart, R. K., & Slade, N. A. (1985). Testing for independence of observations in animal movements. *Ecology, 66*, 1176-1184.

Taggart, M. A., Cuthbert, R., Das, D., Pain, D. J., Green, R. E., Shultz, S., . . . Meharg, A. A. (2006). Diclofenac disposition in Indian cow and goat with reference to Gyps vulture population declines. *Environmental Pollution, 147*, 60-65.

Taggart, M. A., Senacha, K., Green, R. E., Jhala, Y. V., Ragathan, B., Rahmani, A. R., . . . Meharg, A. A. (2007). Diclofenac residues in carcasses of domestic ungulates available to vultures in India. *Environment International, 33*, 759-765.

Tambling, C. J., & du Toit, J. T. (2005). Modelling wildebeest population dynamics: implications of predation and harvesting in a closed system. *Journal of Applied Ecology, 42*, 431-441.

Tarboton, W. R., & Allan, D. G. (1984). *The status and conservation of birds of prey in the Transvaal. Transvaal Museum Monograph, 3*. Pretoria: Transvaal Museum.

Teren, G., & Owen-Smith, N. (2010). Elephants and riparian woodland changes in the Linyanti region, northern Botswana. *Pachyderm, 47*, 18-25.

Thewlis, R. M., Timmins, R. J., Evans, T. D., & Duckworth, J. W. (1998). The conservation status of birds in Laos: a review of key species. *Bird Conservation International, 8*, 1-159.

Thiollay, J. M. (2006a). The decline of raptors in West Africa: long-term assessment and the role of protected areas. *Ibis, 148*, 240-254.

Thiollay, J. M. (2006b). Severe decline of large birds in the Northern Sahel of West Africa: a long-term assessment. *Bird Conservation International, 16*, 1-13.

Thiollay, J. M. (2007). Raptor declines in West Africa: comparisons between protected, buffer and cultivated areas. *Oryx, 41*, 1-8.

Thirgood, S., Mosser, A., Tham, S., Hopcraft, G., Mwangomo, E., Mlengeya, T., . . . Borner, M. (2004). Can parks protect migratory ungulates? The case of the Serengeti wildebeest. *Animal Conservation, 7*, 113-120.

Thomas, D. L., & Taylor, E. J. (2006). Study designs and tests for comparing resource use and availability II. *Journal of Wildlife Management, 70*, 324-336.

Thorn, M., Scott, D. M., Green, M., Bateman, P. W., & Cameron, E. Z. (2009). Estimating brown hyaena occupancy using baited camera traps. *South African Journal of Wildlife Research, 39*, 1-10.

Tomkiewicz, S. M., Fuller, M. R., Kie, J. G., & Bates, K. K. (2010). Global positioning system and associated technologies in animal behaviour and ecological research. *Philosophical Transactions of the Royal Society B-Biological Sciences, 365*, 2163-2176.

Trinkel, M., Funston, P., Hofmeyr, M., Hofmeyr, D., Dell, S., & Slotow, R. (2010). Inbreeding and density-dependent population growth in a small, isolated lion population. *Animal Conservation, 13*, 374-382.

Tsui, J. (2000). *Fundamentals of global positioning system receivers: a software approach*: John Wiley & Sons, Inc.

Tucker, V. A. (1988). Gliding birds: descending flight of the whitebacked vulture, *Gyps africanus*. *Journal of Experimental Biology, 140*, 325-344.

Turnbull, P. C., Diekmann, M., Kilian, J. W., Versfeld, W., de Vos, V., Arntzen, L., . . . Kotze, A. (2008). Naturally acquired antibodies to *Bacillus anthracis* protective antigen in vultures in southern Africa. *Onderstepoort Journal of Veterinary Science 75*, 95-102.

Urbano, F., Cagnacci, F., Calenge, C., Dettki, H., Cameron, A., & Neteler, M. (2010). Wildlife tracking data management: a new vision. *Philosophical Transactions of the Royal Society B-Biological Sciences, 365*, 2177-2185.

Urios, V., Lopez-Lopez, P., Liminana, R., & Godino, A. (2010). Ranging behaviour of a juvenile Bearded vulture (*Gypaetus barbatus meridionalis*) in south Africa revealed by GPS satellite telemetry. *Ornis Fennica, 87*, 114-118.

USGS. (2004). Shuttle Radar Topography Mission, 30 Arc Second scene, Unfilled Unfinished 2.0.

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

Van Aarde, R., & Jackson, T. P. (2007). Megaparks for metapopulations: addressing the causes of locally high elephant numbers. *Biological Conservation, 134*, 289-297.

Van der Merwe, I., Tambling, C. J., Thorn, M., Scott, D. M., Yarnell, R. W., Green, M., . . . Bateman, P. W. (2009). An assessment of diet overlap of two mesocarnivores in the North West Province, South Africa. *African Zoology, 44*, 288-291.

Van der Merwe, P., & Saayman, M. (2005). Game farms as sustainable ecotourist attractions. *Koedoe, 48*, 1-10.

Van der Waal, C., & Dekker, B. (2000). Game ranching in the Northern Province of South Africa. *South African Journal of Wildlife Research, 30*, 151-156.

Van Dyk, G., & Slotow, R. (2003). The effects of fences and lions on the ecology of African wild dogs reintroduced to Pilanesberg National Park, South Africa. *African Zoology, 38*, 79-94.

Van Jaarsveld, J. (1987). Increasing numbers of vultures poisoned in the Kruger National Park. *Vulture News, 18*, 19-21.

Van Wyk, E., Bouwman, H., van der Bank, H., Verdoorn, G. H., & Hofmann, D. (2001). Persistent organochlorine pesticides detected in blood and tissue samples of vultures from different localities in South Africa. *Comparative Biochemistry and Physiology Part C, 129*, 243-264.

Van Wyk, E., van der Bank, F. H., Verdoorn, G. H., & Hofmann, D. (2001). Selected mineral and heavy metal concentrations in blood and tissues of vultures in different regions of South Africa. *South African Journal of Animal Science, 31*, 57-63.

Varland, D. E., Smallwood, J. A., Young, L. S., & Kochert, M. N. (2007). Marking techniques. In D. M. Bird & K. L. Bildstein (Eds.), *Raptor research and management techniques* (pp. 221-236). Surrey, Canada: Hancock House Publishers Ltd.

Virani, M. Z., Kendall, C., Njoroge, P., & Thomsett, S. (2011). Major declines in the abundance of vultures and other scavenging raptors in and around the Masai Mara ecosystem, Kenya. *Biological Conservation, 144*, 746-752.

Wallace, M. P., & Temple, S. A. (1987). Competitive interactions within and between species in a guild of avian scavengers. *Auk, 104*, 290-295.

Ward, J., McCafferty, D. J., Houston, D. C., & Ruxton, G. D. (2008). Why do vultures have bald heads? The role of postural adjustment and bare skin areas in thermoregulation. *Journal of Thermal Biology, 33*, 168-173.

Wartmann, F. M., Purves, R. S., & van Schaik, C. P. (2010). Modelling ranging behaviour of female orang-utans: a case study in Tuanan, Central Kalimantan, Indonesia. *Primates, 51*, 119-130.

Wauters, L. A., & Dhondt, A. A. (1992). Spacing behaviour of red squirrels, *Sciurus vulgaris*: variation between habitats and the sexes. *Animal Behaviour, 43*, 297-311.

Wauters, L. A., Preatoni, D. G., Molinari, A., & Tosi, G. (2007). Radio-tracking squirrels: Performance of home range density and linkage estimators with small range and sample size. *Ecological Modelling, 202*, 333-344.

Wauters, L. A., Verbeylen, G., Preatoni, D., Martinoli, A., & Matthysen, E. (2010). Dispersal and habitat cuing of Eurasian red squirrels in fragmented habitats. *Population Ecology, 52*, 527-536.

White, G., & Garrott, R. (1990). *Analysis of wildlife radio tracking data*. San Diego: Academic Press.

Whiting, M. J., Williams, V. L., & Hibbitts, T. J. (2011). Animals traded for traditional medicine at the Faraday market in South Africa: species diversity and conservation implications. *Journal of Zoology, 284*, 84-96.

Wink, M. (1995). Phylogeny of Old and New World vultures (Aves: Accipitridae and Cathartidae) inferred from nucleotide sequences of the mitochondrial cytochrome b gene. *Journal of Biosciences, 50*, 868-882.

Worton, B. J. (1987). A review of models of home range for animals movement. *Ecological Modelling, 38*, 277-298.

Worton, B. J. (1989). Kernel methods for estimating the utilization distribution in home-range studies. *Ecology, 70*, 164-168.

Worton, B. J. (1995). Using Monte Carlo simulation to evaluate kernel-based home range estimators. *Journal of Wildlife Management, 59*, 794-800.

Xirouchakis, S. M., & Andreou, G. (2009). Foraging behaviour and flight characterstics of Eurasian griffons *Gyps fulvus* in the island of Crete, Greece. *Wildlife Biology, 15*, 37-52.

Yarnell, R. W., Metcalfe, D. J., Dunstone, N., Burnside, N., & Scott, D. M. (2008). The impact of fire on habitat use by the short-snouted elephant shrew (*Elephantulus brachyrhynchus*) in North West Province, South Africa. *African Zoology, 43*, 45-52.

CHAPTER 6

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FORAGING RANGES OF IMMATURE AFRICAN WHITE-BACKED VULTURES (*GYPS AFRICANUS*) AND THEIR USE OF PROTECTED AREAS IN SOUTHERN AFRICA

Foraging Ranges of Immature African White-backed Vultures (*Gyps africanus*) and Their Use of Protected Areas in Southern Africa

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Abstract

Vultures in the *Gyps* genus are declining globally. Multiple threats related to human activity have caused widespread declines of vulture populations in Africa, especially outside protected areas. Understanding of spatial ecology is an important component of species conservation. Despite this, accurate foraging range estimates for the widespread but declining African white-backed vulture (*Gyps africanus*) are lacking. We used GPS-GSM tracking units deployed on six immature African white-backed vultures caught from the wild in South Africa to study their movement patterns, use of protected areas and the proportion of time they spent in the vicinity of supplementary feeding sites. The vultures were tracked for between 101 and 313 days. Their combined foraging ranges extended into six countries in southern Africa (mean (± SE) MCP area = 269,103 ± 197,187 km^2) and three of the vultures travelled more than 900 km from the capture site. All six vultures spent the majority of their tracking periods outside protected areas. South African protected areas were very rarely visited while protected areas in northern Botswana and Zimbabwe were used more frequently. Two of the vultures visited supplementary feeding sites regularly. The results show that immature African white-backed vultures are capable of travelling throughout southern Africa, and their limited use of protected areas leaves them susceptible to the full range of threats in the region. We recommend the use of GPS tracking technology to increase our understanding of the foraging ecology of all vulture species in southern Africa, and assess the risk of exposure to their many threats in the region.

Introduction

Vultures in the *Gyps* genus are obligate scavengers and are the main consumers of ungulate carcasses in African savannahs [1-3]. Their energy efficient soaring flight, keen eyesight and social foraging behaviour enable them to locate sparsely distributed carcasses over a large area, often before their mammalian competitors [2,4,5]. Their scavenging behaviour provides important ecosystem services by recycling carcasses, keeping energy flows higher in food webs, and limiting the development and spread of disease [6,7].

All eight *Gyps* vulture species found globally are currently declining [8]. Since the 1990s three species of *Gyps* vultures have declined by more than 95% in parts of Asia mainly due to accidental poisoning after consuming carcasses of domestic livestock previously treated with the veterinary non-steroidal anti-inflammatory drug (NSAID), diclofenac [8-10]. African *Gyps* vultures, such as the African white-backed vulture (*G. africanus*), are equally as sensitive to the toxic effects of diclofenac and other NSAIDs as their Asian relatives [11,12], raising concerns of potential rapid population declines in the future [13].

Large declines in vulture populations have been documented in many parts of Africa, especially outside protected areas [14-16]. Two of the most serious threats to African vultures are food shortages caused by improved animal husbandry and over-harvesting of wild ungulate populations, and mass poisoning of vultures when they consume carcasses laced with poisons intended to kill predators of livestock [5,14,16]. For example, increasingly frequent poisoning incidents are the most likely cause of a 52% decline in *Gyps* vulture numbers in the Masai Mara ecosystem in Kenya over a 30 year period [16]. Their gregarious feeding behaviour and ability to forage over large areas make *Gyps* vultures particularly susceptible to mass poisoning events which tend to occur most frequently on unprotected farmland [5,17].

Additional threats to vultures in Africa include fatal collisions and electrocutions with power lines [18], illegal harvesting for the traditional beliefs market [19], and the disturbance or loss of breeding sites [20], all of which are more prevalent in unprotected areas. Consequently, several studies have found that vultures are becomingly increasingly restricted to protected areas in different regions of Africa [14-16].

Since the latter half of the twentieth century “vulture restaurants” have been used in southern Africa to provide a source of supplementary food for vultures [21]. Although vulture survival rates have increased in some areas with supplementary feeding schemes [22], the impact of supplementary feeding on vulture foraging ecology is not fully understood [23].

The African white-backed vulture is widespread but declining throughout its range [24,25], prompting calls for its conservation status to be upgraded from Near-threatened to Vulnerable on the IUCN Red List [16,26]. Through re-sightings of marked individuals in southern Africa, immature African white-backed vultures are known to travel extensively [27], but a greater understanding of their movement patterns, foraging ecology and use of protected areas is required to assess their susceptibility to different threats [16].

In this study we use GPS telemetry to estimate the foraging ranges of six immature African white-backed vultures caught from the wild in South Africa. We also assess how regularly they visited protected areas and supplementary feeding sites. We elected to prioritise fitting the limited number of tracking units to immature individuals as we expected them to range further and consequently be exposed to multiple threats across the wider landscape [5,22,28].

Methods

Vulture captures

Vultures were caught at a supplementary feeding site for mammalian and avian scavengers at Mankwe Wildlife Reserve (MWR; 25°13’S, 27 °18’E), approximately 4 km east of Pilanesberg National Park (25°14’S, 27 °05’E) in the North West Province of South Africa (Fig. 6.1). A walk-in cage trap (6 x 3 x 3 m) constructed from a lightweight steel frame overlaid with wire mesh was used to catch the vultures [29]. For at least two days prior to attempted capture attempts domestic livestock or wild ungulate carcasses were placed in and around the cage to attract vultures to the area and allow them to become accustomed to feeding at the site. A carcass was placed inside the cage on the evening before a capture, with a small amount of meat left outside to encourage the vultures to land and feed. All captures were undertaken in the early morning to coincide with the vultures’ normal feeding behaviour and to avoid heat stress. Six immature African white-backed vultures were caught and fitted with GPS-GSM tracking units during three separate captures (Table 6.1).

GPS-GSM tracking units

Hawk105 GPS-GSM tracking units (Africa Wildlife Tracking Ltd., Pretoria, South Africa; www.awt.co.za) were secured onto the back of each vulture using a Teflon® ribbon backpack-style harness enclosed in flexible plastic tubing to prevent skin abrasions [30]. Each unit weighed 170 g (*c.* 3.1% of the mean mass of an African white-backed vulture [5] and was encased in hardened epoxy resin for protection and waterproofing. The units were set to record GPS locations (~10 m accuracy), altitude above sea level, speed and direction of travel, date, time and temperature at three times per day: 07:00, 11:00 and 15:00. The tracking units also recorded a positional dilution of precision (PDOP) value as a measure of the accuracy of each GPS location [31]. The data were transmitted daily by SMS to a secure online database via the GSM network. Whenever a vulture was in an area without GSM coverage, up to 20,000 data points could be stored on the unit which were then transmitted when it returned to an area with coverage. It was anticipated that each unit would record and transmit data for approximately one year. Yellow patagial tags inscribed with a unique four character code were also attached through the patagia of both wings of each captured vulture to allow visual identification of individuals after release.

The procedures were approved by the Animal Use and Care Committee of the University of Pretoria (Protocol: V033-09). 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).

Data analysis

For all spatial analyses the GPS locations were projected to the UTM coordinate system (WGS 1984 UTM Zone 35S) and mapped and analysed using ArcGIS® ArcMap™ 9.3

(Environmental Systems Research Institute, Redlands, California, USA). The degree of autocorrelation of each set of GPS locations was assessed using Schoener's [32] index of autocorrelation in Home Range Tools extension [33] for ArcGIS®.

Distances between consecutive GPS locations were calculated for each vulture using Ranges7 v2.7 [34]. A crude estimation of the total distance travelled per day by an individual was obtained by summing the distances between all GPS locations recorded in a 24 hour period (i.e. (07:00-11:00) + (11:00-15:00) + (15:00-07:00)). For each vulture, the total distance travelled, the mean distance between consecutive locations, and the mean and maximum distance travelled per day were calculated.

Estimates of the foraging ranges traversed by each vulture during their total tracking periods were calculated using three methods to account for potential variation between techniques [35]. Firstly, foraging ranges were delineated with Minimum Convex Polygons (MCPs) using all recorded GPS locations [36,37]. Although MCPs have a tendency to overestimate the actual area occupied by an animal by including outlying locations [35,38], they were used here to compare our estimates with previous tracking studies on *Gyps* vultures (e.g. [28]). Incremental area analysis was carried out in Ranges7 [34] to investigate whether the size of the vultures' foraging ranges represented by MCPs reached an asymptote during the total tracking period [36]. For each individual, MCPs were created by sequentially adding consecutive locations until all locations were used to produce the MCP for the total tracking period. A foraging range area curve was then plotted and asymptotes were identified visually [36].

Secondly, fixed kernel density estimation (KDE) was used to delineate 95% and 50% contours to represent the overall and core foraging ranges, respectively [39]. An *ad hoc* bandwidth ($h_{ad\ hoc}$) designed to reduce over-smoothing of the KDE contours [40,41] was used for KDE calculations. The value of $h_{ad\ hoc}$ was determined by reducing the reference bandwidth (h_{ref}) in increments of 0.05 until the 95% contour became contiguous with no lacunae (i.e. $h_{ad\ hoc} = 0.95 \times h_{ref}$, $0.90 \times h_{ref}$, $0.85 \times h_{ref}$, etc.; [40,41]). A 1000 x 1000 m raster cell size was used for KDE calculations. The Home Range Tools extension [33] for ArcGIS® was used for MCP and KDE analysis.

Thirdly, grid cell range (GCR) estimates were calculated [36] using Hawth's Analysis Tools v3.27 [42]. A 10 x 10 km grid was intersected by the continuous line connecting all consecutive locations for each individual, which represented the shortest assumed path travelled between consecutive locations. Summing the area of the grid cells that were intersected by the path linking the consecutive locations provided an estimate of the size of the overall foraging range, termed the path GCR [43]. The number of GPS locations in each grid cell was counted and core areas (core GCRs) were identified as the cells in which the number of locations was greater than the mean number per cell across the overall range [44]. Path GCR estimates were also calculated for separate complete months (i.e. months with data on >90% of days) for each vulture.

Vulture utilisation of officially protected areas was investigated separately for each vulture at the foraging range scale based on use-availability analysis [45]. A polygon shapefile of protected areas in southern Africa was created using data from the 2010 World Database on Protected Areas (WDPA) containing all IUCN category I-VI protected areas [46] and 'national other areas' (i.e. protected areas uncategorized by IUCN) polygons from the 2003 WDPA [47]. The two datasets were merged into a single polygon shapefile. All areas outside the protected areas polygons were designated as unprotected areas.

Ivlev's electivity index [48] was used to evaluate whether protected areas were used by each vulture in proportion to their availability, and was calculated as $E_i = (U_i - A_i) / (U_i + A_i)$, where E_i is the electivity index value, and U_i and A_i are the use and availability of protected areas, respectively. The proportion of each vulture's 95% KDE contour occupied by protected areas defined their availability to each vulture. Use of protected areas was defined as the proportion of stationary (i.e. < 10 km·h^{-1}) GPS locations that were recorded inside protected areas within the 95% KDE contour. We also calculated the proportion of each vulture's 50% KDE contours occupied by protected areas to estimate their use at the core foraging range scale. Ivlev's electivity index ranges from -1 (completely avoided) to +1 (maximum positive selection), with zero indicating that use of protected areas was proportional to their availability, while positive and negative values indicate greater and less use of protected areas than expected, respectively.

To estimate use of supplementary feeding sites, the proportion of stationary GPS locations recorded within 5 km of known supplementary feeding sites for scavengers in southern Africa was calculated separately for each vulture. The supplementary feeding sites were identified from a combination of databases compiled during questionnaire surveys between 2000 and 2010 ([49], Wolter, unpublished data). Analyses were conducted for the total tracking periods and separately for each complete month for all vultures.

Results

The six vultures fitted with tracking units were all less than four years of age and all but one were tracked continuously for at least 200 days (Table 6.1). One of the vultures (AG332) was tracked for 101 days before the tracking unit stopped transmitting data. This limited tracking period led to the exclusion of data from AG332 from the use of protected areas analysis. The six tracking units recorded a mean of 99.44 ± 0.25% of expected GPS locations, with a mean (± SE) accuracy of 2.4 ± 0.02 PDOP (n = 4,326 locations).

Foraging ranges and distances travelled

The combined foraging ranges of all six vultures extended across much of southern Africa (Fig. 6.1). The vultures traversed path GCRs covering an average (± SE) of 56,683.33 ± 9,210.19 km^2 (Table 6.2, Fig. 6.1A). MCPs included large areas that were never visited by the vultures (Fig. 6.1B). KDE contours delineated realistic range boundaries for three vultures (AG330, AG331 and AG350; Fig. 6.2A-B), but for the three widest ranging vultures they incorporated large areas that were never visited (Fig. 6.2C-D). Foraging range areas presented in the text are from GCR estimates which provided the most realistic representation of the vultures' actual movements.

Foraging range area curves from incremental area analysis reached asymptotes that lasted for at least 50 days for all vultures apart from AG332 (Fig. S6.1). A general pattern of settled periods followed by exploratory movements beyond the existing MCP boundary occurred for all vultures. For all vultures foraging range area curves were asymptotic at the end of their tracking periods, indicating that the tracking periods were long enough to provide representative estimates. The GPS location datasets of all six vultures were significantly autocorrelated, with a mean (± SE) Schoener's index value of 0.019 ± 0.011.

GPS locations were recorded more than 900 km from the capture site for three vultures. Following its capture, AG332 travelled north through Botswana before proceeding to south-east Namibia, travelling 2,502 km and covering an overall foraging range of 28,400 km^2 in 101 days (Fig. 6.2D). AG356 also travelled north immediately after capture, moving through eastern Botswana and western Zimbabwe to the Victoria Falls region (17^{o}55'S, 25^{o}50'E) of Zimbabwe where it remained for a three month period (Fig. 6.2C) before travelling through the Caprivi Strip (Namibia) to south-west Angola, returning to north-east Zimbabwe through northern Botswana. After spending 3.5 months in the NW and Limpopo Provinces of South

Africa, AG032 travelled north through southern Zimbabwe to north-east Botswana and north-west Zimbabwe. During the total tracking period of 206 days AG032 travelled over 8,454 km and occupied an overall range of 74,500 km^2, at one point moving 520 km across the width of south-central Zimbabwe in 2.5 days. AG032 and AG356 entered a total of five and six different countries, respectively (Fig. 6.2C).

The foraging ranges of the remaining three vultures (AG330, AG331 and AG350) extended across the Botswana-South Africa and Zimbabwe-South Africa borders, orientated in a south-west to north-east direction from the Vryburg (21^{o}03'S, 29^{o}21'E) region of South Africa to the West Nicholson (26^{o}57'S, 24^{o}43'E) area of south-west Zimbabwe (Fig. 6.2A). KDE and GCR analysis showed that these three vultures, as well as AG032, used at least two core foraging areas bisected by the South Africa-Botswana border (Fig. 6.2B).

Monthly path GCR estimates ranged from 600 to 22,200 km^2 (mean ± SE = 9,878.26 ± 846.37 km^2; n = 46 months). For three out of five vultures the smallest path GCR estimates were recorded in May (Fig. 6.3). The five vultures that were tracked during both the wet summer (December to April) and dry winter (May to September) periods occupied significantly larger average monthly path GCRs during summer months (mean ± SE = 12,162.00 ± 1,216.55 km^2; n = 5 vultures) compared to winter months (mean ± SE = 8,874.00 ± 1,720.00 km^2; n = 5 vultures) (Wilcoxon signed-rank test: $Z = -2.2023$, $p = 0.043$).

The mean (± SE) distance travelled per day ranged from 22.27 ± 2.13 km for AG356 to 48.86 ± 2.59 km for AG331 (Table 6.3). Three vultures travelled more than 220 km in a single day. AG331 travelled the furthest during the total tracking period, moving 15,293 km in 313 days.

Utilisation of protected areas

Protected areas occupied a mean (± SE) of 4.33 ± 1.50% of the 95% KDE contours of the three vultures that spent the majority of their tracking periods either side of the South Africa-Botswana border (AG330, AG331 and AG350), compared to 32.22 ± 9.75% of the 95% KDE contours of the two vultures that travelled north through southern Africa (AG032 and AG356; Fig. 6.4). A mean (± SE) of 5.21 ± 0.88% of stationary GPS locations within the 95% KDE contours of AG330, AG331 and AG350 were recorded inside protected areas, compared to 35.30 ± 1.13% for AG356 and AG032 (Fig. 6.4). Protected areas occupied a mean (± SE) of 3.15 ± 1.58% of the 50% KDE contours of AG330, AG331 and AG350, compared to 38.62 ± 11.63% for AG356 and AG032 (Fig. 6.4). Assessment of the use of protected areas by AG332 was not conducted due to its short tracking period.

At the overall foraging range scale Ivlev's electivity index values (Fig. 6.5A) indicated that more stationary GPS locations were recorded inside protected areas than expected for three vultures, while fewer than expected were recorded inside protected areas for the other two. At the core foraging range scale Ivlev's electivity index values (Fig. 6.5B) indicated that protected areas occupied a similar proportion of the 50% KDE contours to the 95% KDE contours for three of the vultures, while protected areas occupied a smaller proportion of the 50% KDE contours than expected for the other two. Protected areas were completely absent from the 50% KDE contours of AG331, resulting in an Ivlev's electivity index value indicating maximum avoidance.

South African protected areas were not visited regularly by any vultures (Fig. 6.6), with AG032 never entering a South African protected area in a period of more than 3 months. Pilanesberg NP (25°14'S, 27°05'E) and other relatively large conservation areas in the North West and Limpopo Provinces of South Africa were never visited by any of the vultures, while only two and five stationary locations (both from AG331) were recorded inside Madikwe GR (24^{o}45’S, 26^{o}14’E) and Marakele NP (24^{o}24’S, 27^{o}35’E) respectively. None of the three vultures that spent the majority of their tracking periods in South Africa or southern Botswana spent extended periods inside protected areas.

The two vultures that travelled more extensively through southern Africa visited protected areas more regularly (Fig. 6.6), particularly in northern Botswana and Zimbabwe in the Kavango-Zambezi Transfrontier Conservation Area (TFCA), where they spent extended periods inside wildlife reserves such as Chobe NP (18^{o}08’S, 24 ^{o}43’E) and associated wildlife management areas (WMAs) in northern Botswana, as well as in the Victoria Falls region of Zimbawe (18^{o}02’ S, 25^{o}45’E).

Utilisation of supplementary feeding sites

Excluding AG332 which did not visit a supplementary feeding site after leaving the capture site, the proportion of stationary GPS locations recorded within 5 km of feeding sites for each vulture were 2.98% for AG330, 2.38% for AG331, 33.67% for AG350, 29.35% for AG356 and 11.17% for AG032. The number of feeding sites visited by each vulture ranged from 4 for AG356 to 12 for AG350 (mean ± SE = 6.60 ± 1.40), totalling 19 different sites including the MWR capture site. Two of the sites were in the Victoria Falls region of Zimbabwe, and one was south-east of Gaborone in Botswana. The remaining 16 sites were in South Africa, 14 of which were in the western Limpopo Province and two in the North West Province. MWR was never re-visited by any of the vultures fitted with tracking units after they left the capture site.

Two of the vultures spent a relatively large proportion of their time each month in the vicinity of supplementary feeding sites, with up to 88.73% and 58.03% of stationary GPS locations per month being recorded within 5 km of feeding sites for AG350 and AG356, respectively.

AG350 repeatedly spent extended periods at a privately managed supplementary feeding site approximately 16 km south-east of Gaborone, Botswana (24^{o}42’ S, 25^{o}56’E) with 28.57% of all of its stationary GPS locations within 5 km of that site. From April until July AG356 regularly utilised a site approximately 16 km south-west of Victoria Falls, Zimbabwe (18^{o}02’ S, 25^{o}45’E), with 18.24% of its stationary GPS locations recorded within 5 km of that site. The same vulture was also regularly recorded in the vicinity of a second site located several kilometres west of Victoria Falls town at Victoria Falls Safari Lodge (17^{o}54’ S, 25^{o}48’E), where it was seen feeding several times, identified from its patagial tag number. When data from the five vultures were evaluated collectively, there was a significant negative correlation between the size of monthly path GCRs for months in which at least one stationary GPS location was recorded within 5 km of a feeding site, and the proportion of stationary GPS locations within 5 km of supplementary feeding sites in each corresponding month (r_S (28) = -0.581, p = 0.001, n = 28 months).

Discussion

This study provides the first description of ranging patterns of immature African white-backed vultures tracked from South Africa using GPS tracking methods. The small sample size (n = 6) and relatively short tracking periods (101 – 313 days) require the results to be considered with caution, however. It was also not logistically feasible to verify the activities of the vultures on the ground or the purposes of their flights due to their frequent long distance movements. Despite these limitations, the regular sampling intervals and high accuracy of the tracking units provided a detailed first insight into patterns of space use by immature African white-backed vultures in southern Africa.

The foraging range estimates varied markedly between methods, emphasising the need to use appropriate methods depending on the data available and the aims of the study [41]. As seen previously, both MCPs and KDE contours included large areas that were never visited by some of the vultures, especially the widest ranging individuals [35,38]. Path GCRs reduced the inclusion of unvisited areas and produced the most realistic, but conservative representations of the vultures' movements. The spatial extent of core GCRs and 50% KDE contours corresponded closely (Fig. 6.2) and successfully delineated centres of activity. KDE using the *ad hoc* method of bandwidth selection and GCR methods should both be considered suitable for the analysis of similar vulture tracking data.

The large foraging ranges recorded during this study were expected because immature *Gyps* vultures typically disperse away from their natal origin and move in a nomadic manner from one food source to another [1,5,50]. Although very few foraging range estimates exist for immature African white-backed vultures, one study that tracked an immature Cape vulture (*G. coprotheres*) and an immature African white-backed vulture from Namibia recorded similarly extensive movements across several countries in southern Africa (mean MCP = 482,276 km^2) [28]. The long-distance movements away from the capture site by three of the vultures and previously recorded re-sightings and recoveries of marked individuals more than 900 km from their natal origins [27], confirm that immature African white-backed vultures disperse widely across southern Africa, possibly to avoid competing with adults for the same food supply [5].

In general, foraging range size among vertebrates is inversely related to resource abundance and spatio-temporal predictability [51]. The large foraging ranges and relatively long distances travelled by the vultures indicate that the distribution of their food supply (i.e. ungulate carcasses) was generally unpredictable and sparse, as expected [5,52]. The maximum distances that the vultures travelled in a single day (mean = 207.97 ± 17.44 km) confirm suggestions that they are able to search for carcasses across a vast daily foraging range and that vultures present at a carcass might have arrived from many kilometers away [52].

Although Ivlev's electivity index values (Fig. 6.5A) indicated that three vultures spent more time inside protected areas than expected, only a small proportion (<5%) of stationary GPS locations were recorded inside protected areas for two of those vultures (AG331 and AG350). The low availability (<4%) of protected areas in the 95% KDE contours of both vultures probably caused the Ivlev's electivity index values to reflect a relatively high degree of positive selection despite use only marginally exceeding availability [45]. The limited amount of time that the vultures spent in South African protected areas indicates that they were able to locate sufficient carcasses to meet their energy requirements by regularly foraging on private farmland. This contradicts suggestions that the creation of relatively new protected areas such as Pilanesberg National Park and Madikwe Game Reserve in the late twentieth century would benefit vultures in northern South Africa by providing safe foraging grounds [24,53]. The ungulate populations inside the relatively small fenced protected areas in northern South Africa are regulated primarily by unusually high rates of predation by large carnivores such as lions (*Panthera leo*) rather than other causes of mortality such as malnutrition [54,55]. As vultures are known to feed mainly on ungulates that die from causes other than predation and rarely land at carcasses with large carnivores in attendance [1], their limited use of South African protected areas during this study could be partially explained by lower food availability and elevated levels of competition in fenced reserves containing relatively high densities of large mammalian carnivores [54].

The geographical distribution of protected areas in northern South Africa might also have reduced their accessiblity to the vultures. For example, several relatively large protected areas within the foraging ranges of the vultures were located in mountainous areas (e.g. the Waterberg Mountains; Pilanesberg) which were avoided by all of the tracked vultures (Fig.

S6.2). As African white-backed vultures favour flat, lowland savannah [56] it is possible that some of the protected areas in the region are located in areas lacking suitable environmental characteristics (e.g. topography) for their foraging activity and are therefore rarely visited by the species.

More than 34% of stationary GPS locations of the two vultures that travelled more widely through southern Africa to northern Botswana and Zimbabwe were recorded inside protected areas, all of which were outside South Africa. Both vultures spent extended periods in the large reserves of the Zambezi-Kavango TFCA, and other reserves outside South Africa, where ungulate densities are higher than surrounding unprotected land and disturbance is comparatively low [57-59]. These results support previous suggestions that vultures regularly use protected areas in Botswana and other African countries, probably due to lower levels of anthropogenic disturbance and higher food availability compared to unprotected areas [14-16,20,60], but also show that the tracked vultures spent the majority of their tracking periods outside protected areas. The large amount of time that AG356 spent a short distance from the boundary of a protected area in the vicinity of a supplementary feeding site explains why the Ivlev's electivity index value indicated that the vulture used protected areas less than expected at the overall foraging range scale.

The vultures' core foraging ranges (Fig. 6.2) were located in areas known to be important for African white-backed vultures, and corresponded closely with high reporting rates for the species recorded during ground surveys [5,61]. The distribution of ungulate carcasses was probably the most important factor that influenced the movement patterns of the immature vultures because their principal activity would have been searching for food and they were not restricted to foraging within a certain distance of a nest or roost site [5,62]. Farming of wild and domestic ungulate species is common and widespread in northern South Africa and southern Botswana, where several of the vultures spent a large proportion of their time

[63,64]. It is likely, therefore, that the vultures consumed carcasses of both wild and domestic ungulate species, as previously seen in the study area and elsewhere in South Africa [65,66]. The apparent seasonal variation in foraging range size recorded during this study might have been caused by higher mortality rates of wild ungulate species during the dry winter months [67] increasing the ability of the vultures to locate carcasses in smaller foraging ranges. Although mortality rates of domestic livestock are generally higher in the wet summer months [68] their carcasses are more likely to be found and removed by farmers on commercial livestock farms than on more extensively farmed land, such as game farms [5,65]. The vultures might also have been forced to travel further during the wet summer months when increased vegetation causes a reduction in carcass detectability [69]. It was not possible to verify the purpose of the vultures' movements, however, and as with previous studies that recorded seasonal variations in *Gyps* vulture ranging patterns, the underlying causes remain unclear [28,70].

Two vultures were regularly recorded in the vicinity of specific supplementary feeding sites that they repeatedly visited for extended periods, which suggests that they were able to obtain a relatively large proportion of their food requirements at those sites. *Gyps* vultures frequently use supplementary feeding sites elsewhere in southern Africa [22,28], and the provision of supplementary food at fixed locations has been shown to reduce vulture foraging ranges [70]. Similar patterns were recorded during this study, with smaller monthly foraging ranges recorded during months when the vultures spent a greater proportion of their time in the vicinity of feeding sites. Although not all of the vultures were regularly recorded in the vicinity of feeding sites, it is possible that they visited feeding sites that were not recorded in the database used for this analysis, and so these estimates might be conservative. Further research is required to determine the use of supplementary feeding sites by vultures in southern Africa, and their potential impacts on vulture foraging ecology [23].

Conclusions

Key results of this study are that immature African white-backed vultures are capable of travelling across the entire region of southern Africa and spend a large proportion of their time outside protected areas. Although based on a small sample size, these findings may have important implications for the conservation of African white-backed vultures. If the ranging patterns recorded during this study are repeated across the wider population then immature African white-backed vultures could potentially be exposed to the full range of threats in southern Africa. Their limited use of protected areas and regular use of private farmland, particularly in South Africa, leaves them susceptible to anthropogenic threats such as poisoning by veterinary NSAIDs or predator control measures. Continuing mass poisonings of vultures in southern Africa therefore pose a serious threat to vulture populations from all countries in the region, and co-ordinated trans-national conservation measures will be required to confront the problem. The findings from this study also demonstrate that GPS tracking technology can be used effectively to provide detailed information about vulture movements and land use patterns, and as a tool to inform the planning of vulture conservation strategies. Similar research is required on adult African white-backed vultures and all other declining vulture species throughout Africa.

Supporting Information

Figure S6.1. Foraging range area curves from incremental area analysis of GPS locations from six immature African white-backed vultures.

Figure S6.2. Path grid cell ranges (GCRs) of six immature African white-backed vultures in relation to protected areas and elevation in northern South Africa.

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Author Contributions

Conceived and designed the experiments: WLP KW VN SGW. Performed the experiments: WLP KW. Analysed the data: WLP. Wrote the paper: WLP. Acted as the first author's study supervisor: VN SGW. Edited the manuscript: SGW VN.

Table 6.1. Capture information for six immature African white-backed vultures. Vulture ID, estimated age at time of capture, sex, length of total tracking period, the number of GPS locations that were recorded, and the mean accuracy of each location on the PDOP scale are shown for each vulture.

Vulture ID	**Estimated age at capture**	**Sex**	**Tracking period (Days)**	**Number of GPS locations**	**Mean (±SE) PDOP per location**
AG032	*1st year*	*Male*	*206*	616	2.72 ± 0.06
AG330	*2nd year*	*Male*	*301*	896	2.14 ± 0.04
AG331	*2nd year*	*Male*	*313*	935	3.21 ± 0.05
AG332	*3rd year*	*Female*	*101*	301	2.56 ± 0.07
AG350	*2nd year*	*Female*	*300*	898	2.06 ± 0.04
AG356	*2nd/3rd year*	*Male*	*226*	680	1.77 ± 0.04

* Values of < 3 PDOP indicate very high positional accuracy [31].

Table 6.2. Overall and core foraging range estimates for six immature African white-backed vultures. MCPs including all recorded GPS locations (100% MCP), 95% contours from kernel density estimation (KDE), and path grid cell ranges (GCRs) represent overall foraging ranges. 50% KDE contours and core GCRs represent core foraging ranges. The tracking period and number of GPS locations recorded for each vulture are also shown.

			Foraging range areas (km^2)				
Vulture ID	**Tracking period (days)**	**GPS Locations**	**100% MCP**	**95% KDE**	**50% KDE**	**Path GCR**	**Core GCR**
AG330	301	896	144,568	125,861	29,714	59,400	5,700
AG331	313	935	155,301	145,854	28,044	89,800	11,400
AG350	300	898	124,492	47,132	8,825	43,100	4,200
AG356	226	680	332,451	342,413	34,967	44,900	2,300
AG032	206	616	588,705	582,795	122,465	74,500	4,000
AG332	101	301	439,520	765,483	132,662	28,400	2,700

Table 6.3. Distances travelled by six immature African white-backed vultures. Total distances travelled during total tracking periods, mean (± SE) distances between consecutive GPS locations, maximum and mean (± SE) total distances travelled per day are shown for each vulture.

Vulture ID	Tracking days	Total distance travelled (km)	Mean distance between consecutive locations (km)	Maximum distance travelled / day (km)	Mean total distance travelled / day (km)
AG330	301	7,699.03	8.60 ± 0.61	183.90	25.84 ± 2.04
AG331	313	15,293.49	16.37 ± 0.83	267.43	48.86 ± 2.59
AG350	300	11,273.75	12.57 ± 0.67	241.63	37.58 ± 2.23
AG356	226	5,032.54	7.41 ± 0.62	171.22	22.27 ± 2.13
AG032	206	8,453.76	13.75 ± 1.01	223.48	41.04 ± 2.95
AG332	101	2,502.17	8.34 ± 1.14	160.17	24.77 ± 3.94

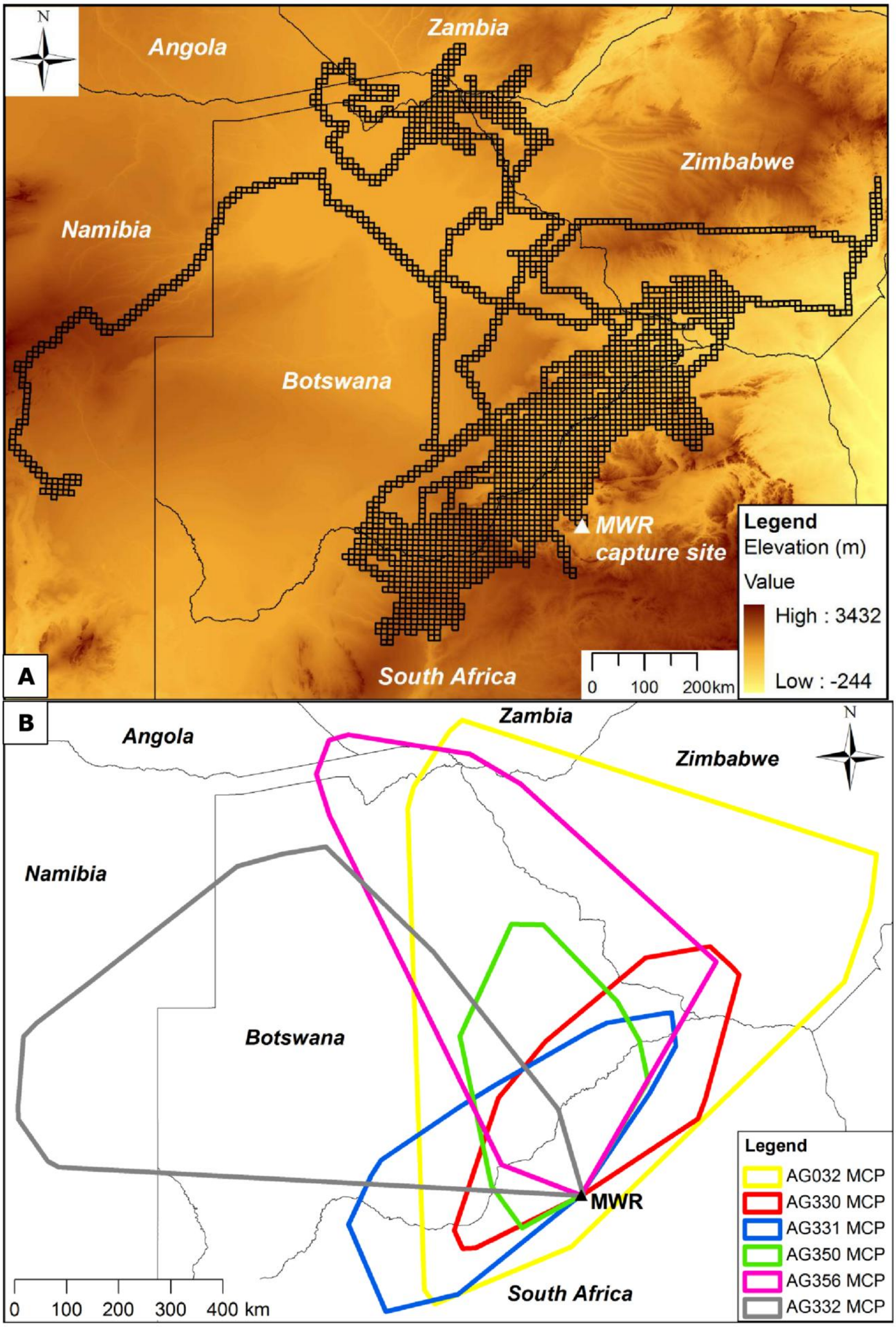
A
N
Angola
Zambia
Zimbabwe
Namibia
Botswana
South Africa
MWR capture site
Legend
Elevation (m)
Value
High : 3432
Low : -244
0
100
200km
B
Angola
Zambia
Zimbabwe
N
Namibia
Botswana
South Africa
MWR
Legend
AG032 MCP
AG330 MCP
AG331 MCP
AG350 MCP
AG356 MCP
AG332 MCP
0
100
200
300
400 km

Figure 6.1. Foraging ranges represented by (A) path GCRs and (B) MCPs for six immature African white-backed vultures. Path GCRs (A) represent 10 x 10 km grid cells intersected by a continuous line between all consecutive GPS locations recorded during the total tracking period of each vulture. Elevation is also shown in (A) [71]. MCPs (B) were created by connecting the outermost GPS locations recorded for each vulture. Mankwe Wildlife Reserve capture site is indicated by a black triangle and “MWR”.

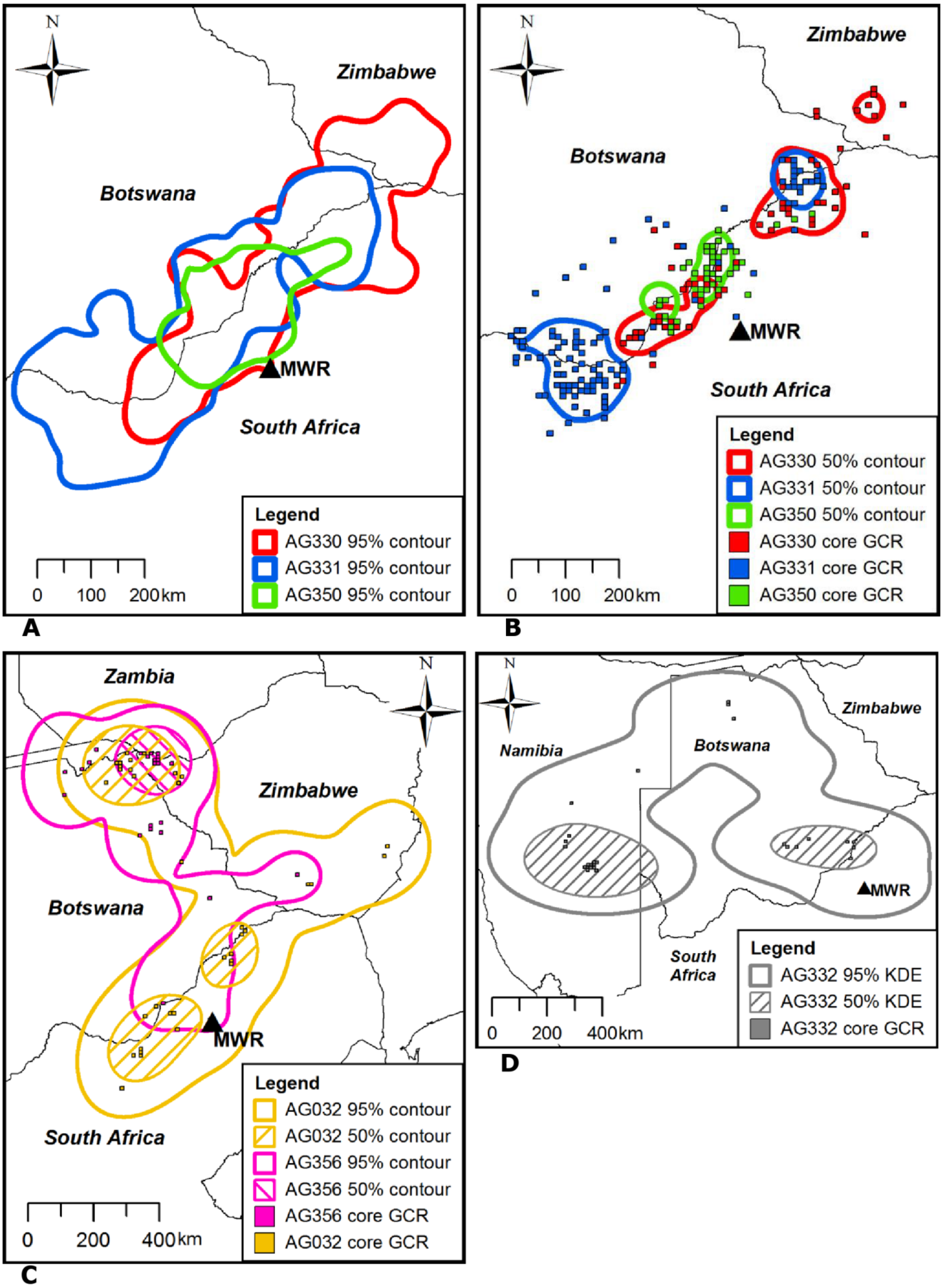
N
Zimbabwe
Botswana
MWR
South Africa
Legend
AG330 95% contour
AG331 95% contour
AG350 95% contour
0 100 200km
A
N
Zimbabwe
Botswana
MWR
South Africa
Legend
AG330 50% contour
AG331 50% contour
AG350 50% contour
AG330 core GCR
AG331 core GCR
AG350 core GCR
0 100 200km
B
Zambia
N
Zimbabwe
Botswana
MWR
South Africa
Legend
AG032 95% contour
AG032 50% contour
AG356 95% contour
AG356 50% contour
AG356 core GCR
AG032 core GCR
0 200 400km
C
N
Namibia
Botswana
Zimbabwe
MWR
South Africa
Legend
AG332 95% KDE
AG332 50% KDE
AG332 core GCR
0 200 400km
D

Figure 6.2. Overall and core foraging ranges for six immature African white-backed vultures. 95% KDE contours represent overall foraging ranges, 50% KDE contours and core GCRs represent core foraging ranges. (A) and (B) show the foraging ranges for AG330, AG331 and AG350; (C) shows the foraging ranges for AG032 and AG356; (D) shows the foraging ranges for AG332. Mankwe Wildlife Reserve capture site is indicated by a black triangle and “MWR”.

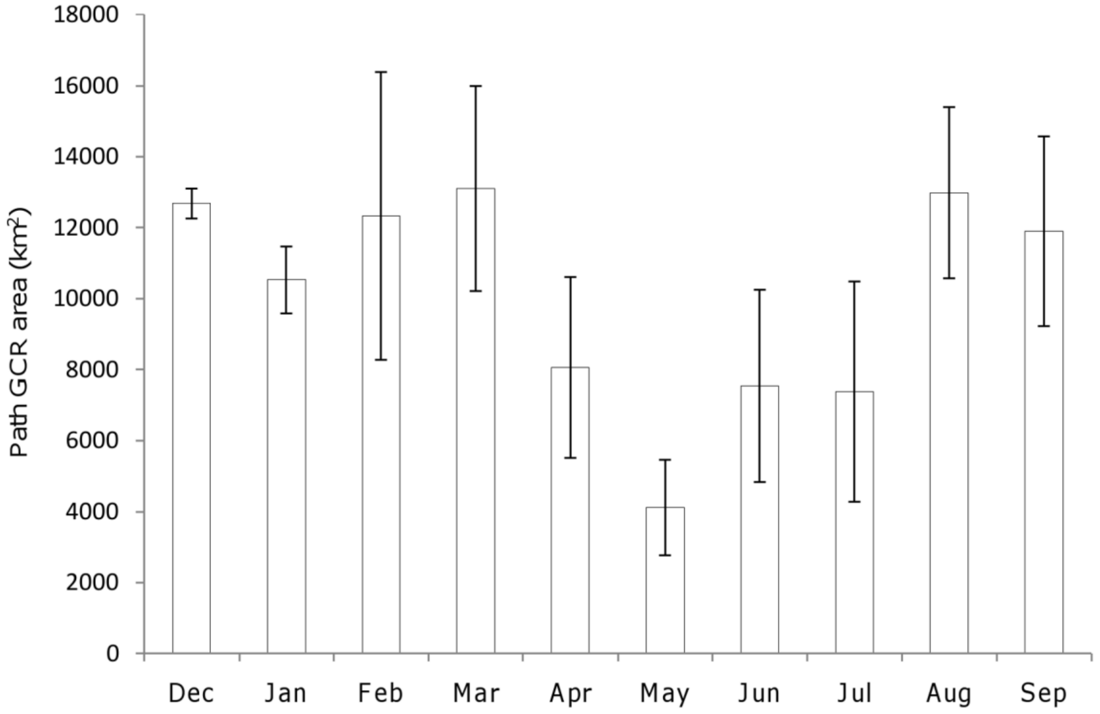

Figure 6.3. Mean (± SE) path GCR estimates for individual months for six immature African white-backed vultures. Due to differences between tracking periods estimates were calculated for four vultures for December to March, and five vultures from April to September, inclusive.

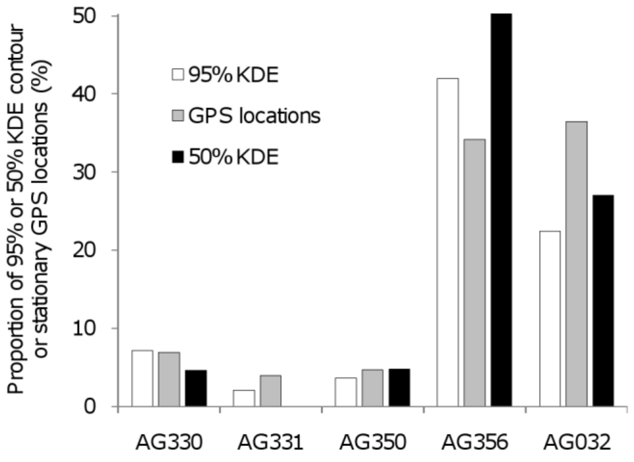

Figure 6.4. Availability and use of protected areas by five immature African white-backed vultures at the overall and core foraging range scales. The proportion of each vulture's 95% KDE contour occupied by protected areas defined their availability to each vulture. At the overall foraging range scale use of protected areas was defined as the proportion of stationary (i.e. < 10 km·h^{-1}) GPS locations within the 95% KDE contour that were recorded inside protected areas . Use of protected areas at the core foraging range scale was defined as the proportion that they occupied of each vulture's 50% KDE contours.

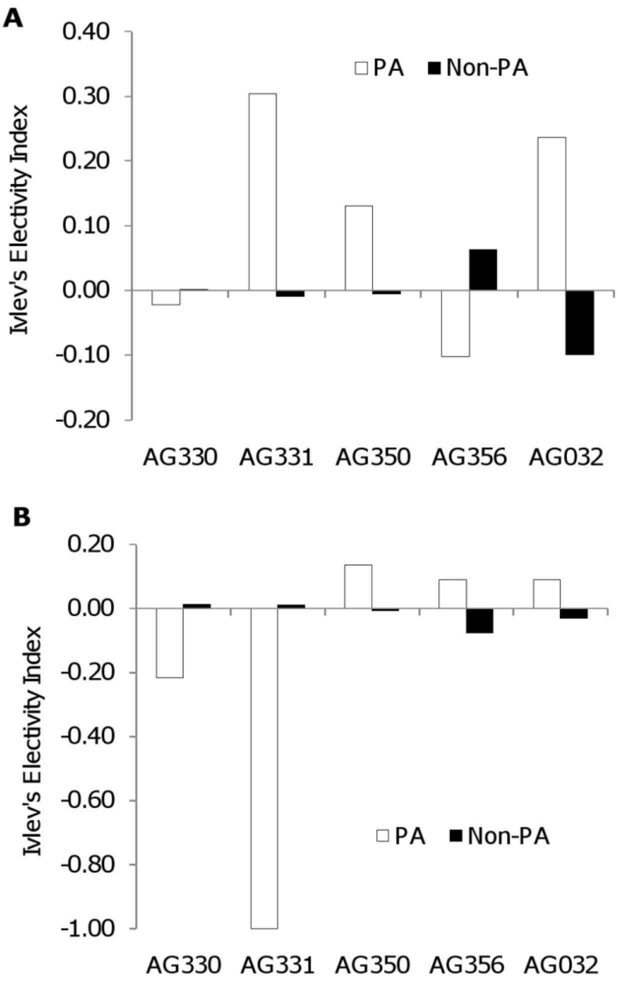

Figure 6.5. Ivlev's electivity index values for protected (PA) and unprotected (Non-PA) areas for five immature African white-backed vultures at the (A) overall and (B) core foraging range scales. Availability was represented by the relative proportions of protected and unprotected areas in each vulture's 95% KDE contour. At the overall foraging range scale (A) use was represented by the proportion of each vulture's stationary GPS locations recorded inside protected and unprotected areas. At the core foraging range scale (B) use was represented the relative proportions of protected and unprotected areas in each vulture's 50% KDE contours. 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.

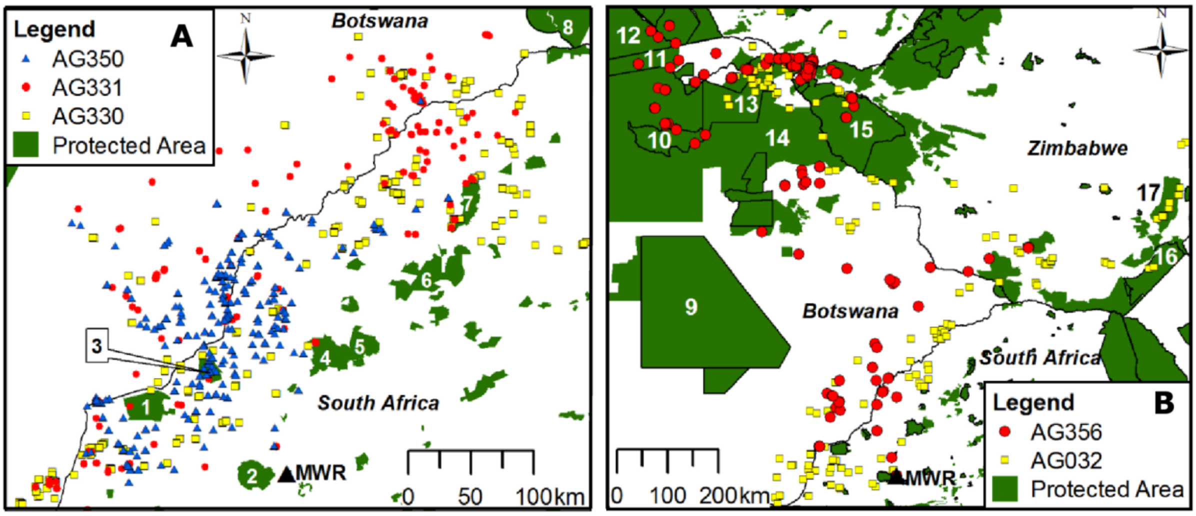

Figure 6.6. Stationary GPS locations of immature African white-backed vultures in relation to protected areas. (A) shows stationary GPS locations from AG330, AG331 and AG350 in relation to protected areas in the North West and Limpopo Provinces of South Africa: 1 = Madikwe GR; 2 = Pilanesberg NP; 3 = Atherstone NR; 4 = Marakele NP; 5 = Welgevonden NR; 6 = Lapalala, Moepel *et al.* reserves; 7 = Wonderkop NR; 8 = Tuli conservation area. (B) shows stationary GPS locations from AG356 and AG032 in relation to protected areas across southern Africa: 9 = Central Kalahari NP; 10 = Moremi GR; 11 = Caprivi GR; 12 = Luiana NP (Angola); 13 = Chobe NP; 14 = Wildlife Management Areas; 15 = Hwange NP; 16 = Gonarezhou NP; 17 = Save Conservancy. Protected area data from [46,47]**.**

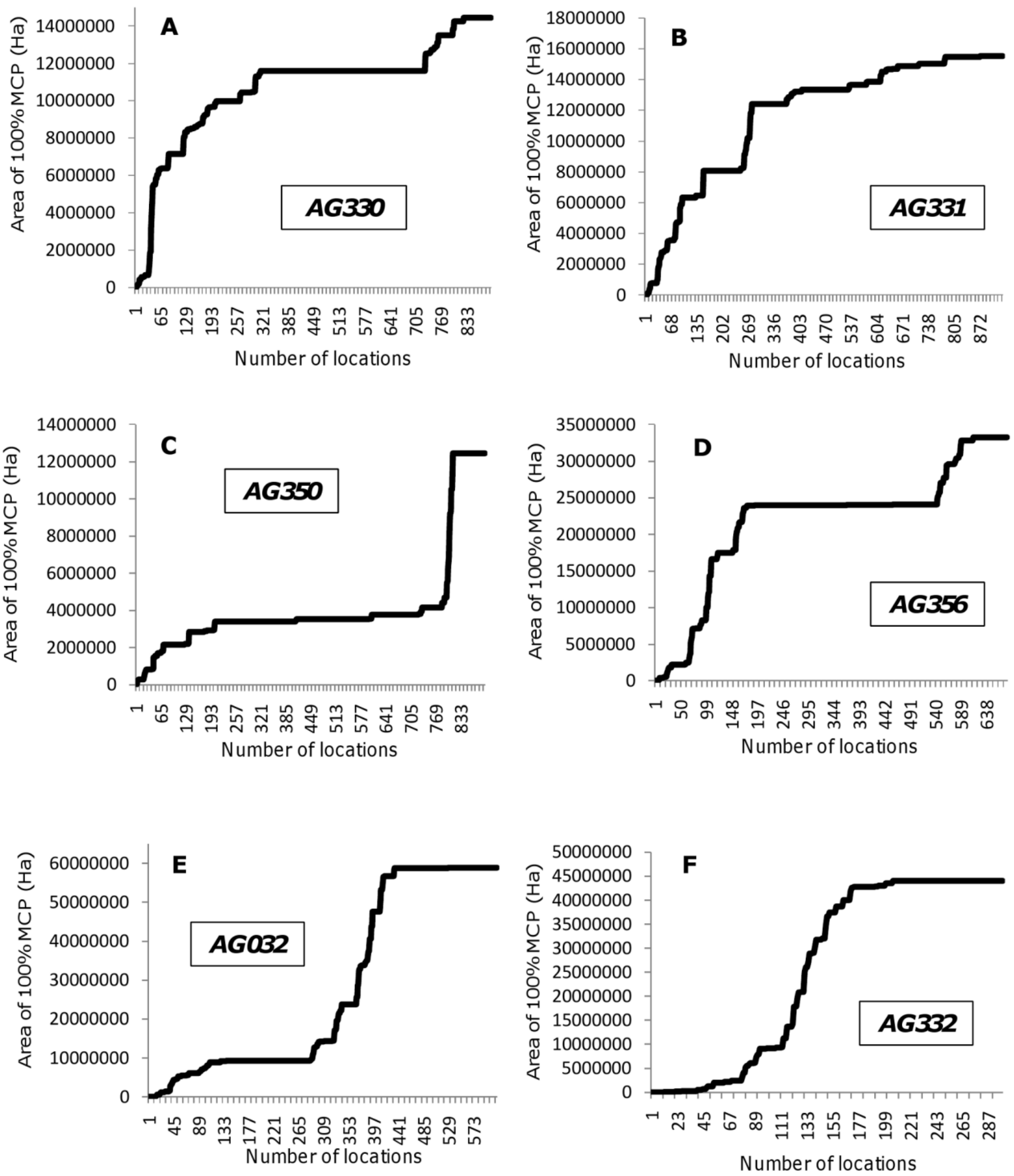

Figure S6.1. Foraging range area curves from incremental area analysis of GPS locations from six immature African white-backed vultures. The number of GPS locations used to generate MCPs by adding consecutive locations until all locations were used is plotted against the area of each MCP. (A) – (F) represent different vultures.

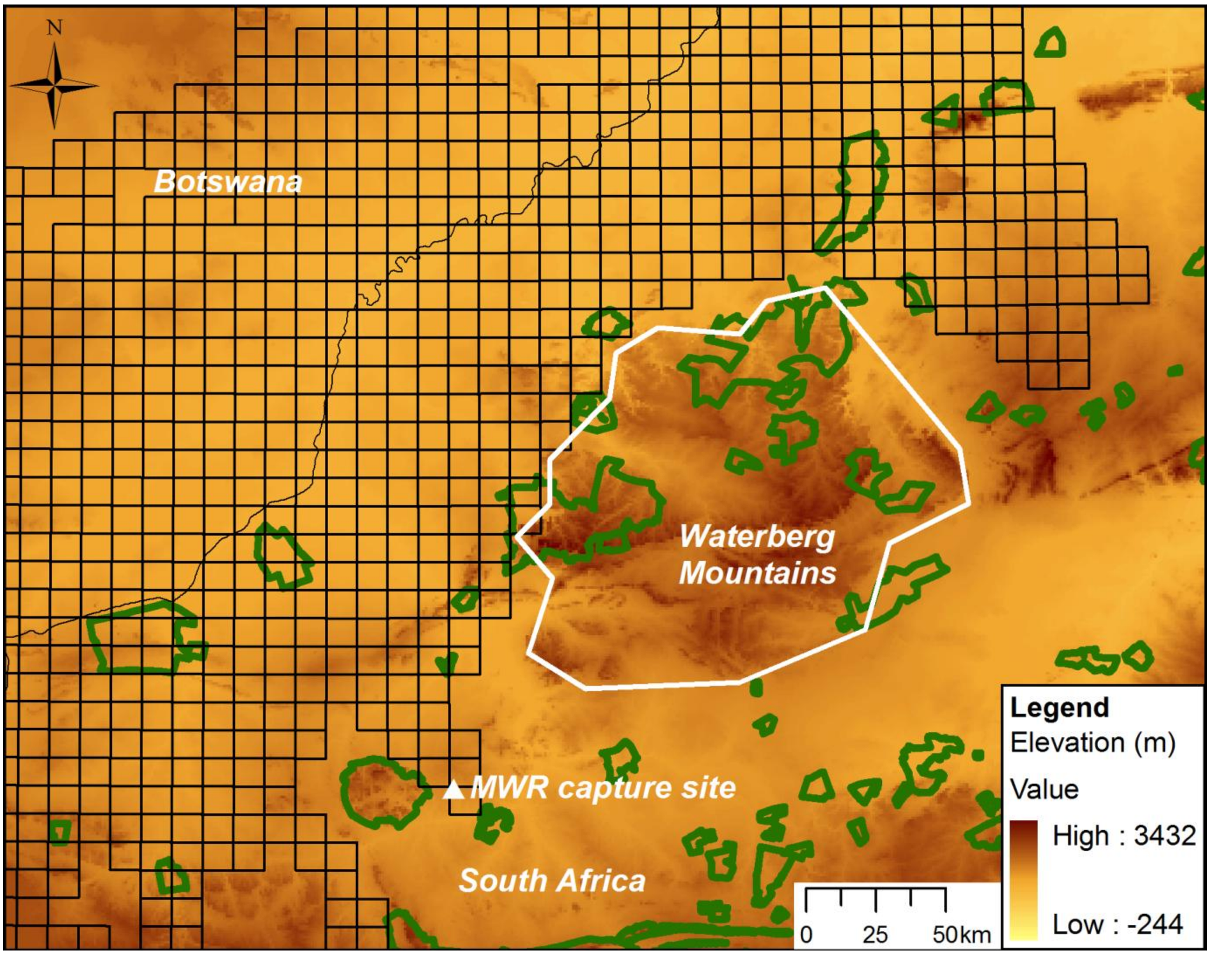

Figure S6.2. Path grid cell ranges (GCRs) of six immature African white-backed vultures in relation to protected areas and elevation in northern South Africa. Path GCRs (hollow squares) represent 100km^2 grid cells entered or travelled through by the vultures. Protected area (hollow green polygons) data are from [46,47]**.** Elevation data are from [71]**.**

References

1. Houston DC (1974) The role of griffon vultures *Gyps africanus* and *Gyps ruppellii* as scavengers. Journal of Zoological Society of London 172: 35-46.

2. Houston DC (1979) The adaptations of scavengers. In: Sinclair ARE, Norton-Griffiths M, editors. Serengeti, Dynamics of an Ecosystem. Chicago: The University of Chicago Press. pp. 263-286.

3. Ruxton GD, Houston DC (2004) Obligate vertebrate scavengers must be large soaring fliers. Journal of Theoretical Biology 228: 431-436.

4. Pennycuick CJ (1972) Soaring behaviour and performance of some East African birds, observed from a motor-glider. Ibis 114: 178-218.

5. Mundy PJ, Butchart D, Ledger JA, Piper SE (1992) The vultures of Africa. London: Academic Press.

6. DeVault TL, Rhodes OE, Shivik JA (2003) Scavenging by vertebrates: behavioural, ecological and evolutionary perspectives on an important energy transfer pathway in terrestrial ecosystems. Oikos 102: 225-234.

7. Sekercioglu CH (2006) Increasing awareness of avian ecological function. Trends in Ecology and Evolution 21: 464-471.

8. Pain DJ, Bowden CGR, Cunningham AA, Cuthbert R, Das D, et al. (2008) The race to prevent the extinction of South Asian vultures. Bird Conservation International 18: S30-S48.

9. Oaks JL, Gilbert M, Virani MZ, Watson RT, Meteyer CU, et al. (2004) Diclofenac residues as the cause of vulture population declines in Pakistan. Nature 427: 630-633.

10. Prakash V, Green RE, Pain DJ, Ranade SP, Saravanan S, et al. (2007) Recent changes in populations of resident *Gyps* vultures in India. Journal of the Bombay Natural History Society 104: 129-135.

11. Naidoo V, Wolter K, Cromarty D, Diekmann M, Duncan N, et al. (2010) Toxicity of non-steroidal anti-inflammatory drugs to Gyps vultures: a new threat from Ketoprofen. Biology Letters 6: 339-341.

12. Naidoo V, Wolter K, Cuthbert R, Duncan N (2009) Veterinary diclofenac threatens Africa’s endangered vulture species. Regulatory Toxicology and Pharmacology 53: 205-208.

13. Anderson MD, Piper SE, Swan GE (2005) Non-steroidal anti-inflammatory drug use in South Africa and possible effects on vultures. South African Journal of Science 101: 112-114.

14. Thiollay JM (2006) The decline of raptors in West Africa: long-term assessment and the role of protected areas. Ibis 148: 240-254.

15. Herremans M, Herremans-Tonnoeyr D (2000) Land use and conservation status of raptors in Botswana. Biological Conservation 94: 31-41.

16. Virani MZ, Kendall C, Njoroge P, Thomsett S (2011) Major declines in the abundance of vultures and other scavenging raptors in and around the Masai Mara ecosystem, Kenya. Biological Conservation 144: 746-752.

17. Green RE, Newton I, Shultz S, Cunningham AA, Gilbert M, et al. (2004) Diclofenac poisoning as a cause of vulture population declines across the Indian subcontinent. Journal of Applied Ecology 41: 793-800.

18. Ledger JA, Annegarn HJ (1981) Electrocution hazards to the Cape vulture *Gyps coprotheres* in South Africa. Biological Conservation 20: 15-24.

19. Hengari GM, Cunningham PL, Adank W (2004) The use of vultures by traditional healers in Namibia. Vulture News 50: 23-28.

20. Monadjem A, Garcelon DK (2005) Nesting distribution of vultures in relation to land use in Swaziland. Biodiversity and Conservation 14: 2079-2093.

21. Friedman R, Mundy PJ (1983) The use of "restaurants" for the survival of vultures in South Africa. Vulture Biology and Management. London: University of California Press. pp. 345-355.

22. Piper SE, Boshoff AF, Scott HA (1999) Modelling survival rates in the Cape Griffon *Gyps coprotheres*, with emphasis on the effects of supplementary feeding. Bird Study 46: S230-238.

23. Deygout C, Gault A, Sarrazin F, Bessa-Gomes C (2009) Modeling the impact of feeding stations on vulture scavenging service efficiency. Ecological Modelling 220: 1826-1835.

24. Anderson MD (2000) African Whitebacked Vulture *Gyps africanus*. In: Barnes KN, editor. The Eskom Red Data Book of Birds of South Africa, Lesotho and Swaziland. Johannesburg, South Africa: BirdLife South Africa. pp. 75-77.

25. BirdLife International (2010) Species factsheet: *Gyps africanus*. Downloaded from http://wwwbirdlifeorg on 1/7/2010.

26. IUCN (2010) IUCN Red List of Threatened Species. Version 2010.2.: Downloaded from www.iucnredlist.org on 1st August 2010.

27. Oschadleus D (2002) Report on southern African vulture recoveries. Vulture News 46: 16-18.

28. Bamford AJ, Diekmann M, Monadjem A, Mendelsohn J (2007) Ranging behaviour of Cape vultures *Gyps coprotheres* from an endangered population in Namibia. Bird Conservation International 17: 331-339.

29. Bamford AJ, Monadjem A, Diekmann M, Hardy ICW (2009) Development of non-explosive based methods for mass capture of vultures. South African Journal of Wildlife Research 39: 202-208.

30. Diekmann M, Scott A, Scott M, Diekmann J (2004) Capture and fitting of satellite- and radio-telemetry equipment onto Cape Griffon vulture *Gyps coprotheres*, African white-backed vulture *Gyps africanus* and Lappet-faced vulture *Torgos tracheliotos* in the Waterberg area, Namibia in 2004. Vulture News 51: 34-45.

31. D'Eon RG, Delparte D (2005) Effects of radio-collar position and orientation on GPS radio-collar performance, and the implications of PDOP in data screening. Journal of Applied Ecology 42: 383-388.

32. Schoener TW (1981) An empirically based estimate of home range. Theoretical Population Biology 20: 281-325.

33. Rodgers AR, Carr AP, Beyer HL, Smith L, Kie JG (2007) Home Range Tools (HRT) for ArcGIS. Version 1.1. Ontario Ministry of Natural Resources, Centre for Northern Forestry Ecosystem Research, Thunder Bay, Ontario, Canada.

34. South AB, Kenward RE, Walls SS (2008) Ranges7: for the analysis of tracking and location data. Online manual. Anatrack Ltd. Wareham, Dorset.

35. Laver PN, Kelly MJ (2008) A critical review of home range studies. The Journal of Wildlife Management 72: 72:290-298.

36. Harris S, Cresswell WJ, Forde PG, Trewhella WJ, Woollard T, et al. (1990) Home range analysis using radio-tracking data - a review of problems and techniques particularly as applied to the study of mammals. Mammal Review 20: 97-123.

37. Mohr CO (1947) Table of equivalent populations of North American small mammals. American Midland Naturalist 37: 223-249.

38. Börger L, Franconi N, De Michele G, Gantz A, Meschi F, et al. (2006) Effects of sampling regime on the mean and variance of home range estimates. Journal of Applied Ecology 75: 1393-1405.

39. Worton BJ (1989) Kernel methods for estimating the utilization distribution in home-range studies. Ecology 70: 164-168.

40. Jacques CN, Jenks JA, Klaver RW (2009) Seasonal movements and home-range use by female pronghorns in sagebrush-steppe communities of western South Dakota. Journal of Mammalogy 90: 433-441.

41. Kie JG, Matthiopoulos J, Fieberg J, Powell RA, Cagnacci F, et al. (2010) The home-range concept: are traditional estimators still relevant with modern telemetry technology? Philosophical Transactions of the Royal Society: Biology 365: 2221-2231.

42. Beyer HL (2009) Hawth's Analysis Tools for ArcGIS version 3.27 (software). URL: http://www.spatialecology.com/htools.

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

44. Horner MA, Powell RA (1990) Internal structure of home ranges of black bears and analyses of home-range overlap. Journal of Mammalogy 71: 402-410.

45. Thomas DL, Taylor EJ (2006) Study designs and tests for comparing resource use and availability II. Journal of Wildlife Management 70: 324-336.

46. IUCN, UNEP (2010) The World Database on Protected Areas (WDPA). UNEP-WCMC. Cambridge, UK. www.protectedplanet.net.

47. IUCN, UNEP (2003) The World Database on Protected Areas (WDPA). UNEP-WCMC. Cambridge, UK.

48. Ivlev VS (1961) Experimental ecology of the feeding of fishes. New Haven: Yale University Press.

49. Piper SE. Vulture restaurants. In: Monadjem A, Anderson MD, Piper SE, Boshoff AF, editors; 2004; Johannesburg, South Africa. Birds of Prey Working Group. pp. 221-227.

50. Newton I (1979) Population ecology of raptors. Berkhamsted, UK: Poyser.

51. Maher CR, Lott DF (2000) A review of ecological determinants of territoriality within vertebrate species. American Midland Naturalist 143: 1-29.

52. Houston DC (1974) Food searching in griffon vultures. East African Wildlife Journal 12: 63-77.

53. Benson PC. Status of vultures in the Northern Province, South Africa. In: Boshoff AF, Anderson MD, Borello WD, editors; 1997; Johannesburg. Vulture Study Group. pp. 21-29.

54. Hayward MW, O'Brien J, Kerley GIH (2007) Carrying capacity of large African predators: Predictions and tests. Biological Conservation 139: 219-229.

55. Tambling CJ, du Toit JT (2005) Modelling wildebeest population dynamics: implications of predation and harvesting in a closed system. Journal of Applied Ecology 42: 431-441.

56. Houston DC (1975) Ecological isolation of African scavenging birds. Ardea 63: 55-64.

57. Gusset M, Swarner MJ, Mponwane L, Keletile K, McNutt JW (2009) Human-wildlife conflict in northern Botswana: livestock predation by Endangered African wild dog *Lycaon pictus* and other carnivores. Oryx 43: 67-72.

58. Parry D, Campbell B (1992) Attitudes of rural communities to animal wildlife and its utilization in Chobe Enclave and Mababe Depression, Botswana. Environmental Conservation 19: 245-252.

59. Lindsey PA, Romanach SS, Davies-Mostert HT (2009) The importance of conservancies for enhancing the value of game ranch land for large mammal conservation in southern Africa. Journal of Zoology 277: 99-105.

60. Bamford AJ, Monadjem A, Hardy ICW (2009) Nesting habitat preferences of the African white-backed vulture *Gyps africanus* and the effects of anthropogenic disturbance. Ibis 151: 51-62.

61. Mundy PJ (1997) Whitebacked vulture Gyps africanus. In: Harrison JA, Allan DA, Underhill LG, Herremans M, Tree AJ et al., editors. The atlas of southern African Birds. Johannesburg: BirdLife South Africa. pp. 160-161.

62. Houston DC (1976) Breeding of white-backed and Rüppell’s griffon vultures, *Gyps africanus* and *Gyps rueppellii*. Ibis 118: 14-43.

63. St John FAV, Keane AM, Edwards-Jones G, Jones L, Yarnell RW, et al. (2011) Identifying indicators of illegal behaviour: carnivore killing in human-managed landscapes. Proceedings of the Royal Society B - Biological Sciences.

64. Van der Waal C, Dekker B (2000) Game ranching in the Northern Province of South Africa. South African Journal of Wildlife Research 30: 151-156.

65. Murn C, Anderson MD (2008) Activity patterns of African White-backed Vultures *Gyps africanus* in relation to different land-use practices and food availability. Ostrich 79: 191-198.

66. Benson PC, Plug I, Dobbs JC (2004) An analysis of bones and other materials collected by Cape vultures at the Kransberg and Blouberg colonies, Limpopo Province, South Africa. Ostrich 75: 118-132.

67. Cronje HP, Reilly BK, MacFadyen ID (2002) Natural mortality among four common ungulate species on Letaba Ranch, Limpopo Province, South Africa. Koedoe 45: 79-86.

68. Mapiye C, Chimonyo M, Dzama K (2009) Seasonal dynamics, production potential and efficiency of cattle in the sweet and sour communal rangelands in South Africa. Journal of Arid Environments 73: 529-536.

69. Bamford AJ, Monadjem A, Hardy ICW (2009) An effect of vegetation on carcass exploitation by vultures in an African savannah. Ostrich 80: 135-137.

70. Gilbert M, Watson RT, Ahmed S, Asim M, Johnson JA (2007) Vulture restaurants and their role in reducing diclofenac exposure in Pakistan. Bird Conservation International 17: 63-77.

71. USGS (2004) Shuttle Radar Topography Mission, 30 Arc Second scene, Unfilled Unfinished 2.0.

APPENDICES

APPENDIX A

Monthly point grid cell range (GCR) estimates for complete months for all vultures

	Monthly point GCR areas (km^2)					
Month	***AG330***	***AG331***	***AG350***	***AG356***	***AG032***	***AG332***
	Point GCR	*Point GCR*	*Point GCR*	*Point GCR*	*Point GCR*	*Point GCR*
December	3,800	4,100	4,000	-	-	3,200
January	3,300	3,500	4,300	-	-	3,000
February	3,600	4,600	5,200	-	-	1,100
March	2,900	5,300	3,400	3,600	-	-
April	700	3,600	1,900	2,400	3,800	-
May	1,000	2,200	1,300	600	2,400	-
June	1,600	3,400	2,900	700	2,000	-
July	1,400	2,900	2,800	800	3,400	-
August	3,500	5,600	4,400	2,400	2,300	-
September	3,300	6,000	1,200	2,300	3,500	-
Mean	*2,510.00*	*4,120.00*	*3,140.00*	*1,828.57*	*2,900.00*	*2,433.33*
± SE	*377.84*	*390.10*	*432.61*	*432.44*	*307.68*	*669.16*

APPENDIX B

Kernel bandwidths (H) selected using the reference (H_{ref}) and *ad hoc* (H_{adhoc}) methods for kernel density estimation (KDE) of foraging ranges for the total tracking periods of all vultures, and the multiples of H_{ref} used for H_{adhoc} KDE

Vulture ID	**H_{ref} bandwidth (km)**	**Multiple of H_{ref} used for H_{adhoc}**	**H_{adhoc} bandwidth (km)**
AG330	45.35	0.50	20.41
AG331	50.12	0.50	25.06
AG350	20.33	0.85	17.28
AG356	58.78	0.95	55.84
AG032	98.62	0.70	69.04
AG332	105.73	0.90	95.16